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Management of Grapevine Fungal Diseases by Using Antagonistic Endophytes - An Environment-Friendly Approach

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ABSTRACT

Grapevine (Vitis vinifera L.) is one of the major crops grown commercially throughout the world. In recent years, there have been major losses to grapevine production due to the challenges caused mainly due to fungal diseases like downy mildew, powdery mildew, grey mold, black rot, and anthracnose. In the last few decades, rampant chemical fertilization and bio-magnification of hazardous chemicals have posed a threat to human health and destroyed the health of the soil as well as crops. For effective management of these fungal diseases of grapes, nowadays, many researchers are conducting various studies on endophytes, which are proven to be better bio-control agents to suppress the growth and development of grapevine phytopathogens. Endophytes are eco-friendly, effective, and easy to apply at field levels, making endophyte-based formulations suppress the growth and development of grapevine pathogens without causing any detrimental effects to the beneficial micro-organisms present at the rhizospheric zone of soil and host plants as compared to the traditional fungicides usage. It also competes with these pathogens for nutrition, space, and colonization. It helps in the production of secondary metabolites with antifungal properties for preventing the growth of fungal pathogens that cause damage to the grapevine crop. It also induces a defense mechanism in grapevine crops against diseasecausing fungal phytopathogens. In this review article, biocontrol mechanisms of endophytes and their potential application in the management of grapevine fungal diseases have been discussed.

INTRODUCTION

Grapevine is one of the major commercial fruit crops grown across 7.3 million hectares worldwide and is used for juice, wine, raisin production, and fresh consumption (Karlsson & Karlsson 2021). The total productivity of grapevine throughout the world in recent years is about 27.42 million metric tons (Statista 2023). In India the grapevine is regarded as a major revenue-generating commercial fruit crop produced for export to other countries; it is expected that India is producing about 2,46,133 tons of fresh grapes with an income value of 334.79 million dollars. Maharashtra is the leading grapevine-producing state of India, which produces over 81% of total grapevine production in India (Indian Grape Forum 2019). The major grapevine fungal diseases that are causing heavy losses to grapevine production throughout the world are Downy mildew, Powdery mildew, Anthracnose, Grey mold, Black rot, etc (Armijo et al. 2016). Endophytes are pervasive and mainly colonize inside the tissues of 300,000 various plant species without causing any detrimental effects to the plants (Narayanan et al.

2022). These endophytes mainly belong to Ascomycota, Actinobacteria, Basidiomycota, Bacteroidetes, Firmicutes, Proteobacteria, and Zygomycota, which are some major prokaryotic and eukaryotic endophytes that were identified till now (Yakop et al. 2019). These endophytes produce various enzymes, hormones, and secondary metabolites, which cause antagonistic effects and antimicrobial activity that inhibit plants from pathogen infection and play a major role in biotechnology (Gunatilaka 2006). Using these natural symbionts provides a chance to increase the production of grapevine while minimizing the use of hazardous pesticides against pathogens (Srivastava et al. 2023).

Endophytes must slowly adapt to these living conditions by gradually interacting with their host plant, including mutualism and antagonism (Dudeja et al. 2012), and can establish themselves in the plant after a process of molecular crosstalk that produces a cornucopia of favorable modifications for the host (Pavithra et al. 2020, Das et al. 2021, Pavithra et al. 2021, Maurya et al. 2024). These endophytes promote the growth and development of their host plant and help them to adapt to environmental changes, and they produce various compounds to sustain symbiosis between host plant and endophytes (Das & Varma 2009). In the present situation, increasing crop production and maintaining ecological sustainability in an eco-friendly manner is possible by using microbial bio-products that include various types of bio-formulations like bio-fertilizers, bio-pesticides, bio-stimulants, bio-inoculants, etc. (Singh et al. 2016). To sustain the goal of increasing crop production and controlling various diseases throughout the world, there is an urgent need to develop microbe-based bio-formulations that are greener and safer alternatives to agrochemicals (Mishra et al. 2015). These microbe-based bio-formulations are strong in comparison to agrochemicals as the formulation includes a single microbe that interacts with the pathogen directly and suppresses its growth and development, which leads to a decrease in disease rate and improves plant growth (Rodrigo et al. 2011).

GRAPEVINE FUNGAL DISEASES AND THEIR IMPACT ON GRAPE PRODUCTION

The major fungal diseases of grapevine (*Vitis vinifera*) as mentioned in Table 1 are powdery mildew, downy mildew, grey mold, black rot, anthracnose which are caused by these phytopathogens like *Uncinula necator*, *Plasmopara viticola*, *Botrytis cinerea*, *Guignardia bidwelli and Elsinoe ampilina* (Armijo et al. 2016). Downy mildew disease causes severe yield losses to the grapevine in vivo when optimum temperate and humidity are present, which is suitable for survival and increases infection-causing capacity, leading to losses of about 40-90% of grapevine (Toffolatti et al. 2018). Powdery mildew disease causes severe losses to the quality and quantity of grapevine. If not managed properly during high disease pressure years, it leads to yield losses of about 75-100% (Fermaud et al. 2016). Anthracnose disease causes yield losses to crop productivity of grapevine about 10-15% and on highly susceptible grapevine varieties due to severe infection on them, crop losses occur up to 100% (Zhi Li et al. 2021). Grey mold disease causes major economic yield losses to the grapevine, about 20-50% throughout the world at post-harvest season, mainly due to rotting of ripe berries (Fedorina et al. 2022). Black rot disease causes yield losses to the grapevine by about 80% due to the availability of its optimum humid condition to produce its primary inoculum and causes infection to the grapevine (Jackson 2014).

VARIOUS TYPES OF ANTAGONISTIC ENDOPHYTES ASSOCIATED WITH HOST PLANTS

Endophytes can reside inside (intercellular) and outside (intracellular) the cells of the host plant, and they can live inside (systematically) and outside (locally) of the host body in a symbiotic relationship with the host without causing any harm to the host plant (Kusari et al. 2012, Lo Presti et al. 2015, Schulz et al. 2015). Endophytes are found existing all over the places of agricultural ecosystems and natural forests and are mainly present in the plant tissues of spermatophytes, ferns, equisetopsids, mosses, liverworts, lycophytes, hornworts, etc. (Kusari et al. 2012, Jeewon et al. 2013, Doilom et al. 2017, Potshangbam et al. 2017). Clavicipitaceous endophytes live as intracellular symbionts, mainly in various grasses. They are found more in the leaves and stems of mother plants as compared to young plants, and these endophytes are transmitted both vertically and horizontally through sexual or asexual spores and seeds, etc. (Yan et al. 2015, Santangelo et al. 2015). Both the fungal and bacterial endophytes have great potential as bio-control agents as they have antagonistic activity (Table 2), which produces various secondary metabolites like antioxidants, bioactive antimicrobial and antiviral metabolites that help in suppressing the growth of various disease-causing phytopathogens, thus reducing the losses caused by them (Gouda et al. 2016).

De Bary (1866) introduced the endophyte term. He defined it as an organism that grows inside of the plant tissues and has a symbiotic relationship with its host without causing any detrimental effects to its host, sometimes helping in providing essential nutrients for the host for its growth and development. Its types are fungal and bacterial endophytes, which act as both obligate or facultative relationships with

Table 1: List of major fungal diseases of grapevine with their causal organisms and peculiar symptoms.

Diseases	Causal organism	Symptoms	References
Downy mildew	Plasmopara viticola	Rough circular yellow discoloration and oily spots on leaves. Whitish	Koledenkova
		downy fungal growth appearance on the lower side of leaves and	et al. (2022)
		stem (sporulation of fungi). Infected shoot tips turn curl (Shepherd's	
		crook). Severely infected leaves turn yellow to brown and finally get	
Dovudomu mildovu	Uncinula necator	dry and dropdown.	Vunava at al
Powdery mildew		Lesions first occur on the lower side of the leaves. Minute orange to	(2021)
		and lower surfaces of leaves and berries. Affected berries finally	(2021)
		dried out and dropped down	
Anthracnose	Elsinoe ampilina	It causes small round spots on the surface of leaves. These spots	Li et al. (2021)
		later become holes on leaves (shot-hole appearance). The appearance	
		of deep elongated cankers with a grevish color in the center and	
		with a black border on the stem. Violet color spots with a greyish	
		appearance in the center appearance on berries. Finally, these infected	
		berries dried and dropped prematurely.	
Grey mold	Botrytis cinerea	It causes necrotic brown spots.	Shen et al.
		Infected berries are covered with greyish substances consisting of	(2021)
	Cuionandia Didwall	spores of the fungus.	
Black rot	Guignarata Blawell	It causes small brown lesions with a border of dark marginal rings	Szabó et al.
		consisting of black pustules (fruiting body of fungi). Infected berries	(2023)
		fist turns white, then purple, and finally turns black color. Severely	
Dina sat	Colletatuichum ann	Infected berries are covered by black pustules.	Usiah at al
Ripe for	Concorrichum spp.	In causes tilly, sufficient, reducisit-brown spots with yellow halos.	(2023)
		herries consisting of small fruiting body structures (acervuli). Infected	(2023)
		fruits turn from light to brown color. The final stage of infection	
		results in the drving and mummification of decaying berries.	
Angular leaf	Psuedopezicula tetraspora	The first appearance of symptoms occurs on leaves. Lesions appear as	Fischer et al.
scorch		faint, yellow spots on the leaf surface and leaf veins and later turn to	(2022)
		reddish-brown color. At severe infection, death of leaf tissue occurs.	
Armillaria root rot	Armillaria mellea	The first appearance of symptoms occurs as stunting of shoots. Later	Calamita et al.
		white mycelial mat appears below the bark of the plant. At severe	(2021)
		infection, and trunk and root of the plant get rotten with a soft and	
	x • 1 • 1 1 • 1 1	spongy appearance, and its color changes from white to dark brown.	
Bot Canker	Lasioaipioaia theobromae	Foliar symptoms may be observed as mild chlorosis or wilting due	DeKrey et al.
		to inhibition of water transport. Berries of infected white-fruited	(2022)
		varieties may develop small, flat lesions with pychidia, with berries	
Dhamana'a	Phomopsis viticola	turning light brown.	Úль Т
Phomopsis	1 nonopolo rincola	small, black spots on the internodes at the base of developing shoots	ot al. (2012)
UIEUACK		usually found on the first three to four basal internodes. It is also	et al. (2013)
		known as the "dead arm"	
Grapevine leaf	Phaeomoniella	Foliar symptoms on established grapevines have been widely	Serra et
stripe	chlamydospora and several species	described and include various types of discoloration, typically	al. (2018).
I -	of Phaeoacremonium	interveinal discolorations evolving into necrotic areas resembling	Calzarano et
		"tiger stripes".	al. (2021)
Botryosphaeria	It is caused by several pathogens,	Symptoms of Botryosphaeria dieback include dead spurs, stunted	Kenfaoui et al.
dieback	primarily Neofusicoccum parvum,	shoots, and bud mortality.	(2022)
	Diplodia seriata, Botryosphaeria		
	stevensii, and Botryosphaeria		
	dothidea. Futuna lata		~
Eutypa dieback	Бтура ши	It is a major trunk disease in grapevines associated with the heavy	Gramaje et al.
Loof blight / Emit	Alternaria alternata. A. vitis	1088 01 production.	2018 Listal (2022)
rot		The unsease attacks both leaves and fruits. Small yellowish spots first	Li et al. (2023)
101		appear along the real margins, which gradually emarge and turn into brownish patches with concentric rings	
Granevine Esca	Phaeomoniella chlamydospora	The typical Esca internal symptoms are vascular discoloration with	Mugnai et al
disease colonizing	Phaeoacremonium aleophilum	the production of dark tarry drops and wood necrosis. In leaves, both	1999. Gramaie
the xylem tissues	-	chlorotic and necrotic areas have typically been described as tiger-	et al. 2018
of vine plants		striped leaves and later as grapevine leaf stripe disease.	

Table 2: Effectiveness of antagonistic endophytes against grapevine phytopathogens.

Endophytes	Effective against grapevine phytopathogens	Reference
Pseudomonas spp.	Phytoplasmas Botrytis cinerea	Gamalero et al. (2017) Gruau et al. (2015)
Burkholderia spp.	Phytoplasmas	Bulgari et al. (2014).
Methylobacterium spp.	Phytoplasmas	Bulgari et al. (2014).
Pantoea spp.	Phytoplasmas Neofusicoccum parvum	Andreolli et al. (2016) Haidar et al. (2021)
Bacillus spp.	Botrytis cinerea Plasmopara viticola	Andreolli et al. (2016). Zhang et al. (2017).
B. subtilis strain AG1	Phaeomoniella chlamydospora and Phaeoacremonium aleophilum	Alfonzo et al. 2009
Bacillus pumilus and Paenibacillus sp. (S19)	Phaeomoniella chlamydospora	Haidar et al. (2016b)
Pseudomonas protegens MP12 strain	Phaeomoniella chlamydospora and Phaeoacremonium aleophilum	Andreolli et al. (2019)
Brevibacillus spp. Lysinibacillus spp. Nocardioides spp. Stenotrophomonas spp. Microbacterium spp.	Botrytis cinerea	Andreolli et al. (2016)
Streptomyces anulatus	Botrytis cinerea	Vatsa-Portugal et al. (2017)
Paraburkholderia phytofirmans strain PsJN	Botrytis cinerea	Ait Barka et al. (2000), MiottoVilanova et al. (2016)
Acinetobacter lwoffi	Botrytis cinerea	Verhagen et al. (2011)
Enterobacter spp. Rahnella aquatilis Paenibacillus spp. Staphylococcus spp. Acremonium spp. Alternaria alternata Epicoccum nigrum	Botrytis cinerea, Plasmopara viticola, Agrobacterium vitis, Xylella fastidiosa	Pacifico et al. (2019)
Paenibacillus spp.	Botrytis cinerea, Plasmopara viticola, Agrobacterium vitis, Xylella fastidiosa Neofusicoccum parvum	Pacifico et al. (2019), Haidar et al. (2021)
Albifimbria verrucaria	Botrytis cinerea, Lasiodiplodia theobromae, Elsinoe ampelina	Li et al. (2000)
Beauveria bassiana	Plasmopara viticola	Rondot and Reineke (2019)
Cochliobolus, Bipolaris, Fusarium, Alternaria, Diaporthe, Phoma and Phomopsis.	Alternaria sp., Sphaceloma sp. And Glomerella sp.	Felber et al. (2016)
Lophiostoma cortisol (from leaves)	Botrytis cinerea	Kulišová et al. (2021)
Alternaria alternata and Fusarium proliferatum	Plasmopara viticola	Mondello et al. (2019), Aleynova et al. (2021)
Acremonium byssoides	Plasmopara viticola	Burruano et al. (2008)

the host plant (Brader et al. 2017). These endophytes colonize the plant tissues, both intercellular and intracellular, and have a mutualistic association with the host in their lifetime. Recent studies show that the health, survival, growth, and development of these host plants are mostly dependent on these endophytes (Hardoim et al. 2015, Potshangbam et al. 2017). Obligate endophytes are those that depend on the host plant metabolism for their survival, and their movement inside the plant occurs through different vectors or vertical transmission (Hardoim et al. 2008). Facultative endophytes are those that can survive outside of the host plant for a certain period of their life cycle, and they are mostly associated with host plants as compared to their natural environment in soil (Abreu-Tarazi et al. 2010).

ROLE OF ANTAGONISTIC ENDOPHYTES IN GRAPEVINE FUNGAL DISEASE MANAGEMENT

Endophytes are helpful in plant growth and provide biotic/

abiotic stress resistance by the production and release of secondary metabolites, plant hormones, antibiotics, and biocides, which leads to improving resistance in plants against abiotic stress and various diseases (Lugtenberg & Kamilova 2009, Compant et al. 2013). The endophytic colonization in the grapevine helps the plant to be in an active state to respond to any attack by grapevine disease-causing pathogens (Martinez-Medina et al. 2016, Mauch-Mani et al. 2017). It is proved by many researchers believe that these endophytes help in triggering defense responses in plants, which provide resistant against various fungal, oomycete, bacterial, and viral pathogens and insects (De Vleesschauwer & Höfte 2009, Van der Ent et al. 2009, Pineda et al. 2010). Some endophyte bacteria like Pseudomonas spp. and Bacillus spp. can produce HCN which helps in breaking summer bud dormancy in grapevine (Shameer & Prasad 2018, Sudawan et al. 2016). The endophytic bacteria Pseudomonas migulae can act as a biocontrol agent against phytoplasmas which causes grapevine yellows disease in grapevine (Gamalero et al. 2017). The bacterial species associated with induced systemic resistance (ISR), such as Burkholderia spp., Methylobacterium spp., and Pantoea spp. the population increased and helped in triggering defense responses for resistance when phytoplasmas attack the grapevine (Bulgari et al. 2014). The endophytic fungus Alternaria alternata, isolated from grapevine leaves, has been reported to be efficacious in controlling downy mildew disease through the production of toxic diketopiperazines metabolites (Musetti et al. 2006, Srivastava et al. 2024). Several other microorganisms, isolated either from rhizosphere or grape fruit surfaces, have also been selected as BCAs over the last decades to control Plasmopara viticola, such as Bacillus subtilis KS1, Lysobacter capsici AZ78, Trichoderma harzianum T39 and Fusarium proliferatum G6 (Perazzolli et al. 2008, Zhang et al. 2017).

In recent studies, the researchers identified various new potential endophytes as biocontrol agents in vitro. Among these potential endophytes, Bacillus licheniformis can secrete lipoproteins, which are biocontrol molecules that help in inhibiting the growth and development of various phytopathogenic fungi in grapevine, mainly against Botrytis cinerea, which causes grey mold disease in grapevine (Favaro et al. 2016, Nigris et al. 2018). The endophytic bacteria i.e., Bacillus spp., Brevibacillus spp., Lysinibacillus spp., Nocardioides spp., Stenotrophomonas spp., Microbacterium spp. and Pantoea spp. also exhibits antifungal activity and induce resistance against Botrytis cinerea phytopathogen causing grey mold disease in grapevine (Andreolli et al. 2016). The most effective endophytes against Botrytis cinerea are Bacillus spp., Pantoea spp., and Pseudomonas spp., respectively. Among them, the bacterial endophyte

Pseudomonas spp. helps in activating defense responses against *Botrytis cinerea* at both local and systemic levels in grapevine (Trotel-Aziz et al. 2008, Verhagen et al. 2011, Gruau et al. 2015).

The endophyte *i.e.*, *Pseudomonas* spp. Colonize the roots of grapevine and exhibits systemic defense response by transfer of molecular signals from roots to leaves, and it shows distinct defense-related gene expression patterns in roots and leaves of grapevine where some genes are associated with causing cell death and hypersensitive response (HR), which stops the infection from Botrytis cinerea from spreading into other cells and tissues of grapevine. It leads to the activation of oxidative burst and production of phytoalexins which helps in reducing the infection caused by Botrytis cinerea in grapevine (Gruau et al. 2015). Streptomyces anulatus is a potential endophytic plant growth-promoting rhizobacterium (PGPR) that exhibits resistance against Botrytis cinerea by activating defense responses in grapevine-like ion fluxes, extracellular alkalinization, protein kinases, oxidative burst, gene expression, and phytoalexin production (Vatsa-Portugal et al. 2017). Paraburkholderia phytofirmans is a potential endophytic plant growth-promoting rhizobacterium (PGPR) which helps in the activation of local immune response by inflation of phenolic compounds, ion fluxes, salicylic acid, and defense gene regulation for inhibiting growth and development of grapevine fungal pathogens mainly Botrytis cinerea (Compant et al. 2005, Bordiec et al. 2011, MiottoVilanova et al. 2016, Patya et al. 2023).

These all of the above-mentioned bacterial endophytes trigger oxidative bursts in tissues of the leaf, callose deposition in stomata, induction of salicylic acid, jasmonic acid, and pathogenesis-related (PR) genes (PR1, PR2, and PR5) in grapevine when infected by grapevine fungal disease-causing pathogens. (Miotto-Vilanova et al. 2016). Some researchers studied and observed that Pseudomonas protegens could colonize inside grapevine tissues, and it helps in inhibiting the growth and development of various phytopathogens such as P. chlamydospore, P. aleophilum, B. cinerea, Alternaria alternata, Aspergillus niger, Penicillium expansum, and N. parvum at in vitro and in vivo (Andreolli et al. 2019). Some bacterial and fungal endophytes such as Curtobacterium spp., Erwinia spp., Pantoae spp., Pseudomonas spp., Xanthomonas spp., Biscogniauxia spp., Cladosporium spp., and Didymella spp., can produce secondary metabolites (stilbene content) in the grapevine cell suspension under in vitro conditions (Aleynova et al. 2021). Grapevine, when inoculated with some endophytes like Acinetobacter lwoffi, Bacillus subtilis, and Pseudomonas fluorescens, is effective in suppressing the growth and development of Botrytis cinerea, causing grey mold disease in grapevine due to the help of these endophytes in synthesis of stilbene

Table 3: Role played by antagonistic endophytes in the management of grapevine diseases.

Endophytes	Role played	Effective against grapevine disease	References
Proteobacteria spp.	Phyto-hormones production	NA	Baldan et al. (2015)
Streptomyces anulatus S37	Activation of protein kinases, induction of defense gene expression, and phytoalexin accumulation	Triggers early and late defense responses, such as ion fluxes, oxidative burst, extracellular alkalinization	Vatsa-Portugal et al. (2017)
Acinetobacter lwoffii	Enzyme Production	Grey mold	Magnin-Robert et al. (2007)
Lophiostoma corticola B. velezensis	Antifungal and antibacterial properties	Grey mold Grey mold, Ripe rot, Downy mildew	Kulisova et al. (2021) Hamaoka et al. (2021)
Bacillus spp. Variovorax spp. Pantoea spp. Staphylococcus spp. Herbaspillurum spp. Sphingomonas spp.	Biocontrol Agents	Grey mold Downy mildew	Bruisson et al. (2019)
Proteobacteria spp. Bacillus spp.	Bio-fertilizers	Grey mold	Baldan et al. (2015)
Proteobacteria spp.	Phosphate solubilization	NA	Baldan et al. (2015)
Penicillium custom Bacillus spp.	Siderophore synthesis	Grey mold	Kulisova et al. (2021) Baldan et al. (2015)
Pseudomonas fluorescens	Secondary metabolites production	Grey mold	Gruau et al. (2015)
Aspergillus pseudodeflectus Beauveria bassiana Aureobasidium pullulans Bacillus subtilis Paenibacillus spp.	Defense responses in host plant	Grey mold Downy mildew Grapevine trunk Grapevine trunk Downy mildew	Kulisova et al. (2021) Rondot and Reineke (2019) Pinto et al. (2018) Trotel-Aziz et al. (2019) Hao et al. (2017)
Paenibacillus spp.	Induce resistance in host plants.	Downy mildew	Haidar et al. (2016)
Penicillium, Aspergillus, Mucor, Alternaria, Cephalosporium, and Geotrichum	Resveratrol	As an antioxidant compound known to increase resistance to biotic stress	Shi et al. (2012), Yang et al. (2016)
Paraburkholderia phytofirmans strain PsJN	Activation of a local immune response characterized by the accumulation of phenolic compounds, salicylic acid (SA) accumulation, ion fluxes, and defense gene regulation	Grey mold	Miotto-Vilanova et al. (2016)

phytoalexins, resveratrol which help activating metabolite composition and triggering defense mechanism in grapevine (Verhagen et al. 2011). It is observed that the endophyte *Arcopilus aureus* produces high resveratrol content in grapevine. A study was conducted on 53 isolates of potential endophytes obtained from various grapevine varieties to observe the resveratrol content produced by various endophytes. Among the endophytes that produce resveratrol content mainly belong to seven genera, *i.e.*, *Aspergillus* spp., *Botryosphaeria* spp., *Penicillium* spp., *Fusarium* spp., *Alternaria* spp., *Arcopilus* spp. and *Lasiodiplodia* spp. (Dwibedi & Saxena 2018). Some important role played by endophytes against grapevine pathogens is mentioned in Table 3.

RECENT APPLICATIONS OF ANTAGONISTIC ENDOPHYTES IN GRAPEVINE FUNGAL DISEASE MANAGEMENT

Nowadays, both fungal and bacterial endophytic applications in agriculture *in vivo* are very beneficial for host plants in which they colonize because these endophytes are ecofriendly with the host plant by promoting growth and development of the plant, act as a biocontrol, help in disease suppression, and stress tolerance, etc (Firdous et al. 2019). Some endophytes application helps the host plants acquire nutrients, production of phytohormones, phytoenzymes, and secondary metabolites, act as biocontrol agents, biofertilizers, exhibit antifungal and antibacterial properties, phosphate



(Source: made by authors).

Fig. 1: Role of endophytes in the growth and development of plants by suppressing the pathogenic microbes.

solubilization, siderophore synthesis, defense responses and induce resistance for suppressing various phytopathogens by inhibiting their growth and development in host plants and prevent them from causing diseases which leads to major losses in crop yield (Santoyo et al. 2016).

Recent studies in endophytes application to grapevine show that some endophytes are helpful in the production of siderophores and exhibit antioxidant and antifungal activity to inhibit grapevine disease-causing pathogens (Fig. 1). Application of Diatrype stigma, Aspergillus niger and Penicillium crustose endophytes in vivo helps in the production of siderophores in grapevine. Application of Penicillium crustosum and Aspergillus pseudodeflectus endophytes in vivo helps in exhibiting antioxidant activity in grapevine. Application of Lophiostoma corticola, and Penicillium crustosum endophytes in vivo helps in exhibiting antifungal activity in grapevine. (Kulisova et al. 2021). Application of Bacillus subtilis and Bacillus pumilus in vivo acts as a biocontrol agent against downy mildew disease of grapevine caused by *Plasmopara vitcola* and helps in the reduction of disease incidence and severity in grapevine (Zhang et al. 2017).

Application of some endophytes like Pantoea agglomerans, Enterobacter spp., Rahnella aquatilis,

Pseudomonas spp., Paenibacillus spp., Staphylococcus spp., Bacillus spp., Burkholderia phytofirmans, Acremonium spp., Alternaria alternata, and Epicoccum nigrum can act as bio-control agents for effective control of various grapevine diseases i.e. grey mold, crown gall, pierce, and downy mildew (Pacifico et al. 2019). In recent days, many endophytic bacteria like Streptomyces spp., Pseudomonas fluorescens, Bacillus spp., Pantoea agglomerans, Acinetobacter aeruginosa, Burkholderia phytofirmans, and Rahnella aquatilis when applied at in vivo these can trigger defense responses and activate secondary metabolites in grapevine which help in effective defense mechanism against various disease-causing pathogens of grapevine. (Compant et al. 2013). It is observed that the application of both *Pantoea* agglomerans and Paenibacillus sp helps in the control of grapevine trunk disease caused by Neofusicoccum parvum. (Haidar et al. 2021). The potential roles and mechanisms of the main endophytes involved in the biotic stress tolerance of grapevine are given in Table 4.

A survey was conducted on various vineyards and observed that there are about 381 culturable bacteria isolated from the inner portion of stems and leaves. Of these isolated bacteria, 30% belongs to genus *Bacillus* spp., and the latter include *Paenibacillus* spp., *Microbacterium* spp.,

Pathogen	Endonhytes	Mechanism associated with the tolerance	Reference
Botrytis cinerea	Acinetobacter Iwoffi (PTA-113 and PTA-	Induced the activities of lipoxygenase (LOX)	Magnin-Robert et al. (2007)
-	152), <i>Pseudomonas fluorescens</i> (PTA-268 and PTA-CT2), <i>Pantoea agglomerans</i> (PTA-AF1 and PTA-AF2), <i>Bacillus</i> <i>subtilis</i> (PTA-271).	phenylalanine ammonia-lyase (PAL), β -1,3 glucanase, and chitinase. Induced the oxidative burst. Accumulated the stress-related metabolites phytoalexin (trans-resveratrol and trans- ϵ -	Trotel-Aziz et al (2008) Verhangen et al. (2011)
	Ulocladium atrum Pseudomonas fluorescens (PTA-CT2).	viniferin. Enhanced chitinase activity. Regulated the expression of defense-related genes in leaf and root, including those with transcriptional factor functions (JAZ9, NAC1, and ERF1), of secondary metabolism (PAL, STS, LOX9, ACCsyn, GST, CHS, CHI, LAND, and ANR), and PR proteins (PR1, PR2, PR3, PR5, and PR6). Induced callose deposition and H ₂ O ₂ production.	Ronseaux et al. (2013) Gruau et al. (2015)
	Bukholderia phytofirmans (PsJN).	JAZ in bacterized plantlets after pathogen challenge.	Miotto-Vilanova et al. (2016)
	<i>Bacillus subtilis</i> (BBG-127, BBG-131, Bs2504, and BBG-125).	Modulated carbohydrate metabolism. Treatment with <i>Bacillus subtilis</i> strains with non- producing lipopeptides, overproducing surfactin, overproducing plipastatin, and overproducing mycosubtilin differentially activated the plant's innate immune response. Modulated genes encode a chitinase (chit4c), a protease inhibitor (pin), a salicylic acid (SA) regulated marker (W17.3), and a glucanase (gluc).	Farace et al. (2015)
	Microbacterium imperial (Rz19M10) Kocuria erythromyxa (Rt5M10) Terribacillus saccharophilus (Rt17M10)	Induced a systemic response that triggers increases in monoterpenes, sesquiterpenes, tocopherols, and membrane sterols (enhanced antioxidant capacity).	Salomon et al. (2016)
	Streptomyces annulus (S37)	Induced rapid and transient generation of H_2O_2 , extracellular alkalinization, and activation of two mitogen-activated protein kinases (MAPKs) followed by the expression of LOX9, PAL, STS, and GST genes in primed cells. Induced defenses modulated by Ca ²⁺ signaling.	Vatsa-Portugal et al. (2017)
Botrytis cinerea, Plasmopara viticola, Xiphinema index nematodes	Paenibacillus spp. strain (B2)	Modulated the expression of defense-related genes CHI, PAL, STS, GST, and LOX and pathogenesis-related protein PR-6. Reduced nematode root infection associated with the expression of genes resistant to nematodes Hero and Hs 1 ^{pro-1} .	Hao et al. (2017)
Rhizobium vitis (Ti) VAT03-9 (tumorigenic)	Rhizobium vitis (ARK-1)	Co-inoculation of ARK-1 with a Ti strain (VATO3-9) into grapevine shoots suppressed the expression of the virulence genes VirA, VirD3, and VirG of VAT03-9.	Kawaguchi et al. (2019)
Flavescence dorée phytoplasma	Pseudomonas migulae (8R6)	Production of 1-aminocyclopropane-1- carboxylate (ACC) deaminase enzyme helps the plant to regulate the level of the stress-related hormone ethylene.	Gamalero et al. (2017).
Diplodia seriata (strains F98.1 and Ds99.7) (Botryosphaeria dieback)	Aureobasidium pullulans strain (Fito-F278)	Modulated genes encoded for plant defense proteins: PR protein 6 (PR-6) and β -1,3 glucanase (Gluc), detoxification and stress tolerance: haloacid dehalogenase hydrolase (Hahl), α -crystalline heat shock protein (HSP), β 1,3- glucanase (GST5), phenylpropanoid pathway: (STS) cell wall (fascAGP) and water stress (Pip2.2).	Pinto et al. (2018).

Table 4: Potential roles and mechanisms of main endophytes involved in biotic stress tolerance of grapevine.

Table Cont....

Pathogen	Endophytes	Mechanism associated with the tolerance	Reference
Neofusicoccum parvum (Botryosphaeria dieback)	Bacillus subtilis (PTA-271)	Antagonized <i>Neofusicoccum parvum</i> by delaying its mycelial growth and detoxifying both (R)- mellein and (-) teremutin. Primed defense genes including PR2 (β-1,3 glucanase), NCED2 (involved in ABA synthesis), and PAL at systemic level after pathogen inoculation.	Trotel-Aziz et al. (2019).
Phaeomoniella chlamydospora (Trunk diseases)	Paenibacillus spp. (S19) Bacillus pumilus (S32)	Induced resistance against trunk disease fungi: induced the expression of defense-related genes PR1, PR10, CHIT3, PAL, STS, CHS, ANTS, CALS, GST, and GLU.	Haidar et al. (2016).

Staphylococcus spp., *Micrococcus* spp., *Stenotrophomonas* spp., *Variovorax* spp., *Curtobacterium* spp. and *Agrococcus* spp., etc (Baldan et al. 2014). These are the major endophytic bacteria in the grapevine that provide both environmental and economic benefits by exhibiting plant growth-promoting hormones, providing required nutrients to the host plant, activating various beneficial microorganisms in soil rhizosphere, protecting host plant against biotic stress (pathogen) attack by aggressively competing against them for nutrient, space, and colonization. These endophytes are eco-friendly and improve the environment surrounding the grapevine without causing any detrimental effects on the soil microbiome in the rhizospheric zone. (Marasco et al. 2018).

Some endophytes like Bacillus spp., Pseudomonas spp., and Micrococcus spp., exhibit beneficial effects to resist various abiotic stresses like arsenic contamination, high temperature, drought, chilling, and salinity, respectively (Pacifico et al. 2019, Parashar & Mudgal 2024). The bacterial endophyte Paraburkholderia phytofirmans slowly gathers trehalose in grapevine to resist various abiotic stress by forming a gel during cellular dehydration to stop excess water loss from the host plant (Fernandez et al. 2012). Pseudomonas spp. is an endophytic bacteria that helps grapevine in resisting against cold conditions by inducing various PR (Pathogenesis) genes that encode chitinase, phenylalanine ammonia-lyase (PAL), lipoxygenase (LOX), and glucanase. Some endophytes can convert detoxification compounds into signaling molecules by decreasing ROS (Reactive oxygen species) concentration with the help of some genes, which particularly encode the enzymes in ROS accumulation in grapevine (Theocharis et al. 2012).

The bacterial endophyte *Bacillus licheniformis* can able to exhibit various secondary metabolites such as monoterpenes (antioxidant activity) and sesquiterpenes (antimicrobial activity) in grapevine to protect the host plant from various abiotic stress (Salomon et al. 2014). *Bacillus licheniformis* is an endophytic bacteria that produces catenoids (antioxidants) in the grapevine that help the host plant survivability under various extremely unfavorable conditions to stop both plant growth and development; it may be due to abiotic/biotic/ environmental changes (Cohen et al. 2018). It is observed that bacterial endophytes like *Bacillus licheniformis* and *Pseudomonas fluorescens* can able to encode genes that induce the expression of ABA synthesis and signaling pathways in grapevine plants (Salomon et al. 2014). Some endophytic fungi like *Septaglomus deserticola*, *Funneliformis mosseae*, *Rhizoglomus intraradices*, *Rhizoglomus clarum*, and *Glomus aggregatum* can alter ABA metabolism when these endophytes are inoculated into grapevine so that they can survive effectively under drought condition (Torres et al. 2018).

Recently, many endophytes have been observed that can help grapevine accumulate protective molecules like melatonin, proline, and carotenoids, which are activated when the host plant suffers from various abiotic stress to help survive through that stress condition (Liu & Brettell 2019). Certain endophytes from grapevine orchards that have been isolated for further investigation can modify the chemical and physical characteristics of both leaves and berries as they ripen. Particularly, fungal endophytes alter the modify the total content of reduced sugar, total flavonoids, total phenols, resveratrol, and PAL activity in grapevine. These endophytes can determine the quality of wine and other edible products produced from grapevine (Yang et al. 2016). Some endophytes, when inoculated, help in enhancing growth and development, improving fruit quality and yield of grapevine, which help in relieving farmers' economic burden by improving profits gained with each fruit sold in the market (Huang et al. 2018). some of the endophytes can exhibit secondary metabolites inside grapevine, which lowers the cost of buying pesticides to control various grapevine diseases and improves economic value by large-scale production of grapevine (Suryanarayanan et al. 2009).

BIOFORMULATION

Role of Endophyte-Based Bioformulation in Sustainable Agriculture

Bioformulations are microbial-based products consisting of beneficial microbes called endophytes, which help in improving plant growth, supply nutrients to plants, and control various diseases caused by phytopathogens in an eco-friendly manner without causing any detrimental effects to the beneficial microbes in the rhizospheric zone and host plants (Burragoni & Jeon 2021). The bio-formulation process in agriculture involves the selection of beneficial microbial strains and a suitable carrier. An appropriate carrier is a vehicle that houses latent live microorganisms and provides a supportive niche to the microbial population (Khan et al. 2023). A bioformulation of an endophyte is said to be good when it is effective, non-polluting, readily biodegradable, with high water retention capacity and sufficient shelf life (Chaudhary et al. 2020).

Endophytic bioformulation products can serve as a sustainable substitute for chemical fertilizers and pesticides. This is because chemical fertilizers can decrease soil fertility when used excessively, increase the possibility of pathogen mutation, and cause resistance to pesticides altogether (Arora & Mishra 2016, Sharma et al. 2023). Bioformulation products comprise active ingredients and inert ingredients. The active ingredient may be living microbe, spores, and their products, which should be in living conditions. It also requires some inert ingredients, *i.e.*, peat, talc, vermiculate, carboxymethylcellulose, and polymers like xantham gum and diatomaceous earth, for bioformulation to be developed successfully. The inert carrier-based bioformulations helped insert antagonistic microbial cells into both the rhizospheric region and plant system through both foliar and soil application for a longer duration (Ardakani et al. 2010, Jorjani et al. 2011). Some additives, i.e., gum, silica gel, methyl-cellulose, and starch, help protect these endophyte bio-formulated products from extreme environmental conditions, which also improve the physical, chemical, and nutritional properties of these products (Schisler et al. 2004).

Nowadays, endophyte-based bioformulation products are essential in sustainable agriculture to protect crops from phytopathogens and decrease disease-prone agricultural zones because of the resistance risk of pathogen mutation caused by using pesticides. Additionally, these bioformulations either directly or indirectly enhance plant growth and development in their native environments (Lugtenberg & Kamilova 2009). There are also some limitations in successfully producing endophyte-based bioformulation products as we know that they consist of living microbes, so extreme care should be taken to maintain microbial load and vigor without contamination of the original product, which determines the quality of the product sold to the market (Kashyap et al. 2023). The development of these products is highly constricted due to a lack of advanced technology, instruments, lack of knowledge,

improper distribution, inexperienced manpower, technical difficulties, and importation laws, which leads to a loss of endophyte viability and decreases the efficacy of these products. Some other major limitations are high production costs and inconsistent performance. These living endophyte cells used in making bioformulations are highly sensitive to external factors, and the person handling them should follow caution during culture, distribution, and application (Arora & Mishra 2016, Xia et al. 2022).

LIMITATIONS OF ENDOPHYTES IN SUSTAINABLE AGRICULTURE

Many endophytes are uncultured and unidentified because databases for endophytes and their metabolites are still unavailable (Xia et al. 2022). Endophytes show specific characteristics towards certain plant species, and they may not act the same on the other plant species, which limits their effectiveness in the application of various crops in the world. Their effectiveness is influenced by some environmental factors like temperature, moisture, and soil characteristics, etc respectively. Their compatibility with agricultural requirements like fertilizers and pesticides is to be considered till now. Some combinations may be synergistic, while some may be antagonistic (Watts et al. 2023). It requires large investments to develop and commercialize endophytic products through numerous research, production, and marketing methods. It may be a challenge for the product to get profits exceeding its initial investment as the small-scale farmers cannot afford it if the price is higher. It is a complex and time-consuming process to get approval from regulatory governing bodies regarding endophytic products as they change from region to region and its landscape navigation difficulty by regulatory bodies limits its commercialization-Even with the recent accomplishments and advancements in endophyte research, there is still a knowledge gap. The relationship between endophytes and plants is still developing, and our understanding of their means of action, long-term impacts, and molecular interactions with the host plant is limited. Their risk in introducing into agricultural systems without proper knowledge about them is more as we must face the unknown consequences (Kaur et al. 2023).

In the quadritrophic system involving fruits, pathogens, and endophytes, the host faces limitations in terms of nutrition and space (Kashyap et al. 2023). Competition with pathogenic microorganisms for niche and nutrition, namely niche exclusion, is a promising mechanism for the use of endophytes in plant disease control (Liarzi & Ezra 2013). Both endophytes and pathogens rely on essential nutrients such as nitrogen, carbon, macro, and micronutrients for their survival (Kumari et al. 2022). However, after the application of microbial biocontrol agents, these agents compete with the target pests or pathogens for space and nutrients by colonizing the same ecological niches or habitats as the target organisms, such as plant surfaces, soil, or water, and trying to establish themselves and proliferate. The biocontrol agents can out-compete the pests or pathogens by utilizing available resources more efficiently, depriving them of essential nutrients, or occupying physical spaces that prevent their establishment. In addition to competing with the target organisms, microbial biocontrol agents may also compete with the native microbial communities (Kumari et al. 2022). Native microorganisms are naturally present in ecosystems and play important roles in nutrient cycling, disease suppression, and maintaining ecosystem balance. The introduction of biocontrol agents can disrupt the existing microbial communities and create competition for resources (Kumar et al. 2020). Endophytes might also be ineffective when the disease is caused by a high presence of pathogens (Lahlali et al. 2014).

FUTURE ASPECTS OF ENDOPHYTES

We must explore, identify, and characterize various new species of endophytes to improve our understanding of their habitat, mode of action, how they interact with host plants, they will have any beneficial effect on that host plant or not as we explore various plant species, we can find novel endophytes with unique characteristics as we know that the endophytes are plant specific. We know that there are many microorganisms in the world. Some may be beneficial to some plants, and the remaining may be harmful to other plants. These beneficial microorganisms we name them as endophytes as their role in plant growth and development is diverse. To create products from these endophytes and apply them at the in vivo level for sustainable agriculture, we must first examine their properties and the impact they will have on the plant to which we intend to apply them.

Additionally, we need to gain a deeper understanding of the molecular interactions between the endophyte and the host plant to gain insight into potential future applications. For conducting molecular studies, we can use techniques such as transcriptomics, proteomics, and metabolomics to know the signaling pathways and gene regulation they do inside the plant. Now, as our understanding of these endophytes improves, we must select endophytes that are beneficial to a specific plant, and we can make bioformulation products of these endophytes, which can improve their survival, colonization, and efficacy on targeted plants when applied *in vivo*. These endophytes-based products are new as they have no records of their effectiveness in reducing abiotic/biotic stress in plants. So, we must investigate their efficacy under real-world conditions long-term to check their effectiveness in reducing the effect of both abiotic/biotic stress on targeted plants so we can apply them risk-free in sustainable agriculture. As the application of these endophytes-based products increases day by day, there is a need for some guidelines and safety standards should be framed by the regulatory bodies so that we can follow these guidelines. Following that these safety standards can be commercialized into the market to be used in agricultural practices.

CONCLUSIONS

In the past three decades, remarkable progress has been made in research on plant disease resistance mechanisms and plant-microbe interactions. Endophytes, colonizing plant tissues, are regarded as naturally occurring agents in plant disease suppression. Most of their success is attributed to the production of a vast array of metabolites. In this review, we studied the management of various fungal diseases of grapevine with the help of various endophytes (may be bacterial or fungal), which are eco-friendly. These endophytes also play a major role in growth and development of grapevine by acquiring nutrients, production of phytohormones, phytoenzymes, secondary metabolites, acting as biocontrol agents, phosphate solubilization, siderophore synthesis, defense responses, and inducing resistance for suppressing various phytopathogens by inhibiting their growth and development in host plants and prevent them from causing diseases which leads to major losses in crop yield of grapevine. Some endophytes help in reducing abiotic stress in the grapevine. Endophytes are reliable and environmentally friendly in plant disease management and crucial for sustainable agriculture. However, to truly achieve their large-scale commercial production and application, we still have some challenges to overcome. Biocontrol effects of endophytes are not stable in field trials. It is necessary to elevate the exploitation of endophytes and their metabolites in the biological control of plant diseases to the multi-omics level as a promising research frontier.

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