A New View of Sooty Blotch and Flyspeck

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Sooty blotch and flyspeck (SBFS) fungi colonize the surface wax layer of the fruit of apple, pear, persimmon, banana, orange, papaya, and several other cultivated tree and vine crops. Because their hyphae, fruiting bodies, and survival structures are melanized (darkly pigmented), SBFS colonies appear as blemishes (Fig. 1). The disease occurs worldwide in regions with moist growing seasons. In addition to cultivated fruit crops, SBFS fungi also grow on the surfaces of stems, twigs, leaves, and fruit of a wide range of wild plants.

SBFS fungi cause no physiological damage to the underlying fruit except an accelerated desiccation of apples during cold storage, presumably due to a damaged wax layer. Nevertheless, SBFS is regarded as a serious disease by fruit farmers and plant pathologists because it can cause substantial economic damage. The smudges and stipples of SBFS often result in downgrading of fruit from premium fresh-market grade to processing use. In eastern North America, high-value apple cultivars can lose as much as 90% of their value in this way. Even when relatively few fruit in an orchard block are blemished, it may not be cost effective to sort them out manually, so entire harvests must be diverted to processing (23,24). Economic damage from SBFS is not limited to North America; losses from SBFS blemishing of apple, pear, persimmon, hawthorn, and other fruit crops occur worldwide. Since economic losses are most common on apple, nearly all of the research on the SBFS complex has focused on this crop.

Eleven years ago, Williamson and Sutton (70) reviewed the etiology, biology, and control of SBFS on apple. Their article remains the only prior review, although SBFS fungi have been studied for nearly 180 years. The present update describes the major shifts that have occurred during the past decade in understanding the genetic diversity of the SBFS complex, clarifying its biogeography and environmental biology, and developing improved management strategies.

Taxonomy, Diversity, Biogeography, and Paradigms

Taxonomy. Reliable identification of SBFS fungi has eluded many generations of mycologists. In general, these fungi are challenging to isolate and grow in pure culture. They grow extraordinarily slowly, so are easily overgrown on agar media by saprophytes. Surface disinfection of the fruit before isolation is not helpful since the epiphytic SBFS fungi are killed as readily as non-SBFS epiphytes. The fact that many SBFS species sporulate rarely or not at all, either on fruit or in culture, frustrates morphological description of species. To compound the problem, colony morphology of an SBFS isolate on fruit can differ radically from that on agar media and varies considerably on media with changes in pH, nutrient source and concentration, and light source.

Williamson and Sutton (70) pieced together the tangled history of SBFS taxonomy from 1832 to 1997. Initially thought to be caused by a single species of fungus, SBFS was reclassified as two

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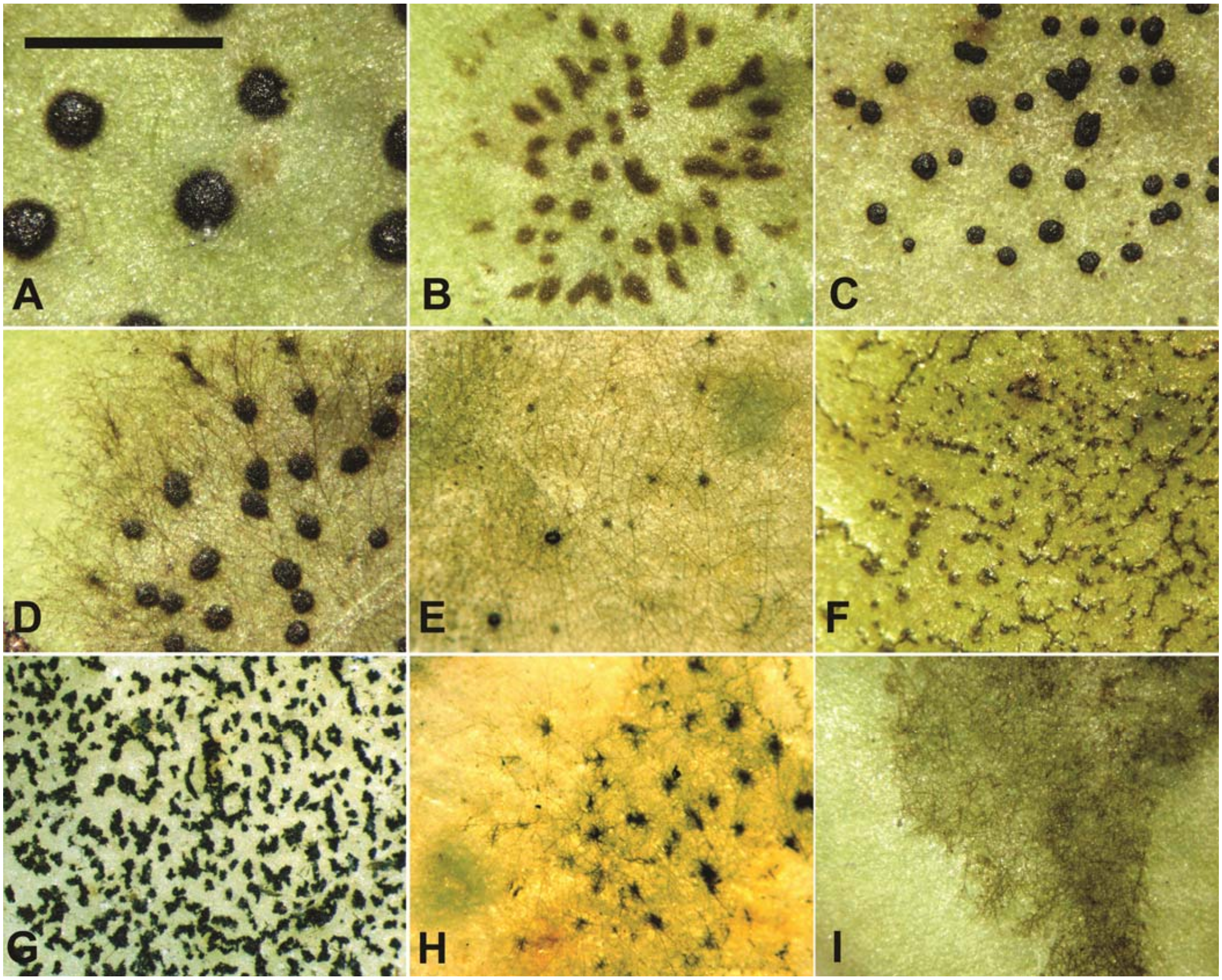

Fig. 1. Appearance on apple fruit of mycelial types of the sooty blotch and flyspeck complex: **A,** flyspeck; **B,** compact speck; **C,** discrete speck; **D and E,** ramose; **F,** ridged honeycomb; **G,** fleck; **H,** punctate; **I,** fuliginous. Bar = 0.5 cm.

species in 1920 (13). One of these, *Gloeodes pomigena*, was thought to cause colonies of the "sooty blotch" morphological type on fruit, i.e., masses of dark mycelium with or without small, black, rounded structures embedded in the mycelium. The other species, which underwent several reclassifications until it became *Schizothyrium pomi* (69) with the presumed anamorph *Zygophiala jamaicensis* (19), was believed to be the causal agent of the "flyspeck" morphological type: clusters of small, black spots with no visible mycelial matrix. This two-disease paradigm—that sooty blotch is one disease caused by a single pathogen species and that flyspeck is a separate disease, also caused by a single species—was firmly embedded in the scientific literature for nearly 80 years (35,70).

The first cracks in the two-disease paradigm appeared in the late 1990s. Many authors had observed that "sooty blotch" colonies on apple fruit encompassed a diverse range of mycelial types (13,26,30,60; Sidebar 1; Fig. 1), but it was assumed that *G. pomigena* could express these multiple types. Then Johnson et al. (34), working with a large collection of isolates from eight eastern U.S. states, established that "sooty blotch" was caused by three species of fungi. A newly described species, *Peltaster fructicola,* was associated with colonies showing the punctate mycelial type, whereas *Leptodontium elatius* was associated with fuliginous colonies and *Geastrumia polystigmatis* with ramose colonies (Fig. 1). As the millennium ended, "sooty blotch" had been broadened to a three-pathogen disease, whereas "flyspeck" remained a single-pathogen disease (70). Although the two-disease paradigm remained standing, it was starting to wobble.

SIDEBAR 1: Mycelial type: In this paper, defined as a categorization of sooty blotch and flyspeck (SBFS) fungi according to general characteristics of colony morphology on fruit. Available evidence indicates that mycelial type is a consistent character within individual SBFS species. Currently recognized mycelial types include ramose, punctate, flyspeck, discrete speck, compact speck, fuliginous, ridged honeycomb, and fleck.

Williamson and Sutton (70) predicted that "it is likely that other fungi will be associated with [SBFS] as the disease is more widely studied throughout the world." They were right. When techniques of molecular genetics were coupled with traditional morphology-based mycological methods, a far more diverse picture began to emerge. Two surveys, encompassing 39 apple orchards in 14 eastern U.S. states, documented that the SBFS complex included at least 60 putative species (3,4,18; Sidebar 2), compared to four species in 1997 (Table 1). These new species belonged to two classes of Ascomycetes, of which the class *Dothideomycetes* accommodated the vast majority, primarily within the order *Capnodiales* (17,18,54). There is also a report of a *Basidiomycete* SBFS species, *Wallemia sebi* (58).

The number of described genera and species has continued to rise as the result of recent extensive surveys conducted on apples in China (38–40,59,72,73; Table 1). For example, five new genera—*Microcyclosporella, Microcyclospora, Phaeothecoidiella, Houjia,* and *Sporidesmajora*—were described, containing nine new SBFS species (22,72). Based on preliminary results from ongoing surveys of apple orchards in Turkey, Norway, Germany, Slovenia, Poland, and Brazil, it is highly likely that many additional SBFS species will be described in the next few years.

How did so many SBFS species remain concealed for so long? The answer lies in their cryptic nature (Sidebar 3). That is, many of the newly discovered genera and species are indistinguishable from one another on the apple surface (Fig. 2). For example, at least 20 SBFS species from the U.S. surveys display the fuliginous mycelial type on apple (18,70). Since most species were also difficult to

SIDEBAR 2: Putative species: A provisional taxonomic unit at the species level, designated on the basis of multiple lines of evidence (e.g., genetic, morphological, physiological, ecological), which has not yet received a Latin binomial.

SIDEBAR 3: Cryptic species: We define cryptic species here as sooty blotch and flyspeck species whose colony morphology on apples is difficult or impossible to differentiate from one another.

Table 1. Taxonomic placement of species and putative species in the sooty blotch and flyspeck (SBFS) complex, prevalence in the United States, countries in which they have been found, mycelial type on apple, and status of completion of Koch's postulates

Class	Order	Family	SBFS species	U.S. Prevalence***	Countries found	Mycelial type	Koch's**
Dothideomycetes	*	*	*Scleroramularia* sp. CS2	6	US, CN	Compact speck	2
			Yeast sp. CS1	14	US	Compact speck	2
	Capnodiales	*	*Peltaster fructicola*	29	US, SB, SV	Punctate	2
			Peltaster sp. P2.1	3	US	Punctate	2
			Peltaster sp. P2.2	5	US	Punctate	2
			Peltaster sp. P2.3	1	US	Punctate	2
			Peltaster sp. P5	0	DE	Punctate	0
			Peltaster sp. P8	2	US	Punctate	2
			Peltaster sp. CN1	0	CN	Punctate	1
		Dissoconiaceae	*Dissoconium aciculare*	10	US	Discrete speck	2
			Dissoconium commune	5	US, CN	Fuliginous	2
			Dissoconium dekkeri	2	US	Discrete speck	2
			Dissoconium mali	1	US, CN	Discrete speck	2
			Dissoconium luensis	0	CN	Ramose	1
			Dissoconium sp. DS2	1	US	Discrete speck	2
			Dissoconium sp. FG5.1	4	US	Fuliginous	2
			Dissoconium sp. FG5.2	2	US,CN	Fuliginous	2
			Dissoconium sp. LF1.1	3	US	Fuliginous	2
			Ramichloridium apiculatum	0	CN	Flyspeck	1
		Micropeltidaceae	*Houjia pomigena*	2	US	Fuliginous	2
			Houjia yanglingensis	2	US, CN	Fuliginous	2
			Passalora-like sp. FG3	2	US	Fuliginous	2
			Phaeothecoidiella illinoisensis	2	US	Punctate	2
			Phaeothecoidiella missouriensis	1	US	Punctate	2
			Sporidesmajora pennsylvaniensis	1	US	Fuliginous	2
			Sterile mycelia sp. RS1	8	US	Ramose	2
			Sterile mycelia sp. RS2	7	US	Ramose	2
			Sterile mycelia sp. RS3.1	2	US	Ramose	2
			Sterile mycelia sp. RS3.2	1	US	Ramose	2
			Sterile mycelia sp. RS4.1	4	US, TK	Ramose	2
			Stomiopeltis sp. RS5.1	2	US	Ramose	2
			Stomiopeltis sp. RS5.2	5	US	Ramose	2
			Sterile mycelia sp. RS6	3	US	Ramose	2
			Sterile mycelia sp. RS7.1	0	TK	Ramose	0
			Sterile mycelia sp. RS7.2	1	TK	Ramose	0
		Mycosphaerellaceae	*Colletogloeopsis*-like sp. FG2.1	11	US	Fuliginous	2
			Ramichloridium sp. FG2.2	2	US	Fuliginous	2
			Ramichloridium sp. FG9	4	US	Fuliginous	2
			Ramularia-like sp. FG10	3	US	Fuliginous	2

(*Continued on next page*)

[a] Countries found: US (United States), CN (China), TK (Turkey), SB (Serbia), SV (Slovenia), DE (Germany), PL (Poland).

[b] * Unable to place at this level. ** Koch's postulates level 0 = not attempted; 1 = sign on inoculated apple; 2 = recovered from sign and internal transcribed spacer (ITS) matched original isolate. *** Number of orchards in which taxon was isolated, from a total of 39 orchards surveyed in 2000 and 2005 (18).

cultivate and routinely failed to produce spores, interspecific differences in mycelial appearance in culture, conidiophores, conidia, and other morphological traits could not be assessed.

Phylogenetic analysis was the catalyst for describing new SBFS taxa by highlighting clades to scrutinize for additional differences. Each new SBFS species was delineated not only by distinct nucleotide sequences of internal transcribed spacer (ITS) and/or large subunit (LSU) regions of ribosomal DNA but also by differences in spore, colony, or hyphal morphology on fruit or in culture (27). Some species distinctions were also corroborated by differences in physiological responses such as fungicide sensitivity (65; Fig. 3), responses to nutrient availability and temperature (7), and ease of removal from apples by postharvest rinsing and brushing (6). Modified versions of Koch's postulates have been used to confirm the identity of SBFS species and putative species (Sidebar 4).

In addition to vastly expanding our knowledge of taxonomic diversity in the SBFS complex, recent work has prompted reclassification of mycelial phenotypes (Fig. 1). Early literature described punctate, ramose, fuliginous, rimate, and flyspeck mycelial types (13,26). In 2005, Batzer et al. (4) re-described the rimate mycelial type as ridged honeycomb to more clearly represent its appearance on apples. They also characterized two new mycelial types, compact speck and discrete speck, which formed clusters of black, sclerotium-like bodies lacking a mycelial matrix but were morphologically distinct from the flyspeck mycelial type sensu *Schizothyrium pomi*. An additional mycelial type, termed fleck, has been proposed (J. C. Batzer, *unpublished data*), and it is likely that further SBFS phenotypes will be described in the near future.

Diversity. We are just starting to discern patterns of SBFS diversity among orchards, regions, and continents. In the surveys of eastern U.S. orchards, for example, 30 SBFS species were relatively rare (found in one or two of 39 orchards), whereas nine spe-

Table 1. (*Continued from previous page*)

Class	Order	Family	SBFS species	U.S. Prevalence***	Countries found	Mycelial type	Koch's**
			Microcyclosporella sp. RH1	23	US, SB, SV, TK, CN, PL	Ridged honeycomb	2
			Microcyclosporella sp. RH2.1	4	US	Ridged honeycomb	2
			Microcyclosporella sp. RH2.2	10	US	Ridged honeycomb	2
			Microcyclosporella mali	12	US, CN, SB, SV, TK	Ridged honeycomb	2
			Microcyclosporella sp. RH4.1	3	US	Ridged honeycomb	2
			Microcyclosporella sp. RH6	1	US	Ridged honeycomb	2
			Microcyclosporella sp. RH7	1	US	Ridged honeycomb	2
			Microcyclosporella sp. RH8	1	US	Ridged honeycomb	2
			Pseudocercospora sp. LLS1	2	US	Fuliginous	2
			Pseudocercospora sp. LLS2	1	US	Fuliginous	2
			Ramularia-like sp. P5	3	US	Punctate	2
		Schizothyriaceae	*Schizothyrium pomi*	38	US, SB, SV, DE, TK	Flyspeck	2
			Zygophiala cryptogama	5	US, CN	Flyspeck	2
			Zygophiala qianensis	0	CN	Flyspeck	1
			Zygophiala cylindrica	0	CN	Flyspeck	1
			Zygophiala tardicrescens	1	US	Flyspeck	2
			Zygophiala wisconsinensis	5	US, CN, TK	Flyspeck (giant)	2
			Zygophiala sp. FS1.9	4	US	Flyspeck	2
			Zygophiala sp. FS3.3	0	TK	Flyspeck	0
			Zygophiala sp. FS3.4	0	CN	Flyspeck	1
			Zygophiala sp. FS5	1	US	Flyspeck	2
			Zygophiala sp. FS6.1	3	US, TK	Flyspeck	2
			Zygophiala sp. FS6.2	0	CN	Flyspeck	1
			Zygophiala sp. FS7	1	US (banana)	Flyspeck	0
		Teratosphaericeae	*Microcyclospora malicola*	9	US, SV, SB, DE, PL	Fuliginous	2
			Microcyclospora tardicrescens	0	SV, TK	Fuliginous	0
			Microcyclospora pomicola	0	SV, DE	Fuliginous	0
			Microcyclospora sp. FS4	1	US	Flyspeck	2
			Microcyclospora sp. FG1.2	1	US	Fuliginous	2
			Microcyclospora sp. FG1.9	2	US	Fuliginous	2
	Dothideales	*Botryosphaeriaceae*	Sterile mycelia sp. MB1	2	US	Ramose	2
			Geastrumia polystigmatis	24	US	Ramose	2
	Myrangiales	*	Sterile mycelia sp. FG6	1	US	Fuliginous	2
Eurotiomycetes	*Chaetothyriales*	*Herpotrichiellaceae*	Sterile mycelia sp. UI-6	2	US	Punctate	2
			Phialophora sessilis	5	US, DE, CN	Fuliginous	2
			Yeast sp. UI-10	1	US	Punctate	2
			Strelitziana mali	0	CN	Punctate	1
			Leptodontidium elatius	4	US	Fuliginous (light)	1
Wallemiomycetes	*Wallemiales*	*Wallemiaceae*	*Wallemia sebi*	0	CN	Punctate	1

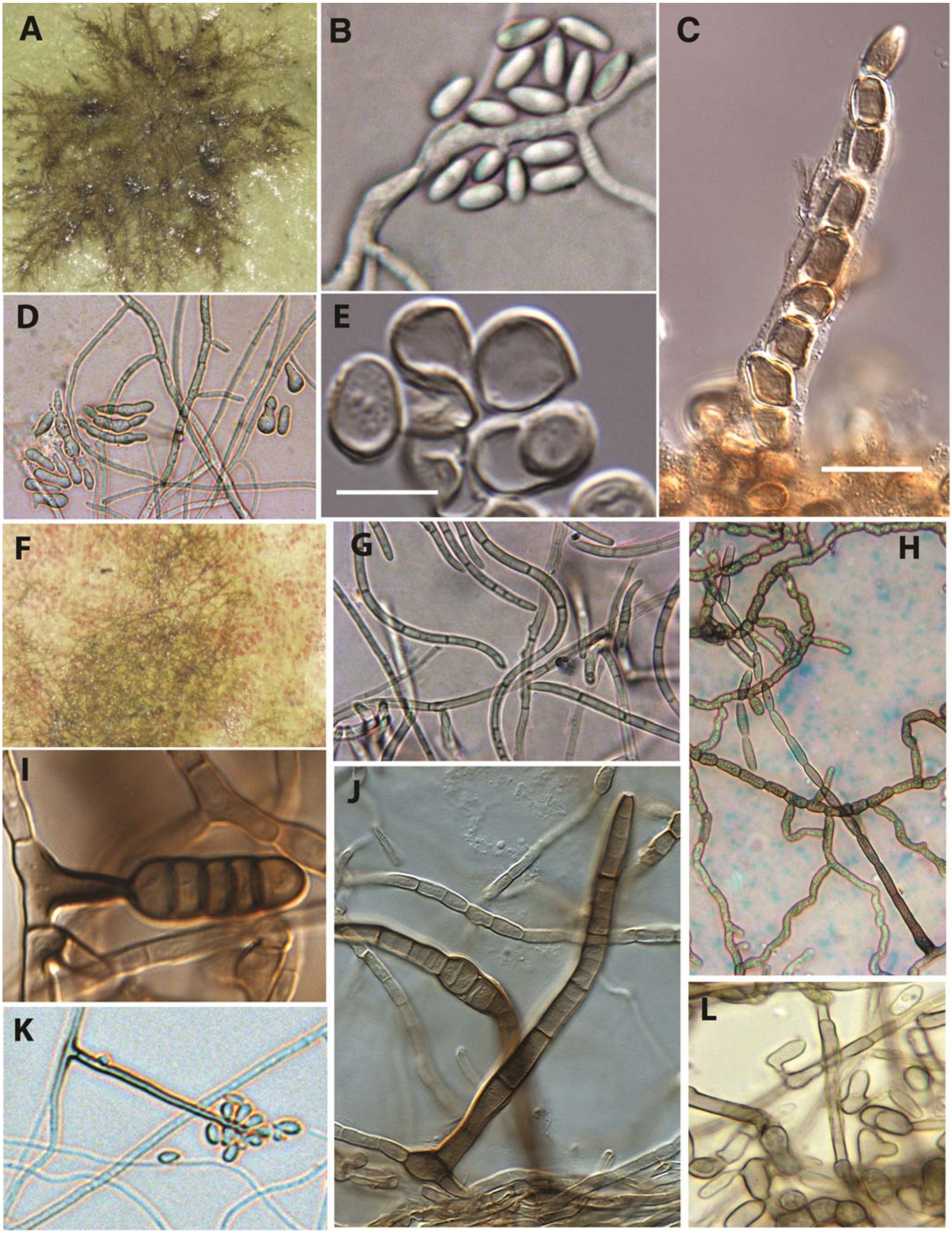

Fig. 2. Conidia of several sooty blotch and flyspeck species that exhibit similar phenotypes on apple. The punctate mycelial phenotype **(A)** is exhibited by *Peltaster fructicola* **(B)**, *Phaeothecoidiella illinoisensis* **(C)**, *Ramularia* sp. P5 **(D)**, and *Phaeothecoidiella missouriensis* **(E)**. The fuliginous mycelial phenotype **(F)** is exhibited by *Micropseudocercospora* sp. FG1.2 **(G)**, *Passalora* sp. FG3 **(H)**, *Houjia yanglingensis* **(I)**, *Sporidesmajora pennsylvaniensis* **(J)**, *Dissoconium* sp. FG5.1 **(K)**, and *Colletogloeum* sp. FG2 **(L)**.

cies were relatively common, occurring in ≥10 orchards (18). The number of species per orchard averaged 7.7, ranging from 2 to 15. Species diversity was strongly affected by fungicide regime in an orchard; there was substantially less diversity in sprayed than in nonsprayed orchards. This discovery appears to fit with evidence that SBFS species can vary at least 20-fold in their sensitivity to fungicides such as thiophanate-methyl (65), which are commonly used against SBFS in the United States. In other words, there is preliminary evidence that fungicide sprays applied during the fruit maturation period select for less sensitive species of SBFS and against more sensitive species. Similar observations have been made in northern Germany, where SBFS is rare in orchards under integrated production but present in organically managed orchards, where it is caused by one economically relevant and several minor species. The greatest species diversity and highest SBFS severity were observed on fruit from orchards with no disease management (R. W. S. Weber, *unpublished data*).

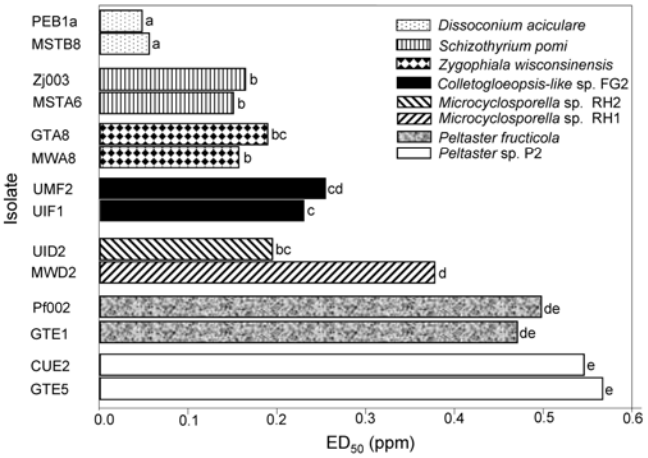

Fig. 3. Estimated ED_{50} of sooty blotch and flyspeck isolates for the fungicide thiophanate-methyl. Bars followed by the same letter are not significantly ($P < 0.05$) different in sensitivity based on Tukey's HSD test (65).

SIDEBAR 4: Koch's postulates for epiphytic pathogens: Fulfillment of Koch's postulates has verified that all 60 of the putative species documented in North America cause sooty blotch and flyspeck (SBFS) signs (18). Koch's postulates needed to be modified in working with epiphytic pathogens such as SBFS by surface-disinfesting immature apples in an orchard using an alcohol spray, applying a preparation of mycelial fragments and/or conidia onto the surface using cotton swabs, and immediately enclosing the inoculated fruit in Japanese fruit bags, which are two-layer bags commonly used in China and Japan to protect apples during the maturation period (18). At harvest, the bags are removed; to complete Koch's postulates, colonies visible on the fruit must match both the mycelial type and internal transcribed spacer sequence of the isolate used as inoculum (4).

Fig. 4. Distribution of cosmopolitan **(A to C)** and regionally restricted **(D to F)** species and putative species within the same genera of the sooty blotch and flyspeck complex based on results of surveys of 39 orchards in 2000 and 2005. **A,** *Schizothyrium pomi*; **B,** *Peltaster fructicola*; **C,** *Microcyclosporella* sp. RH1; **D,** *Zygophiala cryptogama*; **E,** *Peltaster* sp. P2.2; **F,** *Microcyclosporella* sp. RH2. Note that *Zygophiala* is the anamorph genus of *Schizothyrium* (18).

Biogeography. The hypothesis that some SBFS species vary in regional distribution—first proposed by Johnson et al. (34)—has been strongly supported by recent surveys (18). In surveys in the eastern United States, for example, several species were cosmopolitan (e.g., *S. pomi*), whereas others were regional in occurrence (e.g., *Zygophiala cryptogama*) (Fig. 4). These surveys also found that, on average, orchards located west of the Appalachian Mountains had significantly more SBFS species and higher values of species diversity indexes than those located east of the Appalachians (18).

Elsewhere, biogeographic patterns of species distribution are also coming into focus. For example, a survey in China of 27 isolates from orchards in Henan, Liaoning, Gansu, and Shaanxi provinces revealed six *Zygophiala* spp. and provided preliminary evidence that their distribution may differ by region (38). The flyspeck fungus *S. pomi* is common on apples in Serbia and Germany (33; R. W. S. Weber, *unpublished data*) as well as the United States, but is apparently absent from China (38). *Peltaster fructicola, Microcyclospora malicola, Microcyclosporella mali,* and putative species *Microcyclosporella* sp. RH1 have each been found in Serbian, Montenegrian, and German as well as U.S. orchards. In a survey of 14 apple orchards in Serbia and Montenegro, all five species that were found had also been described from the United States (33). Nevertheless, based on present evidence, many SBFS species may be unique to a single continent (18).

Much more information is needed before SBFS biogeographic patterns can be described with confidence. Nevertheless, the existence of regional and continental differences in the assemblage of species invites the hypothesis that the SBFS complex is not composed of the same species assemblage at each location, but rather encompasses a series of assemblages whose composition varies regionally. If so, and if key physiological traits of dominant species such as fungicide and temperature sensitivity (7,65) also vary regionally, it may make sense to customize disease management practices by region. For this purpose, the dominant SBFS species and their environmental biology should be characterized for each fruit-producing region.

Revisiting paradigms. The recent explosion in knowledge of SBFS taxonomy, diversity, and biogeography has demolished the two-disease paradigm that dominated the study of SBFS for 90 years. Abundant evidence now shows that the SBFS complex is highly diverse genetically and physiologically. SBFS species also display a continuum of colony morphologies from mycelial mats lacking sclerotium-like bodies, through intermediate types with both a mycelial matrix and sclerotium-like bodies, to groupings of these bodies without mycelial mats. Each species exhibits only a single mycelial type on apple fruit (4), rather than multiple types as suggested in earlier literature (e.g., 30). As a result, the old two-disease paradigm no longer fits the facts. Instead, SBFS is a disease complex comprised of a large number of fungi whose dominant species may vary with both geographical region and crop management practices (e.g., fungicide use). This new view of SBFS is incorporated into the new edition of the *Compendium of Apple Diseases and Insects* (61).

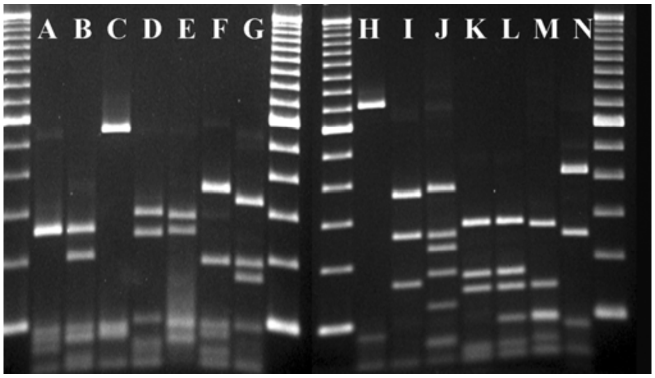

Fig. 5. Using restriction fragment length polymorphism, common members of the sooty blotch and flyspeck complex can be quickly identified to genus or species. After DNA is extracted from mycelium scraped from colonies on apples, polymerase chain reaction amplicons obtained from primers ITS 1-F and Myc 1-R are digested with *Hae*III and run on an agarose gel. Restriction fragment banding patterns can be classified as follows: **A,** *Schizothyrium pomi, Zygophiala cryptogama*, or *Z. tardicrescens*; **B,** *Z. wisconsinensis*; **C,** *Dissoconium aciculare* or *Dissoconium* sp. FG5; **D,** *D. commune*; **E,** *Micropseudocercospora* spp.; **F,** *Microcyclosporella* spp.; **G,** *Colletogloeum* sp. FG2; **H,** *Peltaster fructicola*; **I,** *Peltaster* sp. P2.1; **J,** *Peltaster* sp. P2.2; **K,** *Phaeothecoidiella* spp.; **L,** *Stomiopeltis* sp. RS1; **M,** *Stomiopeltis* sp. RS2; **N,** *Ramularia* sp. L5. Unmarked lanes are 100 base pair ladders (21).

In addition to the two-disease paradigm, other SBFS dogmas also deserve to be laid to rest. Like the lost city of Atlantis, *Gloeodes pomigena* sank from sight a long time ago. This species, accepted as the sole causal agent of "sooty blotch" for nearly 80 years (1920–1997), has not been recovered in any surveys over the past 30 years (4,18,33,34,70,72). It is uncertain whether *G. pomigena* was reassigned as another species or simply disappeared from eastern North America, although the former seems more likely. For example, Batzer et al. (4) described several putative species with morphological characteristics similar to descriptions of *G. pomigena* by Colby (13) and Groves (26). Unless reference cultures of *G. pomigena* can be found for genetic analysis, however, a conclusive solution to this disappearing-species mystery may remain elusive.

Fifty-seven years ago, it was asserted that *Z. jamaicensis,* originally described as the causal agent of banana leaf speckle (41), was the anamorph of the "flyspeck" pathogen then called *Microthyriella rubi*, later renamed *S. pomi* (19,69). Although no direct evidence was presented for making this connection, it persisted as an accepted fact in the SBFS literature (2,70) until a recent study (3) showed that conidial morphology of *S. pomi* is distinct from that described for *Z. jamaicensis* (41). This discrepancy strongly suggests that *Z. jamaicensis* and *S. pomi* are separate but closely related species rather than anamorph/teleomorph stages of the same species (3).

Ecology

A handful of epidemiological studies of *S. pomi* in Massachusetts (15,37) and North Carolina (9), and of *P. fructicola* in North Carolina (34), provide the most detailed information about the environmental biology of SBFS fungi (see 70). These species are readily identifiable on morphological criteria alone, but field studies of cryptic species pose special challenges. For example, the many published studies of *Gloeodes pomigena* ecology (70) should be treated with caution due to uncertainty about the true identity of the SBFS species involved. We know little about the ecology of most of the recently discovered SBFS species.

Molecular tools for ecological studies. New tools are needed to undertake ecological studies of SBFS species. If hundreds or thousands of field samples are involved, isolation and purification in culture, followed by sequencing of rDNA, is impractical due to the slow-growing and generally mulish nature of most SBFS fungi in culture. As a starting point, Duttweiler et al. (21) refined a restriction fragment length polymorphism (RFLP) method proposed by Sun et al. (57) to rapidly identify SBFS fungi directly from mycelium scraped from the apple surface. After DNA was extracted, then amplified with a primer pair specific for the order *Capnodiales*, the restriction enzyme *Hae*III was used to create fragments of the amplicons in order to visualize them on an agarose gel. Duttweiler and co-workers (21) described unique banding patterns for 14 SBFS genera (Fig. 5) and accurately identified a test population of SBFS isolates to either genus or species. The RFLP assay required 2 days compared to several months (or never) for agar plate isolation of many SBFS species, was robust to interference by non-SBFS epiphytes, and resulted in a much higher percentage of identifications than agar plate isolation. This assay needs to be further refined in order to consistently detect SBFS species.

Timing of SBFS inoculation. Separate studies in Poland (25), Germany (43), Brazil (56), and the United States (32) used fruit bags (Fig. 6) to cover apples in nonsprayed orchards at various stages of maturation and assessed SBFS colony development at harvest. All of these studies concluded that colonization of the fruit surface by inoculum can occur throughout the fruit development period, although appearance of the first visible colonies may be delayed until shortly before harvest. Based on results in the Lake Constance region of southern Germany, Mayr et al. (43) suggested that early-season infections were more important than late-season infections (Fig. 7), and therefore that early-season fungicide sprays could outweigh later sprays in impact on SBFS management in that particular region. Ongoing studies in Iowa are using the tools of molecular genetics to discern species-specific patterns of the timing of apple inoculation by SBFS fungi (32).

Timing of appearance of SBFS signs. The period between inoculation of an apple with SBFS fungi and appearance of visible SBFS colonies may vary from a few weeks to several months. The incubation period in Poland was 29 to 45 days (25), and in Brazil up to 48 days (56). Rosenberger's finding that apples incubated in moist chambers at 100% relative humidity produced SBFS signs several weeks sooner than fruit left on the tree (48) emphasized that environment plays a major role in the timing of sign appearance. Apple cultivars that mature relatively early in the summer often escape SBFS damage (8,13). The reason is not entirely clear, but may result from insufficient time to develop visible colonies (8,43). In nonsprayed cultivar trials across 20 site-years in New York, Massachusetts, and Virginia, Biggs and co-workers found that late-maturing cultivars had significantly higher incidence of SBFS than early-maturing ones (8). Similarly, in nonsprayed field trials in Germany on 18 scab-resistant accessions, Mayr and Späth (42) and Mayr et al. (43) noted that the earliest-maturing cultivars consistently had little or no SBFS, whereas mid- to late-season cultivars developed up to 90% disease severity. Sisson et al. (55) applied an RFLP method of Duttweiler et al. (21) to describe phenological patterns of appearance of SBFS colonies on apples in Iowa (Fig. 8). They showed that colonies of two putative species, sterile mycelia spp. RS1 and RS2, consistently became visible first and were also most abundant. A third putative species, *Dissoconium* sp. DS1, appeared several weeks later in the growing season; the number of visible colonies of this taxon increased by 50 to 90% during 3 months of storage at 4°C, whereas the number of new colonies of RS1 and RS2 increased by <5% during storage. This study demonstrated the value of the RFLP technique for making ecological studies feasible.

Temperature. From in vitro studies, Batzer et al. (7) characterized growth response to temperature among five recently discovered SBFS species. For example, *Dissoconium* sp. DS1 had significantly faster mycelial growth rate at 10°C than the other species. Interestingly, this species also had the largest increase in number of colonies during storage at 4°C (55). Comparing temperature responses of SBFS species sampled across climatically distinct regions could yield clues to explaining biogeographic patterns of species distribution.

Fig. 6. Japanese fruit bags are used to protect apple fruit from pathogens and arthropod pests.

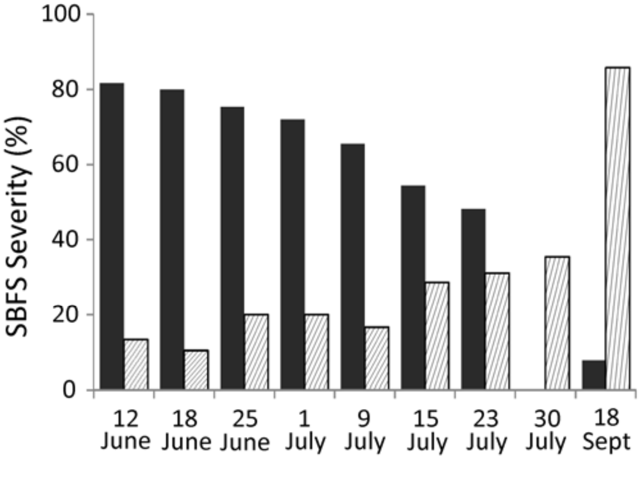

Fig. 7. Severity of sooty blotch and flyspeck (SBFS) signs on nonsprayed apples ('Topaz') at harvest in an orchard in the Lake Constance region of southern Germany in 2008. Solid bars represent means of SBFS severity ratings (43) for 30-apple subsamples that were covered individually by waterproof fruit bags on 2 June (25 days after petal fall); on the dates indicated, apples were removed from bags and subsequently remained uncovered until harvest (18 September). Striped bars represent dates on which subsamples were initially bagged; these apples then remained covered until harvest. Treatments shown for 18 September represent apples bagged since 2 June (solid bar) or exposed for the entire season (striped bar).

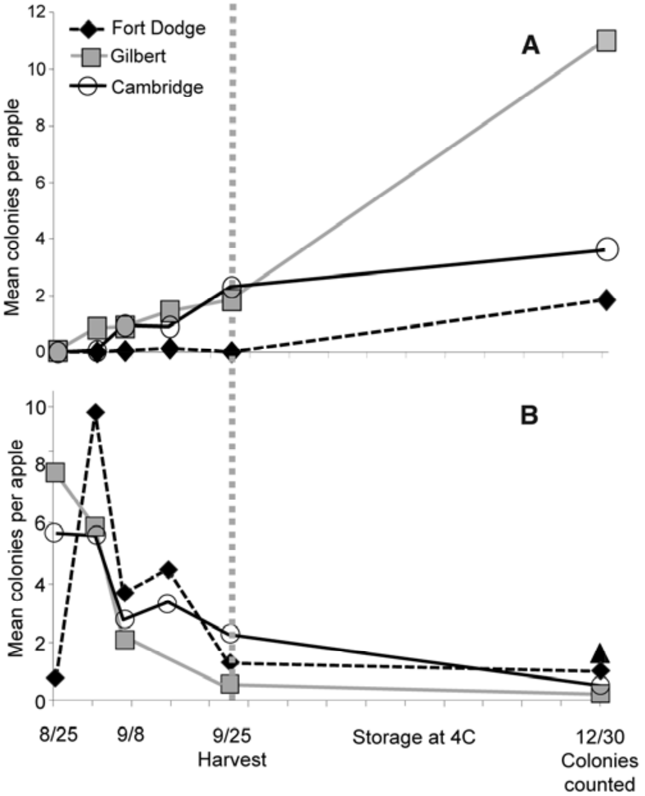

Fig. 8. Time of appearance of colonies and frequency (number of colonies per apple) of the sooty blotch and flyspeck (SBFS) species *Dissoconium aciculare* **(A)** and *Stomiopeltis* sp. RS1 **(B)** in three Iowa orchards in 2006. Newly appearing colonies of SBFS on 30 apples ('Golden Delicious') per orchard were circled weekly with colored pens. After harvest on 25 September (vertical line) and storage for 3 months at 4°C, colonies that had appeared during storage were also marked. Species were identified using restriction fragment length polymorphism (21) and sequencing of the internal transcribed spacer region of rDNA (55).

Nutrient availability. Wrona and Grabowski (71) showed that the first appearance of SBFS signs on maturing apples coincided with an upsurge of fructose and glucose in the apple flesh and on the exterior of the peel. This report supported the hypothesis that an increase in available nutrients on the apple surface during maturation influences the timing of SBFS colony appearance, and helped to explain why SBFS incidence and severity often spike sharply near the end of the growing season. Strong morphological responses of several SBFS species to apple juice concentration in vitro (7) provided additional evidence of the importance of nutrient stimulus. In some cases, these sugars may trigger rapid development of SBFS colonies arising from inoculum that arrived on the apple much earlier in the season (32).

Sources of inoculum for orchard infections. SBFS fungi colonize the epicuticular wax layer of many species of trees, shrubs, and vines in addition to several cultivated fruit crops (2,30,34,44; Fig. 9). For managed orchards, a major source of inoculum for SBFS epidemics may be alternative plant species—so-called reservoir hosts—growing along the orchard borders (Fig. 10).

The clearest evidence for this link was provided recently by field

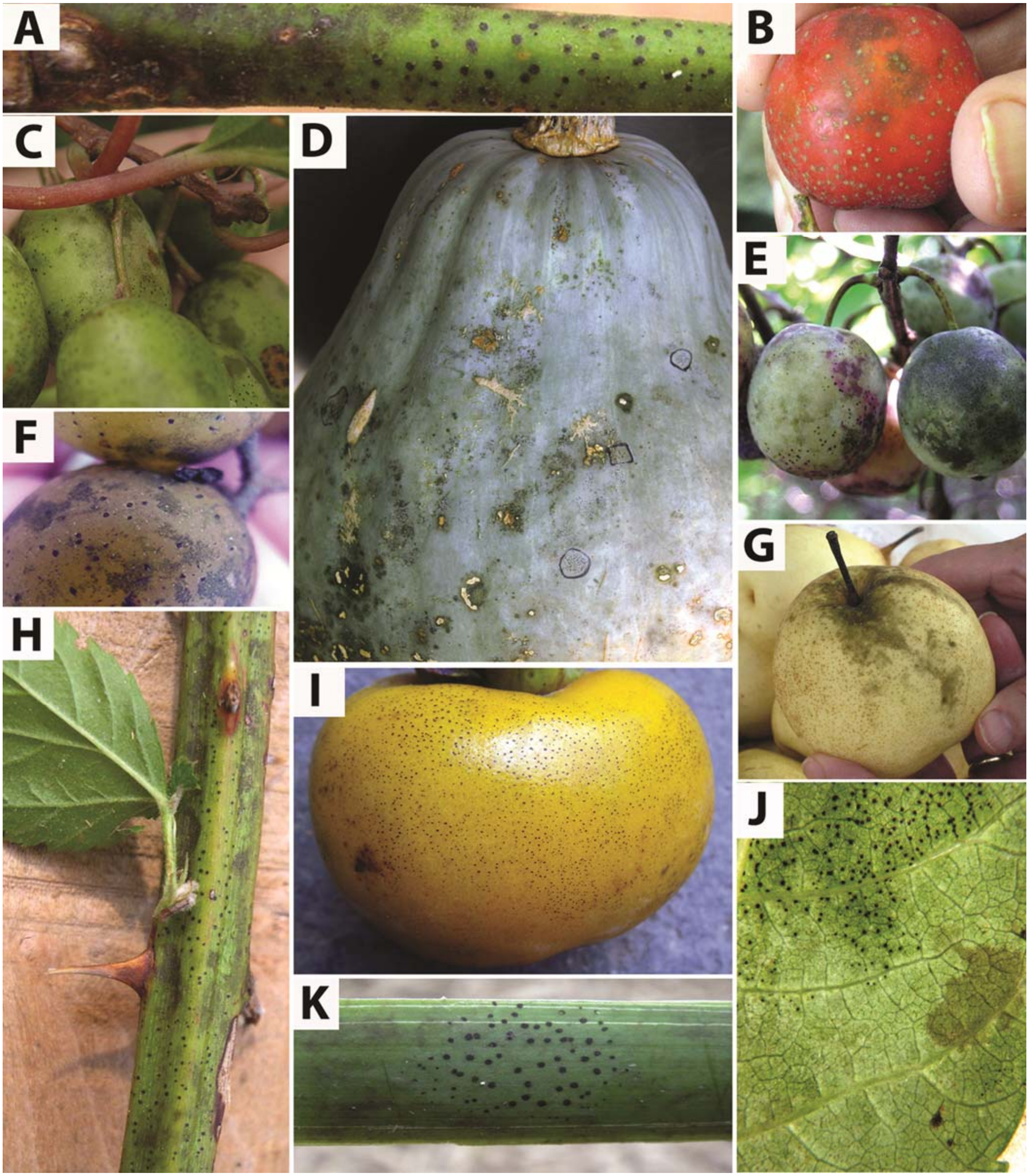

Fig. 9. Sooty blotch and flyspeck colonies on: **A,** sassafras stem; **B,** crabapple; **C,** hardy kiwi; **D,** Hubbard squash; **E,** wild plum; **F,** grape; **G,** Asian pear; **H,** blackberry cane; **I,** persimmon; **J,** leaf of wild grape; and **K,** bamboo.

studies of *Schizothyrium pomi* on common blackberry (*Rubus allegheniensis*) in Massachusetts (15). The timing of *S. pomi* ascospore maturity on blackberry in the spring was driven primarily by air temperature. Cooley and co-workers speculated that the major source of inoculum for nearby apple orchards was not ascospores, but rather conidia that developed on blackberry or other reservoir hosts later in the growing season. *S. pomi* has also been recovered from scores of additional reservoir host species (70).

Very little is known about the occurrence of specific SBFS species on hosts other than apple (70). A complicating factor in interpreting previous host range studies is that the true taxonomic status of most SBFS fungi from earlier studies is now in doubt. For example, reservoir host studies of *Gloeodes pomigena* are difficult to interpret because the species was probably misidentified (70).

The advent of molecular genetic analysis has sparked new interest in exploring host range, since it is now possible to verify the identity of cryptic species. For example, some of the same SBFS species that infest apple also produce signs on fruit of other crop species such as persimmon (36,59), pawpaw (28), winter squash (D. Mayfield, Iowa State University, *unpublished data*), avocado, grape (45), banana, carambola (star fruit), and mango (47). Recent surveys in China revealed SBFS species colonizing the stem surfaces of two species of bamboo (74) and two species of Chinese medicinal plants (75). In Costa Rica, SBFS species have been found on stem sheaths of banana and oil palm (*Elaeis oleifera*) as well as the nut husks of beach almond (*Terminalia catappa*) (M. M. Díaz Arias and J. C. Batzer, *unpublished data*). Despite these new findings, we have barely scratched the surface in describing relationships of SBFS fungi with host plants.

The role of SBFS inoculum sources within apple orchards also deserves closer study. Once SBFS fungi have colonized an orchard, they may become permanently established there, causing new infections from within the plot in subsequent years. Fruit mummies (the remains of apple fruit aborted by the tree at various stages of the growing season; Fig. 11) harbor inoculum of many plant-pathogenic fungi (e.g., 31), and such a role has also been demonstrated for *Peltaster* sp. in Northern Germany by exposing surface-sterilized apples to water run-off from mummies collected from a heavily infested orchard (R. W. S. Weber, *unpublished data*). Apple cultivars can differ greatly in their tendency to retain fruit mummies. The progress of SBFS caused chiefly by *Peltaster* sp. was monitored in an organic orchard planted with alternating rows of two late-maturing cultivars Dalinbel (retaining mummies for 1 to 2 years) or Topaz (dropping most of its mummies within days of fruit abortion). While the timing of onset of SBFS signs was similar for both cultivars, disease incidence was significantly higher in Dalinbel than Topaz (Fig. 12). It is also possible that there are inherent genetic differences in susceptibility of apple cultivars to SBFS fungi, but unequivocal data on this topic have not been published.

Fig. 10. Apple orchard border in Massachusetts. Orchard is at left, nonmanaged woodland is at right. Reservoir hosts in such woodlands can contribute inoculum for sooty blotch and flyspeck outbreaks in orchards.

Management

The economic threat of SBFS to apple growers is high in the eastern half of North America, and has increased in several other apple-growing regions of the world during the past decade. In northern Europe, for example, SBFS has risen in economic importance due to accelerating demand for organically produced apples

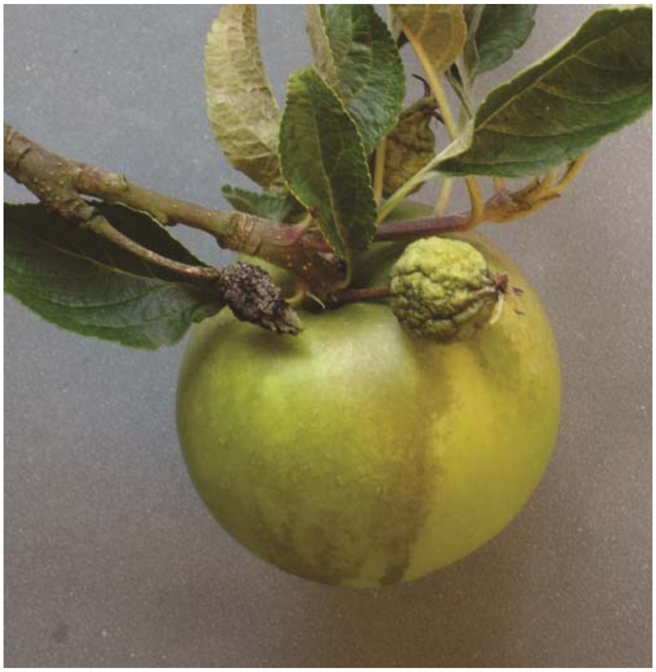

Fig. 11. Sooty blotch and flyspeck signs on a maturing apple ('Dalinbel') associated with an overwintered fruit mummy (left) in an organically managed orchard in northern Germany.

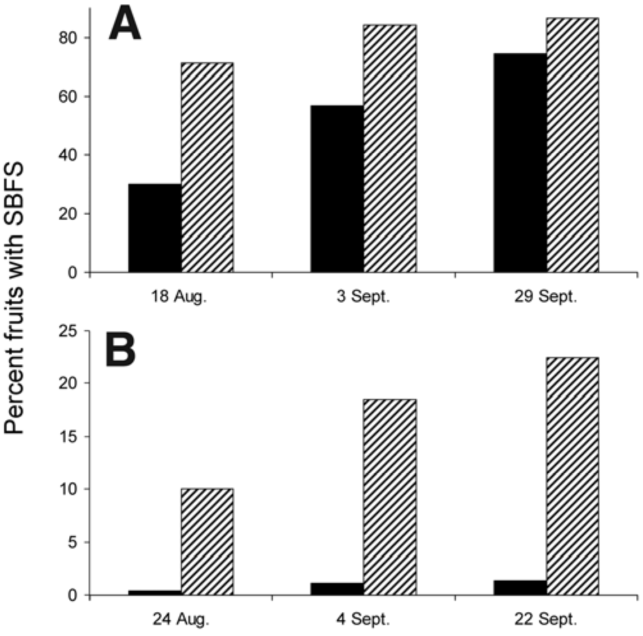

Fig. 12. Sooty blotch and flyspeck (SBFS) severity on apple 'Topaz' (black bars) and 'Dalinbel' (striped bars) during the 2008 **(A)** and 2009 **(B)** growing seasons in an organic orchard in Jork (northern Germany). Trees of the two cultivars were located in adjacent rows (200 m long) in the center of the orchard. Severity of SBFS infection was recorded for 100 arbitrarily selected fruit in each of 10 trees per row (R. W. S. Weber, *unpublished data*).

(66). Although organic orchards in this region are usually planted with scab-resistant cultivars, the high risk of SBFS damage requires fungicides to be sprayed on a preventive schedule during the summer (65). As a result, field research and scientific meetings on SBFS management have increased in northern Europe (11,42,43,66) and southern Brazil (56). In China, the predominant apple-growing country in the world, an intensified emphasis on growing cosmetically acceptable fresh fruit for export and domestic use has heightened interest in SBFS management.

Fungicides. In the United States, the selection of effective fungicides against SBFS has broadened since 2000, partially filling a gap created by withdrawal of registration of ethylene bis-dithiocarbamate (EBDC) fungicides for mid- to late-season use in 1989 (70). In the midwestern and northeastern United States, for example, the strobilurin fungicides kresoxim-methyl and trifloxystrobin controlled SBFS in apple orchards as effectively as the existing standard treatment of thiophanate-methyl plus captan (1,48). However, because of their highly specific mode of action, strobilurins are at risk for resistance development, so their use on apples is restricted to only a few non-consecutive sprays per season. They are also substantially more expensive per application than older fungicides such as EBDCs, thiophanate-methyl, or captan, adding to the pressure on growers to use fungicides more judiciously than in the past.

The search for effective organic methods of SBFS management is intensifying. In the United States, spraying a commercial formulation of potassium bicarbonate, an organically approved fungicide, at 2-week intervals provided a measure of SBFS control but was significantly less effective than conventional fungicides (1). Field trials in Switzerland with a different potassium bicarbonate fungicide, also applied at 2-week intervals, resulted in excellent SBFS control that was superior to that of other organically approved fungicides, including a commercial formulation of coconut soap (64). In U.S. trials, both calcium chloride and phosphites provided excellent control of SBFS when combined with captan (14,50,51,62,63).

In northern Europe, scab-resistant orchards receiving few or no fungicide sprays often escape SBFS entirely during the first year after planting, but experience gradually worsening disease pressure in subsequent years (67). Speculating that SBFS inoculum could build up and overwinter on apple trees in these orchards, Trapman et al. (67) and Mayr and Späth (42) applied copper oxychloride or lime sulfur to trees at high rates just before bud break in the spring. SBFS control was not acceptable, however, leading them to conclude that dormant-season fungicide sprays were much less effective than summer sprays. In preliminary field trials on scab-resistant apple cultivars in southern Germany, Mayr et al. (43) found that six sprays per season of potassium bicarbonate plus wettable sulfur, or of potassium carbonate in a soap formulation, suppressed SBFS effectively, resulting in >85% marketable apples, compared to 7% for an unsprayed control.

Disease-warning systems. Disease-warning systems are decision aids that can help growers reduce their costs by applying fungicide sprays only when justified by a substantive risk of economic loss from a disease (12). Like most warning systems, those targeting SBFS use weather data as inputs. Development of SBFS warning systems began in North Carolina, where Brown and Sutton (10) related cumulative hours of leaf wetness duration (LWD) to timing of appearance of the first signs on apples. Various modifications of Brown and Sutton's LWD-based system, aimed at determining the period of time between the first-cover fungicide spray (7 to 14 days after petal fall) and the subsequent (second-cover) fungicide spray, were validated in field trials in North Carolina, Kentucky, and Iowa during the late 1990s (70) and more recently in Brazil (56).

When the Brown-Sutton-Hartman warning system (as it came to be called) was moved from the Southeast to the Northeast United States, modifications were needed to reflect the differing weather conditions and SBFS species complex (18) in the Northeast. Williamson and Sutton (70) described Rosenberger's development of a dual-threshold warning system for New York growers (49). In New York and New England, *S. pomi* is the predominant species in the complex. Hours of LWD are accumulated beginning at petal fall to account for timing of maturation of *S. pomi* conidia on reservoir host plants near the orchard; these conidia act as primary inoculum for infections on apples in the orchard (15). Rosenberger's warning system, as it is currently used, recommends application of the second-cover fungicide spray when 270 hours of LWD have accumulated since petal fall. Following this spray, additional fungicide sprays are applied when a total of 5.1 cm of rain has fallen or 21 days have passed, whichever occurs first (D. Rosenberger, Cornell University, *personal communication*).

In field trials in the Upper Midwest United States (Iowa, Wisconsin, and Illinois) during 2001 and 2002, the Brown-Sutton-Hartman system performed well in university orchards, but incidence of SBFS was higher than with conventional spray timing in 12 of 28 commercial orchards, suggesting that the warning system needed to be modified for this region (1). In subsequent field trials, timing of the first appearance of SBFS signs in unsprayed orchards in Wisconsin and Iowa was predicted more accurately by cumulative hours of relative humidity (RH) ≥97% after the first-cover spray than by LWD, rainfall, air temperature, or combinations of these parameters (20). RH was a more accurate predictor than LWD because dew was the predominant cause of wet hours in the Upper Midwest. In contrast, in North Carolina, where most wet hours were caused by rainfall, LWD was a more accurate predictor. Because SBFS warning systems traditionally place sensors within the canopy of apple trees in orchards, and LWD sensors under tree canopies are much more prone to local site variation than RH sensors during dew periods (5), dew-dominated climates are more subject to LWD measurement errors than rain-dominated climates. As a result, LWD worked better as a predictor of SBFS risk in a rain-dominated climate (North Carolina), whereas RH worked better in a dew-dominated climate (the Upper Midwest). This outcome reinforced the caution that SBFS warning systems need to be thoroughly validated in field trials before being adopted by growers in a new region.

Analyzing and modifying practices that could influence warning system behavior are making the systems more robust for grower use. For example, 3 years of field experiments in Iowa and Wisconsin orchards showed that the performance of the Brown-Sutton-Hartman warning system was often compromised by low-volume spraying (≤473 liters/ha) (70), but only sporadically by poor pruning of apple trees (M. L. Gleason and P. S. McManus, *unpublished data*). In southern Brazil, however, summer pruning enhanced the performance of the Brown-Sutton-Hartman system (56). These observations are defining decision rules to ensure that SBFS warning systems perform reliably in each apple production region.

In northern Europe, the proprietary RIMpro decision-support system, originally developed to time fungicide sprays against scab, now includes a SBFS warning system module for organic fungicides (67). This warning system was assessed in preliminary field trials in the Lake Constance region of Southern Germany during 2005 (42) and is currently being further validated in a multi-year trial (U. Mayr, *unpublished data*).

Bagging fruit. In China and Japan, apple fruit are routinely sealed individually in air-permeable, double-layer bags from 3 to 4 weeks after fruit set until harvest (Fig. 6). The outer, opaque layer is removed shortly before harvest in order to allow the fruit to color normally. Bagging can be highly effective against SBFS since the bags prevent spores from reaching the fruit. The bagging strategy has several potential pitfalls, however. In Iowa orchards, for example, preliminary field studies found that numerous SBFS spores landed during the earliest weeks of fruit development, before bagging would normally occur (S. I. Ismail, Iowa State University, *unpublished data*). Therefore, fruit could be inoculated prior to bagging (Fig. 13). Another liability is the fact that bags must be installed and removed by hand. In China, for example, it is anticipated that bagging may become cost prohibitive as labor costs rise. In addition, bagging offers no protection against foliar diseases, so fungicides must still be applied preventively where these diseases pose a risk of severe leaf damage or defoliation. This factor partially negates the protective advantage of bagging.

Early-maturing cultivars. As discussed earlier, cultivars may differ in their susceptibility to SBFS colonization. Whereas early-ripening cultivars may escape SBFS altogether, late-maturing varieties, particularly those retaining their fruit mummies, are at high risk (8; R. W. S. Weber, *unpublished data*). Minimizing SBFS by choosing appropriate cultivars for new orchards is therefore possible. However, criteria such as yield, market demand, long-term storability, and susceptibility to a wide range of diseases are likely to be given higher priority by commercial apple growers than reduction of SBFS risk.

Postharvest eradication. Fresh-market grade of SBFS-infested apples can be restored by postharvest dip treatments in chlorine bleach followed by brushing on a commercial grading line, effectively removing the blemishes or at least making them invisible (13,29). This practice is in wide use, partially to eradicate SBFS signs but also to suppress fruit and human pathogens that might otherwise accumulate in water flumes used in fruit packing lines. In a follow-up study, Batzer et al. (6) found that SBFS severity was reduced by dip-and-brush treatments using chlorine bleach or fruit soap. Removal of SBFS blemishes was not complete on heavily infested apples, certain mycelial types were more difficult to remove than others, and removal efficacy was affected by apple cultivar.

Outlook

A series of discoveries during the past decade has radically changed our perception of SBFS. At the same time, questions are piling up faster than answers. Some of these questions have been languishing for decades, whereas others are new. We raise a few of them here in the hope of stimulating research aimed at finding answers.

What roles do SBFS species play in natural and managed ecosystems? This question has received little attention to date. Since SBFS fungi are successful colonizers of the surfaces of many plant species, it is tempting to speculate that they may serve as decomposers once these tissues senesce and die. Other epiphytic fungi fulfill such a saprophytic role (46). In some instances, SBFS fungi may provide a food source for invertebrates such as snails which graze on plant surfaces (Fig. 14), but the ecological significance of these interactions is unclear.

Could fungi causing SBFS on some plants also be pathogens of other plants? Crous and Groenewald (16) proposed the “pogo stick” hypothesis to explain the interesting observation that host-specific plant parasites in the genus *Mycosphaerella* also colonize nonhost plants and other substrates, for example as endophytes or epiphytes. These fungi can produce inoculum on such nonhosts, which may have survival value in increasing the odds that they will encounter their hosts. So far there is no direct evidence to support either parasitic or saprophytic roles of SBFS species. However, gaining deeper insight into the ecological niches of the SBFS fungi could provide clues on how to suppress them on vulnerable fruit crops.

Where did SBFS fungi come from? Given the recent rapid progress in reconstructing evolutionary scenarios for dozens of fungal taxa, as well as our accumulation of thousands of SBFS isolates, it should now be possible to deduce the ancestry of SBFS fungi. It is intriguing to note that many plant-pathogenic fungal species are closely related to SBFS clades at the order, family, and genus levels in SBFS phylogenetic trees of the LSU region of rDNA (4,18). Did SBFS species therefore evolve from plant-parasitic ancestors? Alternatively, many characteristics of SBFS fungi closely resemble those of fungi that grow on rocks (52,53) and as lichen symbionts (54). Like these fungi, SBFS species are extremophiles, colonizing environments with wide variations in light levels and water availability, and they must function as oligotrophs since their substrate is likely to be nutrient-poor most of the time. Both groups show similar adaptations such as melanization of hyphae and spores, absence of sexual cycles (and sometimes asexual cycles too), extremely slow growth rates, formation of conidia by low-energy methods such as budding, and secretion of a mucilaginous matrix around hyphae. Many rock and lichen inhabitants, like almost all SBFS fungi, are in the order *Capnodiales*, and several of these species are highly homologous to SBFS species in BLAST searches. Could SBFS fungi therefore have evolved from rock- or lichen-inhabiting fungi? An effort to reconstruct the evolutionary origins of SBFS fungi is underway by several authors of this paper.

How are SBFS species arranged in space and time? Beyond a few hints from recent studies, we need to better define spatial patterns in species occurrence and predominance at different scales: from orchard to orchard in a locality, among geographic regions, and across continents. The occurrence of a SBFS species in one country but not another may prompt the latter to classify it as a quarantine pest and take measures to prevent its introduction on imported apples. What is the relative importance of management regime (especially fungicide use), reservoir host plant assemblage, and climate in SBFS biogeography? Furthermore, how persistent are patterns of species predominance and occurrence in given orchards from year to year, and what factors influence annual and longer-term changes in the species assemblage? Studies in northern Germany (R. W. S. Weber, *unpublished data*), Massachusetts (68), and southern Brazil (56) revealed spatial gradients of SBFS inci-

Fig. 13. Signs of sooty blotch and flyspeck on an apple inside a Japanese fruit bag in a commercial apple orchard in China.

Fig. 14. Trails provide evidence of snail grazing through sooty blotch and flyspeck colonies on a fallen apple fruit.

dence that peaked along orchard borders, suggesting that SBFS risk could be mapped for individual orchard blocks based on proximity to inoculum sources (68).

How do disease cycles differ among SBFS species? The epidemiology of most SBFS species is unexplored territory. By targeting the most important species in an apple production region, we can learn basic information that could lead to more effective management of the disease. For example, how far does inoculum travel from reservoir hosts to fruit in orchards? Preliminary data from orchards in Massachusetts suggest that conidia of SBFS species travel a few hundred yards at most (15). How does this range vary among targeted SBFS species? Furthermore, which phenological and weather factors affect spore release by these species? Although it has been assumed that the major source of SBFS inoculum for U.S. orchards is outside rather than within the orchard (15), we must verify where SBFS inoculum is coming from. For growers, is it worthwhile to spray or remove reservoir host species in order to reduce the risk of SBFS outbreaks? We continue to need faster and more precise tools for epidemiological studies, including not only improved RFLP assays but also newer approaches such as macroarrays.

How can SBFS be managed more effectively? We need to integrate reduced-risk fungicides, warning systems, and associated practices such as appropriate spray volume for each geographic region and for organic as well as conventional management. Key questions for warning system validation include whether it is effective to focus primarily on the first-appearing species on the crop in a region, how SBFS warning systems should be integrated into management practices for concurrent diseases such as apple scab and fruit rots (47), and how they can be integrated into organic apple production. As with many other pathosystems, definitive studies of the economic impact of proposed new management schemes are sorely needed.

Questions aside, the past decade has dramatically altered our perception of the SBFS complex. The ongoing, DNA-driven revolution in fungal taxonomy (16) provided the tools for revealing more than 60 species in the complex, compared to four in 2000. What previously appeared to be two diseases—"sooty blotch" and "flyspeck"—turned out to be a spectrum of intergraded mycelial types, each represented by numerous cryptic species. It is now clear that SBFS is a vast disease complex rather than two distinct diseases. By using molecular tools, we have also started to unlock long-held secrets of SBFS such as patterns of diversity, biogeography, and environmental biology. Recent advances in disease management, including effective reduced-risk and organic fungicides as well as wider validation of disease-warning systems, have potential to save money for apple growers while minimizing pesticide loads on apples and the environment.

Dedication

This article is dedicated to Dr. Kenneth D. Hickey (Professor Emeritus, Penn State University Fruit Research and Extension Center, Biglerville, PA), an influential pioneer in the study of sooty blotch and flyspeck.

Literature Cited

1. Babadoost, M., Gleason, M. L., McManus, P. S., and Helland, S. J. 2004. Evaluation of a wetness-based warning system and reduced-risk fungicides for management of sooty blotch and flyspeck of apple. HortTechnology 14:27-33.
2. Baker, K. F., Davis, L. H., Durbin, R. D., and Snyder, W. C. 1977. Greasy blotch of carnation and flyspeck of apple: Diseases caused by *Zygophiala jamaicensis.* Phytopathology 67:580-588.
3. Batzer, J. C., Díaz Arias, M. M., Harrington, T. C., Gleason, M. L., Groenevald, J. C., and Crous, P. W. 2008. Four species of *Zygophiala* (Schizothyriaceae, Capnodiales) are associated with the sooty blotch and flyspeck complex on apple. Mycologia 100:246-248.
4. Batzer, J. C., Gleason, M. L., Harrington, T. C., and Tiffany, L. H. 2005. Expansion of the sooty blotch and flyspeck complex on apples based on analysis of ribosomal DNA and morphology. Mycologia 97:1268-1286.
5. Batzer, J. C., Gleason, M. L., Taylor, S. E., Koehler, K. J., and Monteiro, J.


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Dr. Zhang is an associate professor in the College of Plant Protection at Northwest A&F University. Her research interests on pathogen biology and integrated management of apple diseases include Marssonina blotch, SBFS, bitter rot, and postharvest diseases.

Ms. Díaz Arias received bachelor's degrees in biotechnology and agronomy from Technological Institute of Costa Rica and University of Costa Rica (UCR). Her M.S. degree in crop protection from UCR, on characterization of SBFS diversity and biogeography, included a research internship at ISU. Her Ph.D. research at ISU focuses on determining relative frequency of root-related *Fusarium* species on soybean in Iowa and their relationship with soybean cyst nematode.

Dr. Sutton is a professor in the Department of Plant Pathology at North Carolina State University. He has a joint appointment in research, extension, and teaching. His research and extension activities have focused on the epidemiology, biology, and management of summer diseases of apples and vinifera grapes in the southeastern United States. He has taught courses on epidemiology and plant disease control and fruit diseases and their management and has recently led the development of curriculum for plant pathology students interested in careers in extension and industry.


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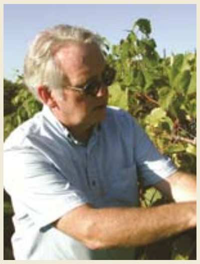
Daniel R. Cooley


Ulrich Mayr


Roland W. S. Weber


Keith S. Yoder


Emerson M. Del Ponte


Alan R. Biggs


Bernhard Oertel

Dr. Crous is director of the CBS Fungal Biodiversity Centre in Utrecht, Netherlands, and is appointed as professor at the Universities of Wageningen and Utrecht (Netherlands), Stellenbosch and Pretoria (South Africa). He is directly involved in training phytomycologists in Europe, Asia, and Africa, and has published widely on the taxonomy of plant pathogenic fungi. His research focuses primarily on taxonomy of plant pathogenic members of Dothideomycetes, specifically *Botryosphaeria*, *Mycosphaerella, Phoma,* and their relatives.

Dr. Ivanović is a plant pathologist at the University of Belgrade, Serbia. He received his B.S. degree in 2005 and his Ph.D. degree in plant pathology from the Faculty of Agriculture, University of Belgrade, in 2010. He was a visiting fellow in the plant pathology departments at University of Florida (2007) and Iowa State University (2008). His current research focuses on diagnosis and biological control of bacterial and fungal diseases of fruit and vegetable crops.

Dr. McManus is Vaughan-Bascom Professor of Plant Pathology at the University of Wisconsin-Madison, where she has been on the faculty since 1995. She earned her B.S. degree in botany from UW-Madison and M.S. and Ph.D. degrees from Michigan State University. Her research and extension programs are focused on the biology and management of diseases of temperate fruit crops.

Dr. Cooley has worked for nearly 30 years in integrated management of diseases of temperate fruit crops. He received an A.B. from Harvard College, M.S. from the University of Vermont in horticulture, and Ph.D. from the University of Massachusetts Amherst in plant pathology. His professional focus has been on the ecology of diseases, and on applying knowledge of disease ecology to management of plant diseases, including disease forecasting models, fungicidal and nonfungicidal management methods, and evaluation of environmental impacts of disease management.

Dr. Mayr holds a degree in agricultural science and completed his Ph.D. at the Munich Technical University on the identification of phenolic compounds in apple and their influence on apple scab resistance. After postgraduate research work at the INRA fruit breeding station in Angers (FR), since 1996 he has been active at the Kompetenzzentrum Obstbau – Bodensee (KOB) in Bavendorf near Ravensburg, South West Germany. At the KOB, he is group leader for pipfruit cultivar selection and also responsible for organic fruit growing research. Since autumn 2006, he has been leader of the Baden-Württemberg central cultivar collection.

Dr. Weber received his B.Sc. and Ph.D. from the University of Exeter (UK) before joining the University of Kaiserslautern (Germany) in 1999, and the Northern German Fruit Production Centre in 2006. As a whole-organism mycologist, his interests include secondary metabolites, taxonomy, ecophysiology, and plant pathology, culminating in the publication of a new edition of John Webster's *Introduction to Fungi*. Dr. Weber has established a mycology laboratory and contributes to the advisory service, focusing on new diseases and fungicide resistance.

Dr. Yoder received a Ph.D. in plant pathology from Michigan State University and has been Research and Extension Tree Fruit Pathologist with Virginia Tech University's Ag Research and Extension Center, Winchester, VA, since 1976. Dr. Yoder's long-term research focus has included alternative management strategies for the many tree fruit diseases in the region, fungicide activity spectrum and resistance management, strategies for managing fire blight, disease susceptibility and resistance of new apple cultivars, and apple powdery mildew economic thresholds.

Dr. Del Ponte has been a professor at the Universidade Federal do Rio Grande do Sul (UFRGS), Brasil, since 2006. He received a Ph.D. in plant pathology in 2004 from the Universidade Federal de Pelotas, having conducted part of the work in the Department of Plant Pathology, Cornell University, as a visiting fellow in 2002. Prior to joining UFRGS, he was a postdoctoral research associate at Iowa State University. His research activities focus on disease modeling and forecasting, molecular epidemiology, and quantitative aspects of epidemics on cereal and fruit crops in subtropical regions.

Dr. Biggs is professor of plant pathology and extension specialist for tree fruit diseases at West Virginia University's Kearneysville Tree Fruit Research and Education Center. In 1983, Dr. Biggs was appointed research scientist with Agriculture Canada at the Vineland, Ontario, Research Station, a position he held until 1989, when he moved to TFREC. He served as Editor-In-Chief of *Plant Disease* from 2000 to 2002. His research interests include alternative disease control strategies for fruit production, potential uses of calcium for disease suppression, woody plant defense mechanisms, and electronic communications in extension plant pathology.

Dr. Oertel is a researcher at INRES, Agricultural Faculty, University of Bonn, in mycology and chemistry. His research topics include sooty blotch fungi on apple, fungal diseases of ananas, phylogeny of mycorrhizal fungi, mycotoxins, fungal inventory of Central Europe, and other topics. He teaches wine science and fruit growing.

E. B. A. 2008. Spatial heterogeneity of leaf wetness duration in apple trees and its influence on performance of a warning system for sooty blotch and flyspeck. Plant Dis. 92:164-170.

6. Batzer, J. C., Gleason, M. L., Weldon, B., Dixon, P. M., and Nutter, F. W., Jr. 2002. Evaluation of postharvest removal of sooty blotch and flyspeck on apples using sodium hypochlorite, hydrogen peroxide with peroxyacetic acid, and soap. Plant Dis. 86:1325-1332.
7. Batzer, J. C., Hernández Rincon, S., Mueller, D. S., Petersen, B. J., Le Corronc, F., McManus, P. S., Dixon, P. M., and Gleason, M. L. 2010. Effect of temperature and nutrient concentration on the growth of six species of sooty blotch and flyspeck fungi. Phytopathol. Mediterr. 49:3-10.
8. Biggs, A. R., Cooley, D. R., Rosenberger, D. A., and Yoder, K. S. 2010. Relative susceptibility of selected apple cultivars to sooty blotch and flyspeck. Online. Plant Health Progress doi:10.1094/PHP-2010-0726-01-RS.
9. Brown, E. M., and Sutton, T. B. 1993. Time of infection of *Gloeodes pomigena* and *Schizothyrium pomi* on apple in North Carolina and potential control by an eradicant spray program. Plant Dis. 77:451-455.
10. Brown, E. M., and Sutton, T. B. 1995. An empirical model for predicting the first symptoms of sooty blotch and flyspeck of apples. Plant Dis. 79:1165-1168.
11. Buchleither, S., and Späth. 2007. Regenflecken – nach wie vor ein ungelöstes Problem. Öko-Ostbau 3:3-7.
12. Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. John Wiley & Sons, New York.
13. Colby, A. S. 1920. Sooty blotch of pomaceous fruits. Trans. Ill. Acad. Sci. 13:139-179.
14. Cooley, D. R., Autio, W. R., and Krupa, J. 2007. Calcium salts and other alternatives to conventional fungicides for management of the summer disease complex of apple, 2006. Plant Disease Management Reports 1:PF051 Online publication. doi: 10.1094/PDMR01
15. Cooley, D. R., Lerner, S. M., and Tuttle, A. F. 2007. Maturation of thyriothecia of *Schizothyrium pomi* on the reservoir host *Rubus allegheniensis.* Plant Dis. 91:136-141.
16. Crous, P. W., and Groenewald, J. Z. 2005. Hosts, species, and genotypes: Opinions versus data. Australas. Plant Pathol. 34:463-470.
17. Crous, P. W., Schoch, C. L., Hyde, K. D., Wood, A. R., Gueidan, C., de Hoog, G. S., and Groenewald, J. Z. 2009. Phylogenetic lineages in the *Capnodiales*. Stud. Mycol. 64:17-47-S7. doi:10.3114/sim.2009.64.02
18. Díaz Arias, M. M., Batzer, J. C., Harrington, T. C., Wang Wong, A., Bost, S. C., Cooley, D. R., Ellis, M. A., Hartman, J. R., Rosenberger, D. A., Sundin, G. W., Sutton, T. B., Travis, J. W., Wheeler, M. J., Yoder, K. S., and Gleason, M. L. 2010. Diversity and biogeography of sooty blotch and flyspeck fungi on apple in the eastern and midwestern United States. Phytopathology 100:345-355.
19. Durbin, R. D., Davis, L. H., Snyder, W. C., and Baker, K. F. 1953. The imperfect stage of *Mycothyriella rubi*, cause of flyspeck of apple. Phytopathology 43:470-471.
20. Duttweiler, K. B., Gleason, M. L., Dixon, P. M., Sutton, T. B., McManus, P.S., and Monteiro, J. E. B. A. 2008. Adaptation of an apple sooty blotch and flyspeck warning system for the Upper Midwest United States. Plant Dis. 92:1215-1222.
21. Duttweiler, K. B., Sun, G. Y., Batzer, J. C., Harrington, T. C., and Gleason, M. L. 2008. An RFLP-based technique for identifying fungi in the sooty blotch and flyspeck complex on apple. Plant Dis. 92:794-799.
22. Frank, J., Crous, P. W., Groenewald, J. Z., Oertel, B., Hyde, K. D., Phengsintham, P., and Schroers, H.-J. 2010. *Microcyclospora* and *Microcyclosporella*: Novel genera accommodating epiphytic fungi causing sooty blotch on apple. Persoonia 24:93-105.
23. Gold, H. J., and Sutton, T. B. 1986. A decision analytic model for chemical control of sooty blotch and flyspeck diseases of apple. Agric. Systems 21:129-157.
24. Gold, H. J., and Sutton, T. B. 1988. Past orchard performance as a guide to decisions on the use of fungicides to control sooty blotch and flyspeck. Crop Prot. 7:258-266.
25. Grabowski, M., and Wrona, B. 2004. An investigation of the date of sooty blotch primary infection and duration of incubation period for selected apple cultivars. Folia Hortic. 16:73-77.
26. Groves, A. B. 1933. A study of the sooty blotch disease of apples and causal fungus *Gloeodes pomigena.* Virginia Agric. Exp. Stn. Bull. 50:1-43.
27. Harrington, T. C., and Rizzo, D. M. 1999. Defining species in the fungi. Pages 43-70 in: Structure and Dynamics of Fungal Populations. J. Worrall, ed. Kluwer Academic Press.
28. Hemnani, K., O'Malley, P. J., Tanović, B., Batzer, J. C., and Gleason, M. L. 2008. First report of seven species of sooty blotch and flyspeck fungi on *Asimina triloba* in Iowa. Plant Dis. 92:1366.
29. Hendrix, F. F., Jr. 1991. Removal of sooty blotch and flyspeck from apple fruit with a chlorine dip. Plant Dis. 75:742-743.
30. Hickey, K. D. 1960. The sooty blotch and flyspeck diseases of apple with emphasis on variation within *Gloeodes pomigena* (SCW.) Colby. Ph.D. diss. Pennsylvania State University, State College, PA.
31. Holmes, J., and Rich, A. E. 1970. The influence of the retention of immature apple mummies by certain cultivars on the overwintering of *Physa lospora obtusa*. Phytopathology 60:452-453.
32. Ismail, S. I., Batzer, J. C., Mayfield, D. A., and Gleason, M. L. 2010. Phenology of natural inoculation of apples by sooty blotch and flyspeck fungi in Iowa apple orchards. (Abstr.) Phytopathology 100:S54.
33. Ivanović, M. M., Ivanović, S. M., Batzer, J. C., Tatalović, N., Oertel, B., Latinović, J., Latinović, N., and Gleason, M. L. 2010. Fungi in the Apple sooty blotch and flyspeck complex from Serbia and Montenegro. J. Plant Pathol. 92:65-72.
34. Johnson, E. M., Sutton, T. B., and Hodges, C. S. 1997. Etiology of apple sooty blotch disease in North Carolina. Phytopathology 87:88-95.
35. Jones, A. L., and Aldwinckle, H. S., eds. 1990. Compendium of Apple and Pear Diseases. American Phytopathological Society, St. Paul, MN.
36. Latinović, J., Batzer, J. C., Duttweiler, K. B., Gleason, M. L., and Sun, G. 2007. First report of five sooty blotch and flyspeck fungi on *Prunus americana* in the United States. Plant Dis. 91:1685.
37. Lerner, S. M. 1999. Studies on the biology and epidemiology of *Schizothyrium pomi*, causal agent of flyspeck disease of apple. M.S. thesis. University of Massachusetts, Amherst.
38. Li, H., Zhang, R., Sun, G., Batzer, J. C., and Gleason, M. L. 2010. New species and record of *Zygophiala* on apple fruit from China. Mycol. Prog. 9:245-251. DOI 10.1007/s11557-009-0633-1.
39. Li, H. Y., Zhang, R., Sun, G. Y., and Gleason, M. L. 2009. First report of sooty blotch and flyspeck fungi on hawthorn in China. Plant Dis. 93:670.
40. Ma, Y., Zhang, R., Sun, G., Zhu, H., Tang, M., Batzer, J. C., and Gleason, M. L. 2010. A new species of *Zygophiala* associated with the flyspeck complex on apple from China. Mycol. Prog. 9:151-155. DOI 10.1007/s11557-009-0635-z.
41. Martyn, E. B. 1945. A note on banana leaf speckle in Jamaica and some associated fungi. Commonw. Mycol. Inst. Mycol. Pap. 13:1-5.
42. Mayr, U., and Späth, S. 2008. Sooty blotch of apple: Efficacy of different application strategies. Pages 82-86 in: Ecofruit – Proc. 13th Int. Conf. Cult. Techniques Phytopathol. Problems Organic Fruit Growing. FÖKO, Weinsberg, Germany.
43. Mayr, U., Späth, S., and Buchleither, S. 2010. Sooty blotch research – a progress report. Pages 70-77 in: Ecofruit - Proc 14th Int. Conf. Organic Fruit Growing. FÖKO, Weinsberg, Germany.
44. Nasu, H., and Kunoh, H. 1987. Scanning electron microscopy of flyspeck of apple, pear, Japanese persimmon, plum, Chinese quince, and pawpaw. Plant Dis. 71:361-364.
45. Nasu, H., Shintaro, F. and Yokoyama, T. 1985. *Zygophiala jamaicensis* Mason, a causal fungus of flyspeck of grape, Japanese persimmon, and apple. Ann. Phytopathol. Soc. Jpn. 51:536-545.
46. Osono, T. 2006. Role of phyllosphere fungi of forest trees in the development of decomposer fungal communities and decomposition processes of leaf litter. Can. J. Microbiol. 52:701-716.
47. Perez-Martinez, J. M., Batzer, J., Ploetz, R., and Gleason, M. 2009. Avocado, banana, carambola, and mango are hosts of members of the sooty blotch and flyspeck complex. (Abstr.) Phytopathology 99:S102.
48. Rosenberger, D. A., Meyer, F. W., Ahlers, C. A., and VanCamp, K. L. 2002. Apple disease control with strobilurin, DMI and contact fungicides, 2001. Fungic. Nematicide Tests 57:PF15 doi: 10.1094/FN57.
49. Rosenberger, D. A., Meyer, F. W., and Engle, C. A. 1997. Timing summer fungicides for sooty blotch and flyspeck, 1996. Fungic. Nematicide Tests 52:23.
50. Rosenberger, D. A., Meyer, F. W., and Rugh, A. 2008. Effectiveness of ProPhyt used alone or with other fungicides to control summer disese of apples, 2007. Plant Disease Management Reports 2: PF032 Online publication. doi: 10.1094/PDMR02
51. Rosenberger, D. A., Meyer, F. W., and Rugh, A. 2009. Controlling flyspeck, sooty blotch and fruit decays with fungicides applied during summer, 2008. Plant Disease Management Reports 3: PF011. Online publication. doi: 10.1094/PDMR03.
52. Ruibal, C., Gueidan, C., Selbmann, L., Gorbushina, A. A., Crous, P. W., Groenewald, J. Z., Muggia, L., Grube, M., Isola, D., Staley, J. T., Lutzoni, F., and de Hoog, G. S. 2009. Phylogeny of rock-inhabiting fungi related to *Dothideomycetes.* Stud. Mycol. 64:123-1337.
53. Ruibal, C., Platas, G., and Bills, G. F. 2008. High diversity and morphological convergence among melanised fungi from rock formations in the Central Mountain System of Spain. Persoonia 21:93-110.
54. Schoch, C. L., Crous, P. W., Groenewald, J. Z., Boehm, E. W. A., Burgess, T. I., de Gruyter, J., de Hoog, G. S., Dixon, L. J., Grube, M., Gueidan, C., Harada, Y., Hatakeyama, S., Hirayama, K., Hosoya, T., Huhndorf, S. M., Hyde, K. D., Jones, E. B. G., Kohlmeyer, J., Kruys, Å., Li, Y. M., Lücking, R., Lumbsch, H. T., Marvanová, L., Mbatchou, J. S., McVay, A. H., Miller, A. N., Mugambi, G. K., Muggia, L., Nelsen, M. P., Nelson, P., Owensby, C. A., Phillips, A. J. L., Phongpaichit, S., Pointing, S. B., Pujade-Renaud, V., Raja, H. J., Rivas Plata, E., Robbertse, B., Ruibal, C., Sakayaroj, J., Sano, T., Selbmann, L., Shearer, C. A., Shirouzu, T., Slippers, B., Suetrong, S., Tanaka, K., Volkmann-Kohlmeyer, B., Wingfield, M. J., Wood, A. R., Woudenberg, J. H. C., Yonezawa, H., Zhang, Y., and Spatafora, J. W. 2009. A class-wide phylogenetic assessment of Dothideomycetes. Stud. Mycol. 64:1-15. doi:10.3114/sim.2009.64.01.
55. Sisson, A. J., Batzer, J. C., Waxman, K. B., Hemnani, K., and Gleason, M. L. 2008. Phenology of sooty blotch and flyspeck fungi on apples in Iowa. (Abstr.) Phytopathology 98:S147.
56. Spólti, P. 2009. Epidemiologia e controle de fuligem e sujeira de mosca em

macieira (Malus × domestica Borkh) no sul do Brasil. M.Sc. thesis. Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil.

57. Sun, G. Y., Leandro, L. F., Batzer, J. C., Harrington, T. C., and Gleason, M. L. 2004. Specific PCR primers to identify sooty blotch and flyspeck fungi on apple in the Midwest U.S. (Abstr.) Phytopathology 94:S100.
58. Sun, G., Zhang, M., Zhang, R., Ma, H., and Gleason, M. L. 2006. *Wallemia* – a genus newly recorded from China. Mycotaxon 95:277-280.
59. Sun, G. Y., Zhang, R., Li, H. Y., and Gleason, M. L. 2008. Diversity of fungi causing flyspeck signs on apple in China. (Abstr.) Phytopathology 98:S153.
60. Sutton, A. L., and Sutton, T. B. 1994. The distribution of the mycelial types of *Gloeodes pomigena* on apples in North Carolina and their relationship to environmental conditions. Plant Dis. 78:668-673.
61. Sutton, T. B., Alwinckle, H. S., and Walgenbach, J. F., eds. 2010. Compendium of Apple and Pear Diseases and Insects. American Phytopathological Society, St. Paul, MN. In press.
62. Sutton, T. B., Brown, E. M., and Anas, O. 2007. Summer disease control with reduced risk fungicides, 2006. Plant Disease Management Reports 1: PF007. Online publication. doi: 10.1094/PDMR03.
63. Sutton, T. B., Brown, E. M., Anas, O., and Meister, C. W. 2006. Efficacy of phosphorus-containing fungicides on summer diseases of apples, 2005. Fungic. Nematicide Tests 61: PF004. Online publication. doi: 10.1094/FN61.
64. Tamm, L., Amsler, T., Schärer, H., and Refardt, M. 2006. Efficacy of Armicarb (potassium bicarbonate) against scab and sooty blotch on apples. Pages 87-92 in: Ecofruit - 12th Int. Conf. Cult. Technique Phytopathol. Problems Organic Fruit-Growing. M. Boos, ed. FÖKO, Weinsberg, Germany.
65. Tarnowski, T., Batzer, J., Gleason, M., Helland, S., and Dixon, P. 2003. Sensitivity of newly identified clades in the sooty blotch and flyspeck complex on apple to thiophanate-methyl and ziram. Online. Plant Health Progress doi:10.1094/PHP-2003-1209-01-RS.
66. Trapman, M. 2004. A simulation program for the timing of fungicides to control sooty blotch in organic apple growing. First results in 2003. Pages 56-66 in: Ecofruit – Proc. 11th Int. Conf. Cult. Techniques Phytopathol. Problems Organic Fruit-Growing, FÖKO, Weinsberg, Germany.
67. Trapman, M., Tamm, L., and Fuchs, J. G. 2004. The effectiveness of winter treatments with copper or lime sulphur to control sooty blotch on apple. Pages 67-72 in: Ecofruit – Proc. 11th Int. Conf. Cult. Techniques Phytopathol. Problems Organic Fruit-Growing. FÖKO, Weinsberg, Germany.
68. Tuttle, A., Bergweiler, C., Hall, J., Reisner, L., Christle, S., Autio, W., and Cooley, D. 2002. Development of a model for predicting flyspeck risks in blocks of apple trees. Fruit Notes 67:5-8.
69. von Arx, J. A. 1959. Ein Beitrag zur Kenntnis der Fliegenfleckenpilze. Proc. Koninkl. Nederl. Acad., ser. C 62:333-340.
70. Williamson, S. K., and Sutton, T. B. 2000. Sooty blotch and flyspeck of apples: Etiology, biology, and control. Plant Dis. 84:714-724.
71. Wrona, B., and Grabowski, M. 2004. Etiology of apple sooty blotch in Poland. J. Plant Prot. Res. 44:293-297.
72. Yang, H. L., Sun, G. Y., Batzer, J. C., Crous, P. W., Groenewald, J. Z., and Gleason, M. L. 2010. Novel fungal genera and species associated with the sooty blotch and flyspeck complex on apple in China and the United States. Persoonia 24:29-37.
73. Zhang, R., Yang, H., Sun, G., Li, H., Zhuang, J., Zhai, X., and Gleason, M. L. 2009. *Strelitziana mali*, a new species causing sooty blotch on apple fruit. Mycotaxon 110:477-485.
74. Zhang, R., Zhuang, J., Sun, G., and Gleason, M. L. 2010. *Strelitziana africana*—A species newly recorded from China. Mycotaxon 113:485-492.
75. Zhuang, J., Zhu, M., Zhang, R., Yin, H., Lei, Y., Sun, G., and Gleason, M. L. 2010. *Phialophora sessilis*, a species causing flyspeck signs on bamboo in China. Mycotaxon 113:405-413.