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Stealth Pathogens: The Sooty Blotch and Flyspeck Fungal Complex

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Abstract

Sooty blotch and flyspeck (SBFS) fungi produce superficial, dark-colored colonies on fruits, stems, and leaves of many plant genera. These blemishes are economically damaging on fruit, primarily apple and pear, because they reduce the sale price of fresh fruit. Fungicide spray programs can control SBFS but are costly and impair human and environmental health; thus, less chemically intensive management strategies are needed. Although the scientific study of SBFS fungi began nearly 200 years ago, recent DNA-driven studies revealed an unexpectedly diverse complex: more than 100 species in 30 genera of Ascomycota and Basidiomycota. Analysis of evolutionary phylogenetics and phylogenomics indicates that the evolution of SBFS fungi from plant-penetrating ancestors to noninvasive ectophytic parasites was accompanied by a massive contraction of pathogenicity-related genes, including plant cell wall–degrading enzymes and effectors, and an expansion of cuticle-degradation genes. This article reviews progress in understanding SBFS taxonomy and ecology and improving disease management. We also highlight recent breakthroughs in reconstructing the evolutionary origins of these unusual plant pathogens and delineating adaptations to their ectophytic niche.

INTRODUCTION

Fungi in the sooty blotch and flyspeck (SBFS) complex are among the most noticeable plant-associated microbes. Their dark-colored colonies are conspicuous to the naked eye as superficial inhabitants on numerous tree and vine crops, including apple, pear, persimmon, banana, mango, orange, plum, and papaya as well as hundreds of noncrop species. Drawn by these intriguing colonies, mycologists began to investigate SBFS fungi nearly 200 years ago (99).

Despite their exclusively surface-dwelling nature, SBFS fungi are economically important pathogens of several tree fruit crops, especially apple. The fruit blemishing caused by their dark blotches and clusters of black dots often precludes fresh-market sale. Diverting SBFS-infected apples to alternative uses such as juice, sauce, and pies salvages some revenue, but more than 90% of the profit can be lost from high-value cultivars (124). Severely infected apples also lose value because they become desiccated in cold storage (87).

Scientific research on SBFS was minimal until recently. Several factors contributed to the slow pace of research progress. For example, standard surface-sterilization procedures often kill SBFS fungi. They grow so slowly in culture that they are often overgrown by other fruit-inhabiting fungi. Most SBFS species do not sporulate on fruit surfaces; therefore, they must be coaxed to sporulate in culture, and some flatly refuse to do so. Colony morphology is only marginally helpful as a clue for species identification because cryptic species are commonplace. These difficulties apparently dissuaded all but a few mycologists and plant pathologists from pursuing SBFS studies.

Research by Turner B. Sutton and colleagues (112) at North Carolina State University during the 1980s and 1990s reinvigorated SBFS research. Their publications on SBFS ecology, etiology, epidemiology, taxonomy, and management sparked the interest and participation of many other groups around the world and ushered in a new era of faster progress. A review by Williamson & Sutton (124) placed their group's research in the context of historical and concurrent efforts. More recently, DNA-based fungal identification and phylogenetic analysis triggered a new burst of SBFS research that revealed a far more diverse species assemblage than previously known and opened new directions for research. Much of this progress was reviewed by Gleason et al. (42). The current decade has seen a third wave of major advances in understanding SBFS. Studies of the evolutionary origins of this unique group provided a basis for exploring adaptive mechanisms. Genomic and transcriptomic studies revealed the profound evolutionary changes that accompanied the transition of SBFS fungi to their surface-dwelling niche. Recent field and laboratory studies have also begun to clarify how SBFS species grow and proliferate on the fruit surface. This review is comprehensive but highlights these recent advances and the many questions they have raised.

TAXONOMY

Taxonomy claims a central role in the story of SBFS research. Confusion about the identity of the causal fungi thwarted progress for more than 150 years (42). Application of DNA sequence information to SBFS taxonomy revealed unexpected taxonomic diversity and facilitated studies of the etiology and environmental biology of component species. A brief summary of the taxonomic history follows; additional details are in prior reviews (42, 75, 124).

Morphology of SBFS colonies on the fruit surface is a consistent character (42). However, several genera produce similar morphologies, also called mycelial types (9, 16, 32, 36) (**Figure 1**). Species identification combines sequence information for the internal transcribed spacer (ITS) and large subunit (LSU) regions of rDNA with morphological evidence in culture because SBFS fungi rarely produce spores on apple fruit. A modified Koch's postulates approach for confirming

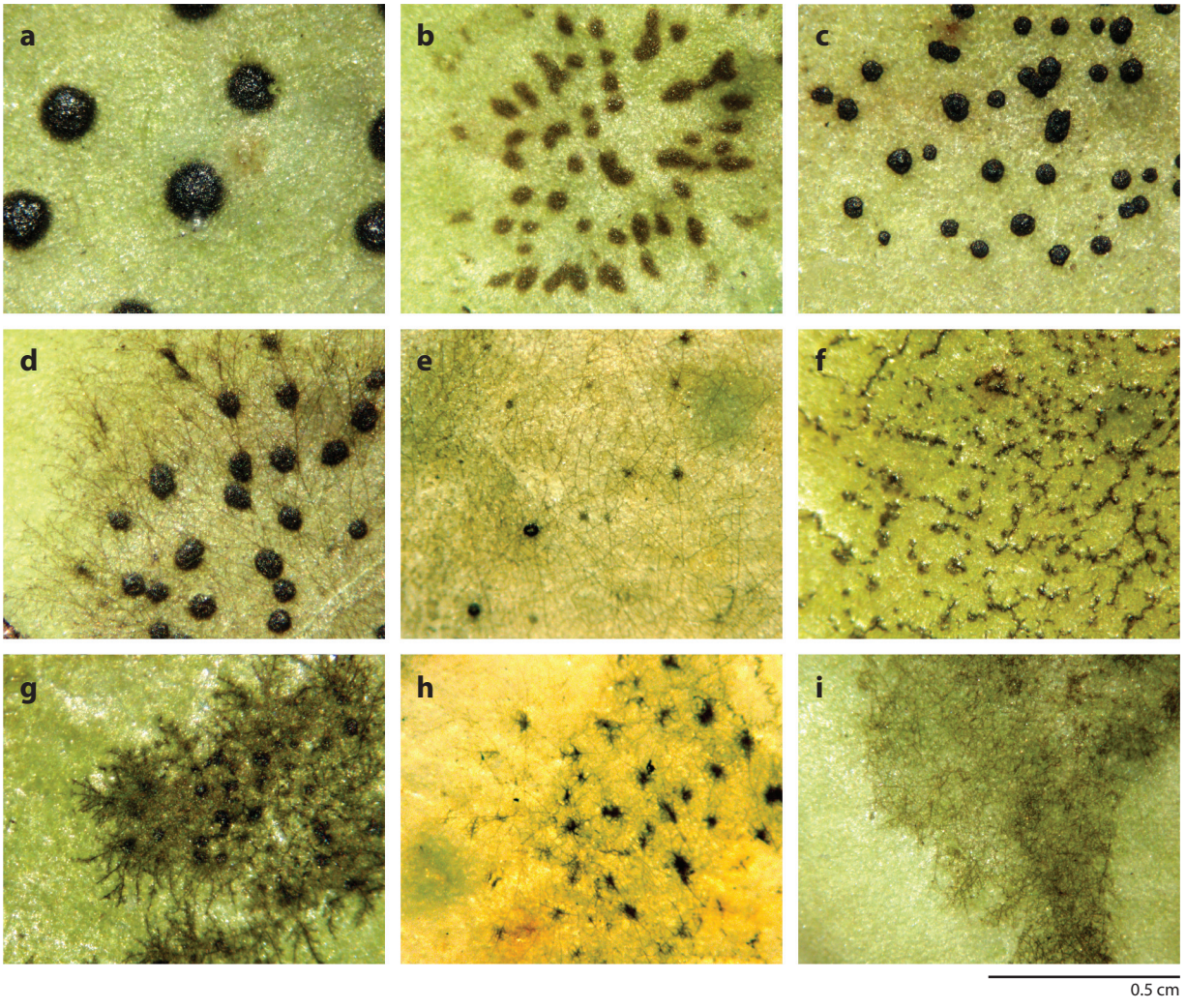


Figure 1

Appearance on apple skin of mycelial types of fungi in the sooty blotch and flyspeck (SBFS) complex. (*a*) Flyspeck. (*b*) Compact speck. (*c*) Discrete speck. (*d*) Ramose caused by *Stomiopeltis* spp. (*e*) Sparse ramose caused by *Geastrumia* spp. (*f*) Ridged honeycomb. (*g*) Arborescent punctate. (*h*) Punctate. (*i*) Fuliginous. Figure adapted from Gleason et al. (42) with permission from the publisher.

pathogenicity requires inoculation of the fruit surface with a pure culture, incubation until the expected mycelial type becomes visible, reculturing from the colony, and identification of the inoculated isolate using molecular tools (9, 34, 49).

The convoluted tale of SBFS taxonomy began with designating *Dothidea pomigena* Schwein. as the sole causal agent of SBFS (99). It was later renamed *Asteroma pomi* (Desm.) Lév. (72), then *Phyllachora pomigena* (Schwein.) Sacc. (97), and finally *Leptothyrium pomi* A. Selby (100). SBFS was later viewed as two distinct diseases, sooty blotch and flyspeck, caused by *P. pomigena* and *L. pomi*, respectively (51). Colby (25) described the sooty blotch pathogen [at that time named *Gloeodes pomigena* (Schwein.) Colby] as having a mycelial mat, whereas colonies of the flyspeck pathogen had clusters of sclerotium-like bodies without a mycelial mat. Baines (7) further cemented the

two-disease, two-species paradigm of sooty blotch and flyspeck. The flyspeck pathogen was first renamed *Microthyriella rubi* Petr. and then *Schizothyrium pomi* (Mont.) Arx (120). *Zygophiala jamaicensis* Mason, a cause of flyspeck on banana, was assumed to be the anamorph of *S. pomi* (33). In the late 1990s, sooty blotch was revised as a three-species complex encompassing *Leptodontium elatius* (F. Mangenot) de Hoog, *Peltaster fructicola* Eric M. Johnson, T.B. Sutton & Hodges, and *Geastrumia polystigmatis* Bat. & M.L. Farr (61).

The addition of DNA-based phylogenetic analysis to the morphological description revealed that SBFS is a highly diverse disease complex (9) that, to date, has expanded to more than 100 named and putative species worldwide (**Table 1**). This is arguably the most diverse plant-pathogen complex ever documented. SBFS species reside almost entirely in the phylum Ascomycota, primarily in the Dothideomycetes order Capnodiales but also in Eurotiomycetes. Several SBFS species also reside in the phylum Basidiomycota. Genera that have been erected to accommodate newly described SBFS species include *Cyphellophora*, *Devriesia*, *Dissoconium*, *Houjia*, *Microcyclospora*, *Microcyclosporella*, *Ochroconis*, *Phaeothecoidiella*, *Phialophora*, *Pseudoveronaea*, *Ramichloridium*, *Scleroramularia*, *Sporodesmajora*, *Strelitziana*, *Uwebraunia*, *Wallemia*, and *Zasmidium* (36, 39, 47, 73–75, 78, 109, 122, 129, 132, 133, 135, 137). Although many new species have been described, the numerous *Stomiopeltis* putative species found across the Northern Hemisphere lack Latin binomials because they do not sporulate in culture, although sporulation has been observed rarely on overwintered apples (1). SBFS isolates with ITS sequences similar to those of *Stomiopeltis*-like spp. have been identified from mango and banana and have been placed in the genus *Chaetothyrina* (54). In contrast, *Phaeococcus*-like sp. CS1 produces only budding spores without mycelium in culture but forms darkened sclerotium-like bodies on fruit and other hard surfaces (13), so CS1 has also evaded formal description. The historically referenced *G. pomigena* has not been isolated since its initial description nearly 100 years ago (25), and no preserved specimens have been found. *S. pomi* and *Z. jamaicensis* were proved to be members of a species complex rather than sexual and asexual stages of the same species, and *Z. jamaicensis* is now recognized as one of at least 16 *Schizothyrium* anamorphs (14, 38, 79, 134). A single species in the Basidiomycota genus *Wallemia* (Wallemiomycetes, Wallemiales) was reported to cause SBFS symptoms (109).

The DNA-driven revolution in SBFS taxonomy erased the long-standing dogma of two diseases—sooty blotch and flyspeck—each caused by a single pathogen species. We now recognize that SBFS is a pathogen complex that incorporates a spectrum of intergraded mycelial types and is composed of species assemblages that vary with geographic region and disease management regime (32, 42).

ECOLOGY

Disease Cycles

Most of the meager information about SBFS disease cycles comes from studies of a few species in the eastern United States whose spores are morphologically distinct (21, 27, 61, 71, 89). Many studies conducted before DNA-based identification became available were hampered by uncertainty about species identification, but several general patterns emerged. For example, SBFS fungi colonize a wide range of trees, shrubs, and vines in and around apple orchards (7, 25, 52, 61). Baines (7) and Hickey (52) reproduced SBFS symptoms on apple fruit from inoculum obtained from apple, crabapple, blackberry, willow, sycamore, sassafras, wild grape, and smooth sumac (124). Using molecular methods, numerous SBFS species were detected on presumptive additional reservoir hosts (42, 49, 69, 80, 82). Conidia produced on reservoir hosts move by wind and rain to orchards at almost any time during the fruit development period (55, 61, 112).

Table 1 Taxonomic placement, species names, mycelial type, geographic region, prevalence, GenBank accession numbers, and references for sooty blotch and flyspeck species and putative species

Order, Family	Species names	Mycelial type on host	Geographic region reported	Prevalence	GenBank accession	References
Ascomycota, Dothideomycetes						
Uncertain	*Phaeococcus*-like sp. CS1	Compact Speck	USA	Regional	AY598891	13, 32
Capnodiales	*Peltaster fructicola*	Punctate	Bulgaria, China, Germany, Norway, Serbia, Turkey, USA (Eastern)	Worldwide	AY598886	15, 16, 23, 32, 57, 82, 90, 123
	Peltaster cerophilus	Punctate	Germany, Norway, Poland, Slovenia, Spain	Regional	KF646817	15, 16, 84, 87
	Peltaster gemmifer	Punctate	USA (Midwest)	Regional	AY598890	32, 94
	Peltaster crataegi	Punctate	China	Regional	NS	23
	Peltaster punctatum	Punctate	China	Regional	NS	23
	Peltaster rosacearum	Punctate	China	Regional	NS	23
	Peltaster sp. Ch8	Punctate	China	Regional	MF075292	93
	Peltaster sp. 65rap	Punctate	Germany	Rare	JN573668.2	84
Uncertain	*Neopeltaster mali*	Punctate	China	Regional	KT582276	23
Capnodiales, Schizothyriaceae	*Schizothyrium pomi*	Flyspeck	Germany, Norway, Serbia, Slovenia, Turkey, Spain, USA (Eastern)	Worldwide	AY598848	15, 16, 36, 57, 83
	Zygophiala cryptogama	Flyspeck	China, Spain, USA (Eastern)	Worldwide	AY59854	8
	Zygophiala cylindrica	Flyspeck	China, Spain, Turkey, USA (Eastern)	Worldwide	FJ941848	76, 83
	Zygophiala qianensis	Flyspeck	China	Rare	KF806030	79
	Zygophiala tardicrescens	Flyspeck	USA (Midwest)	Rare	AY598856	8
	Zygophiala wisconsinensis	Large flyspeck	China, Republic of Korea, Turkey, USA (Midwest)	Worldwide	AY598853	10, 40, 64, 83
	Zygophiala jamaicensis	Flyspeck	Jamaica	Regional	NS	81
	Zygophiala emperorae	Flyspeck	China	Regional	KF646710	40
	Zygophiala trispora	Flyspeck	China	Rare	KF646711	40
	Zygophiala musae	Flyspeck	China	Rare	KF646707	39
	Zygophiala inaequalis	Flyspeck	China	Rare	KF646709	39
	Zygophiala longispora	Flyspeck	China	Rare	KF646708	39
	Zygophiala montenegroensis	Flyspeck	Montenegro	Rare	KJ730237	131
	Schizothyrium sp. FS7	Flyspeck	Spain, Turkey	Regional	JX042476	83
	Schizothyrium sp. FS8	Flyspeck	Spain	Rare	NS	J.C. Batzer, unpublished results
	Schizothyrium sp. FS9	Flyspeck	Spain	Rare	NS	J.C. Batzer, unpublished results
Capnodiales, Pseudoveronaea	*Pseudoveronea obclavate*	Fuliginous	USA (Midwest)	Rare	AY598877	9, 73
	Pseudoveronea ellipsoidea	Fuliginous	China, USA (Eastern)	Worldwide	FJ425205	23, 32, 67

(*Continued*)

Table 1 (*Continued*)

Order, Family	Species names	Mycelial type on host	Geographic region reported	Prevalence	GenBank accession	References
Capnodiales, Dissoconiaceae	*Dissoconium acciculare*	Discrete speck	USA (Midwest)	Regional	JQ622083	16, 74
	Dissoconium sp. CPC 18969	Discrete speck	USA (Georgia)	Rare	JQ622084	16, 68
	Dissoconium sp. 1	Discrete speck	Germany, Norway	Regional	KP400569	15, 16
	Dissoconium sp. 2	Discrete speck	Germany, Norway	Regional	KP400570	12, 15
	Ramichloridium apiculatum	Fuliginous	China	Regional	KC986373	109, 121
	Ramichloridium luteum	Fuliginous	China	Rare	EU329730	74
	Ramichloridium cucurbitae	Fuliginous	USA (Midwest)	Rare	NR 120082	68
	Ramichloridium mali	Fuliginous	China	Rare	EF627452	109
	Ramichloridium punctatum	Punctate	USA (Midwest)	Rare	JQ622086	74
	Ramichloridium sp.	Fuliginous	Spain	Rare	NS	J.C. Batzer, unpublished results
	Uwebraunia commune	Ramose	USA (Eastern)	Regional	AY598876	9, 31, 74
	Uwebraunia dekkeri	Punctate	USA (Eastern)	Regional	FJ425204	32, 74
	Uwebraunia musae	Fuliginous	India	Regional	EU514225	4
	Zasmidium angulare	Discrete speck	USA (Eastern)	Rare	JQ622088	32, 74
Capnodiales, Terato-sphaeriaceae	*Devresia stretziea*	Discrete speck	China	Rare	JX294932	78
	Devresia pseudoamericana	Unknown	Germany	Local	GU570527	36
	Microcyclospora malicola	Fuliginous	Germany, Norway, Slovenia, Spain, USA (Eastern)	Worldwide	GU570537	15, 16, 36, 84
	Microcyclospora pomicola	Fuliginous	Germany, Norway, Spain	Regional	GU570539	11, 12, 81
	Microcyclospora tardicrescens	Fuliginous	Germany, Norway, Spain	Regional	GU570541	12, 16, 81
	Microcyclospora sp.	Fuliginous	Spain	Rare	NS	J.C. Batzer, unpublished results
	Microcyclospora sp. FG1.3	Fuliginous	Germany	Rare	KP400567	15
	Microcyclospora sp. FG1.4	Fuliginous	Germany	Rare	KP400568	9
Capnodiales, Phaeothecoidiel-laceae	*Houjia pomigena*	Fuliginous	China, USA (Eastern)	Regional	AY598885	129
	Houjia yanglingensis	Fuliginous	China, USA (Eastern)	Regional	FJ147166	129
	Passalora-like sp. FG3	Fuliginous	USA (Eastern)	Regional	AY598926	16
	Phaeothecoidiella illinoisensis	Arborescent punctate	USA (Eastern)	Regional	AY598879	129
	Phaeothecoidiella missouriensis	Arborescent punctate	USA (Eastern)	Regional	AY598917	129
	Phaeothecoidiella sp. N1.7E6	Arborescent punctate	Norway	Regional	KJ719560	15
	Translucidithyrium thailandicum	Flyspeck	Thailand	Regional	MG993045	130
	Sporidesmajora pennsylvaniensis	Arborescent punctate	USA (Eastern)	Regional	FJ147167	31, 129

(*Continued*)

Table 1 (*Continued*)

Order, Family	Species names	Mycelial type on host	Geographic region reported	Prevalence	GenBank accession	References
	Chaetothyrina musarum	Flyspeck	Thailand	Regional	KX372275	54
	Chaetothyrina guttulata	Punctate	Thailand	Regional	KX372277	54
	Stomiopeltis sp. RS1	Ramose	USA (Midwest)	Regional	AY598882	9
	Stomiopeltis sp. RS2	Ramose	USA (Midwest)	Regional	AY598883	9
	Stomiopeltis sp. RS3.1	Ramose	USA (Eastern), Spain	Regional	FJ147160	1, 32
	Stomiopeltis sp. RS3.2	Ramose	USA (Eastern)	Regional	FJ147161	32
	Stomiopeltis sp. RS3.3	Ramose	Spain	Rare	NS	J.C. Batzer, unpublished results
	Stomiopeltis sp. RS3.4	Ramose	Spain	Rare	NS	J.C. Batzer, unpublished results
	Stomiopeltis sp. RS4.0	Ramose	USA (Eastern)	Regional	FJ147162	1, 32
	Stomiopeltis sp. RS4.1	Ramose	Turkey	Regional	JQ358787	83
	Stomiopeltis versicolor	Ramose	USA (Eastern)	Regional	FJ438375 AY160172	1, 32
	Stomiopeltis sp. RS6	Ramose	USA (Eastern)	Regional	FJ425198	32
	Stomiopeltis sp. RS7.1	Ramose	Turkey	Regional	JQ358788	81
	Stomiopeltis sp. RS7.2	Ramose	Turkey, Spain	Regional	JX042483	81
	Stomiopeltis sp. It-s	Flyspeck	Japan	Regional	LC190412	2
Capnodiales, Mycosphaerellaceae	*Microcyclosporella mali*	Ridged honeycomb	Germany, Iran, Norway, Poland, Serbia, Slovenia, Spain, Turkey, USA (Eastern)	Worldwide	GUS570539 GUS570540	9, 11, 15, 16, 32, 36, 48, 87
	Ramichloridium sp. RH4	Ramose	USA (Eastern)	Regional	FJ425198	32
	Ramichloridium sp. RH5	Ramose	USA (Eastern)	Regional	FJ425200	32
	Colletogloeum-like sp. FG2	Fuliginous	USA (Eastern)	Regional	AY598870	9, 31
Botryosphaeriales	*Geastrumia polystigmatis*	Ramose/ Fuliginous	Bulgaria, Spain, USA (Eastern)	Worldwide	FJ147177	32, 59, 61, 90
	Geastrumia sp. S1	Ramose	Brazil, Spain	Worldwide	NS	J.C. Batzer, unpublished results
	Geastrumia sp. G2	Ramose	Germany, Norway	Regional	KR187108	15, 16
	Scolecobasidium musae	NA	China	Rare	JQ364738	47
Venturiales, Sympoventuriaceae	*Scolecobasidium musae*	NA	China	Rare	JQ364738	47
Pleosporomycetidae						
Pleosporales	*Scleroramularia abundans*	Compact speck	Turkey, USA (Midwest)	Worldwide	FR716675	73, 83
	Scleroramularia benaniensis	Compact speck	China, USA, Spain	Worldwide	FR716679	73
	Scleroramularia asiminae	Compact speck	USA (Midwest)	Regional	FR716677	73
	Scleroramularia pomigena	Compact speck	USA (Midwest)	Regional	FR716682	73
	Scleroramularia shaanxiensis	Compact speck	China	Regional	FR716683	73
	Scleroramularia musae	Compact speck	China	Rare	KR010464	37
	Pleosporales sp. G1	Punctate	Germany	Rare	KR187107	16

(*Continued*)

Table 1 (*Continued*)

Order, Family	Species names	Mycelial type on host	Geographic region reported	Prevalence	GenBank accession	References
Eurotiomycetes						
Chaetothyriales	Chaetothyriales sp. S1	Punctate	Spain	Rare	NS	J.C. Batzer, unpublished results
	Chaetothyriales sp. F1	Fuliginous	Turkey	Rare	JX014309	83
	Chaetothyriales sp. S2	Ramose	Spain	Rare	NS	J.C. Batzer, unpublished results
	Chaetothyriales sp. G6	Fuliginous	Germany	Rare	KP400572	16
	Chaetothyriales sp. G7	Ridged honeycomb	Germany	Rare	KP400573	16
	Chaetothyriales sp. G8	Fuliginous	Germany	Rare	KP400574	16
Chaetothyriales, Cyphellophoraceae	*Cyphellophora phyllostachydis*	Ramose	China	Rare	KP010371	37
	Cyphellophora sessilis	Ramose	China, Germany, Poland, Spain, USA (Eastern)	Worldwide	KP400571	16, 32, 75, 87, 109, 137
	Cyphellophora astocarpi	Ramose	China	Rare	KP010367	39
	Cyphellophora musae	Ramose	China	Rare	KP010368	39
Chaetothyriales, Herpotrichiellaceae	*Exophiala xenobiotica*	Fuliginous	Germany	Rare	KP400575	16
	Leptodontidium elatius	Light fuliginous	USA (Southern)	Regional	AY598931	58
	Exophiala sp. G4	Punctate	Germany	Rare	KP400576	16
	Neophaeococcomyces catenatus	Punctate	Germany	Rare	KP400577	16
Basidiomycota						
Wallemiales	*Wallemia qianyangensis*	Punctate	China	Regional	NS	R. Zhang, unpublished results
	Wallemia sebi	Punctate	China	Regional	NS	109
	Wallemia longxianensis	Fuliginous	China	Regional	NS	R. Zhang, unpublished results
	Wallemia longxianensis	Fuliginous	China	Regional	NS	R. Zhang, unpublished results

Abbreviations: NA, not available; NS, not submitted.

Phenology

Colonies on apples become visible from several weeks to several months after inoculation (27, 89, 113, 125), depending on weather and nearness to harvest. Secondary spread on a single fruit or among several fruits can occur during subsequent wet periods (14, 93, 124). Overwintering can apparently occur on apple fruit and other reservoir hosts (1, 17, 49). Ismail et al. (55) documented significant interspecific differences in the timing of inoculum arrival among eight prevalent SBFS species. In the same orchard, Batzer et al. (11) noted that certain SBFS species developed visible colonies earlier in the fruit development period than did other species.

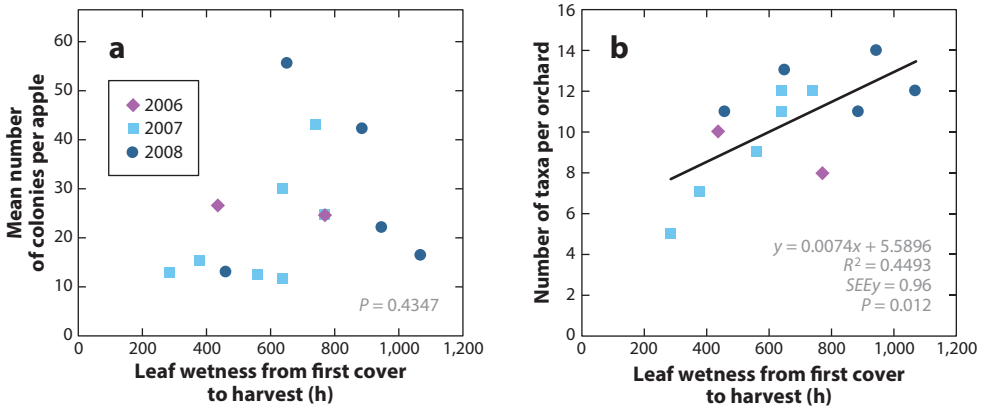


Figure 2

The relationship of leaf wetness hours during the growing season to (*a*) the mean number of colonies of sooty blotch and flyspeck (SBFS) per apple and (*b*) the species richness per orchard year (14). *P* is the observed significance level for rejecting the null hypothesis that the number of colonies per apple (panel *a*) and the number of taxa per orchard (panel *b*) can be predicted by leaf wetness; *y* is the predicted number of taxa in an orchard based on leaf wetness; R^2 shows that leaf wetness explained 44.93% of the variation in the number of taxa per orchard; and SE*y* shows that leaf wetness predicted the number of taxa within 0.96%. Abbreviations: *P*, linear regression *P* value; R^2, coefficient of determination; SE*y*, standard error of the estimate; *y*, species richness estimate. Figure adapted from Batzer et al. (14) with permission from the publisher.

Environmental Adaptations

The duration of moist periods strongly impacts the activity of these surface-dwelling fungi. Many studies have connected SBFS symptom severity to extended periods of rain, dew, or high humidity (22, 34, 101, 111), and SBFS diversity on apples may be similarly affected (**Figure 2**) (14). Free water on the fruit surface promotes both mycelial growth and, in some SBFS species, budding of spores that can travel down the fruit in water droplets, forming new colonies in a distinctive streaked pattern (**Figure 3**). Leaf wetness duration (LWD), relative humidity, and rainfall are key weather inputs to SBFS warning systems (see the section titled Management).

Many SBFS species have relatively broad temperature optima (13, 60), although mycelial growth differs significantly among some species at 10°C and 30°C (13). The broad temperature optima among prevalent SBFS species in the eastern United States may explain why temperature is not an important input to warning systems developed for this region (22, 34).

Nutrient availability on apple fruit alters drastically during the growing season. The cuticle environment is low in nutrients during the early phases of fruit development when internal tissues are composed mainly of complex carbohydrates. As fruit mature, however, simple sugars and organic acids leak through the peel to the exterior (125). This pulse of nutrients coincides with a late-season upsurge in SBFS colony growth. Rapid acceleration of mycelial growth in several SBFS species in response to apple juice has also been demonstrated experimentally (13).

The pH of the apple surface is usually ~4.0 (41, 126). The SBFS species *P. fructicola* grew on media within a pH range of 4–6, but very slowly at pH < 4 or > 6 (24). In contrast, *Ramichloridium luteum* grew across a much wider pH range (<1–8) (23). However, the optimal pH for both species was 4, which helps to explain why they are well adapted to the apple surface microenvironment.

Figure 3

Drip pattern of *Peltaster* sp. colonies on apple fruit. This pattern occurs when budding conidia or yeast-like conidia move downward on the fruit in rain or dew droplets.

SBFS fungi need protection against desiccation and ultraviolet radiation on fruit surfaces. In in vitro experiments using polyethylene glycol 6000 (PEG-6000), which is widely used for simulating drought stress (24, 65, 85), it was shown that *P. fructicola* grew on media amended with osmotic potential ranging from −1.5 MPa to −4.9 MPa. *R. luteum* was also highly drought resistant, growing even on media with an osmotic potential of −10.3 MPa (B. Wang, personal communication). These results suggest that SBFS is well adapted to cope with persistently dry conditions on the waxy epicuticle. SBFS fungi deploy several adaptations to mitigate UV damage (121, 127); for details, see below in the section titled Evolution and Adaptive Mechanisms.

Dimorphism

Several SBFS fungi, including *Microcyclosporella* spp. and *Peltaster* spp., are dimorphic, exhibiting both hyphal and yeast-like stages (23, 24, 74). This ability enables them to respond to radical shifts in microenvironmental conditions that occur on plant surfaces. Nutritional conditions may contribute to morphological shifts. For example, in a low-nutrient cultural environment, such as water agar or adjusted SNA medium not containing carbon or nitrogen sources, *P. fructicola*

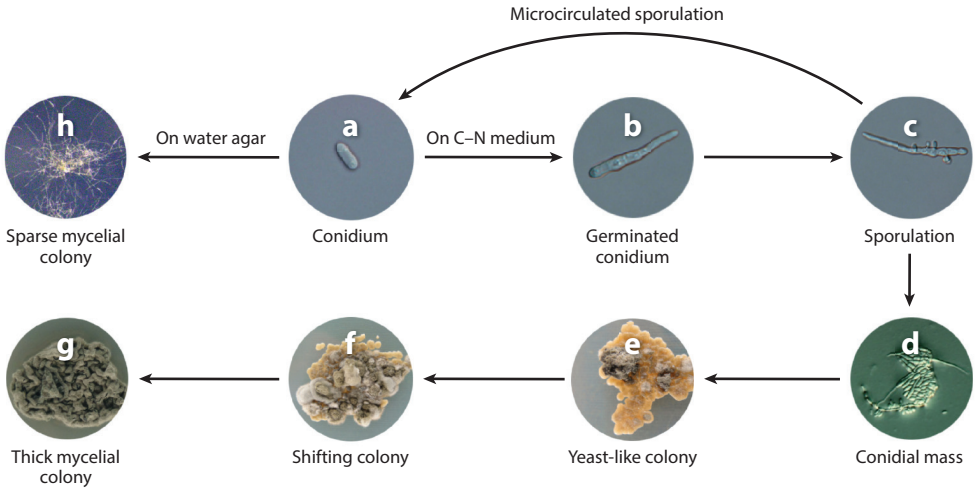


Figure 4

Dimorphic shifts of *Peltaster fructicola* between hyphal and yeast-like stages, based on results from Chen (24). (*a*) Conidium. (*b*) Conidium producing germ tubes at either end on agar containing C–N source medium. (*c*) Microcyclic sporulation from germinated conidium. (*d*) Conidial mass. (*e*) Yeast-like colony. (*f*) Shift from yeast-like to hyphal colony morphology. (*g*) Extensive mycelial colony formed after multiple weeks in culture. (*h*) Sparse mycelial colony formed on water agar or adjusted SNA (synthetic nutrient agar) medium not containing carbon or nitrogen sources.

exhibited mainly mycelial growth, whereas adding glucose (0.5 g/L) or KNO_3 (1 g/L) induced formation of yeast-like colonies (24). Fruit surface nutrition therefore can trigger morphological shifts in at least some SBFS fungi (**Figure 4**).

Spatial Dynamics

Available evidence suggests that SBFS inoculum typically travels no more than several hundred meters from reservoir hosts on orchard borders into apple orchards (27, 108), although inoculum can also originate from apple or other hosts within orchards (124). Gao and coworkers used scanning electron microscopy to track the proliferation of *Zygophiala wisconsinensis* colonies on individual apple fruit, documenting the formation of sclerotium-like bodies from hyphae as well as subsequent dissolving of intercalary hyphae (38). Preliminary evidence from Iowa field experiments suggested that there were distinctions among SBFS species in spatial dissemination patterns; for example, *Peltaster* spp., which produce blastospores on infected fruit by means of budding, were more likely than other prevalent SBFS species to undergo secondary spread on fruit (14, 55). Subsequently, Rosli (93) showed that *Peltaster gemmifer* was much more likely to spread from apple to apple on the same tree than was the nonsporulating SBFS species *Stomiopeltis* sp. or the larger-celled microcyclic conidia of *Microcyclosporella* sp., confirming the existence of major differences among SBFS taxa in capacity for short-distance spatial dissemination.

Biogeography

Characterizing patterns of distribution of SBFS species among orchards and geographic regions took on practical importance with the discovery that species can differ significantly in environmental optima (118), tolerance to temperature extremes (13), and sensitivity to fungicides (115). Knowing which species are most prevalent can potentially lead to improved SBFS management,

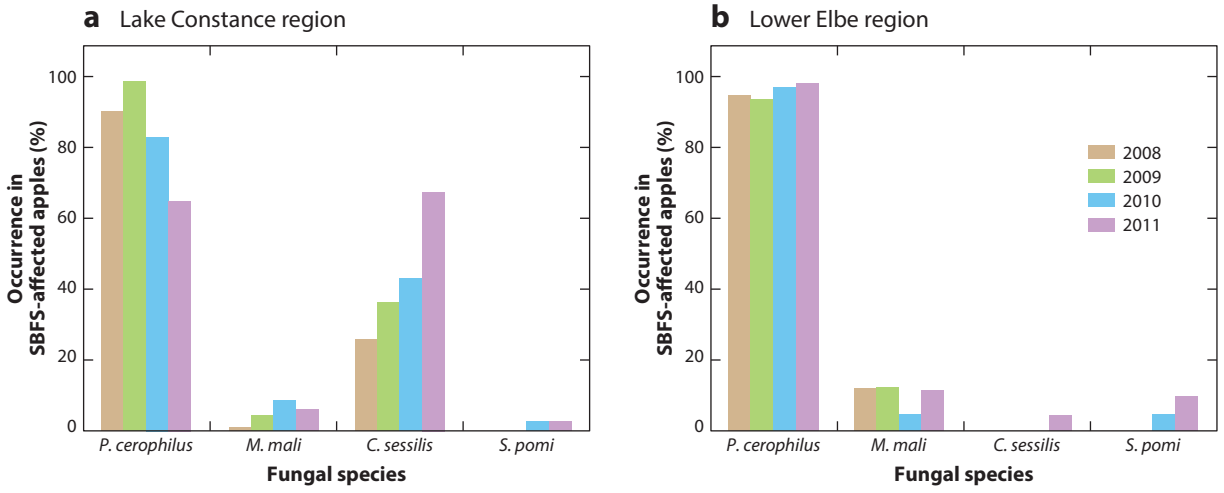


Figure 5

Frequency of occurrence of the four most commonly occurring sooty blotch and flyspeck (SBFS) fungi on apples in the (*a*) Lake Constance and (*b*) Lower Elbe regions of Germany (16). Abbreviations: *P. cerophilus*, *Peltaster cerophilus*; *M. mali*, *Microcyclosporella mali*; *C. sessilis*; *Cyphellophora sessilis*; *S. pomi*; *Schizothyrium pomi*. Figure adapted from Batzer et al. (16) with permission from the publisher.

for example, by altering fungicide selection and/or developing regionally based SBFS warning systems (16, 22, 34, 94, 117, 118).

Plant pathologists and mycologists had long suspected that SBFS assemblages varied among geographic regions (61, 111), but DNA-supported species identification has begun to clarify these distinctions (**Table 1**). A study of 39 apple orchards in the eastern United States provided persuasive evidence that some SBFS species were ubiquitous, whereas others were regional (32). Additional apple surveys have shown that some taxa, e.g., certain species of *Schizothyrium*, *Peltaster*, and *Microcyclosporella*, are apparently worldwide in distribution (16, 32, 36, 57, 76, 77, 83), whereas others are subcontinental or local in distribution (16). The management regime clearly impacts the SBFS assemblage; organically managed orchards may differ from conventionally managed orchards and abandoned orchards in both species diversity and prevalence (12, 16, 32). Studies on several continents documented that local SBFS species assemblages and prevalence patterns tend to persist across multiple growing seasons (**Figure 5**) (14, 16, 55).

Host Range

SBFS hosts include many fruits and hundreds of noncrop species. However, cross-inoculation tests suggested that there are clear host range differences (23, 40). Gao et al. (40) revealed that *Z. wisconsinensis* could be isolated from a wide range of hosts, including several in Rosaceae (apple, plum, hawthorn) and Ebenaceae (persimmon). In contrast, five species of this genus, including *Zygophiala emperorae*, *Zygophiala longispora*, *Zygophiala trispora*, *Zygophiala musae*, and *Zygophiala inaequalis*, were isolated from Japanese banana (*Musa basjoo*) fruit, but only *Z. emperorae* and *Z. longispora* could produce colonies on apple fruit (40).

MANAGEMENT

SBFS is an economically important disease on apples worldwide when fruit production periods coincide with moist environmental conditions. Most management-related research has occurred

in the eastern half of North America, where SBFS is a major apple disease under both conventional and organic production. However, it is also a major concern on organic apples in northern Europe and under conventional management in Brazil, Pakistan, and Korea (e.g., 17, 63, 64, 106, 107, 114).

Fungicides

Spraying fungicides has been a mainstay of SBFS management for 130 years. Williamson & Sutton (124) chronicled how changes in fungicide use in the United States have impacted SBFS management success in different eras; here, we capsulize the main historical transitions.

The first fungicide used on apples during summer and fall (the fruit development period) was the Bordeaux mixture (a mixture of copper sulfate and lime) (66, 67). The primary target of these sprays was often fungal fruit rots rather than SBFS, but good to excellent control of SBFS was also noted (51). By 1910, lime sulfur was coming into use for summer sprays because it caused less phytotoxicity than the Bordeaux mixture.

In the late 1940s and 1950s, lime sulfur gave way to new synthetic fungicides such as ferbam and captan, alongside DDT and lead arsenate for insect-pest management. However, Groves (45) noted that an upsurge of SBFS damage accompanied this change, in part because the inorganic fungicides were more active against SBFS fungi. Meanwhile, growers began to tank mix fungicides with insecticides to minimize the number of spray trips through the orchard. Lead arsenate also enhanced the activity of captan, enabling growers to extend spray intervals 25 days longer than with captan alone (52). The extraordinarily long residual activity of DDT and lead arsenate meant that fewer pesticide (and thus fungicide) sprays were applied (52).

Registration of ethylene bis-dithiocarbamate (EBDC) fungicides in the late 1950s and early 1960s ushered in another era. Their primary advantage was considerably longer periods of residual (postapplication) activity than that of captan. Along with captan, EBDC fungicides were the mainstays for SBFS management until the early 1990s. However, loss of lead arsenate and the advent of concentrate spraying during the 1970s and 1980s undermined the effectiveness of SBFS control. Concentrate spraying, i.e., using much higher concentrations but lower volumes of water than in previous eras, gained favor because it saved time and money, but poorer spray coverage led to SBFS control failures, particularly within fruit clusters and on the back sides of fruit (20). Because of its shortcomings, highly concentrated spraying eventually lost popularity where SBFS was a major management challenge.

The increasing use of benzimidazole fungicide against SBFS and fruit rots in the 1980s, often in combination with captan, proved to be fortuitous when the US Environmental Protection Agency banned the use of EBDC fungicides within 77 days of harvest—effectively eliminating their use in summer sprays. This change triggered another resurgence in SBFS-incited losses. Subsequently, tank mixes of a benzimidazole fungicide plus captan for control of summer diseases became common practice.

Several fungicide classes were added to the SBFS management toolbox during the past 20 years. A number of strobilurin [also known as quinone outside inhibitor (QoI)] and succinate dehydrogenase inhibitor (SDHI) fungicides have excellent activity against SBFS fungi, and combination products such as pyraclostrobin (a QoI) plus boscalid (an SDHI) are recommended for preharvest sprays because of relatively long residual activity (29). However, QoI and SDHI fungicides are at risk for resistance development by many fungal pathogens of apples; thus, the number of sprays per season is limited by label restrictions. In addition, using these newer fungicides is considerably costlier per application than older products. Phosphite fungicides have been valuable as mixing partners with captan during summer in situations where other fungicides have reached their label-specified limit on the number of sprays per season (91).

Warning Systems

An earlier review (42) provided a detailed timeline of the progress in developing warning systems to time fungicide sprays for SBFS. After summarizing these events, we describe more recent advances.

Disease-warning systems are decision aids to help growers improve the effectiveness and efficiency of management practices by utilizing information about the weather, pathogen, and/or crop. Most SBFS warning systems have used weather and crop information as inputs. With few exceptions (117, 118), most research on SBFS warning systems has focused on fungicide spray timing under conventional rather than organic production.

The first published work on modeling the level of SBFS risk, by Gold & Sutton (44) in North Carolina, input parameters for disease progress, initial and residual fungicide efficacy, cost of control, and market prices for apples but did not explicitly consider weather conditions. Brown & Sutton (22) found that the timing of the first appearance of SBFS colonies on apples could be predicted by summing the number of hours of leaf wetness (LWD) from the day on which the first-cover fungicide spray (7 to 14 days after the last flower petals fell off) occurred until a threshold was reached. In field trials in North Carolina, Kentucky, and Brazil, using this Brown–Sutton–Hartman warning system saved several sprays per season without compromising SBFS control (103, 104, 107, 124).

The Brown–Sutton–Hartman system was modified for use in other US regions. In New York, Rosenberger et al. (92) added a rain threshold to the LWD threshold. In the Upper Midwest, control failures that occurred when using the Brown–Sutton–Hartman system (6) triggered research showing that a relative humidity (RH)-based threshold, i.e., cumulative hours of RH $\geq$ 97%, predicted SBFS risk more accurately than LWD (34). In field tests in Iowa, using the new Gleason–Duttweiler warning system saved an average of 2.6 fungicide sprays per season with no loss of SBFS control and was cost-effective for orchard sizes $>$1 ha (94).

In an overview of SBFS warning systems, Cooley et al. (28) questioned the value of using LWD as an input parameter because of its high level of spatial variability in tree canopies (**Figure 6**) (8) and lack of calibration standards (95). They also perceived the need for faster and more efficient communication of spray timing advice to growers and for incorporating more site-specific information such as cultivar, tree size, canopy density, and distance to potential inoculum sources to improve warning system reliability and efficacy.

Organic Fungicide Programs

The increasing popularity of organically grown apples in North America and northern Europe spurred efforts to optimize SBFS control using organically certified fungicides. Most organic trials have used apple cultivars with genetic resistance to apple scab (caused by the fungus *Venturia inaequalis*, whose primary infection period occurs in the springtime), focusing instead on the management of summer diseases such as SBFS and fungal fruit rots. Ellis et al. (35) compared organic and conventional fungicide programs on scab-resistant and scab-susceptible cultivars in Ohio, concluding that organic programs for SBFS were effective during dry summers but failed to provide acceptable control in wet summers. Several studies assessed biological control formulations (31) and kaolin-based particle films (43, 116), but levels of SBFS suppression were often inferior to conventional fungicides. Methionine–riboflavin and potassium bicarbonate reduced SBFS incidence and severity but were insufficient to achieve commercially acceptable control in Wisconsin (3). In Massachusetts, Cooley et al. (27) evaluated several combinations of calcium compounds along with potassium bicarbonate and a commercial biological control formulation, with similar results.

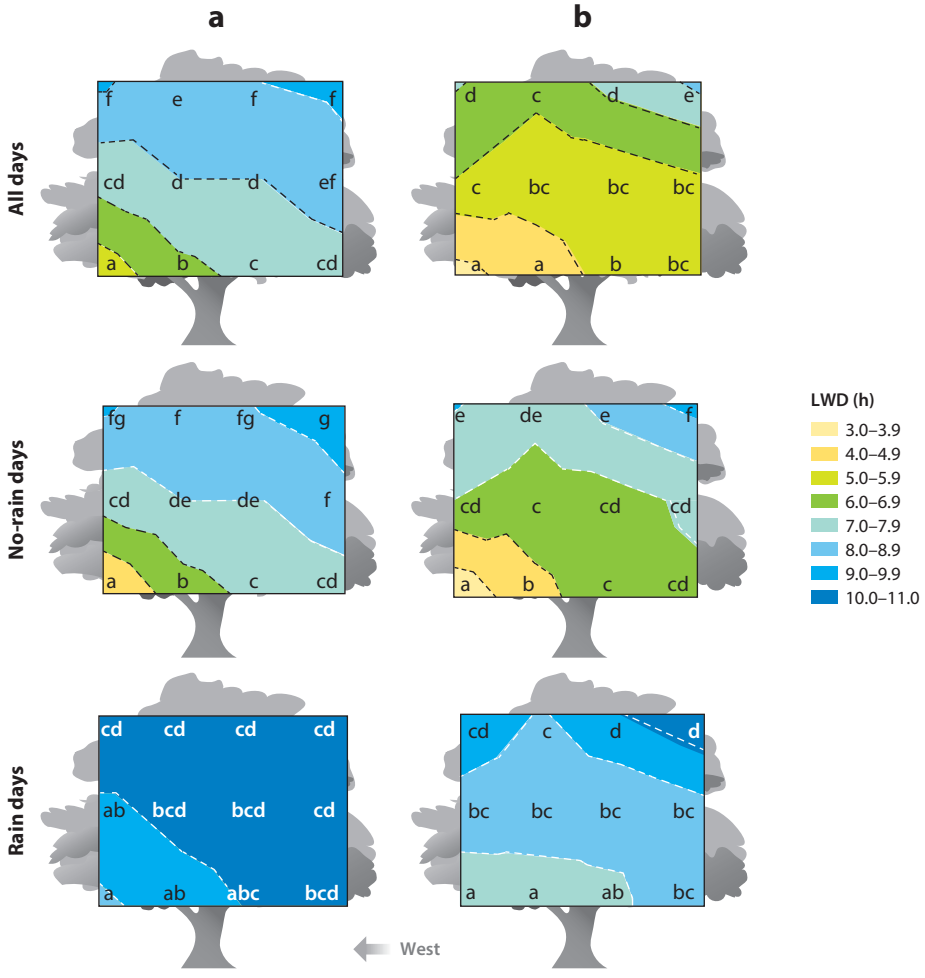


Figure 6

Statistical comparison of mean daily leaf wetness duration (LWD) among 12 canopy positions in semidwarf apple trees in orchards in Iowa, USA. (*a*) Summarized measurements made by LWD sensors at an orchard in Gilbert, Iowa, during the 2001, 2002, and 2003 growing seasons. (*b*) Summarized measurements from four Iowa orchards in 2003. Daily data sets were partitioned into rain days (measured rainfall ≥0.25 mm) and no-rain days. Dashed lines separate 1-h differences in LWD. Canopy positions that do not share the same letters are significantly different from each other ($P < 0.05$) (10). Figure adapted from Batzer et al. (10) with permission from the publisher.

In European apple orchards, SBFS is a major challenge for organic production (118). Spray options include lime sulfur, potassium soap, and coconut soap, but the efficacy of coconut soap has been inconsistent (114). Potassium bicarbonate formulations gave encouraging SBFS suppression on scab-resistant cultivars in Germany (106) and Switzerland (114). Winter treatments with copper or lime sulfur were evaluated to eliminate overwintering SBFS inoculum, but control was inferior to summer application of organic sprays (118). As part of the RIMpro apple management program, Trapman (117) developed a warning system for SBFS that incorporates relative humidity, LWD, and cultivar information and has been widely used by organic apple growers in Europe.

Cultural Control

Several cultural control recommendations, designed to reduce the risk of outbreaks, date back to the beginning of SBFS management efforts.

Site selection. A basic recommendation for SBFS management is to plant orchards on upper slopes and wind-exposed sites. These sites dry more rapidly after wetting periods and are thus less conducive to SBFS outbreaks (100, 102).

Pruning. Pruning opens up the tree canopy to accelerate dryoff and facilitates penetration of fungicide sprays (52). Both dormant-season pruning (68, 89) and summer pruning (26) can reduce SBFS risk. Batzer et al. (12) showed that dormant pruning in Iowa and Wisconsin enhanced the effectiveness of the Brown–Sutton–Hartman warning system in timing fungicide sprays.

Fungicide spray volume. Like pruning, spraying with an adequate volume of water helps to ensure thorough coverage of fruit and thereby more effective control of SBFS (124). Field trials by Batzer et al. (12) reinforced the value of so-called dilute spraying (at least 935 liters/ha on mature semidwarf trees) to ensure the effectiveness of the Brown–Sutton–Hartman warning system.

Cultivar selection. SBFS colonies are more visible on yellow or green cultivars than red ones (7, 25, 51). Russeting on the fruit surface, which is characteristic of some apple cultivars, suppresses SBFS colony development (18). Maturity date also exerts a major influence: short-season, early-maturing cultivars are less likely to develop SBFS infections than later-maturing cultivars. This trend holds true across a wide range of scab-susceptible, scab-resistant, and cider cultivars (**Figure 7**) (19, 86, 106). Early-maturing cultivars may escape SBFS because there is insufficient time during the fruit development period to allow for colony development (19).

Management of reservoir hosts and fruit mummies. Conidia from SBFS species probably travel no more than a few hundred meters on air currents, so it is likely that inoculum for SBFS outbreaks originates within or near orchards (27, 112). In the southeastern United States, Hickey

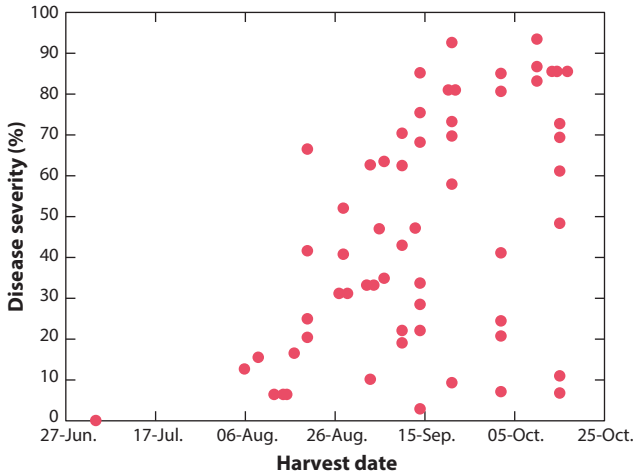


Figure 7

Influence of harvest date on severity of sooty blotch and flyspeck for more than 60 scab-resistant apple cultivars and selections in the Lake Constance region of Germany (106). Figure adapted from Späth & Mayr (106) with permission of the publisher and the authors.

Figure 8

Colonies of a *Peltaster* sp. on apple cultivar Dalinbel associated with an overwintered fruit mummy in an organically managed orchard in northern Germany.

(52) and Sutton et al. (113) recommended mowing commonly occurring reservoir hosts, such as *Rubus* spp., near orchard borders during the fruit development period to reduce SBFS risk on apples; however, there is no experimental evidence to support this recommendation.

Several apple cultivars retain dried fruit that was aborted at various stages of development (mummies); these mummies can persist on the tree for up to three years (**Figure 8**) (17). In Germany, Beer et al. (17) demonstrated that the mummy-retaining cultivar Dalinbel had a higher incidence of SBFS than the nonretaining cultivar Topaz, although both matured at the same time. In their field trials, removal of mummies reduced the incidence of the SBFS fungus *Peltaster cerophilu*s on cv. Dalinbel.

Fruit bagging. Placing apples in two-layer bags during the fruit development period is a widespread practice in China and Japan. The bags protect the fruit from certain pathogens (including SBFS fungi) and pest insects. The opaque outer layer is removed several weeks before harvest to allow the fruit to develop their normal mature color. This strategy has been highly effective in protecting fruit quality but has several limitations. One constraint is that bagging is highly labor intensive. In addition, the widespread use of bagging in Chinese orchards has triggered an upsurge in black spot and fruit rot caused by the fungal pathogen *Trichothecium roseum* (30); these diseases occur only on bagged apples.

Postharvest dip treatments. Postharvest dip treatments with various surfactants can remove SBFS colonies, suppress other postharvest pathogens, and kill human pathogens. Multiple dip solutions, from chlorine bleach to sodium bicarbonate and various fruit soaps, followed by

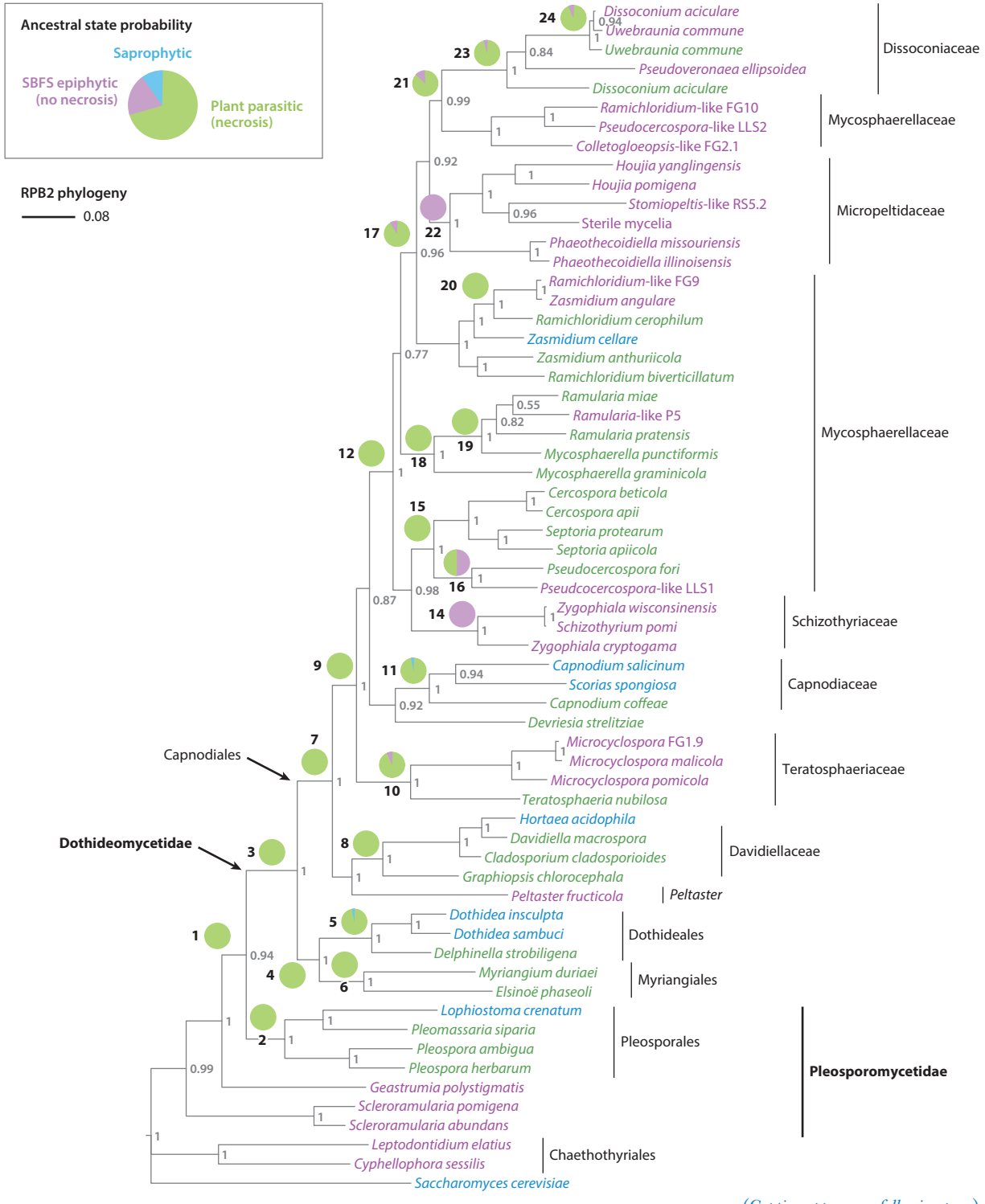
brushing remove most but not all SBFS colonies, and removal success varies among SBFS species (5, 11, 50).

EVOLUTION AND ADAPTIVE MECHANISMS

Recent research has clarified how SBFS fungi evolved and how they adapted to their unique plant-surface niche. Ismail et al. (55) used ancestral state reconstruction to determine whether SBFS species arose from parasites, saprophytes (i.e., fungi that feed on dead plant material), or both. They examined two genes: (*a*) the 28S region of the nuclear ribosomal DNA (28S rDNA), which is widely used for assessing evolution of symbiosis in Ascomycota (98), and (*b*) the RNA polymerase II subunit gene (*RPB2*), which is a single-copy protein-coding gene with a slow rate of sequence divergence that allows it to reliably resolve deep phylogenetic relationships in the Dothideomycetes (98). Each set of gene sequences was generated from 23 SBFS species from 15 genera, mostly in the order Capnodiales. These were aligned with sequences obtained from plant-penetrating parasites (PPPs) and saprophytes from seven families within the Dothideomycetes. The PPPs and saprophytic fungi were selected based on BLAST (basic local alignment search tool) nucleotide searches, using the 28S rDNA that showed high similarity to SBFS species (56). Phylogenetic trees were constructed separately for the 28S ribosomal DNA region and the RNA polymerase II gene (*RPB2*) data sets using Bayesian analysis. A Bayesian ancestral state reconstruction using a Markov chain Monte Carlo (MCMC) analysis showed a high level of support for plant-penetrating parasitism as the ancestral state of SBFS fungi (**Figure 9**). This conclusion was strongly supported by phylogenomic studies documenting evolutionary divergence of SBFS species from hemibiotrophic relatives (121, 127).

These latter studies documented reductive evolution from plant-penetrating parasitism to SBFS's plant-surface niche. A drastic reduction in the number and activity of genes involved in plant cell wall degradation, secondary metabolism, and secreted peptidases and effectors accompanied a loss of the ability to penetrate and colonize living cells (121, 127, 128) (**Figure 10**). However, genes facilitating survival on plant surfaces were more numerous and/or active than in necrotrophic or hemibiotrophic fungi. For example, genes responsible for the production of cutinases and secreted lipases, which are associated with breaking down the cuticle components cutin and epicuticular waxes, respectively, were either retained or increased markedly in number in comparison to PPP species (121, 127). On the basis of a transcriptomics analysis, Wang et al. (121) noted four additional stress-response mechanisms that help the SBFS species *R. luteum* to thrive on plant surfaces: melanin, lysozymes, aquaporin, and the HOG pathway. Melanin, whose production by *P. fructicola* was documented by Xu et al. (127), protects fungi from UV irradiation, high temperatures, and desiccation. Lysozymes break down peptidoglycans in bacterial cell walls, conferring a competitive advantage over phyllosphere bacteria (88). Aquaporins, which are membrane proteins that enhance tolerance to osmotic stress, were highly upregulated in *R. luteum*. Finally, the high osmolarity glycerol (HOG) pathway, a signaling pathway associated with response to osmotic stress (136), was active in this SBFS species. Revealing this diverse suite of adaptations and gene losses has dramatically advanced understanding of the evolutionary journey of SBFS fungi.

To gain a broader perspective on the evolution of SBFS fungi, Xu et al. (127) conducted comparative genome analyses pairing three taxonomically diverse SBFS species in the order Capnodiales with three closely related PPP species. As with *P. fructicola* (127) and *R. luteum* (121), these three SBFS species had considerably smaller genomes than their PPP counterparts and were relatively deficient in genes associated with plant-penetrating parasitism. The Xu et al. (127) study strengthened the evidence that evolution to the SBFS niche has occurred independently in



(Caption appears on following page)

Figure 9 (*Figure appears on preceding page*)

RPB2 phylogeny with a Bayesian Markov chain Monte Carlo analysis of ancestral state reconstruction of ecological niches of sooty blotch fungi and related taxa. Posterior probabilities for each of three niches—sooty blotch and flyspeck (*purple*; referred to here as epiphytic, now known as ectophytic), plant-penetrating parasitic (*green*; referred to here as plant parasitic), and saprophytic (*blue*)—are represented in pie charts at each reconstructed node (55). Abbreviation: SBFS, sooty blotch and flyspeck. Figure adapted from Ismail et al. (55) with permission from the publisher.

multiple Ascomycete taxa. Despite genomic differences among these five SBFS species (121, 127, 128), their similarities suggested convergent evolution toward low-energy lifestyles associated with the austere environmental conditions (62) on plant surfaces.

Scanning electron micrograph images of *P. fructicola* and *R. luteum* showed that SBFS fungi could partially dissolve the subtending cuticle and become embedded in it (**Figures 11** and **12**) (121, 127). This finding was contrary to Belding et al.'s (18) conclusion that *P. fructicola* was unable to degrade the apple cuticle. Three possible advantages to embedding in the cuticle rather than simply perching atop it include (*a*) increased access to nutrients, primarily sugars and organic acids that leak from fruit as they mature (127), (*b*) firmer attachment by the fungus to the hydrophobic fruit surface, reducing the risk of washoff (127), and (*c*) less exposure to environmental extremes.

Epiphytes can multiply and grow on the surface of healthy plants without exerting any adverse impacts on the host (70). Along with cutinase and secreted lipase production, the visual evidence of cuticle degradation supports Xu et al.'s (127) view that SBFS fungi occupy an ecological niche as ectophytes rather than epiphytes. Ectophytes, unlike epiphytes, can penetrate the nonliving surface layers of plants (e.g., the epicuticular wax layer and the cuticle). Like epiphytes, however, ectophytes do not penetrate the living cells underlying the cuticle. This ectophytic niche may be unique among phytopathogenic fungi. Xu et al. (127) note that the evolutionary story of the SBFS complex does not fit the generalization that saprophytic fungi were the ancestors of hemibiotrophic plant pathogens, which then evolved into either necrotrophs or obligate biotrophs (105). Instead, SBFS fungi took a different evolutionary road to reach their plant-parasitic niche: from PPPs to ectophytes. Xu et al. (127, 128) and Wang et al. (121) contended that SBFS fungi are a distinct type of biotroph, requiring live hosts from which they extract essential nutrients, but without killing, or even invading, host cells or tissues (**Figures 13** and **14**). Available evidence indicates that SBFS fungi deploy few elicitors, none of which contact living cells, so they do not trigger host defense responses. They are therefore true stealth pathogens, permanently undetected by plant hosts.

The evolutionary forces driving SBFS fungi from a plant-penetrating niche to an ectophytic niche are unclear. However, this change may have enabled them to escape host specialization and thereby survive during periods of rapid environmental change.

OUTLOOK

Major segments of the SBFS disease cycle remain undescribed. Knowledge of the timing of sporulation and dissemination is nonexistent for almost all species (27, 112). Coupling spore trapping with DNA-based species identification could (*a*) clarify how weather conditions influence species-specific spore release and dissemination patterns, (*b*) resolve persistent questions about the primary sources of SBFS inoculum for orchard outbreaks, and (*c*) determine whether management of reservoir hosts along orchard borders can be effective as an SBFS management strategy.

Processes that govern growth and dissemination of SBFS colonies on fruit are likewise poorly understood. Gao et al. (40) described the ramifications and subsequent dissolution of hyphae that occur in successive waves of colony enlargement, but the genetic mechanisms underlying these processes remain obscure. Rosli (93) determined that *P. fructicola* produced abundant single-celled secondary conidia on apple surfaces and readily spread from fruit to fruit by means of splash

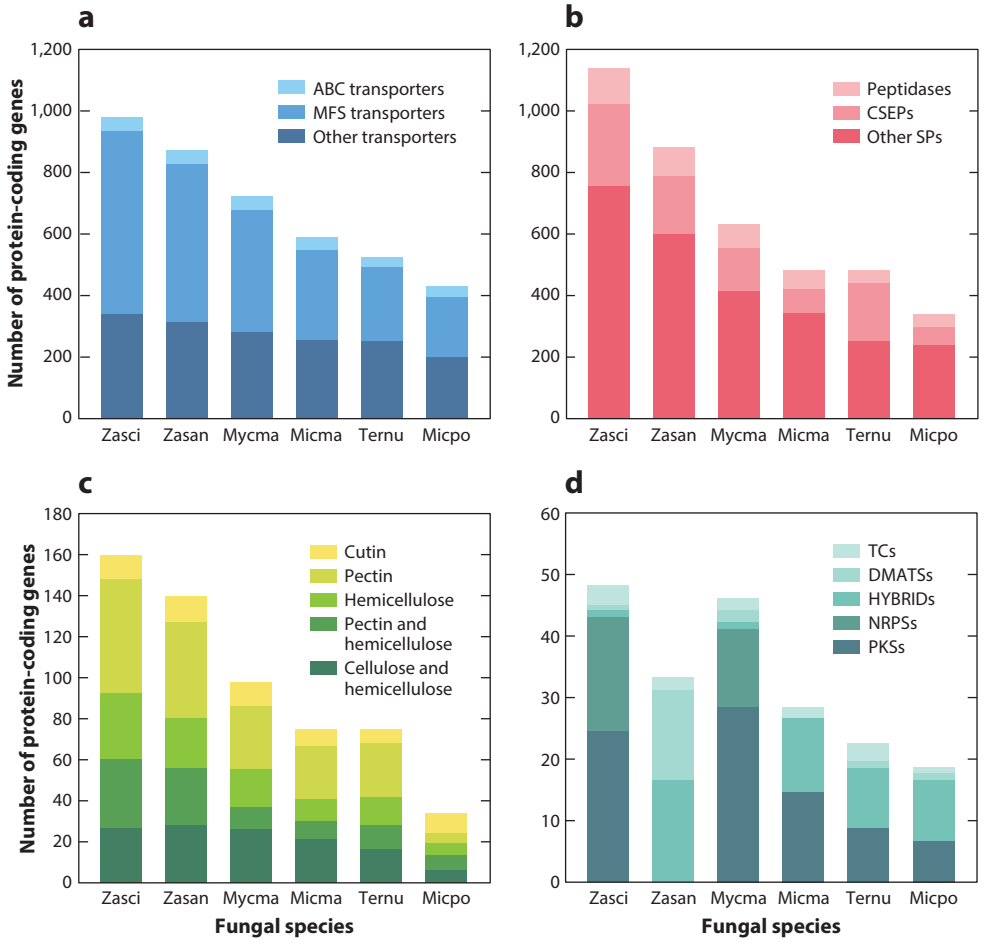


Figure 10

Plant pathogenicity-related protein-coding genes in six species of fungi investigated by Xu et al. (128). (*a*) Membrane transporters. ABC transporters, MFS transporters, and all other transporters (*dark blue*) are shown. (*b*) Secreted proteins (SPs), including peptidases, candidate secreted effector proteins (CSEPs), and all the other SPs. (*c*) Plant cell wall–degrading enzymes, including cutinases, degrading enzymes for pectins, hemicelluloses, both pectins and hemicelluloses, and both celluloses and hemicelluloses. (*d*) Secondary metabolite biosynthesis core enzymes, including PKSs, NRPSs, PKS-NRPSs, DMATSs, and TCs. *Mycosphaerella madeirae* (Mycma) and *Teratosphaeria nubilosa* (Ternu) cause necrotic leaf spots on eucalyptus foliage, and *Zasmidium citri* (Zasci) causes leaf and fruit lesions on most citrus and related hosts. In contrast, *Microcyclosporella mali* (Micma), *Zasmidium angulare* (Zasan), and *Microcyclospora pomicola* (Micpo) are SBFS species that colonize the surfaces of apples. Abbreviations: ABC, ATP-binding cassette; DMATS, dimethyl allyl tryptophan synthase; HYBRIDs, the hybrid PKS-NRPS gene; MFS, major facilitator superfamily; NRPS, nonribosomal peptide synthase; PKS, polyketide synthase; TC, terpene cyclase. Figure adapted from Xu et al. (128) with permission from the publisher.

dispersal, whereas two other SBFS species with differing reproductive strategies showed less or no secondary spread. However, the dynamics of the proliferation of other SBFS species within orchards are unknown. Surup et al. (110) and Venkatasubbaiah et al. (119) reported finding mycotoxin production in SBFS fungi, but the nature of the interactions of these fungi with other plant-surface microflora has not been investigated.

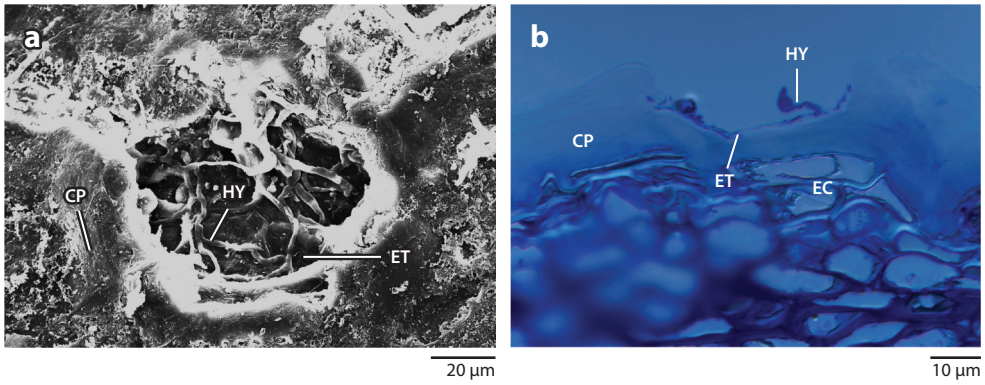


Figure 11

Degradation of the cuticle proper beneath sclerotium-like bodies of *Peltaster fructicola* on apple fruit (127). (*a*) Cuticle degradation under scanning electron microscopy. (*b*) Cross sections showing degradation of the cuticle. Abbreviations: CP, cuticle proper; EC, epidermal cell; ET, eroded trace; HY, hypha. Figure adapted from Xu et al. (127) with permission from the publisher.

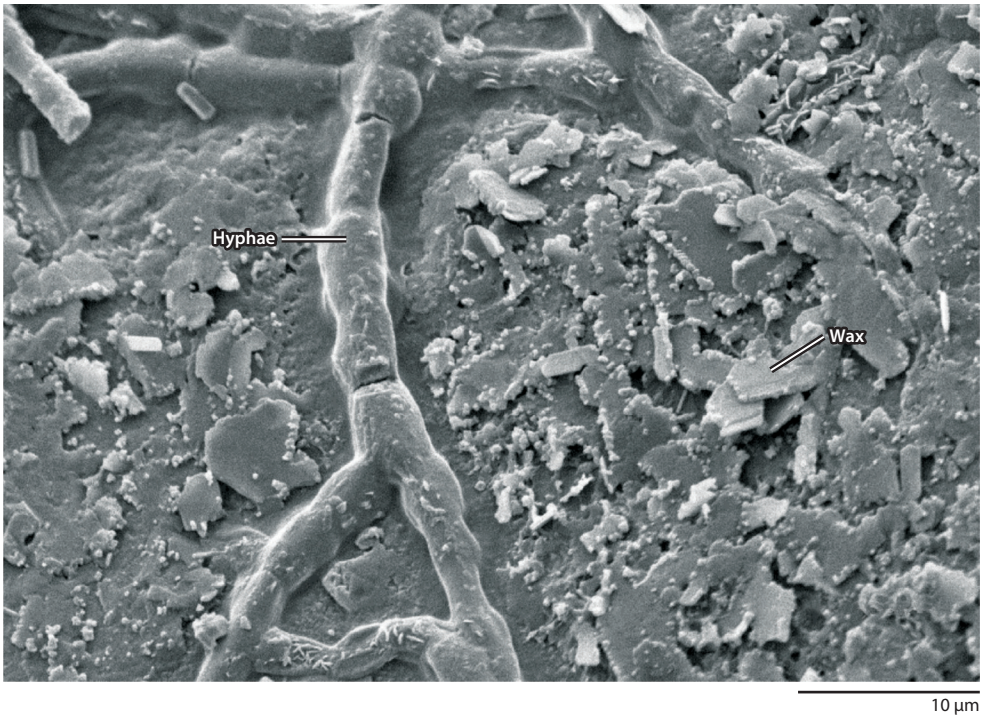


Figure 12

Scanning electron microscopy showing disappearance of waxy crystals around a hyphal network of *Ramichloridium luteum* (121). This disappearance indicates that *R. luteum* can efficiently degrade apple wax. Figure adapted from Wang et al. (121) with permission from the publisher.

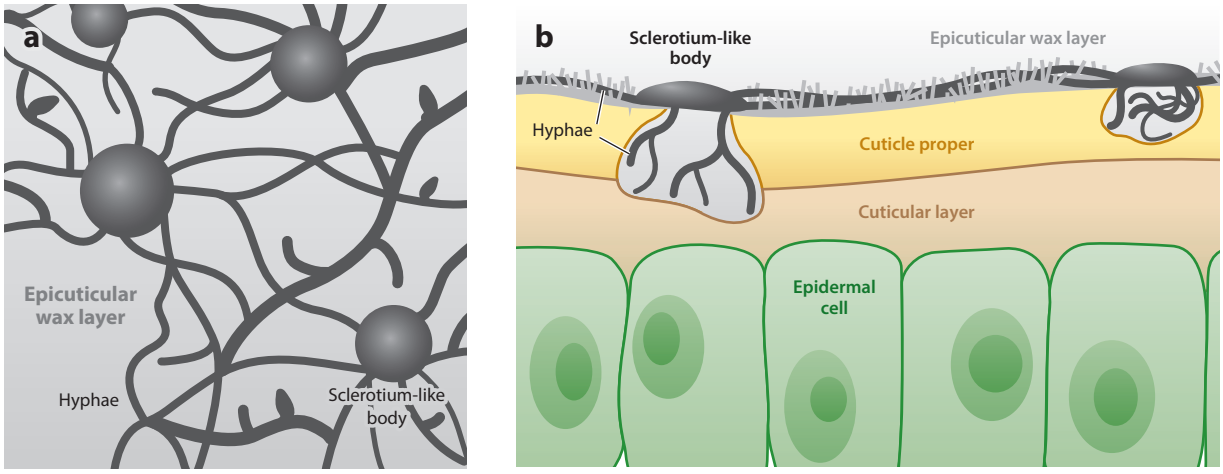


Figure 13

Inferred colonization pattern of *Peltaster fructicola* on apple fruit (127). (*a*) Overhead view of *P. fructicola* growing on the fruit surface. (*b*) Lateral view of *P. fructicola* growing on the fruit surface. Figure adapted from Xu et al. (127) with permission from the publisher.

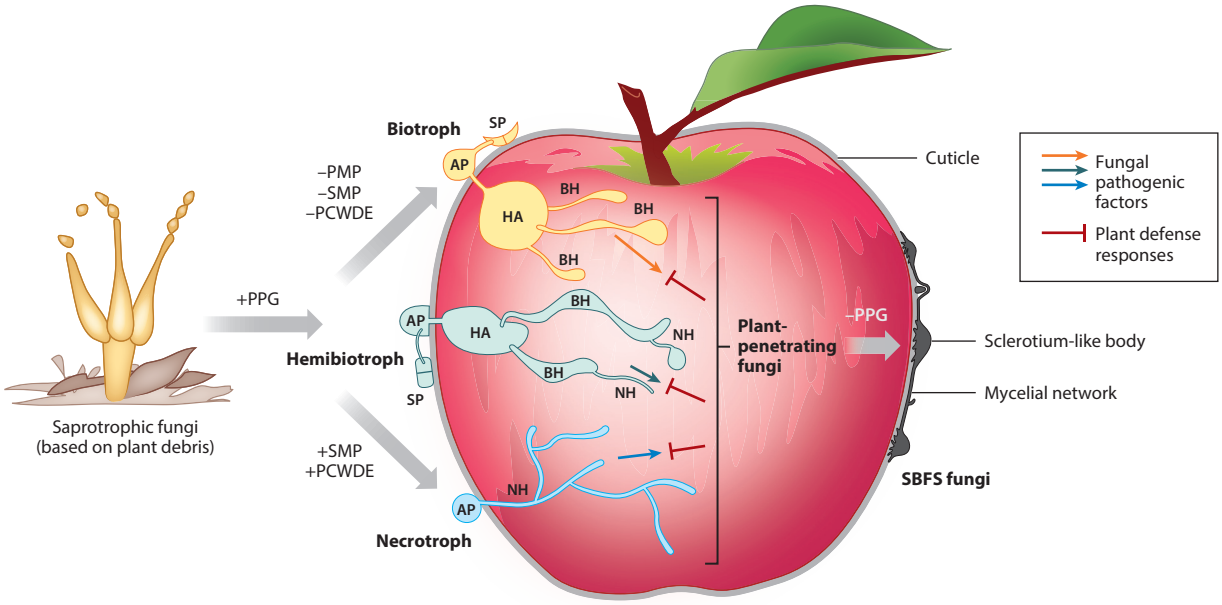


Figure 14

Schematic representation of a hypothesis for the evolutionary route of sooty blotch and flyspeck fungi (127). Abbreviations: AP, appressorium; BH, biotrophic hyphae; HA, haustorium; NH, necrotrophic hyphae; PCWDE, plant cell wall–degrading enzyme; PMP, primary metabolism pathway; PPG, plant pathogenicity–related gene; SBFS, sooty blotch and flyspeck; SMP, secondary metabolism pathway; SP, spore. Figure adapted from Xu et al. (127) with permission from the publisher.

There are compelling public health and environmental rationales to seek effective alternatives to the use of fungicides as the mainstay of SBFS control. Recent advances in teasing apart SBFS species complexes and uncovering adaptive strategies create a foundation for finding effective alternative control strategies that reduce or eliminate the need for chemical fungicides.

The hypothesis that colonization of the fruit surface by SBFS fungi does not alert host defenses lacks conclusive proof at this point, despite evidence that the SBFS fungi do not produce the types of enzymes associated with host-pathogen chemical combat. It would be useful to pursue omics studies from the host side to test this noncombatant hypothesis.

Finally, the evolutionary position of SBFS fungi among fungal epiphytes, which are located primarily in Dothideomycetes, needs clarification. Available evidence suggests that rock-inhabiting fungi in Chaetothyriomycetes were ancestral to other fungal epiphytes, including SBFS, in Dothidiomycetes (46, 96) and that other nutritional guilds emerged after fungi began to colonize plants (53). However, evolutionary relationships among major groups of fungal epiphytes and ectophytes, e.g., sooty molds, black dots, black mildews, and the SBFS complex, remain to be resolved.

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Errata

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