



# Bioprospecting of endophytes associated with *Solanum* species: a mini review

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## Abstract

Endophytes are considered the repository of bioactive compounds as they contain a wide variety of chemically and structurally diverse secondary metabolites. The endophytes associated with *Solanum* species have been studied for the last few years. Therefore, the present study aimed to discuss the bioactive compounds produced by endophytes associated with *Solanum* species and their biological activities. Our study reveals that among the *Solanum* species, only 13 species have been studied in the context of endophytes so far. Overall, a total number of 98 bioactive compounds have been reported from endophytes associated with *Solanum* species, of which 64 compounds are from fungi and 34 compounds from bacteria. These bioactive compounds belong to different chemical groups such as sterols, flavonoids, volatiles, and many others and exhibited diverse biological activities including antimicrobial, anticancer, antiparasitic, antioxidants, and plant growth-promoting activity. Moreover, the endophytic fungi were reported to produce two compounds that are often present in the host plants. These condensed data may open the door for further research and provide details on potent endophytes associated with *Solanum* species.

**Keywords** Bioactive compounds · Biological activity · Endophytes · *Solanum*

## Introduction

The utmost step in the research on endophytes is the selection of an economically important and promising host plant. The reason behind the selection of host plants is to understand the plant–endophyte interaction as well as to discover new bioactive compounds produced by those endophytes that could be helpful in the pharmaceutical industry. In this respect, plants of ethnomedicinal value are excellent candidates for the study of endophytes, as endophytes can imitate the biochemistry of their colonized host plant to stimulate similar types of bioactive compounds or derivatives which are even more bioactive than the types of their host plants (Sadrati et al. 2013). For example, capsaicin is produced by an endophytic fungus *Alternaria alternata* from *Capsicum annum*, which is a key compound of the host plant

(Devari et al. 2014). Anticancer drug taxol is produced by *Lasiodiplodia theobromae* which is an endophytic fungus of the medicinal plant *Morinda citrifolia* (Pandi et al. 2011). Similarly, camptothecin is reported from the endophytic bacteria *Paenibacillus polymyxa* found in *Camptotheca acuminata* (Nchabeleng 2017). However, such phenomena might be the consequence of horizontal gene transfer (HGT) between the endophytes and host plants (Sachin et al. 2013).

The *Solanum* is the largest and most representative genus in the family Solanaceae that comprises more than 2000 species (Kaunda and Zhang 2019). The genus is very rich in economically important species that include both food crops and ornamental plants. Besides, the species of *Solanum* is well known for ethnopharmacological applications due to the presence of various bioactive compounds. There are about 670 compounds including alkaloids, terpenes, flavonoids, lignans, steroidal saponins, steroidal sterols, phenolic compounds, coumarins, and many more compounds documented by Kaunda and Zhang (2019) in their review. In addition, it is reported that the wild variety of traditional or indigenous vegetables belonging to *Solanum* has higher nutritional value than domesticated species (Mili et al. 2021). Furthermore, they are grown healthy in the wild with

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no care at all compared to other domesticated species. It is believed that such type of feature may be due to the outcome of plant–microbe interaction, in particular, endophytes that colonize the interior. Several studies have demonstrated that the endophytes associated with these plants confer increased resistance to biotic and abiotic stress, and improve yield and quality by supplying different secondary metabolites to the host.

Numerous studies on the endophytes from various species of *Solanum* have been conducted in recent years, including topics such as diversity, antimicrobial activity, secondary metabolite, application in bioremediation, and many more. A total number of 13 species of *Solanum* have been studied for endophytes, and these are *Solanum nigrum* L., *S. rostratum*, *S. xanthocarpum* L., *S. tuberosum* L., *S. mauritianum* Scop., *S. surattense*, *S. trilobatum* L., *S. lycopersicum* L., *S. elaeagnifolium*, *S. sodomaeum* and *S. bonariense*, *S. violaceum*, and *S. melongena* L. Among 13 species, only 8 species have been investigated for endophyte-derived compounds to date. In this review, we shall highlight the bioactive compounds produced by the endophytes associated with the different species of *Solanum* and their potential uses in the agriculture and pharmaceutical aspects.

## Diversity of endophytes associated with *Solanum* species

### Endophytic bacteria

The diversity of endophytic bacteria has extensively been studied from different species of *Solanum* in the last two decades. A large number of endophytic bacteria such as *Deinococcus radiopugnans*, *Melissococcus pluton*, *Saccharococcus thermophilus*, *Burcella melitensis*, *Stomatococcus mucilaginosus*, *Streptococcus pyogenes*, *Staphylococcus aureus*, *Salinococcus roseus*, *Gemella haemolysans*, *Klebsiella pneumoniae*, *Buttiauxella agrestis*, *Pediococcus damnosus*, *Bacillus subtilis*, *Coproccoccus eutactus*, and *Aerococcus viridians* are reported from species *Solanum trilobatum* L., an important medicinal plant commonly distributed in southern India (Bhuvanewari et al. 2013). Endophytic bacteria, *Serratia* sp. IU01 and *Enterobacter* sp. IU02, isolated from *Solanum nigrum*, alleviate cadmium (Cd) stress response by their antioxidant potentials, phosphate solubilization activity, and indole acetic acid production (Ullah et al. 2019). Another strain *Serratia* sp. RSC-14 improves the phytoextraction abilities of *S. nigrum* in Cd contamination (Khan et al. 2015). Furthermore, Chen et al. (2010) studied the diversity of the endophytic bacterial population associated with the Cd-hyperaccumulator plant *Solanum nigrum* L. grown in mine tailings. The results revealed that a total number of 61.93% Proteobacteria, 12.18% Bacteroidetes, 2.03%

Firmicutes, and 18.78% Actinobacteria occurred of which *Sphingomonas* and *Pseudomonas* were found to be dominant genera. The endophytic bacteria *Pseudomonas fluorescens* isolated from *Solanum melongena* L. showed an antagonistic role against *Ralstonia solanacearum* that causes wilting diseases of solanaceous crops (Ramesh et al. 2009). The species *Solanum lycopersici* L. is one of the staple vegetable crops that harbor endophytic bacteria belonging to different genera, such as *Acinetobacter*, *Arthrobacter*, *Bacillus*, *Microbacterium*, *Pantoea*, *Pseudomonas*, and *Stenotrophomonas* (López et al. 2021). Another study reports that the leaf of *S. lycopersici* L. harbors rich diversity of endophytic bacteria belonging to Proteobacteria (90%), Actinobacteria (1.5%), Planctomycetes (1.4%), Verrucomicrobia (1.1%), and Acidobacteria (0.5%) (Romero et al. 2014). Moreover, *Bacillus subtilis* and *Paenibacillus* sp. were also reported from the *S. lycopersici* L. by Iqbal et al. (2018). In addition, two plant growth-promoting endophytic bacteria such as *Bacillus* sp. str. SV101 (KU043040) and *B. tequilensis* str. SV104 (KU976970) were also isolated from stems of *Solanum elaeagnifolium* (Abdalla et al. 2016).

### Endophytic fungi

A series of studies have been carried out on endophytic fungi from plants belonging to *Solanum*. Mohammad Golam Dastogeer et al. (2020) isolated endophytic fungi from the stem of *Solanum lycopersicum* Mill. plants, belonging to 29 unique operational taxonomic units (OTUs) with 97% ITS gene sequence identity. Among them, *Fusarium* (45.1%), *Alternaria* (12.8%), *Gibberella* (12.0%), and *Dipodascus* (6.8%) were the dominant genera. A large number of endophytic fungi such as *Alternaria helianthi*, *Fusarium* sp., *Penicillium funiculosum*, *Phomopsis* sp., *Acremonium* sp., *Aspergillus niger*, *A. flavus*, *Cladosporium* sp., *Trichoderma* sp., *Myrothecium* sp., *Geotrichum* sp., *Colletotrichum* sp., *Humicola* sp., and many mycelia sterile are reported from *S. lycopersicum* species (Abayneh et al. 2022). Besides, endophytic fungi *A. flavus* is reported from *S. nigrum* (El-Hawary et al. 2016). Similarly, *S. tuberosum* L. a worldwide staple vegetable harbors a wide range of endophytic fungi such as *Alternaria tenuissima*, *A. flavus*, *A. niger*, *A. ochraceus*, *A. oryzae*, *Chaetomium cervicicola*, *Curvularia lunata*, *Fusarium equiseti*, *F. nygamai*, *F. oxysporum*, *Lasiodiplodia theobromae*, *Penicillium funiculosum*, *P. minioluteum*, *P. pinophilum*, *P. polonicum*, *P. rubens*, *Stemphylium vesicarium*, *Trichoderma harzianum*, and *Ulocladium* sp. identified by Yasser et al. (2019) in Egypt. In addition, three species of endophytic *Cephalotrichum* such as *Cephalotrichum asperulum*, *C. gorgonifer*, and *C. tenuissimum* are reported from *S. tuberosum* L. in Iran (Mamaghani et al. 2022). A total of 9 fungal endophytes *Aureobasidium pullulans*, *Paracamarosporium leucadendri*, *Cladosporium* sp., *Collectotrichum*

*boninense*, *Fusarium* sp., *Hyalodendriella* sp., *Talaromyces* sp., and *Penicillium chrysogenum* were isolated from the leaves and unripe fruits of *Solanum mauritianum* (Pelo 2020). Furthermore, Vieira et al. (2012) reported several endophytic fungi such as *Arthrotrichum foliicola*, *Colletotrichum gloeosporioides*, *Coprinellus radians*, *Glomerella acutata*, *Diatrypella frostii*, *Phoma glomerata*, *Mucor* sp., *Phlebia subserialis*, *Phoma moricola*, *Phanerochaete sordida*, and *Colletotrichum* sp. associated with a Brazilian medicinal plant *Solanum cernuum* Vell.

## Bioactive compounds from endophytes associated with *Solanum* species

In recent times, endophytes have received a great deal of attention in agriculture and pharmaceutical industries because of their ability to synthesize a wide range of bioactive metabolites. Researchers have reported hundreds of natural compounds with antimicrobial, antioxidant, anticancer, and many other properties. In the present review, a total number of 98 bioactive metabolites were encountered from endophytes associated with different species of *Solanum* (Table 1). The highest compounds were recorded from endophytes of *S. lycopersicum* L. with 34 compounds followed by *S. mauritianum* Scop. (24 compounds), and *S. nigrum* L. (10 compounds). Moreover, there are 7 compounds from endophytes of each species of *S. surattense*, *S. trilobatum* L., *S. tuberosum* L., 6 compounds from *S. xanthocarpum*, and 3 compounds from *S. rostratum* so far (Fig. 1).

### Sterols

Ergosterol (1), ergosterol peroxide (2), and cerevisterol (11) were the main sterol compounds obtained from the endophytes associated with *Solanum* species (Fig. 2). Sterols in endophytes of *Solanum* have indicated possession of anticancer, antifungal, and antiplasmodial features. Meza-Menchaca et al. (2020) isolated and purified ergosterol peroxide (2) from *Pleurotus ostreatus* and tested its efficacy as an anticancer compound *in-vitro*. The results revealed that a gradual increase in ergosterol peroxide (2) dose correlates with a loss of viability in HeLa and CaSki cervical cell lines. Furthermore, the amoebicidal activity of ergosterol peroxide (2) against *Entamoeba histolytica* is studied and found that the compound (2) produced a strong cytotoxic effect against amoebic growth with inhibitory concentration  $IC_{50} = 4.23$  nM (Meza-Menchaca et al. 2015). Furthermore, cerevisterol (11) alleviates inflammation via the suppression of mitogen-activated protein kinase/nuclear factor  $\kappa$ B/activator protein 1 (MAPK/NF- $\kappa$ B/AP-1) and activation of the nuclear factor erythroid 2-related factor 2/heme oxygenase-1

(Nrf2/HO-1) signaling cascade as reported by Alam et al. (2020).

### Volatiles

A wide range of volatile compounds is synthesized and released by both endophytic fungi and bacteria. There are several hundreds of volatile compounds often including alkenes, alcohols, ketones, terpenes, benzenoids, pyrazines, acids, and esters reported to be released by endophytes (Effmert et al. 2012; Lemfack et al. 2014). They are well known for their inhibitory potential against different phytopathogens in different ways such as modifying microorganism behavior, population dynamic, gene expression, and antagonizing within the microbial communities (Tyc et al. 2017). López et al. (2021) detected many volatile compounds (65-98) (Fig. 3) from endophytic bacteria associated with *Solanum lycopersici* L. which were reported to be having antifungal properties against plant pathogens *Alternaria alternata* and *Corynespora cassiicola*. Likewise, the endophytic fungi associated with *S. mauritianum* Scop. are reported to produce many volatile antibacterial compounds such as seircardine A (54), 2-pentadecanone (61), hexacosane (63), and tridecanoic acid methyl ester (64) (Pelo 2021). It is reported that the compound tridecanoic acid methyl ester (64) has antibacterial activity against *Enterococcus faecalis* MCC 2041 T and *Salmonella enterica* serovar Typhimurium MTCC 98, at a dose of  $375 \mu\text{g mL}^{-1}$  and  $750 \mu\text{g mL}^{-1}$ , respectively (Misra et al. 2022). This compound induces the autolysis of bacterial cells by disrupting cellular morphology.

### Flavonoids

Many flavonoids have been identified from endophytes associated with *Solanum* (Fig. 4). A primary flavonoid Quercetin (37) was isolated from endophytic fungi *Penicillium roqueforti* (CGF-1) and *Trichoderma reesei* (CGF-11) associated with *S. surattense* (Ikram et al. 2019). Quercetin (37) can inhibit the early stages of viral infection, interact with proteases important to viral replication and reduce inflammation from infection (Di Petrillo et al. 2022). In addition, quercetin (37) inhibits the growth of different drug-resistant Gram-positive and Gram-negative bacteria as well as fungi by different mechanisms such as cell membrane damage, change of membrane permeability, inhibition of synthesis of nucleic acids and proteins, reduction in expression of virulence factors, mitochondrial dysfunction, and preventing biofilm formation (Nguyen and Bhattacharya 2022). In another study, Jan et al. (2019) reported four important flavonoids such as *p*-hydroxyl benzoic acid (39), diadzein (40), genistein (41), and myricetin (42) from endophytic fungi *Meyerozyma caribbica* isolated from *S. xanthocarpum* L. These compounds

**Table 1** Bioactive compounds produced by fungal endophytes associated with different species of *Solanum*

Sl. No	Compound	Producing endophytes	Host plant	Biological properties	References
1	Ergosterol	<i>Aspergillus</i> sp. (SNFSt), <i>Lasiodiplodia theobromae</i> (SNFF)	<i>Solanum nigrum</i> L.		El-Hawary et al. (2017)
2	Ergosterol peroxide	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.		El-Hawary et al. (2017)
3	Indole-3-carboxylic acid (ICA)	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.	Plant growth regulator	El-Hawary et al. (2017)
4	Indole-3-acetic acid (IAA)	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.	Plant growth regulator	El-Hawary et al. (2017)
5	(S,S)-sapinofuranone B	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.		El-Hawary et al. (2017)
6	Penicellic acid	<i>Aspergillus</i> sp. (SNFL)	<i>S. nigrum</i> L.	Mycotoxin	El-Hawary et al. (2017)
7	Cyclo(leu-pro)	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.		El-Hawary et al. (2017)
8	Cyclo(Phe-Pro)	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.		El-Hawary et al. (2017)
9	3-indolaldehyde	<i>Aspergillus</i> sp. (SNFSt), <i>L. theobromae</i> (SNFF)	<i>S. nigrum</i> L.		El-Hawary et al. (2017)
10	Adenosine	<i>Purpureocillium</i> sp.	<i>S. rostratum</i>	Plant growth regulator activity	Kuchkarova et al. (2020)
11	Cerevisterol	<i>Purpureocillium</i> sp.	<i>S. rostratum</i>	Plant growth regulator activity	Kuchkarova et al. (2020)
12	Thymine	<i>Purpureocillium</i> sp.	<i>S. rostratum</i>	Plant growth regulator activity	Kuchkarova et al. (2020)
13	Lovastatin	<i>Phomopsis vexans</i>	<i>S. xanthocarpum</i>	Lowering blood cholesterol	Parthasarathy and Sathiyabama (2015)
14	Isosativenediol	<i>Bipolaris eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
15	Dihydroprehelminthosporo	<i>B. eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
16	Helminthosporol	<i>B. eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
17	Drechslerines C	<i>B. eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
18	Drechslerines A	<i>B. eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
19	Secolongifolene diol	<i>B. eleusines</i>	<i>S. tuberosum</i>		Man-si et al. (2015)
20	Solamargine	<i>Aspergillus flavus</i>	<i>S. nigrum</i>	Cytotoxic	El-Hawary et al. (2016)
21	Destruxin A	<i>Metarhizium brunneum</i>	<i>S. tuberosum</i>	Insecticidal, anti-viral	Ríos-Moreno et al. (2016)
22	Alkaloids <sup>a</sup>	<i>Fusarium</i> sp., <i>Cladospodium</i> sp., <i>Paracamarosporium leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
23	Flavonoids <sup>a</sup>	<i>Fusarium</i> sp., <i>Cladospodium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
24	Glycosides <sup>a</sup>	<i>Fusarium</i> sp., <i>Cladospodium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
25	Phenols <sup>a</sup>	<i>Fusarium</i> sp., <i>Cladospodium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
26	Quinones <sup>a</sup>	<i>Cladospodium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
27	Saponins <sup>a</sup>	<i>Fusarium</i> sp., <i>Cladospodium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	antibacterial	Pelo et al. (2021)

**Table 1** (continued)

Sl. No	Compound	Producing endophytes	Host plant	Biological properties	References
28	Eicosane	<i>Fusarium</i> sp., <i>Clad- osporium</i> sp., <i>P. leuca- dendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
29	2-methyloctacosane	<i>Fusarium</i> sp., <i>Clad- osporium</i> sp., <i>P. leuca- dendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
30	2-pentadecanone, hexa- cosane	<i>Fusarium</i> sp., <i>Clad- osporium</i> sp., <i>P. leuca- dendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
31	Tridecanoic acid methyl ester	<i>Fusarium</i> sp., <i>Clad- osporium</i> sp., <i>P. leuca- dendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo et al. (2021)
32	Phenols <sup>a</sup>	<i>Penicillium roque- forti</i> (CGF-1), <i>Tricho- derma reesei</i> (CGF-11)	<i>S. surattense</i>		Ikram et al. (2019)
33	Steroids <sup>a</sup>	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>		Ikram et al. (2019)
34	Tannins <sup>a</sup>	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>		Ikram et al. (2019)
35	Ferulic acid	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>	Antioxidant	Ikram et al. (2019)
36	Cinnamic acid	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>	Flavoring agent	Ikram et al. (2019)
37	Quercetin	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>	Anticancer	Ikram et al. (2019)
38	Rutin	<i>P. roqueforti</i> (CGF-1), <i>T. reesei</i> (CGF-11)	<i>S. surattense</i>	Antioxidant, anti-inflam- matory	Ikram et al. (2019)
39	<i>p</i> -hydroxyl benzoic acid	<i>Meyerozyma caribbica</i>	<i>S. xanthocarpum</i> L.	Antioxidant, Anticancer	Jan et al. (2019)
40	Diadzein	<i>M. caribbica</i>	<i>S. xanthocarpum</i> L.	Antioxidant, Anticancer	Jan et al. (2019)
41	Genistien	<i>M. caribbica</i>	<i>S. xanthocarpum</i> L.	Antioxidant, Anticancer	Jan et al. (2019)
42	Myricetin	<i>M. caribbica</i>	<i>S. xanthocarpum</i> L.	Anti-oxidant, anticancer, antidiabetic and anti- inflammatory	Jan et al. (2019)
43	Caffeoyl-D-glucose	<i>M. caribbica</i>	<i>S. xanthocarpum</i> L.	Antioxidant	Jan et al. (2019)
44	Glycine, N- (phenyl acetyl)-,ethyl ester	<i>Curvularia lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
45	Penta—decanoic acid,14- methyl-, methyl ester	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
46	4-(6-Methoxypyridazinyl- 3-amino)- 1,2—naphtho- quinone	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
47	4-(6-Methoxypyridazinyl- 3-amino)- 1,2—naphtho- quinone	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
48	9,15-Octadecadienoic acid, methyl ester, (ZZ)	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
49	[3-Methyl- 2—(4 -nitro phenyl) – 4 -oxo-1,2,3,4 tetrahydro-phthalazin- 1yl], acetic acid, methyl ester	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
50	Octa—decanedioic acid,3,16-dioxo-, dime- thyl ester	<i>C. lunata</i>	<i>S. trilobatum</i> L.		Kannan et al. (2016)
51	L-Cladinose	<i>P. leucadendri</i>	<i>S. mauritianum</i> Scop.	Microside antibiotic	Pelo (2020)

**Table 1** (continued)

Sl. No	Compound	Producing endophytes	Host plant	Biological properties	References
52	Lachnophyllum ester	<i>P. leucadendri</i>	<i>S. mauritianum</i> Scop.	Antifungal, antioxidant	Pelo (2020)
53	Rishitin	<i>P. leucadendri</i>	<i>S. mauritianum</i> Scop.	Antifungal	Pelo (2020)
54	Seiricardine A	<i>P. leucadendri</i>	<i>S. mauritianum</i> Scop.	Phytotoxin	Pelo (2020)
55	1,8-Diazacyclotetradecane-2,9-dione	<i>Penicillium chrysogenum</i>	<i>S. mauritianum</i> Scop.		Pelo (2020)
56	L-Ascorbic acid	<i>P. chrysogenum</i>	<i>S. mauritianum</i> Scop.	Vitamin	Pelo (2020)
57	6-octadecanoate	<i>P. chrysogenum</i>	<i>S. mauritianum</i> Scop.		Pelo (2020)
58	Ochrolifuanine A	<i>P. chrysogenum</i>	<i>S. mauritianum</i> Scop.	Antiplasmodium	Pelo (2020)
59	2-nitroimidazo[2,1-b][1,3]oxazole	<i>Fusarium</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
60	Eicosane	<i>Cladosporium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
61	2-pentadecanone	<i>Cladosporium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
62	2-methyloctacosane	<i>Cladosporium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
63	Hexacosane	<i>Cladosporium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
64	Tridecanoic acid methyl ester	<i>Cladosporium</i> sp., <i>P. leucadendri</i> , <i>Talaromyces</i> sp.	<i>S. mauritianum</i> Scop.	Antibacterial	Pelo (2020)
65	2,3-butanediol	<i>Bacillus</i> sp., <i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
66	3-hydroxi-2-butanone	<i>Bacillus</i> sp., <i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
67	2-methyl butanoic	<i>Bacillus</i> sp., <i>Acinetobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
68	3-methyl butanol	<i>Bacillus</i> sp., <i>Stenotrophomonas</i> sp., <i>Acinetobacter</i> sp., <i>Arthrobacter</i> sp., <i>Microbacterium</i> sp., <i>Pantoea</i> sp., <i>Pseudomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
69	Dihydro-2-methyl 3(2H)-thiophenone	<i>Bacillus</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
70	3-methyl butanoic	<i>Pseudomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
71	6-methyl-2-heptanone	<i>Stenotrophomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
72	S-methyl-3-methyl butan-othionate	<i>Stenotrophomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
73	X-methyl-2-nonanone	<i>Stenotrophomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
74	S-methyl-3-methyl butan-othionate	<i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
75	X-methyl-2-nonanone	<i>Acinetobacter</i> sp., <i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
76	Phenyl ethyl alcohol	<i>Acinetobacter</i> sp., <i>Stenotrophomonas</i> sp., <i>Arthrobacter</i> sp., <i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)

**Table 1** (continued)

Sl. No	Compound	Producing endophytes	Host plant	Biological properties	References
77	2-nonanone	<i>Stenotrophomonas</i> sp., <i>Arthrobacter</i> sp., <i>Microbacterium</i> sp., <i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
78	Thiometanol	<i>Stenotrophomonas</i> sp.,	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
79	2-heptanol	<i>Stenotrophomonas</i> sp., <i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
80	5-methyl-2-heptanone	<i>Stenotrophomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
81	Nonano	<i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
82	Geranylacetone	<i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
83	1-decanol	<i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
84	1-octanol	<i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
85	X-methyl-2-tridecanone	<i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
86	2-tridecanone	<i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
87	9-decen-1-ol	<i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
88	Octanoic	<i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
89	Isopentyl acetate	<i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
90	3-methyl butanoic	<i>Bacillus</i> sp., <i>Stenotrophomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
91	2-methyl butanol	<i>Stenotrophomonas</i> sp., <i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
92	2-undecanone	<i>Stenotrophomonas</i> sp., <i>Microbacterium</i> sp., <i>Pseudomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
93	x-methyl-2-undecanone	<i>Acinetobacter</i> sp., <i>Microbacterium</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
94	2-octen-1-ol	<i>Acinetobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
95	5-methyl-2-heptanone	<i>Acinetobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
96	x-tridecen-2-one	<i>Pseudomonas</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
97	2-heptanone	<i>Arthrobacter</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)
98	2-nonanol	<i>Pantoea</i> sp.	<i>S. lycopersici</i> L.	Antifungal	López et al. (2021)

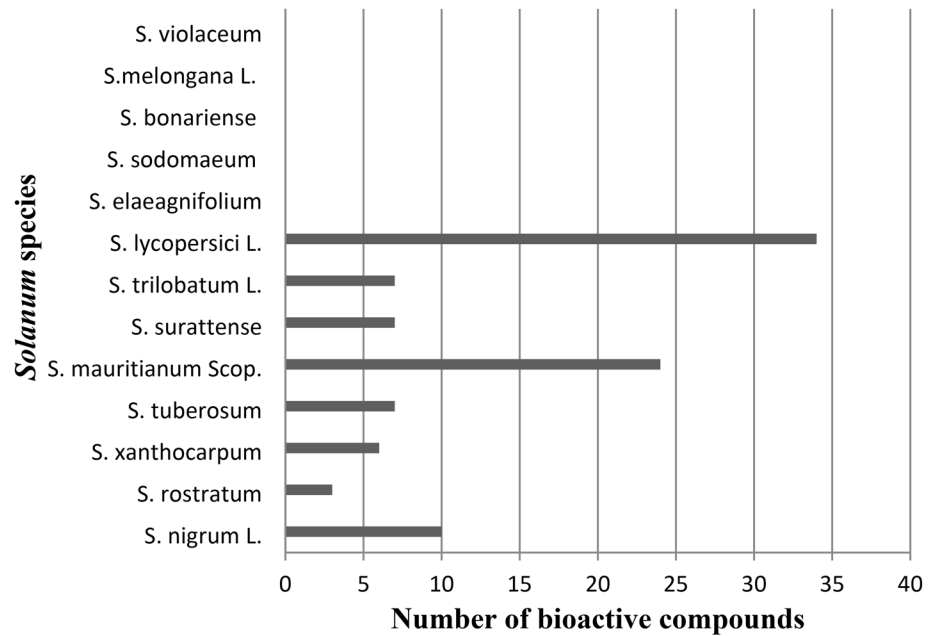
The compounds numbered and bolded (in brackets) in the manuscript represent the serial number of compounds given in Table 1

<sup>a</sup>Not specifically mentioned the compound names in the cited literature and considered as a single compound for the statistical analysis

are believed to exhibit a wide range of biological activities including anti-oxidant, anticancer, antidiabetic, and anti-inflammatory activities. The role and mechanisms of myricetin (**42**) in cancer treatment are extensively studied by several researchers. The inhibition of breast and lung cancer cell proliferation through inhibiting microtubule affinity regulating kinase (MARK4) ( $IC_{50} = 3.11 \mu M$ ) which regulates the initial stages of cell division and a druggable target for various cancers is studied by Anwar et al. (2022). Myricetin (**42**) promoted cytotoxicity in HCT-15 cells via activating the apoptotic genes such as the Bcl-2-associated X Protein (Javed et al. 2022). Furthermore, myricetin (**42**) also acts as an anticancer agent by targeting various cell signaling pathways such as phosphatidylinositol 3-kinase/protein kinase B (PI3K/Akt) and associated mammalian target of rapamycin (mTOR) pathway, rapidly accelerated

fibrosarcoma/mitogen-activated protein kinase/extracellular signal-regulated kinase (Raf/MEK/ERK) pathway, nuclear factor kappa-B (NF- $\kappa$ B) pathway, Janus kinase/signal transducers and activators of transcription (JAK/STAT) pathway, transforming growth factor-beta/mothers against decapentaplegic (TGF $\beta$ /Smad) pathway, tumor necrosis factor  $\alpha$ /tumor necrosis factor receptor (TNF $\alpha$ /TNFR) signaling, bone morphogenetic proteins/mothers against decapentaplegic (BMP/SMAD) and BMP-downstream pathways, Wnt/ $\beta$ -catenin pathways, intrinsic apoptotic pathway, and many others highlighted by different researchers (Javed et al. 2022). Similarly, genistein (**41**) possesses strong anti-inflammatory activities through inhibition of various signaling pathways such as NF- $\kappa$ B, prostaglandins (PGs), inducible nitric oxide synthase (iNOS), proinflammatory cytokines, and reactive oxygen species (ROS) (Goh et al. 2022). Likewise, daidzein

**Fig. 1** Number of identified bioactive compounds isolated from crude extracts of endophytes associated with different *Solanum* species



(40) is reported to alleviate doxorubicin-induced heart failure via the mitochondrial sirtuin-3/forkhead box O-3a (SIRT3/FOXO3a) signaling pathway (Li et al. 2022).

### Other compounds

Apart from the above compounds, many other compounds that include terpenoids, alkaloids, phenols, and plant growth regulators (3, 4) were obtained from endophytes colonizing the plant species of *Solanum* (Fig. 5). For example, ochrolifuanine A (58) is one of the important alkaloids reported to possess antitrypanosomal activities against *Trypanosoma brucei* parasites which are responsible for Human African Trypanosomiasis (HAT) (Norhayati et al. 2022). A pharmaceutically important compound lovastatin (13) which lowers blood cholesterol is obtained from endophytic fungi *Phomopsis vexans* associated with *S. xanthocarpum* (Parthasarathy and Sathiyabama 2015). Additionally, some plant-derived compounds of *Solanum* species such as rishitin (53) and solamargine (20) are reported to be produced by endophytic fungi associated with *S. nigrum* and *S. mauritianum* Scop., respectively. The compound rishitin (53) is a terpenoid compound that has good antifungal properties (Pelo, 2021), whereas solamargine (20) has cytotoxic properties (El-Hawary et al. 2016). Some mycotoxins such as penicillic acid (6) and destruxin A (21) were also reported from endophytes of *Solanum* causing paralysis and killing insects (Bogus et al. 2021; Wang et al. 2021). In this respect, endophytes can be used as a source of insecticidal agents in food processing industries and sustainable agriculture.

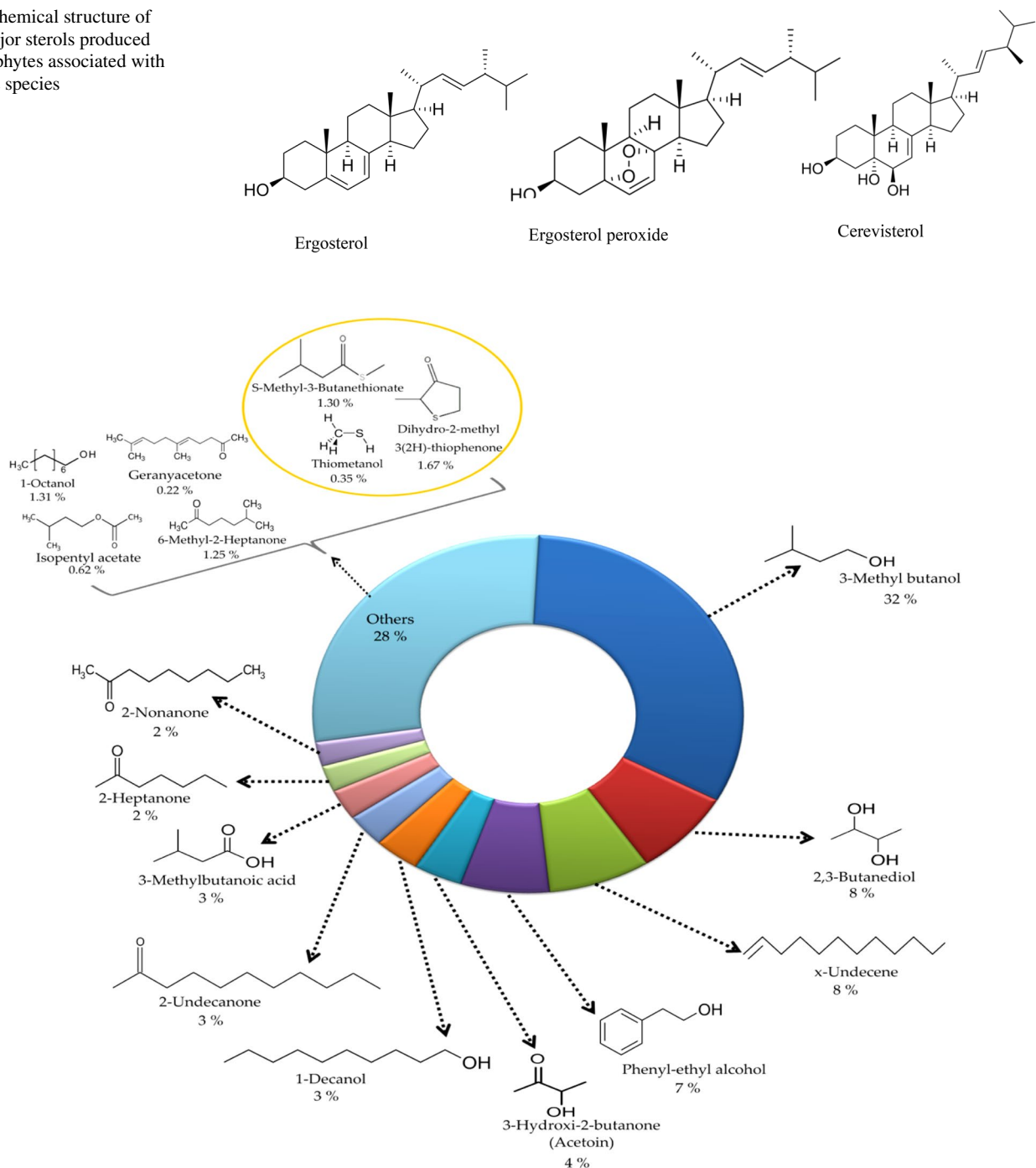
### Biological activity of endophytes associated with *Solanum* species

#### Antimicrobial activity of endophytic fungi

The number of antimicrobial drug-resistant pathogens has been increasing in recent years, leading to a health crisis that has become one of the greatest concerns to global health. The resistance capacity of infectious pathogens against antimicrobial drugs resulted in patients' longer hospital stays, higher health costs, and greater patient mortality (Kouipou and Boyom 2019). Therefore, it is very urgent to find out new antimicrobial agents to treat microbial infections and this emergency is the engine of exploration of endophytes from *Solanum* species as a source of bioactive metabolites. In a previous study, it is reported that cell-free supernatants and agar plugs of *Alternaria* sp., *Cladosporium tenuissimum*, *Mycosphaerellaceae* sp., *Curvularia beasleyi*, and *Alternaria alternata* isolated from fruits of *Solanum violaceum* Ortega showed potent antimicrobial activity against human pathogenic nosocomial organisms such as *Staphylococcus aureus*, *Escherichia coli*, and *Klebsiella pneumonia* (Manasa et al. 2021). Moreover, *Curvularia beasleyi* exhibited antifungal activity also against *Candida albicans* and *C. tropicalis* with an inhibition zone of  $20 \pm 2$  mm in agar well diffusion plates. The endophytic fungi such as *Alternaria tenuissima*, *Fusarium equiseti*, *Penicillium funiculosum*, *P. pinophilum*, *P. rubens* isolated from different parts of *S. tuberosum* L. have shown significant ( $P < 0.05$ ) antimicrobial activity against *Candida albicans*, *Salmonella typhimurium*, *Sarcinaventriculi*, *S. aureus* (Yasser et al. 2019).



**Fig. 2** Chemical structure of three major sterols produced by endophytes associated with *Solanum* species

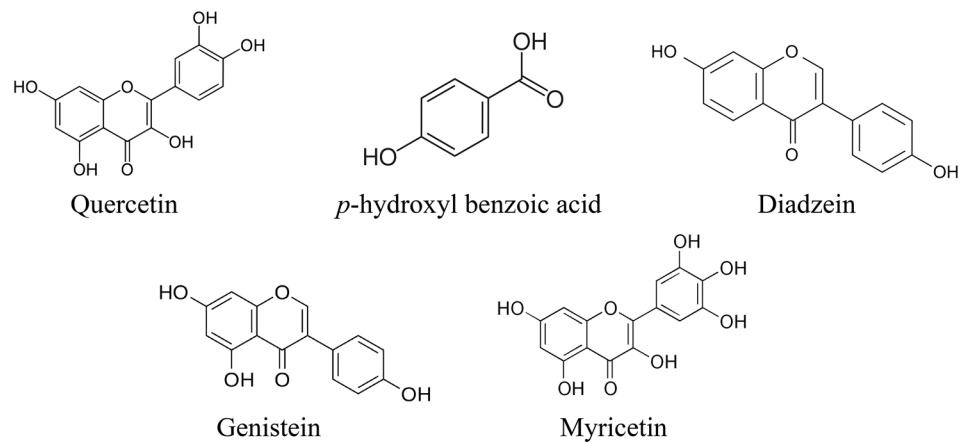


**Fig. 3** Some volatile compounds produced by endophytic bacteria isolated from *S. lycopersici* L. exhibiting strong antifungal activity (Source: López et al. 2021)

In addition, *A. tenuissima* and *Lasiodiplotia theobromae* showed antimicrobial activity against *S. aureus*, *F. oxysporum* against *Salmonella typhimurium*, *S. riculi*, and *Stemphylium vesicarium* against *S. riculi* (Yasser et al. 2019). Crude extracts of endophytic fungi *Paracamarosporium leucadendri* associated with *S. mauritanum* inhibit bacterial pathogens such as *Mycobacterium bovis*, *Klebsiella*

*pneumoniae*, and *Pseudomonas aeruginosa* at a concentration of  $6\mu\text{g mL}^{-1}$ . Additionally, crude extracts of *Fusarium* sp. also showed antimicrobial activity against *M. bovis*, *M. smegmatis*, and *K. pneumonia* at  $9\mu\text{g mL}^{-1}$ . In addition, the nonpolar fraction of the cultural filtrate of *Penicillium roqueforti* (CGF-1) and *Trichoderma reesei* (CGF-11) isolated from *S. surattense* reflected the antibacterial activity

**Fig. 4** Chemical structure of some important flavonoids produced by endophytes associated with *Solanum* species



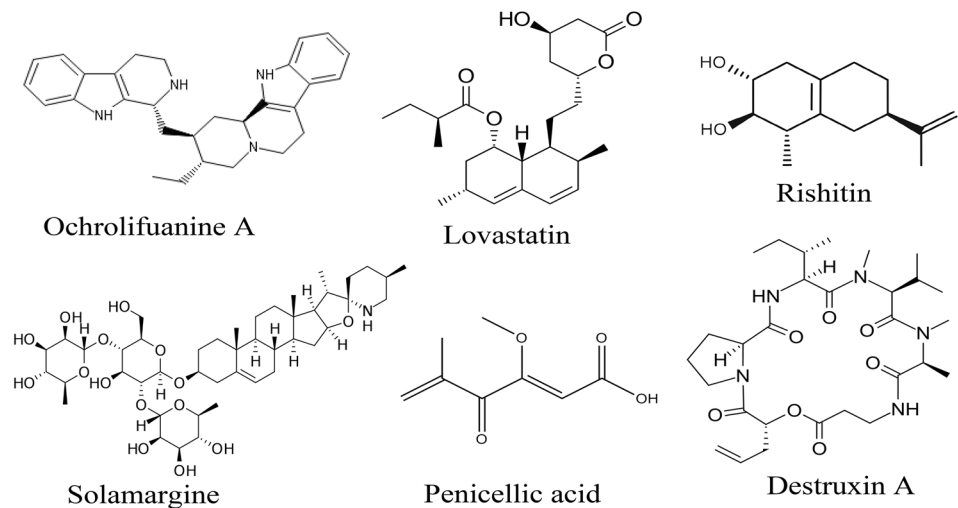
against phytopathogenic bacteria such as *Xanthomonas oryzae*, *Pseudomonas syringae*, *Agrobacterium tumefaciens*, and *Ralstonia solanacearum* (Ikram et al. 2019). This antimicrobial activity might be due to the presence of ferulic acid, cinnamic acid, quercetin, and rutin confirmed by high-performance liquid chromatography (HPLC) analysis.

### Antimicrobial activity of endophytic bacteria

Endophytic bacteria are well known to have a wide range of secondary metabolites because of which they have demonstrated significant biological control potential in vitro. An antagonistic endophytic bacteria *Pseudomonas* sp. isolated from *S. melongena* L. suppressed bacterial wilt pathogen *Ralstonia solanacearum* in eggplant (*Solanum melongena* L.) (Ramesh et al. 2009). Besides, the endophytic bacteria such as *Stenotrophomonas maltophilia*, *Bacillus* sp., *Azotobacter chroococcum*, *Serratia marcescens* associated with *Solanum sodomaeum* and *Solanum bonariense* have also been evaluated and found to be the most efficient in reducing

disease severity by 82–96% over control (Aydi-Ben-Abdallah et al. 2020). Uche-Okerefor et al. (2019) studied the antimicrobial activity of metabolite extracts from *Pantoea* sp. associated with *S. mauritanum* and showed an efficient inhibition against *E. coli*, *S. aureus*, *K. pneumoniae*, and *Pseudomonas aeruginosa* with the concentrations ranging from 0.0625 to 8.0000 mg mL<sup>-1</sup>. Two strains of *Bacillus* such as *Bacillus amyloliquefaciens* Sa08 and *B. subtilis* Og04 isolated from *Solanum lycopersicum* L. have also been reported to have inhibitory activity against *Fusarium oxysporum* causing severe wilt diseases with inhibitory zones of 15.67 and 19.43mm, respectively (Adedire et al. 2023). On the other hand, endophytic actinobacteria such as *Streptomyces* sp. TP199 and *Streptomyces* sp. A2R31 associated with *Solanum tuberosum* subsp. *tuberosum* L. were found to inhibit the growth of the *Pectobacterium carotovorum* subsp. *carotovorum* and *Pectobacterium atrosepticum* which are responsible for the blackleg and soft rot of potato tubers (Padilla-Gálvez et al. 2021).

**Fig. 5** Chemical structure of some biologically active compounds produced by endophytes associated with *Solanum* plants



## Plant growth-promoting (PGP) activity

In addition to antimicrobial activity, endophytes can promote plant growth and development through various mechanisms such as the synthesis of siderophore, production of indole-3 acetic acid (IAA), phosphate solubilization, biological nitrogen fixation, and biological control of phytopathogens (Mili et al. 2021). Two fungal endophytes, *Fusarium tricinctum* RSF-4L, and *Alternaria alternata* RSF-6L isolated from leaves of *S. nigrum* were examined for their plant growth-promoting activity in Dongjin rice plants (Khan et al. 2015). The results revealed that the plant growth traits such as chlorophyll content, root–shoot length, and biomass production were significantly ( $< 0.05$ ) improved when culture filtrates (CFs) of the endophytes were applied. Subsequently, gas chromatography/mass spectrometry (GC/MS) analyses of the CFs of those endophytes revealed the production of IAA which is important for plant growth and development. Furthermore, endophytic *Streptomyces* sp. strain DBT204 isolated from *S. lycopersicum* L. also showed the production of antibiotics (trimethoprim, fluconazole, chloramphenicol, nalidixic acid, rifampicin, and streptomycin) and two phytohormones (IAA and kinetin) as confirmed by ultra-performance liquid chromatography (UPLC-ESI-MS/MS) analysis (Passari et al. 2016). Singh et al. (2019) isolated heat (45–47 °C)-tolerant endophytic bacteria such as *Rhizobium pusense* (MS-1), *Bacillus flexus* (MS-2), *B. cereus* (MS-3), *Methylophilus flavus* (MS-4), and *Pseudomonas aeruginosa* (MS-5) from roots of *S. lycopersicum* L. and examined for PGP activity. The results showed that all the isolates have the potentiality of phosphate solubilization, IAA production, siderophore production, ammonia production, HCN production (except isolate MS-4), and nitrate reductase synthesis. Moreover, four heavy metals-resistant endophytic bacteria such as *Serratia nematodiphila* LRE07, *Enterobacter aerogenes* LRE17, *Enterobacter* sp. LSE04, and *Acinetobacter* sp. LSE06, isolated from Cd hyperaccumulator *S. nigrum* L. grown in metal-polluted soil, were screened for PGP activity (Chen et al. 2010). The *in vitro* results revealed that all the endophytes show excellent PGP activity such as the production of 1-aminocyclopropane-1-carboxylic (ACC) deaminase ( $0.27\text{--}0.46 \mu\text{M } \alpha\text{-KB mg}^{-1} \text{ h}^{-1}$ ), IAA ( $45.83\text{--}107.45 \text{ mg L}^{-1}$ ), siderophores ( $0.377\text{--}0.921 \lambda \lambda_0^{-1}$ ), and phosphate solubilization ( $206.21\text{--}382.23 \text{ mg L}^{-1}$ ) activity. In another study, four endophytic bacteria, *Pseudomonas palleroniana* B10, *P. fluorescens* B17, *Bacillus subtilis* B25, and *B. aryabhatai* B29, were isolated from *S. lycopersicum* L. and reported to induce root growth in greenhouse experiment by producing IAA and solubilized phosphate (Cochard et al. 2022). Furthermore, endophytic bacteria such as *Stenotrophomonas maltophilia*, *Bacillus* sp. SV81, *Azotobacter chroococcum*

S11, and *Serratia marcescens* S14 associated with *Solanum sodomaicum* and *S. bonariense* are reported to control the wilting disease of tomato induced by *Fusarium oxysporum* f. sp. *lycopersici* as well as exhibited IAA production and phosphate solubilization activity (Aydi-Ben-Abdallah et al. 2020).

## Conclusion and future aspects

The present study reveals that the endophytic community associated with *Solanum* species is extremely varied and produces a wide variety of bioactive compounds. Therefore, endophytes associated with *Solanum* may serve as a source of chemically novel compounds for potential use in medical, agricultural, and other industries. This review has reflected that endophytes from *Solanum* have tremendous antimicrobial activity against both human pathogens and phytopathogens. Few endophytes were reported to produce metabolites mimicking the host metabolites, thereby providing an alternate source for the isolation of important natural products with potential pharmaceutical value. Such characteristics lay the foundation for further investigations on endophytes that could be potentially used in sustainable agriculture and the pharmaceutical industry. Future research has to be made on biochemistry, molecular, and genetics to identify the regulatory gene involved in the biosynthesis pathway of metabolites, which may scale up the production of pharmaceutically significant endophyte-derived compounds and enhance our understanding of endophytic biodiversity for human welfare.

Although from the perspectives of ethnopharmacology and phytochemistry, *Solanum* is one of the most studied major genera of medicinal plants, the endophytic community has not been well researched in this biome. Our study shows that among ~ 2000 species only 13 have been investigated for their colonized endophytes, and about 1987 *Solanum* spp. are yet to be explored for the endophytes and their producing metabolites.

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**Data availability** Data will be made available as per the journal policy.

## Declarations

**Conflict of interest** The author has no conflict of interest.

**Ethical approval** Not applicable.

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