Talaromyces flavus: An Important Rhizospheric Inhabitant

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B. M. Bashyal, Prashantha S. T., and Rashmi Aggarwal

Abstract

The *Talaromyces*' story started about 100 years ago, with isolation and description of the first strain, albeit under another name. It continued with taxonomic studies, secondary metabolites identification, and the study of their effect on biological models. Subsequently, it continued with attempts to apply this strain in agriculture for biocontrol of phytopathogenic microorganisms and culminated with the study of *T. flavus* genetic equipment. Biological studies with metabolites such as vermiculine, vermistatin, dehydrolatenusin, or purpactins have broadened our horizons in immunology, cancer treatment, or metabolic diseases. This chapter describes some of the important metabolites produced and the role of *T. flavus* as biocontrol agent in sustainable agriculture system.

Keywords

Talaromyces flavus · Biological control · Phytopathogen · Secondary metabolites · Glucanase · Chitinase

10.1 Introduction

Talaromyces flavus is the most common species of the genus *Talaromyces*, which has been studied and applied as a biocontrol agent, a producer of secondary metabolites or enzymes. *T. flavus* is an extremely variable species found in soils and on organic materials that undergo slow decomposition. The species is widespread in its distribution but it is most commonly reported from the warmer regions

B. M. Bashyal (✉) · P. S. T. · R. Aggarwal
Division of Plant Pathology, ICAR-Indian Agricultural Research Institute, New Delhi, India

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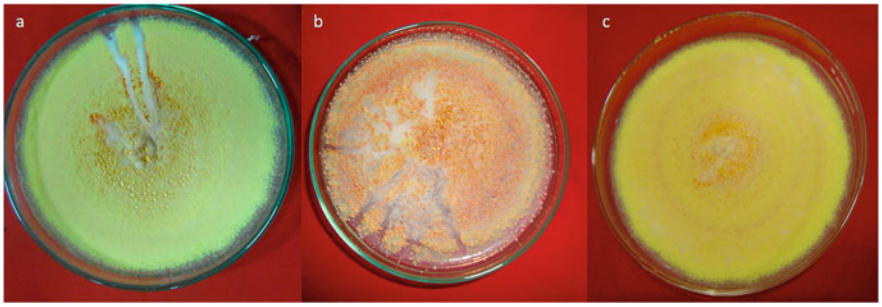

Fig. 10.1 *Talaromyces flavus* isolates showing different colony characteristics: (**a**) *Tf1*, (**b**) *Tf2*, and (**c**) *Tf3*

of the world. It also occurs in foods, probably as a contaminant (Pitt and Hocking 2009). Dangeard (1907) provided a detailed report of *Penicillium vermiculatum*, which Benjamin (1955) relocated to the genus Talaromyces, and Orr et al. (1963) demonstrated the identity of this strain with *Gymnoascus flavus* described by Klocker (1902). *Arachniotus indicus* (Chattopadhyay and Das Gupta 1959) and *P. liani* were also declared identical with *T. vermiculatus* (Ghosh et al. 1961). Stolk and Samson (1972) redefined the genus *Talaromyces* and distinguished two new varieties of *T. flavus*, namely *T. flavus* var. *flavus* (isolates varies in color and colony characteristics; Fig. 10.1) and *T. flavus* var. *macrosporus*.

10.2 Classification

Species classified in the phylum Ascomycota, class Eurotiomycetes, order Eurotiales, family Trichocomaceae, and genus *Talaromyces* are as follows (MycoBank 2010):

- *Talaromyces flavus* (Klocker) Stolk and Samson (1972)
- Basionym: *Gymnoascus flavus* Klocker (1902)
- Synonyms: *Arachniotus indicus* Chattopadhyay and Das Gupta (1959)
- *Talaromyces flavus* var. *flavus* (Klocker) Stolk and Samson (1972)
- Synonyms: *Penicillium liani* Kamyschko (1962), *T. vermiculatus* (Dangeard) Benjamin (1955), *G. flavus* Klocker (basionym), *A. indicus* Chattopadhyay and Das Gupta (1959), *A. indicus* var. *major* Chattopadhyay and Das Gupta (1959)

Status conidialis (anamorphs):

- *P. vermiculatum* Dangeard (1907)
- *P. liani* Kamyschko (1962), *Penicillium vermiculatum* Dangeard (1907)
- Synonym: *Eupenicillium vermiculatum* (Dang.) Ram and Ram (1972)

Teleomorphs:

- *P. dangeardii* Pitt (1979)
- *T. flavus* var. *flavus* (Klocker) Stolk and Samson (1972)

10.3 Secondary Metabolites

The organic soluble metabolites of this fungus include D-glucono-1,4-lacton, 5-hydroxymethylfurfural, 4,6-dihydroxy-5-methylphthalimide, methyl-4-carboxy-5-hydroxyphethalal dehydrate, hexaketide, 7-hydroxy-2,5-dimethylchromone, 3-hydroxymethyl-6,8-dimethoxycoumarin, altenusin, desmethyldehydroaltenusin, talaroflavone, deoxytalaroflavone, 2-methylsorbic acid, sorbic acid, bromomethylsorbic acid, and bromosorbic acid (Ayer and Racok 1990a). Some of the above-mentioned metabolites (2-methylsorbic acid, sorbic acid, bromomethylsorbic acid, and bromosorbic acid) play a fundamental role in the biogeochemical cycling of phosphorus (P) in natural and agricultural ecosystems. Some of the metabolites produced by the *T. flavus* are reported in Table 10.1.

10.4 Enzymes

Esterase/amidase from *P. vermiculatum* stereoselectively hydrolyzed only 2R,3S enantiomer from the synthetically prepared monoalkylesters or dialkylamides of racemic phosphomycin (Demain et al. 1972). Amine oxidase (EC 1.4.3.4) catalyzes the oxidative deamination of amines by the formation of aldehyde, hydrogen peroxide, and ammonia. *T. flavus* var. *flavus* isolated from a soil sample collected from a rice field produced amine oxidase stable up to 40 °C with the optimum pH in a range of 7.5–8.5. This enzyme was intended to be used in biochemical analysis, e.g., determination of the freshness of meat by assaying tyramine or other amines (Matsumoto and Takada 1984). α-Amylase and glucoamylase *P. vermiculatum* precultured on amylose gel and cultured on a medium containing corn starch secreted crude α-amylase (EC 3.2.1.1), which was further purified on a cross-linked starch (Augustín et al. 1983). Thermostable amylases are used for starch hydrolysis in the liquefaction step of industrial starch syrup production. *T. flavus* secreted a thermophilic glucoamylase (EC 3.2.1.3), which exhibited peak activity at 50 °C and a pH of 4.0–4.8 (Hang and Woodams 1993). Chitinase: *T. flavus* grown in the presence of chitin produced two chitinases (EC 3.2.1.14). The isolated enzymes with a molecular mass of 41 and 32 kDa decomposed the cell wall of *Verticillium dahliae*, *Sclerotinia sclerotiorum*, and *Rhizoctonia solani* (Duo-Chuan et al. 2005) at the optimum pH between 4.0 and 5.0, respectively and 40 °C. *P. vermiculatum* produced dextranase (EC 3.2.1.11) at the optimum temperature between 50 and 55 °C and pH in a range of 5.0–5.5. It hydrolyzed dextran to isomaltose, isomaltotriose, and glucose (Sun et al. 1988). The main application field of dextranases is sugarcane processing. The use of dextranases has also been extended to dental care as a

Table 10.1 List of important metabolites produced by *T. flavus*

S. no.	Secondary metabolite	Description	Reference	Function
1	Coumarins	3-Hydroxymethyl-6,8-dimethoxycoumarin (III)	Ayer and Racok (1990a)	Endophytic fungus *Pestalotiopsis* sp.
		Talacoumarins A (**1**) and B (**2**)	He et al. (2007)	
2	Chromones	2,5-Dimethyl-7-hydroxychromone (IV)	Ayer and Racok (1990a)	Until now, chromone IV has only been isolated from higher plants, e.g., *Bupleurum longicaule* wall and *Lycopus europaeus* L.
3	Short-chain organic acids	(–)-*Trans*-2,3-epoxysuccinic acid (V)	Sakaguchi et al. (1939), Martin and Foster (1955)	Antibiotic activity
		Fosfonochlorin (VI)	Hendlin et al. (1969)	
		2-Methylsorbic acid (VII)	Proksa et al. (1992a)	
	Phthalide derivatives	4,6-Dihydroxy-5-methylphthalide (IX) 2-Formyl-5-hydroxyterephthalic acid	Ayer and Racok (1990a)	Antioxidant activity
		Rubralide C (XV)	Kimura et al. (2007)	Antioxidant activity
		Funiculosic acid (XI)	Qureshi et al. (1980)	Antioxidant activity
4	Vermistatin and derivatives	Vermistatin (XVI, F)	Fuska et al. (1979a)	Vermistatin (XVI) is a cytotoxic agent without any marked antibiotic effect. This compound inhibited the utilization of precursors of nucleic acid and protein synthesis in Ehrlich ascites

(continued)

Table 10.1 (continued)

S. no.	Secondary metabolite	Description	Reference	Function
				carcinoma cells and suppressed proliferation of P388 cells in vitro (Fuska et al. 1979a)
5	Altenusin, dehydroaltenusin, and derivatives	Altenusin (XXIX)	Ayer and Racok (1990b)	Anticancerous
		Dehydroaltenusin (XXX), desmethyldehydroaltenusin (XXXI) together with the structurally related talaroflavone (XXXII) and deoxytalaroflavone (XXXIII)	Ayer and Racok (1990b)	Anticancerous
	(–)-Mitorubrin and related compounds	(–)-Mitorubrin (XXXV) and (–)-mitorubrinol (XXXVI)	Proksa et al. (1994, 1997)	Suggested for the treatment of trypanosomiasis, Chagas' disease, malaria, or coccidiosis (Hayashi et al. 1996)
6	Purpactin, penicillide, and related compounds	Vermixocins A (XL) and B (XLI)	Proksa et al. (1992b)	Acts as an acyl-CoA:cholesterol acyltransferase inhibitor
7	Vermiculine and derivatives	Vermiculine (XLVI)	Fuska et al. (1972)	Antimicrobial
		Vermiculinol (XLVII) and vermiculidiol (XLVIII)	Massias et al. (1989)	Antimicrobial
	Vermicillin	–	Fuska et al. (1979a, b)	Affected the synthesis of RNA in leukemia P388, EAC, NK/Ly, and L 1210 cells and suppressed the proliferation of P388 cells
8	TAN-2177A and B	Esterified oligopeptides TAN-2177A and B (LII) and (LIII)	Tozawa et al. (1996)	Specific inhibitors of squalene synthase may inhibit cholesterol biosynthesis

(continued)

Table 10.1 (continued)

S. no.	Secondary metabolite	Description	Reference	Function
9	Saccharides and polysaccharides	D-Glucono-1,4-lactone	Ayer and Racok (1990a)	Fungicidal activity
		Talaron	Mizuno et al. (1974)	

toothpaste additive, since dextran has been shown to be involved in dental plaque formation (Galvez-Mariscal and Lopez-Munguia 1991). *T. flavus* var. *flavus* cultured aerobically at 28 °C for 48 h on a medium containing fructan-afforded fructanase (EC 3.2.1.80), which has been applied in the production of fructose from Jerusalem artichokes (Ishibashi et al. 1974). *T. flavus* secreted α-D-galactosidase in the presence of 6-deoxyglucose. The crude enzyme was composed of three isoenzymes. The most important isoenzyme, αGal-1, showed a different regioselectivity than the other two isoenzymes. Purified αGal-1 catalyzed the transglycosylation of *tert*-butanol and split off D-galactose from raffinose and stachyose. This enzyme, inhibited by α-D-galactopyranosylazide, D-xylose, melibiose, or lactose (Simerská et al. 2007), catalyzed the reaction of 4-nitrophenyl-α-D-galactopyranoside (LXX) and its 6-acetyl derivative LXXI to 4-nitrophenyl-α-Dgalactopyranosyl-(1→3)-6-*O*-acetyl-α-D-galactopyranoside (LXXII) (Simerská et al. 2003). A mixture of biosides, which composed of 86.5, 3.5, and 8.0% of LXXIII, α(1→2), and α(1→6) regioisomers, respectively, was prepared after incubation of LXX with α-D-galactosidase from *T. flavus* (Weignerová et al. 2001). *P. vermiculatum*, grown in a culture enriched with α-1,3-glucan, secreted a remarkable amount of α-1,3-glucanase (EC 3.2.1.84). The production of this enzyme was stimulated by the addition of surfactants Tween 80 or Tergitol NPX to the culture medium (Reese et al. 1972). The antifungal activity of this enzyme was studied in relation to its role in mycoparasitic processes, especially in degradation of the host cell wall (Sanz et al. 2004). Glucose oxidase (EC 1.1.3.4) catalyzes the oxidation of β-D-glucose to gluconic acid and hydrogen peroxide using molecular oxygen as the electron acceptor. *T. flavus* produces glucose oxidase, which is involved in the biocontrol of fungal plant pathogens. Pectinolytic enzymes are important for several industrial applications such as improving juice yields and clarity. Other areas of application include the paper and pulp industry, waste management, animal feed preparation, or the textile industry. *T. flavus*, precultured for 24 h on a solid substrate culture like passion fruit peel and then transferred into a new medium supplemented with 0.5–0.8% citrus pectin, secreted pectinesterase (EC 3.1.1.11) and polygalacturonase (EC 3.2.1.15) into the medium. High levels of pectinases cultivated in solid state fermentation using citrus pulp pellets were produced by *T. flavus* isolated from Brazilian soil (Siessere and Said 1989). Phytase, an enzyme that breaks down the indigestible phytic acid/phytates (inositol penta-, tetra-, and triphosphate) found in grains and oil seeds, was produced by *T. flavus* cultured in a medium containing up

to 6% of saccharides and 2% of nitrogen-containing compounds (Jiang et al. 2007). Proteinase K (EC 3.4.21.64), a serine protease, is used in molecular biology because it rapidly inactivates nuclease, which might otherwise degrade the DNA or RNA during purification and maintains its activity in the presence of chemicals that denature proteins. Proteinase K was secreted by *T. flavus* in media containing goat hairs. The highest enzyme production was observed at pH 6.5 after a 9-day incubation and the isolated raw enzyme was separated into two fractions characterized by a molecular mass of 31.5 and 36.75 kDa, respectively (Mohawed and Badran 1995). The purified product was tested as an antifungal agent against brown spot disease caused by *Botrytis fabae* on a bean of *Vicia faba* (Haggag et al. 2006). α-L-Rhamnosidase *T. flavus* produced an extracellular α-L-rhamnosidase when incubated with inducers such as L-rhamnose, rutin, or naringin but not hesperidin (Monti et al. 2004). Fungal α-L-rhamnosidases have applications mainly in the food industry (Yadav et al. 2010). The enhancement of wine aroma by enzymatic hydrolysis of terpenylglycosides was also studied (Spagna et al. 2000). Cell wall-degrading enzymes, such as β-1,3-, β-1,4-, and β-1,6-glucanases, cellulase, and chitinase, are involved in the antagonistic activity of biocontrol agents against phytopathogenic fungi (Madi et al. 1997; Inglis and Kawchuk 2002). Some of the enzymes produced by *Talaromyces flavus* are listed in Table 10.2.

10.5 *Talaromyces flavus* in Biological Pest Control

T. flavus suppresses Verticillium wilt of tomato (Dutta 1981), aubergine (Fahima and Henis 1995; Marois et al. 1982), potato (Fravel et al. 1986), or cotton (Nakova 2003) and parasitizes *Sclerotium rolfsii* (Madi et al. 1992, 1997), *Sclerotinia sclerotiorum* (McLaren et al. 1986), *Rhizoctonia solani* (Boosalis 1956), and *Gaeumannomyces graminis* var. *tritici* (Mohammadi and Ghanbari 2015).

Dethoup et al. (2007) characterized 122 isolates of *Talaromyces flavus* from 45 soil samples in 38 provinces of Thailand. *Talaromyces flavus* isolates were found in both non-agricultural and agricultural soil in Chiang Mai and Mae Hong Son provinces following heat and alcohol treatments. Twenty isolates of *T. flavus* were selected for antagonistic tests against 15 species of plant pathogenic fungi in vitro and in the greenhouse. All the selected isolates of *T. flavus* inhibited the mycelial growth of *Phytophthora palmivora*, *P. parasitica*, *Peronophythora litchii*, *Colletotrichum capsici*, *C. gloeosporioides*, *Pestalotiopsis guepinii*, *Phyllosticta* sp., *Curvularia lunata*, *Helminthosporium maydis*, *H. oryzae*, and *Fusarium oxysporum*. However, none of the isolates controlled *Pythium aphanidermatum*, *Lasiodiplodia theobromae*, *Rhizoctonia solani*, and *Sclerotium rolfsii* in vitro. However, in the greenhouse experiment, 20 isolates of *T. flavus* controlled stem rot of mung bean, caused by *S. rolfsii*, 7 and 14 days inoculation, and 6 isolates gave control up to 30 days inoculation. Bashyal (2018) reported that *T. flavus* is effective against *Fusarium fujikuroi* responsible for bakanae disease in rice (Fig. 10.2).

Cell wall-degrading enzymes, such as β-1,3-, β-1,4-, and β-1,6-glucanases, cellulase, and chitinase, are involved in the antagonistic activity of biocontrol agents

Table 10.2 List of the important enzymes produced by *Talaromyces flavus*

S. no.	Enzyme	Functions
1	Acetyl hexosaminidase	Fungal β-*N*-acetyl hexosaminidase (EC 3.2.1.52) catalyzes the hydrolysis and transfers β-GlcNAc and β-GalNAc (*N*-acetyl galactosamine
2	Amine oxidase	Amine oxidase (EC 1.4.3.4) catalyzes the oxidative deamination of amines by the formation of aldehyde, hydrogen peroxide, and ammonia
3	α-Amylase, glucoamylase	Thermostable amylases are used for starch hydrolysis in the liquefaction step of industrial starch syrup production
4	Chitinase	Decomposed the cell wall of *Verticillium dahliae*, *Sclerotinia sclerotiorum*, and *Rhizoctonia solani*
5	Dextranase	It hydrolyzed dextran to isomaltose, isomaltotriose, and glucose (Sun et al. 1988). The main application field of dextranases is sugarcane processing
6	Fructanase	It has been applied in the production of fructose from Jerusalem artichokes
7	Galactosidase	Purified αGal-1 catalyzed the transglycosylation of *tert*-butanol and split off D-galactose from raffinose and stachyose
8	α-1,3-Glucanase	The antifungal activity of this enzyme was studied in relation to its role in mycoparasitic processes, especially in degradation of the host cell wall
9	Glucose oxidase	Glucose oxidase (EC 1.1.3.4) catalyzes the oxidation of β-D-glucose to gluconic acid and hydrogen peroxide using molecular oxygen as the electron acceptor. *T. flavus* produces glucose oxidase, which is involved in the biocontrol of fungal plant pathogens
10	β-Glucosidase	The enzyme showed the capacity to resolve diastereoisomeric mixtures of alkyl β-D-glucopyranosides
11	Pectinase	Pectinolytic enzymes are important for several industrial applications such as improving juice yields and clarity
12	Phytase	Phytase, an enzyme that breaks down the indigestible phytic acid/phytates (inositol penta-, tetra-, and triphosphate) found in grains and oil seeds, was produced by *T. flavus* cultured in a medium containing up to 6% of saccharides and 2% of nitrogen-containing compounds
13	Proteinase K	Proteinase K, a serine protease (EC 3.4.21.64), is used in molecular biology because it rapidly inactivates nuclease, which might otherwise degrade the DNA or RNA during purification and maintains its activity in the presence of chemicals that denature proteins
14	α-L-Rhamnosidase	Fungal α-L-rhamnosidases have applications mainly in the food industry (Yadav et al. 2010)

against phytopathogenic fungi (Madi et al. 1997; Inglis and Kawchuk 2002). In addition, *T. flavus* antagonizes *Verticillium dahliae* by parasitism and antibiosis (Fahima et al. 1992; Marois et al. 1984). Microsclerotia of *V. dahliae* were suppressed by a culture filtrate of *T. flavus* and this effect was attributed to the action of glucose oxidase (Fravel and Roberts 1991; Kim et al. 1988). In a recent study, the

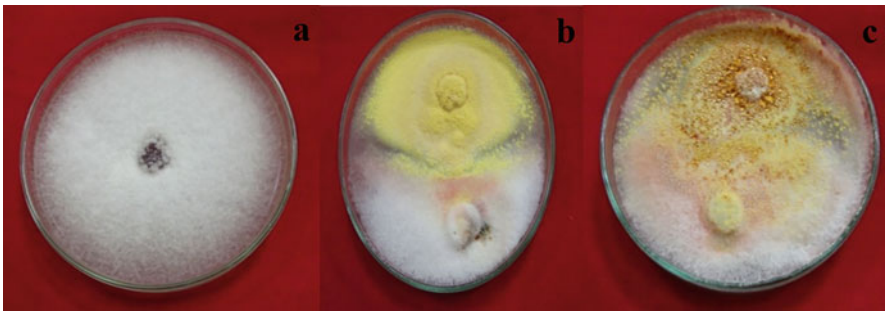

Fig. 10.2 Dual culture assay of *Fusarium fujikuroi* with different isolates of *Talaromyces flavus*: (**a**) control, (**b**) *Fusarium fujikuroi* + Tf_1, and (**c**) *Fusarium fujikuroi* + Tf_2

effect of seed treatments of *Talaromyces flavus* on sugar beet seedling damping-off disease under greenhouse conditions reported that the isolates reduced the percentage of damping-off disease from 40 to 7.5% compared to infected control (Naraghi et al. 2012). Furthermore, in another field study, a significant decrease in the incidence of sugar beet seedling damping-off disease was observed along with increase in yield in treatments containing antagonistic fungi *T. flavus* and *T. harzianum* compared to the control (Naraghi et al. 2014; Lamichhane et al. 2017). Further, improved growth was reported on cotton and potato when they were treated with biocontrol agent *Talaromyces flavus* (Naraghi et al. 2012). Bashyal et al. (2020) reported increased drought tolerance in *T. flavus*-treated rice seedlings.

Chattopadhyay and Das Gupta (1959) isolated *T. flavus* from paddy rhizosphere and reported phosphate-solubilizing activity of *T. flavus* under in vitro conditions that positively influenced the growth of the rice, *Cicer arientinum*, and *Vigna radiata* under greenhouse conditions. He further reported that *T. flavus* have the capacity to convert insoluble phosphorus to soluble form.

Haggag et al. (2006) purified proteases from the culture filtrate of *T. harzianum* and *T. flavus* and tested for their antifungal activity against brown spot disease caused by *Botrytis fabae* on faba bean. *T. flavus* exhibited high levels of extracellular protease activity compared with *T. harzianum*. Germination and growth rate, extracellular polygalacturonase (*PGase*), and carboxymethyl cellulase (*CMCase*) activities of *Botrytis fabae* were inhibited by the purified protease at a concentration of 40–120 U/ml. Growth and extracellular production of *B. fabae* were completely inhibited by the protease enzyme of *T. flavus* at a concentration of 80 U/ml, while protease from *T. harzianum* was effective at 120 U/ml. Proteases were effective in reducing brown spot disease severity and pathogen sporulation on faba bean leaves inoculated with *B. fabae*.

Glucose oxidase, secreted by *T. flavus*, retards hyphal growth and kills microsclerotia of *V. dahliae* in vitro, probably by generating toxic peroxide (Kim et al. 1988; Stosz et al. 1996), but only if a sufficient amount of glucose is available (Murray et al. 1997). Partial disintegration of melanin was observed near hyphae of *T. flavus* colonizing sclerotia of *S. sclerotiorum* (McLaren et al. 1989). The

inhibition of germination and melanin formation in sublethally heated microsclerotia of *V. dahliae* and additive suppression by sublethal heating and *T. flavus* treatment was studied (Tjamos and Fravel 1995). A glucose oxidase gene was located and isolated, and mutants of *T. flavus* with both high and low production ability of this enzyme were constructed. A high level of glucose oxidase in tobacco and cotton as a result of the expression of its gene from *T. flavus* was associated with phytotoxic effects such as reduced root growth, slow germination on culture medium, or reduced lateral root formation (Murray et al. 1999).

To increase the effectiveness of *T. flavus* isolates obtained from greenhouse cucumbers and field-grown tomatoes, five chemical stabilizers were evaluated. Based on the results of previous studies, the most effective substrate for the growth, sporulation, and stability of *T. flavus* isolates related to the above-mentioned plants was a mixture of rice bran and peat moss. Different chemical stabilizers were mixed with the above-mentioned substrate containing spore suspensions of various *T. flavus* isolates. Completely randomized experiment was conducted under greenhouse conditions with seven treatments and three replications. The results of this study indicated that treatments containing sodium nitrate and D-cycloserine were more effective than those containing other stabilizers (Bahramiyam et al. 2016).

Fravel et al. (1986) evaluated the use of pyrophyllite clay (Pyrax), milled chitin, maize cobs, fish meal, neem cake, groundnut hulls, soya fiber, and wheat bran to make alginate prill with or without ascospores of *T. flavus*. The formulations were compared for their ability to induce *T. flavus* to control Verticillium wilt of aubergine in the greenhouse in field soil and to increase populations of *T. flavus* in three field soils (two loamy sands, one silty clay). Survival of *T. flavus* in prill at 5 °C or ambient temperature (22–24 °C), as well as the carbon (C) and nitrogen (N) contents of the prill, was also determined. Two formulations (maize cobs and pyrophyllite) consistently enhanced biocontrol activity.

10.6 Conclusion

Talaromyces flavus is a significant soil-inhabiting fungus that produces important metabolites and enzymes that have established their effects on biological models. The application of its enzymes has enabled stereoselective preparation of many useful saccharides. *T. flavus* is a very variable species and not all of its secrets have as yet been uncovered. At the same time, this microbe was utilized as biological control agent against many important diseases. However, genomic studies are lacking on this fungal species. Further, emphasis should be given on genes involved in secondary metabolite production, whole genome studies of this microbe, and tripartite interaction to understand this fungal species further.

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