REVIEW
Schizophyllum commune as a Ubiquitous Plant Parasite

Shuhei TAKEMOTO[1,3], Hitoshi NAKAMURA[1]*, Erwin[2,4],
Yuji IMAMURA[2] and Takanori SHIMANE[1]

[1] Plant Pathology Research Team, National Institute of Fruit Tree Science, National Agriculture and Food Research Organization (Tsukuba, Ibaraki 305–8605, Japan)

[2] Research Institute for Sustainable Humanosphere (RISH), Kyoto University (Gokasho, Uji, Kyoto 611–0011, Japan)

Abstract

Schizophyllum commune is a sap-rot basidiomycete and cosmopolitan species. The fungus is also recognized as a plant pathogen that causes wood rot on living trees, and many plant species including fruit and ornamental trees have been recorded as hosts. In this paper, previous studies on the plant parasitism of *S. commune* and related information to date were reviewed, in addition to the unique characters of the fungus. Though the fungus is only a poor wood decomposer in vitro, it preferably invades living tissues of plants including bark and sapwood, being exceptional as a wood-rot basidiomycete. Basidiospores are abundantly ejected in the air, and pruning wounds, freeze injuries and sunscald lesions are major infection courts for them. Wood-rot disease by the fungus is promoted by drought, freezing temperatures and other weather conditions unfavorable for plants; the fungus is adapted to such adverse environmental conditions. It is expected that, depending on plant species and localities, ongoing global warming enhances plant damage, which may predispose plants to fungal infection. Schizophyllum rot possibly helps other wood-rot pathogens to infect and establish. More attention should be paid to the wood-rot disease complex in which *S. commune* is involved. In conclusion, various aspects on the biology of *S. commune* still remain to be studied in relation to the mechanism of its pathogenesis.

Introduction

The split gill fungus *Schizophyllum commune* is a cosmopolitan species of wood-rot basidiomycetes. The fungus is common throughout the world and very popular as an edible mushroom in some regions, e.g. Mexico[41] and Peninsular Malaysia[31].

It is generally considered that *S. commune* causes sap rot[46,50], though some researchers thought that the fungus caused heart rot[42,60,61]. In the personal observations of the authors (Nakamura et al., unpublished), sporocarps of the fungus were often found on the bark of dead trees, or even on the dead branches and trunks of living trees soon after they had lost viability. The fungus seems to colonize wood faster than any other wood-rot fungi. Some researchers regarded *S. commune* as a mere wound parasite or even a saprophyte[10], but others recognized the fungus as a plant pathogen[26,56], causing 'Schizophyllum rot' on living trees.

Recently, the authors[15] isolated a basidiomycete from cankerous tissue of a living *Shorea smithiana* (light red meranti) tree after a forest fire in Kalimantan, Indonesia, and identified the fungus as *S. commune*. The fungus produced white rot on test pieces *in vitro* which was similar to the early-stage decay observed in the cankerous part of the naturally infected tree[15]. These findings suggested a possible pathogenicity of *S. commune* against *S.*

Present address:

[3] Environmental Biofunction Division, National Institute for Agro-environmental Sciences (Tsukuba, Ibaraki 305–8604, Japan)

[4] Laboratory of Wood Anatomy and Biology, Faculty of Forestry, Mulawarman University (Jln. Ki Hajar Dewantara No. 1, Samarinda 75123, East Kalimantan, Indonesia)

*Corresponding author: e-mail nakamh@affrc.go.jp

smithiana that might lead to continuous storage loss in the forest. Schmidt[46] noted that the fungus was a serious wood destroyer in tropical regions, but no more details on the pathogenic relationship between the fungus and tropical lumber trees were suggested.

There have been a few reviews on the biology of *S. commune* with reference to its pathogenicity[10,16,19,44]. Although they are of scientific and practical significance, recent studies on the fungus have not been integrated in terms of its pathogenic nature. This paper intended to review major studies concerning plant parasitism of *S. commune* and related information, including the aggressive nature of *S. commune*.

Schizophyllum rot in Japan

One of the earliest studies on *S. commune* in Japan was made by Kitajima[27]. He mentioned that the fungus was found all over Japan, mainly inhabiting timber of broad-leaf trees (e.g. railroad ties of *Fagus crenata* (Japanese beech) wood[25]), as well as that of coniferous trees. Although the major interest of Kitajima[27] was to preserve construction timber, he also introduced some studies from abroad dealing with plant parasitism of the fungus. Among the literature, living trees of *Ulmus* sp. (elm), *Tilia* sp. (lime), *Fagus* sp. (beech), *Picea rubens* (red spruce), *Prunus salicina* (Japanese plum), and ornamental *Prunus* sp. were recorded as host species of the fungus.

Akai and Nagatomo[3] pointed out that the fungus prevailed on all kinds of merchantable timber woods, and often caused '*fuke*-discoloration rot', i.e. discoloration of living tissues due to their resistance reaction to fungal invasion. This problem seriously arose in Hokkaido when broad-leaf trees became utilized for the pulp industry. A series of studies was done for preserving raw pulpwoods during storage in the forest and yard. Wood Processing Division, Hokkaido Forest Products Research Institute[63] warned of the economic loss of *Betula* spp. (birch) wood due to discoloration rot by sap-rot fungi including *S. commune*. The loss of pulpwood was very serious in storage yards in Tomakomai and Ebetsu, Hokkaido with more than 95% of logs decayed, and *S. commune* was nominated as one of the 4 most frequent wood-rot fungi there[38]. Decay experiments in the laboratory and yard revealed that the fungus could rapidly intrude logs from the cut surfaces, but that the fungus was a poor wood decomposer[39,40].

Wood-rot disease of living trees caused by *S. commune* in Japan might have been first recorded by Togashi et al.[57,58] in basic researches on the diseases of crop plants in Iwate, northern Japan. *Malus pumila* (apple), *P. persica* (peach), *P. avium* (sweet cherry) and *P. mume* (Japa-

nese apricot) were recorded as host species. Togashi[56] published a textbook of the diseases on fruit trees. In the book, *S. commune* was described as a wood-rot pathogen that parasitized *M. pumila* and other stone-fruit trees via wounds and potentially caused considerable loss. Although its virulence was quite low, wood-rot disease was recorded also on *Castanea crenata* (Japanese chestnut) tree, and designated as Schizophyllum rot[22]. Ito[23] regarded *S. commune* as a wood-rot pathogen parasitizing branches and trunks of living broad-leaf trees. Hayashi[18] described the fungus as one of the early colonizers on pruning wounds of *Prunus* spp. (flowering cherries). He mentioned that the management of cherry trees had recently changed to remove branches and limbs for esthetic purpose, which provided wood-rot fungi with an infection court, and emphasized the importance of appropriate care for artificial wounds with antifungal pastes. Recently, a series of surveys on wood-rot diseases of ornamental cherry trees was done in several localities in the Kanto area[47–49], central Japan, to clarify the distribution pattern of wood rot pathogens involved and risk factors. In their studies, *S. commune* was suggested to prefer branch stubs after pruning to naturally declining branches.

Based on the studies mentioned above, *S. commune* is accepted as a wood-rot pathogen in Japan. In fact, a compendium[26] and the check list of plant diseases in Japan[4] include descriptions on the fungus and the wood-rot disease it causes. Although there has been no record on *Pyrus pyrifolia* var. *culta* (Japanese pear) as a host plant, our recent observations in a mature orchard in Tsukuba, central Japan, indicated that 12% of the trees suffered from the fungus, which was more serious than other host plant cases in Japan (e.g. 3.3% of *Prunus* spp. trees[49]). Results from inoculation experiments on young shoots of *P. pyrifolia* var. *culta* by the authors (Takemoto et al., unpublished) will briefly be presented later in this review.

Wood-decay ability

Previous studies commonly pointed out that *S. commune* was only a poor destructor of dead wood. Soshiroda[52] studied the decay ability of 3 wood-rot basidiomycetes on 6 coniferous woods. *Schizophyllum commune* seldom caused weight loss (0–0.49%) on the wood blocks after 6-month incubation at 28°C on water-saturated sawdust, though the loss of compressive strength was considerable (5.7–44.6%). Similarly, only a little weight-loss was reported on the sapwood of *F. crenata*[3] and *Pinus thunbergii* (Japanese black pine)[35]. Sahashi et al.[45] reported that weight-loss caused by the fungus was less than 1.5% for *Cryptomeria japonica* (*Sugi*, or Japanese cedar) woodchip, heartwood and sapwood, and less than 3.7%

for *Liriodendron tulipifera* (tulip tree) heartwood and sapwood.

Schmidt[46] regarded the fungus as a primary colonizer of raw woods, especially of *Fagus* sp., after felling. Odajima and Oyama[39,40] showed that though only a little weight loss was observed on wood pieces tested, the fungus could rapidly intrude raw pulpwoods from the cut ends, i.e. 12-cm depth for *T. japonica* (Japanese lime) and 15-cm depth for *B. platyphylla* var. *japonica* (Japanese white birch) after 1-month incubation. Erwin et al.[15] compared wood rot naturally occurring in a living tropical lumber tree, *Shorea smithiana* (light red meranti) between naturally- and artificially infected wood blocks from the same tree. Detailed observations revealed that both natural and artificial samples had white rot with a simultaneous decay pattern, though the weight loss was only 1.8% after 12-week incubation at 26°C in laboratory[15]. Species identification of the fungus involved was first based on sequencing of DNA[15], but later confirmed by the morphology of sporocarps and mating compatibility tests (Takemoto et al., unpublished).

Anatomical observations of diseased wood by Putterill[44] revealed that the fungus had cellulolytic activity. *In vitro* experiments, however, indicated no lignolytic[40,44] or peroxidase activity[44]. Cellulolytic activity of *S. commune* was induced when the culture medium was amended with cellobiose, cellulose, xylan[62], carboxymethyl cellulose, or filter paper fragments[54], but suppressed with glucose, fructose or sucrose[62]. The enzymatic activity was most inductive at the germling stage of basidiospores[62]. Xavier-Santos et al.[64] compared polygalacturonase activity among 72 basidiomycete isolates belonging to 42 species. Though the results varied within species, the 5th most active isolate was *S. commune*. De Vries et al.[13] demonstrated significant laccase activity from dikaryotic mycelium cultured at 30°C in the dark, while monokaryons genetically related to the dikaryon generally failed to produce laccase.

Parasitism on living plants

Togashi[56] and Kishi[26] noted that *S. commune* is a wound parasite on some stone fruit trees, and that the fungus might cause a considerable loss on debilitated or poorly managed trees. In fact, the fungus has been recognized as a wood-rot pathogen for fruit trees[1,4,6,11,19,22,26,29,32–34,42–44,56–58,60], ornamental trees[26,49,51] and lumber trees[15,37].

Schizophyllum commune cannot invade living plant tissues without injuries. One of the exceptional cases was reported for *M. pumila* fruits, which were infected at the stem end and the calyces[30]. Usually, the infection of *S. commune* is likely to occur via a physical wound, e.g.

pruning[1,18,32,33,43,46,49,51,60], freeze injury[11,12,22,32,43], sunscald lesion[22,44,50], a lesion made by other pathogens[36,43,57,58], fire scar[15,46,50], and dead branch stubs[37,49]. Host plant species of *S. commune* with reference to mode of infection are listed in Table 1. Recently, it was pointed out that global warming may enhance the incidence of sunscald, late frost damage and even freezing injury, depending on locality and tree species[53]. Therefore, appropriate care of trees suffering from such climatic damage will be of increasing importance to manage wood-rot diseases caused by *S. commune* and other basidiomycetous pathogens.

Previous studies suggested that environmental stresses, e.g. low temperatures in winter and drought in summer[42] and overhumidity[51], might promote disease incidence. Sinclair et al.[50] also stated that the fungus might aggressively colonize trees stressed by heat, drought and large wounds. Hemmi[19] also pointed out that, in Chinese inland areas, extreme drought and strong sunlight prevented the normal curing of pruning wounds, which facilitated fungal colonization. He concluded in the review that the pathogenicity of *S. commune* might be affected by regional factors such as climate. Some researchers stated that decreased plant vigor might facilitate the infection of *S. commune*[16]. To prevent the infection of the fungus, trees should be fertilized and nursed appropriately[19,56]. Resistance levels against the fungus varied among cultivars of *P. armeniaca* (apricot) trees[42] and *M. pumila* fruits[30]. In addition to these environmental and host factors, inherent characters of the pathogen should also be involved in pathogenesis and intensity of the disease. However, there have been no studies in which *S. commune* isolates were compared in virulence. This should be clarified in future.

Some researchers observed that *S. commune* invaded living and sound tissues of woody plants. Putterill[44] conducted inoculation experiments on *P. communis* (almond), *P. armeniaca* and *P. persica* trees and reported that the fungus showed pathogenicity in the latter two species. He observed a characteristic gumming in the vessels and cells of the wood. The rotten part of the wood was clearly distinguished from the healthy part with a distinct line[44]. Hemmi[19] concluded that the fungus could gradually invade and kill sound tissues after colonizing trees at wounded sites. Snieškienė and Juronis[51] reported that the fungus destroyed the bark tissue of *T. cordata* (small-leaved lime). Similarly, bark rot was observed on *P. persica* trees infected by the fungus[32]. Dai[11] confirmed the pathogenicity of *S. commune* to *P. persica* saplings by inoculation tests. In our unpublished studies, *S. commune* isolates were examined for their pathogenicity on young shoots of *P. pyrifolia* var. *culta* using field plants and fragments of dormant shoots. All the dikaryotic and

Table 1. Host plant species of *Schizophyllum commune* and its infection mode

Latin name	Common name	Infection site	Infection court	Reference
ACERACEAE				
Acer platanoides	Norway maple	TB		42
A. saccharum	Sugar maple	TB	DB	37
ANACARDIACEAE				
Mangifera indica	Mango	TB		41
Pistacia vera	Pistachio	TB		34
Rhus typhina	Staghorn sumac	TB		42
ARECACEAE				
Elaeis sp.	Oil palm	seed and germ		14
BETULACEAE				
Betula spp.	Birch	TB		42
CONVOLVULACEAE				
Ipomoea batatas	Sweet potato	rhizome	IN	43
DIPTEROCARPACEAE				
Shorea smithiana	Light red meranti	TB	FS	15
FABACEAE				
Acacia pennatula	*Huizache* [Spanish]	TB		41
Erythrina americana	Coral tree	TB		41
Robinia pseudacacia	Black locust	TB		42
FAGACEAE				
Castanea crenata	Japanese chestnut	TB	FI, SS	22, 26
C. mollissima	Chinese chestnut	TB		26
Quercus sp.		TB		42
OLEACEAE				
Fraxinus angustifolia	Narrow-leaved ash	TB		42
POACEAE				
Saccharum spp.	Sugar canes	TB		2
Sorghum bicolor	Sorghum	grain		17
RHIZOPHORACEAE				
Rhizophora mangle	Mangrove	TB		41
ROSACEAE				
Malus pumila	Apple	fruit	NO, IN	5, 30
		TB	LS, PW	6, 19, 33, 43, 44, 56, 57, 58
Prunus armeniaca	Apricot	TB	IN, SS	26, 29, 32, 42, 44
P. avium	Sweet cherry	TB		58
P. davidiana	David peach	TB		32
P. domestica	Plum	TB	SS	41, 44
P. mume	Japanese apricot	TB		26, 58
P. persica	Peach	TB	FI, IN, PW, SS	1, 11, 32, 43, 44, 57, 58, 60
P. pseudocerasus	Chinese cherry	TB		11, 32
P. salicina	Japanese plum	TB		11, 16, 32
P. serrulata	Japanese flowering cherry	TB		32
Prunus spp.	Flowering cherries	TB	DB, PW	18, 26, 49
Pyrus pyrifolia var. *culta*	Japanese pear	TB	IN	Takemoto et al., unpublished
SALICACEAE				
Populus sp.	Poplar	TB		41, 42
Salix babylonica	Weeping willow	TB		42
TILIACEAE				
Tilia cordata	Small-leaved lime	TB	FI, PW	12, 51
Tilia sp.	Lime	TB		42
VITACEAE				
Vitis vinifera × *caribea*	Grape	TB		20

TB: tree body including trunk, branches and twigs. DB: dead branch stubs, IN: inoculation wound, FS: fire scar, FI: freeze injury, SS: sunscald, NO: natural openings, LS: lesion made by other pathogens, PW: pruning wound and other mechanical injuries. The reference numbers are the same as those used in the text.

monokaryotic isolates were more or less pathogenic irrespective of their original host plants, showing white rot bordered with bluish discolored zones on the radial cut surface of wood (Fig. 1). The internal rot symptoms were similar to those described by Essig[16] and Liu et al.[32].

As well as these wood and bark tissues, the fungus can invade other living tissues and organs of plants. Dikin et al.[14] proved that the fungus caused brown rot on the seed and germ of oil palm, *Elaeis* sp. Gramineous plants such as *Saccharum* spp. (sugar cane)[2] are parasitized by the fungus. Rhizomes of *Ipomoea batatas* (sweet potato)[43] and some fruits[5,30] were also infested. Because the fungus is known as a possible producer of mycotoxin on sorghum grain[17], infestation of such fruits and rhizomes might lead to problems of food contamination. *Schizophyllum commune* sometimes inhabits living plant tissues without noticeable symptoms. For instance, Nakazawa and Harada[36] revealed that mycelium of the fungus persisted for three months or more in the sound tissue around the inoculation wounds on *M. pumila* shoots. The fungus was even reported as an endophyte from healthy pods of a tropical tree species *Theobroma gileri*[55]. All the facts mentioned in this section suggest that *S. commune* has enough potential to colonize, and sometimes aggressively invade, living tissues of plants.

Omnivory

Schizophyllum commune can occur on a broad range
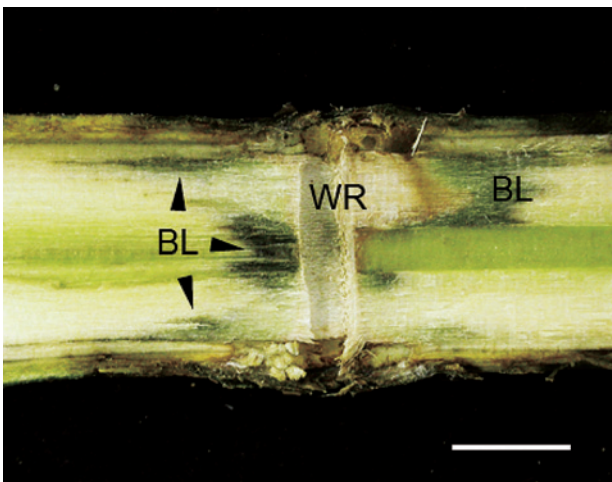
Fig. 1. Typical internal symptoms caused by *Schizophyllum commune* on *Pyrus pyrifolia* var. *culta*

A dormant shoot was drilled with 1.5 mm-diameter bit, inoculated with a *S. commune* isolate growing on a toothpick and incubated at 25°C for 1 month in a growth chamber.
White rot (WR) bordered with bluish discolored zone (BL) can be observed on the radial cut surface. Bar = 5 mm.

of substrates: more than 260 species belonging to 150 genera of plants were listed by Cooke[10], and similarly 32 species in 22 genera of woody plants in Japan by Kobayashi[28]. The fungus parasitizes diverse plants (Table 1). Although they solely represent sporadic observations and experimental results, our unpublished study indicated that 5 *S. commune* isolates showed uniform pathogenicity on *P. pyrifolia* var. *culta* (Rosaceae, Rosales), irrespective of host plant species from which they had been isolated, including *S. smithiana* (Dipterocarpaceae, Malvales). These facts suggest that individual fungal isolates have a broad host range, and are thus considered to be omnivorous. To confirm this hypothesis, further inoculation experiments on several plant species are needed. Gene flow across *S. commune* populations parasitizing different host species should also be examined to test a possibility of host differentiation.

Possible involvement in complex diseases

Schizophyllum commune readily invades plants from lesions made by other pathogens. Poole[43] observed that the fungus infected living *M. pumila* trees at the shoots fire-blighted by a pathogenic bacterium *Erwinia amylovora*. Togashi et al.[57,56] recorded that Schizophyllum rot on *M. pumila* trees accompanied Nectria canker (*Neonectria galligena* = *Nectria galligena*) and Valsa canker (*V. ceratosperma*). Preventive spraying for microbial diseases may also be effective to control Schizophyllum rot. Nakazawa and Harada[36] also isolated *S. commune* from Valsa canker on a *M. pumila* tree; however, the fungus caused apparently no harm against the tree and even suppressed the growth and colonization of *V. ceratosperma*. These results may partly be explained by the observations of Tzean and Estey[59], who considered *S. commune* to be a destructive mycoparasite.

Another possible mode of the complex disease is that the secondary infection of wood-rot pathogens occurs following Schizophyllum rot. Since the fungus is a competent cellulose decomposer but has little lignolytic activity[40,44], the lignin/cellulose ratio of wood increases after colonization of the fungus. Its vegetative mycelium mostly exists near the living wood[44], and the heartwood, if any, may remain intact. This may promote habitat segregation between *S. commune* and secondary fungi with lignolytic activity to cause heart-rot.

Wilson[61] reported that sporocarps of *Schizophyllum* sp. occurred through burrows of *Xyleborus dispar*, a secondary borer, implying a relationship between the fungus and the beetle. Reversely, the authors (Nakamura et al., unpublished) observed that an allied species *X. saxeseni* preferably burrowed the tree trunk at the emerging points

of *S. commune* sporocarps (Fig. 2). An ambrosia fungus of *X. saxeseni* was often isolated together with *S. commune* from the wood around beetle galleries, which implied that *S. commune* might coexist with the ambrosia fungus in the wood (Nakamura et al., unpublished). *Schizophyllum commune* appears to do no harm to *X. saxeseni* in terms of nutrition supply. Also, the fungus does not attack the beetle directly. Although there is no evidence of close physiological relationships between the fungus and the beetle, they may be synergistic to expand wood rot when inhabiting together.

Discussion

Schizophyllum commune is an omnivorous plant pathogen that invades living tissues from wounds and potentially causes rot. The aggressiveness and omnivory of *S. commune* are unique among wood-rot basidiomycetes. In the case of *Botrytis cinerea*, an omnivorous plant-pathogenic ascomycete of necrotrophic nature, the resistance to oxygenic stresses and the high productivity of

Fig. 2. **An entrance hole (arrow) of *Xyleborus saxeseni* at the emerging point of *Schizophyllum commune* sporocarps**
   Bar = ca. 5 mm.

polygalacturonase are known as important pathogenicity factors[9]. Similarly, some isolates of *S. commune* can produce polygalacturonase more abundantly than many other wood-rot basidiomycetes[64]. The strong resistance to dryness[7], high temperature[21,27,30,45] and salinity[8] may have some relation to the resistance to oxygenic stresses.

Schizophyllum commune is basically a sap-rot fungus and seems to be specialized in fresh plant tissues including bark. Basidiospores are abundantly ejected in the air[24], and play an important role for infection. Germlings of basidiospores have high cellulolytic activity[62] but laccase production is suppressed[13] *in vitro.* These findings indicate that germlings are more adapted to fresh substrates than decayed wood with a high lignin/cellulose ratio. All these features characterize *S. commune* as a plant parasitic sap-rot fungus and early colonizer of wood rather than a wood decomposer.

In the genus *Schizophyllum*, only the species *commune* is worldwide[10], while *S. fasciatum* and *S. umbrinum* have a limited distribution circumscribing Mexico, Central America and the Caribbean[10,41]. According to Olivo-Aranda and Herrera[41], the latter 2 species seem to be less resistant to dry or cold climate than *S. commune*. Possibly, pathogenicity might be one of the key factors for *S. commune* to prevail in the world, as well as its stress resistance; plant parasitism has not been known for other *Schizophyllum* species, except a *S. umbrinum* specimen found on a living tree of *Acacia* sp.[41]. Comparative studies among the *Schizophyllum* species should contribute to better understanding the biology of *S. commune*, an aggressive and omnivorous plant parasite.

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