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REVIEW ARTICLE

# Microbial biocontrol agents against chilli plant pathogens over synthetic pesticides: a review

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**Abstract**

India is amongst the top countries consuming, producing and exporting chillies. Chilli (*Capsicum annuum*), known as chilli peppers, belongs to the family Solanaceae. Heavy losses have been observed in the yield due to diseases caused by bacterial, fungal and viral pathogens. Over utilization of synthetic agents to control these diseases causing pathogens have raised serious biological and ecological issues. Along these lines, late endeavours have been centred on utilizing natural ways for controlling plant pathogens. Interest in biological control using microbial agents has increased over the past years as an alternative to chemicals which are toxic to the environment and lead to the development of resistant pathogenic populations. Biological control using microorganisms is a more environmentally friendly alternative and is utilized either on its own or as a part of integrated management strategy to reduce the use of synthetic agents. This research approach reviews various pathogen causing diseases in the *Capsicum annuum*, toxicity of the chemical agents used for controlling the pathogens and the biocontrol agents against chilli phytopathogens along with their suggested mode of action. This article will deepen our knowledge about the consistent beneficial effects of microbial biocontrol agents.

**Keywords** Biocontrol · Chilli · Disease · Pathogen · Toxicity

## Introduction

Chillies (*Capsicum annuum*) also known as 'mirchi', are an indispensable ingredient in Indian cuisine. They were brought in Asia by Portuguese navigators in the 16th Century. Chilli plant belongs to Solanaceae family, are herbaceous annuals, have glabrous or pubescent lanceolate leaves, white flowers and fruit that vary in length, colour and pungency depending on the cultivar (Stommel et al. 2018). They are rich in Vitamin C (ascorbic acid), E (tocopherols and tocotrienols), P (citrin), B1 (thiamine), B2 (riboflavin), B3 (niacin) and provitamin A (β-carotene) (Gopalakrishnan 2007; Bosland et al. 2012). They are also known to be a good source of flavonoids, carotenoids and xanthophylls (Lee et al. 1995). India has been amongst the major countries producing, consuming and exporting chillies. A rising demand for chillies combined with higher value acknowledgment in the domestic market has spurred farmers to expand areas under chilli cultivation for export (Surepeddi and Giridhar 2015). However heavy yield loss of Chilli crop is observed across the country due to diseases caused by both abiotic and biotic factors.

## Abiotic factors affecting chilli plant

Non-living factors responsible for crop damage include extreme levels of temperature, moisture and light, change in nutrients and pH, air pollutants and overdose of pesticides (Peter and Hazra 2012). The major abiotic factor which cause stress conditions in the chilli plant is deficiency or toxicity of the macro and micronutrients. Deficiency of the nutrients may lead to conditions like stunted growth of the plant, chlorosis of leaves, limited foliage and reduced size of fruits. Excessive nutrients are also harmful for the plant and may lead to burning of foliage and root system (Balakrishnan 1999). Due to factors like inconsistent watering, calcium deficiency, increased soil salinity or excessive applications of nitrogen fertilizers; Blossom-End rot is observed in chilli fruit which results in early fruit drop (Taylor and Locascio 2004). This condition manifests in the water soaked lesions on immature fruits, resulting as a prime location for microbial infections by opportunistic

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disease causing pathogens. Exposure to intense sunlight results in 'Sun scalding' where wrinkling of foliage is observed making the plant light-coloured and papery textured. Occasionally fruit skin is affected and cracked open (Rabinowitch et al. 1983). Presence of air pollutants such as peroxyacetyl nitrate (PAN) is reported to cause stunting, chlorosis and even senescence in the chilli plant leaves (Goyal et al. 2020).

## Diseases caused by microbial pathogens in chilli plant

Losses incurred in agriculture due to microbial pathogens sums up to around 16% globally (Oerke 2006). The growth and yield of a chilli plant is most affected by bacterial, fungal and viral pathogens (Gachomo et al. 2003). Disease symptoms have been noticed in seedlings, mature plant, fruit or leaves depending on the phytopathogen that attacks the plant. Table 1 enlists the diseases caused by microbial phytopathogens in chilli plants along with the symptoms associated with the disease. Wilting and rotting are manifested in the mature plants by soil borne fungal pathogens belonging to genera *Macrophomina, Phytophthora, Rhizoctonia, Sclerotinia, Fusarium, Sclerotium* and *Verticillium*. Bacterial wilt is particularly caused by a bacterium *Ralstonia solanacearum* leading to the death of the plant (Sanogo 2003). Fungus belonging to genera *Pythium* or *Phomopsis* show damping off symptoms in seeds or young seedlings. Infected seeds fail to germinate and the damaged seedlings generally rot, causing the seedling to wilt and eventually die, or collapse from the ground line (Mishra et al. 2013). Leaves of the plant affected by bacterial pathogens (*Xanthomonas* sp.) and fungal pathogens (*Leveillula* sp., *Alternaria* sp. or *Cercospora* sp.) show powdery mildew and spot symptoms. Formation of mosaic pattern on leaves, curling of leaves, vein bending, mottling of leaves is mostly caused by the viral pathogens affecting the plant (Damiri 2014). Chilli fruits are primarily affected by abiotic factors which can eventually lead to secondary infection by fungal pathogens belonging to the genera *Colletotrichum or Phytophthora*. These pathogens can attack fruit directly or can attack tissue weakened by environmental factors (Reddy 2009; Naik and Savitha 2014).

## Use of synthetic pesticides for controlling chilli crop pathogens and the associated problems

The term pesticide in agriculture refers to a component or mixture of components to prevent, control, reduce or inhibit a pest (bacteria, fungi, virus, nematodes, vectors and even unwanted species of plants or animals) interfering with the production, processing, storage or marketing of any agricultural commodity. Synthetic pesticides are those which are formulated or manufactured using chemical processes using chemically synthesized components or by chemically changing any component derived from natural sources (Stoytcheva 2011). For any pest problem, chemical agents are usually preferred over organic ones as they are cheaper, readily available and have longer shelf life than the later. They are mostly broad-spectrum agents thus can be applied against various pests. They are even known to be more persistent in nature thus reducing the frequency of application in the field, which in turn saves time and economics (McCoy and Frank 2020). However due to such properties of persistency and broad spectrum activity, the indiscriminate use of synthetic pesticides has resulted in serious biological and ecological problems (Whipps 2001; Muthukumar et al. 2008). Table 2 summaries the chemical agents used against chilli plant pathogens and the reported toxicity of each agent. As reported by Pimentel (1995), only < 0.3% of chemical pesticides showed interaction and inhibition only of target pathogens. Most of the chemical pesticides affect the beneficial organisms in the soil which assist natural processes of mycorrhizal colonization, transformation or fixation of nitrogen, improvement of soil porosity and fertility (Aktar et al. 2009). Overuse of pesticides has also resulted in acquirement of resistance by the target pathogens. Some of the chemical agents are seen to be converted to toxic byproducts in the soil thus hampering other plants, animals and even humans (Smith and Perfetti 2020). Studies have revealed many associated adverse effects of the pesticides on human health viz. irritation of eyes and skin, mutations and carcinogenicity, disruption of endocrine functions, impaired reproductive capacity, atherogenicity and interference with neural transmission in the central and peripheral nervous system (Pruett et al. 2001; Atreya and Sitaula 2011; Budzinski and Couderchet 2018). Synthetic pesticides have been detected into aquatic systems due to field runoff or leaching, thus affecting the multiple developmental stages of aquatic life and even wild life (Nabi et al. 2019). Aragaki et al. (1994) has reported the phytotoxicity in a higher plant due to decomposition of a fungicide in water. Disruption of endocrine function, ovarian toxicity, oxidative stress and neuropathological effects has been identified in animals due to toxic chemical agents (Moser et al. 2001; Lu et al. 2004; Tahir and Nour 2009). Considering the risks associated with synthetic pesticides, there is need to shift to biological ways of controlling phytopathogens.

**Table 1** Disease causing phytopathogens in *Capsicum annuum*

| Sr. no. | Disease | Causative agent | Symptoms |
|---|---|---|---|
| Fungal diseases | | | |
| 1 | Charcoal Rot (Shahid et al. 2016) | *Macrophomina phaseolina* | Blackening of lower stem and taproot is observed under the epidermis due to the numerous microsclerotia formation. This gives the plant tissue charcoal-sprinkled appearance. As the disease advances, leaves turn yellow, then wilt turning brown and eventually plant dies off |
| 2 | Damping off (Majeed et al. 2018) | *Pythium aphanidermatum* | In pre-emergence damping off, the growing points are damaged in the initial stages of seed germination before they come out through the soil. In post emergence damping off, the seedlings topple over the ground due to the collar rotting and rapid shrinkage, followed by spreading to the cortical tissue of the hypocotyls, basal stem and developing taproot resulting in death of plants |
| 3 | Fruit rot/Die-back/Anthracnose (Than et al. 2008; Machenhalli 2014) | *Colletotrichum capsici/Colletotrichum gloeosporioides/Colletotrichum truncatum/Colletotrichum acutatum/Colletotrichum scovillei* | Irregular water drenched spots appear on fruits which later become dark depressed lesions with various acervuli in concentric rings. Acervuli formation begins from the focal point of lesion and move towards periphery. They blend and get to be distinctly papery. The infected parts turn black and gets wrinkled and ultimately the fruit shrivels, dries up, rots and fall down. The pathogen may also attack the fruit stalk along the stem causing die-back symptoms. Branches and twigs show necrosis and the entire top of the plant may wither away. Disease spreads quickly under hot and humid conditions |
| 4 | Leaf spot/blight (Mishra et al. 2013) | (i) *Alternaria solani/Alternaria alternata* | Circular to oblong spots are observed with light grey to white centres and dark brown margins. Small spots coalesce to each other in extreme diseased condition prompting to defoliation. These leaf spots are covered with a dark greyish brown to black spores which sporulate in moist conditions |
| | | (ii) *Cercospora capsici* | Angular or irregular shaped chlorotic lesions observed which later on turn greyish brown with profuse sporulation at the focal point of the spot. Severely infected leaves drop off prematurely |
| 5 | Phomopsis Blight/soft rot (Gopalakrishnan 2007) | *Phomopsis vexans/Diaporthe vexans* | Infected seeds may bring about damping off in the nursery. Lower leaves of seedlings show clearly defined circular brown spots with lighter centre. These spots are papery, often crack and may have short holes. Sometimes infected leaves show big irregular lesions and stems shows lesions with constriction which start from basal part of nodal portion as grey dry rot. This prompts to drying of few twigs or partial wilting of the portion of the plant. Pale to light brown sunken spots develop on the old fruits which expand and coalesce to cover the entire fruit leading to fruit rot |

**Table 1** (continued)

| Sr. no. | Disease | Causative agent | Symptoms |
|---|---|---|---|
| 6 | Phytophthora blight/Fruit rot/root rot/leaf blight (Majid et al. 2016) | *Phytophthora capsici* | Occur as crown rot from soil inoculums. At initial stages shrivelling of plants occur due to infection of root and lower portion of the stem. Purplish black lesions are also observed at collar region. Dark green water soaked spots appear later on the fruits which enlarges rapidly to cover the entire surface causing rotting of the fruit. On leaves water soaked bleached spots appear resulting in blight |
| 7 | Powdery mildew (Peshama et al. 2017) | *Leveillula taurica* | Whitish spots smaller in size and of circular shape are observed on lower leaf surface. As the disease progresses the entire leaf surface gets covered with dirty white powdery development which are seen in patches. The infection begins from the older leaves but gradually covers the whole plant. Diseased leaves eventually drop off leaving fruits exposed to sunscald |
| 8 | Rhizoctonia root rot (Mannai et al. 2018) | *Rhizoctonia solani* | Affects seedling and mature plants and induce dry rot of collar region and root rot which leads to wilting and death of chilli plants. It is easily identified by presence of white mycelia. It also shows symptoms of damping off |
| 9 | White/Sclerotia rot (Saharan and Mehta 2008) | *Sclerotinia sclerotiorum* | It is shown up as water soaked rotting of leaves at petiole, stalk and stump region. White mycelium growth is observed all over the infected portion. Seed production of crops is severely affected by this disease collapsing the entire inflorescence. The total rotted portion is converted into compact mat in later stages followed by hard black sclerotial body formation |

**Table 1** (continued)

| Sr. no. | Disease | Causative agent | Symptoms |
|---|---|---|---|
| 10 | Wilt (Mullen 2001; Bhat et al. 2003; Suryanto et al. 2010) | (i) *Fusarium oxysporum/Fusarium solani/Fusarium pallidoroseum* | Along with the wilting of the plant, leaf chlorosis and vascular discoloration is observed. Symptoms may appear at 2 stages *viz*. seedling and adult plant stage. Foliage of affected seedling turns yellow and dries there off. On adult plant initially, slight drooping of leaves is seen which led to drying of leaves starting from lower ones extending from root to stem region followed by wilting symptom. Increased temperature and moisture are conducive to symptom development |
| | | (ii) *Sclerotium rolfsii* | The infected plants may show dry root rot, collar rot or stem rot. Rotting of the plant is followed by wilting and eventually plant dies off |
| | | (iii) *Verticillium dahliae/Verticillium albo-atrum* | Slight chlorosis of the lower leaves is observed during initial stages which continue until the leaves become bright yellow, wilt and eventually fall off the plant. During warmer times of the day, plant shoots and overall foliage wilt. Internal vascular tissue of the main stems closer to the crown has a tan to light brown discoloration. Infected plants may exhibit physiological changes such as decreased photosynthesis, increased plant transpiration and respiration. Even if the infected plants do not die completely, plant development and yields can be essentially decreased |
| Bacterial diseases | | | |
| 1 | Leaf spot (Roach et al. 2018) | *Xanthomonas campesthis* pv. *vesicatoria* | Raised spots arise on young leaves and are yellowish green to dark brown in colour and on older leaves dark, water soaked spots arise which are not raised. Later they appear as straw coloured centre and dark margins. The spots are depressed on the upper leaf surface whereas on the lower leaf surface the spots are raised and slab like. As the bacteria spread along the veins, the spots appear angular. Leaves drop off on turning yellow due to severe spotting. Infected seedlings often lose their foliage except their top leaves. As the disease progress, the spots may enlarge, turn black and become rough giving a scabby appearance. Bacterial spot of pepper is described as blight because of large water-soaked lesions that later become necrotic. On the fruits, smaller blister like spots occur at the early stages and later gain a warty appearance. The disease results in defoliation and severely spotted fruits, both of which cause massive yield losses |
| 2 | Soft Rot (Djami-Tchatchou et al. 2019) | *Pectobacterium caratovorum* | Penetrates and infects the chilli fruit through broken peduncles and calyx resulting in soft rot. As the infection progresses, the entire fruit is reduced to a watery mass |

**Table 1** (continued)

| Sr. no. | Disease | Causative agent | Symptoms |
|---|---|---|---|
| 3 | Wilt (Sanogo 2003; Tahat and Sijam 2010) | *Ralstonia solanacearum* | The bacterium invades the roots causing wilting of the host plant as a consequence of rapid colonization and multiplication in the vascular tissue, followed by light tan to yellow–brown discoloration of the vascular tissue. Affected leaves turn yellow and remain wilted. The plants attacked by this disease rot, wilt, and eventually die |
| Viral diseases | | | |
| 1 | Chilli mosaic virus disease ( Gopalakrishnan 2007) | *Tobacco mosaic (TMV)/Tomato mosaic (ToMV)/Cucumber mosaic virus* | TMV and ToMV cause light and dark green mosaics and distortion of leaves. Vein clearing, yellowing, mottling are characteristic symptoms. Necrotic flecks and spots can also appear on leaves. Stunted growth of infected plant is observed which does not normally bear fruits. If formed fruits are small, deformed, with chlorosis and necrosis in skin. Ring spot and necrotic spot symptoms are mostly seen in case of cucumber mosaic virus on the leaves or fruits of sweet pepper along with mild to moderate mosaic pattern |
| 2 | Leaf curl virus disease (Mishra and Chauvey 2018) | *Pepper leaf curl virus (PepLCV)* | The early symptoms include curling of the leaves toward the midrib at early plant growth stage thus getting deformed. Along with abaxial and adaxial curling; enations, heavy crinkling or puckering, chlorosis or yellowing and size reduction of leaves are observed. This is accompanied by shortening of internodes and petioles, blistering of inter veinal areas and thickening and clearing of the veins. Flower buds abscise before attaining full size and pollen development is hampered, leading to either no fruit set or setting of tiny fruits without any commercial value. In the advanced stages of disease, auxiliary buds are stimulated producing a cluster of small leaves and plant appears bushy with stunted growth producing no fruit |
| 3 | Pepper mottle virus disease (Peter and Hazra 2012) | *Pepper Mottle Virus* | Mottling is observed over the entire leaf surface especially in interveinal areas. Fruit becomes distorted and show mosaic pattern |
| 4 | Potato virus disease (Peter and Hazra 2012) | *Potato Virus Y* | Vein bending is seen along with the leaf distortion and plant stunting |
| 5 | Tomato spotted wilt (Mishra et al. 2013) | *Tomato Spotted Wilt Virus (TSWV)* | Leaves develop black small irregularly shaped to circular spots along with chlorotic and necrotic ring spots. Stems and shoots show black streak or lesions. Fruits develop chlorotic ring, patches and lesions. Severely infected plants are stunted and may wilt |

**Table 2** Toxicity of chemical agents used to control plant pathogens

| Sr. no. | Chemical agents | Pathogen | Toxicity | References |
|---|---|---|---|---|
| 1 | 1,3-Dichloropropene | *Ralstonia solanacearum* | Probable human carcinogen<br>Moderate to high aquatic toxicity | Markovitz and Crosby (1984)<br>Krijgsheld and Van der Gen (1986) |
| 2 | Azoxystrobin | *Sclerotium rolfsii* | Hazardous to the aquatic environment | van Wijngaarden et al. (2014) |
| 3 | Bavistin/Carbendazim | *Alternaria solani*<br>*Cercospora capsici*<br>*Colletotrichum capsici*<br>*Leveillula taurica*<br>*Phomopsis vexans*<br>*Sclerotinia sclerotiorum* | Disturb endocrine function in humans and wildlife, lead to impaired reproductive capacity, and have other toxic effects on sexual differentiation, growth, and development | Lu et al. (2004) |
| | | | Induce aneuploidy | Morinaga et al. (2004) |
| 4 | Bayleton | *Leveillula taurica* | Toxicological and pathological effects in animals | Bentley et al. (2000)<br>Tahir and Nour (2009) |
| 5 | Benlate | *Leveillula taurica* | Phytotoxic | Aragaki et al. (1994) |
| 6 | Blitox/copper oxychloride | *Colletotrichum capsici*<br>*Fusarium spp.*<br>*Phytophthora capsici*<br>*Pythium aphanidermatum*<br>*Rhizoctoni solani*<br>*Xanthomonas campesthis* | Hampers growth rate of juveniles and cocoon production in earthworms | Helling et al. (2000) |
| 7 | Captan | *Colletotrichum capsici*<br>*Fusarium spp.*<br>*Phytophthora capsici*<br>*Pythium aphanidermatum*<br>*Rhizoctonia solani* | Possible carcinogenic hazard | Bridges et al. (1972) |
| 8 | Chloropicrin | *Ralstonia solanacearum*<br>*Verticillium dahlia*<br>*Verticillium alboatrum* | Airborne-irritant | Goldman et al. (1987) |
| 9 | Chlorothalonil | *Alternaria solani*<br>*Cercospora capsici*<br>*Colletotrichum capsici* | Airborne-irritant | Lensen et al. (2007) |
| 10 | Dazomet | *Sclerotium rolfsii* | Hampers development of mycorrhiza-forming fungi | Iyer and Wojahn (1976) |
| | | | Anti-thyroid activity | Buxeraud et al. (1992) |
| 11 | Dithane M45 | *Colletotrichum capsici*<br>*Colletotrichum gloeosporioides* | Potential mutagenic and carcinogenic agent | Hemavathi and Rahiman (1993) |
| 12 | Flutolanil | *Sclerotium rolfsii* | Toxic effects on multiple developmental stages of aquatic life | Yang et al. (2016) |
| 13 | Fosetyl-Al | *Fusarium spp.*<br>*Phytophthora capsici*<br>*Pythium aphanidermatum*<br>*Rhizoctoni solani* | Reduced growth of roots and inhibition of mycorrhizal colonization | Sukarno et al. (1998) |
| 14 | Hexaconazole | *Colletotrichum capsici* | Shows genotoxic effects<br>Result in thyroid endocrine toxicity and other toxicity in aquatic fishes | Yilmaz et al. (2008)<br>Yu et al. (2013)<br>Wang et al. (2015) |
| 15 | Karathane | *Leveillula taurica* | Mutagenic, Clastogenic and Cytotoxic | Çelik et al. (2005) |
| 16 | Mancozeb | *Alternaria solani*<br>*Cercospora capsici*<br>*Fusarium spp.*<br>*Phytophthora capsici*<br>*Pythium aphanidermatum*<br>*Rhizoctoni solani*<br>*Sclerotinia sclerotiorum* | It degrades into ethylethiourea (ETU) which shows sperm abnormalities. It affects the central and peripheral nervous systems and causes endocrine disruption. It is carcinogenic – particularly affecting the thyroid teratogenic (interfering with embryonic development), and a general irritant | Atreya and Sitaula (2011) |
| 17 | Mercuric chloride | *Xanthomonas campesthis* | Genotoxic potential in a variety of organisms including humans and aquatic species | Betti et al. (1992)<br>Bolognesi et al. (1999) |

**Table 2** (continued)

| Sr. no. | Chemical agents | Pathogen | Toxicity | References |
|---|---|---|---|---|
| 18 | Metam sodium | *Sclerotium rolfsii* | Irritant, adverse effects on both non-target plants and soil microbes, potential for immunological, developmental, carcinogenic, and atherogenic effects | Pruett et al. (2001) |
| 19 | Methylbromide | *Sclerotium rolfsii* | Potent ozone depletor<br>Central and peripheral neurotoxic effects | Ristaino and Thomas (1997)<br>DeHaro et al. (1997) |
| 20 | Propiconazole | *Leveillula taurica* | Interferes with embryonic development of aquatic animals | Kast-Hutcheson et al. (2001) |
| 21 | Propineb | *Phytophthora capsici* | Carcinogenic in animals | Guven et al. (1998) |
| 22 | Tebuconazole | *Sclerotium rolfsii* | Neurobehavioral deficits and neuropathology in animals | Moser et al. (2001) |
| | | | Disrupts physiological activity in fish | Sancho et al. (2010) |
| 23 | Thiophanate-methyl | *Sclerotium rolfsii* | Prolonged exposure is considered as a cytogenetic hazard | Capriglione et al. (2011) |
| 24 | Thiram | *Colletotrichum capsici*<br>*Fusarium spp.*<br>*Phytophthora capsici*<br>*Pythium aphanidermatum*<br>*Rhizoctoni solani* | Potential mutagenic and carcinogenic agent | Hemavathi and Rahiman (1993)<br>Perocco et al. (1989) |
| 25 | Topsin | *Leveillula taurica* | Ovarian toxicity and oxidative stress in animals | Sakr et al. (2011) |

## Biocontrol agents against phytopathogens infecting chilli plants

Recent efforts have been focused on developing natural or biological control for the management of plant diseases for increasing the yield. Biocontrol is a safer option as it avoids environmental pollution and is specific to target pathogens. Being from a natural source they don't tend to pose any harm to plants, animals or humans. According to Eilenberg (2006), "biological control or biocontrol is the use of living organisms to suppress the population density or impact a specific pest organism, making it less abundant or less damaging than it would otherwise be". In other words, biological control is a phenomenon related to the antagonism between microorganisms (Cook 1985). Numerous microorganisms have been shown to be capable in suppressing plant pathogens and are therefore considered as biological control agents (BCAs). Table 3 summarizes BCAs against plant pathogens affecting chilli crops along with the suggested mode of action. Single BCA may show different modes of action against a phytopathogen which may be expressed sequentially, concurrently or synergistically. There are three main modes of antagonism exhibited by a candidate BCA against a phytopathogen: direct antagonism, indirect antagonism and mixed path antagonism (Pal and Gardener 2006).

## Direct antagonism

Direct antagonism, involves the principle of parasitism or predation. In predation, the predator (in this case a BCA) kills the prey (a phytopathogen) for its survival. Some predatory bacteria use the cytoplasmic constituents of other bacteria as a source of nutrition, thereby killing the later (Köhl et al. 2019). Parasitism is a biological interaction wherein the parasite (in this case a BCA) lives on or inside a host (a phytopathogen), thus harming the later. This type of antagonism is termed as hyperparasitism or mycoparasitism/mycophagy (when target pathogen is a fungus). In mycoparasitism, a BCA secretes lytic enzymes that lyse the fungal cell wall leading to the leakage or disorganisation of cell contents. Hyphal deformation (abnormal swelling, curling and branching of mycelia), vacuolization and disintegration have also been reported. This results in a decrease of pathogen population or even complete inhibition (Heydari and Pessarakli 2010). A study carried out by Sid Ahmed et al. (1999) evaluated *Trichoderma harzianum* as a biocontrol agent for root rot caused by *Phytophthora capsici* in pepper plants. The study revealed how the hypha of *Trichoderma harzianum* coils around those of *Phytophthora capsici* resulting in vacuolization and disintegration of the hyphae of later. Another study exhibited coiling, vacuolation and swelling of the hyphae of *Colletotrichum truncatum* by *Burkholderia rinojensi*, resulting in inhibition of the pathogen, thus suppressing the anthracnose in chillies (Sandani et al. 2019).

**Table 3** BCAs against plant pathogens affecting chilli crops and their mode of action

| Sr. no. | Pathogen | Bioagent | Suggested mode of action | References |
|---|---|---|---|---|
| 1 | *Alternaria alternata* | *Bacillus spp.* | Hyperparasitism | Sid et al. (2003) |
| 2 | *Cercospora capsici* | *Lactobacillus plantarum* | Induced Systemic Resistance | Adedire et al. (2019) |
| 3 | *Colletotrichum acutatum* | *Bacillus vallismortis* | Induced Systemic Resistance | Park et al. (2013) |
| 4 | *Colletotrichum capsici* | *Pichia guilliermondii*<br>*Trichoderma harzianum*<br>*Pseudomonas fluorescens*<br>*Ophiocordyceps sobolifera* | Induced systemic reistance<br>Hyperparasitism<br>Induced systemic reistance<br>Antibiosis | Chanchaichaovivat et al. (2007)<br>Nantawanit et al. (2010)<br>Ekefan et al. (2009)<br>Anand et al. (2010)<br>Jaihan et al. (2016) |
| 5 | *Colletotrichum gloeosporioides* | *Bacillus subtilis*<br>*Streptomyces sp.*<br>*Pseudomonas aeruginosa*<br>*Streptomyces philanthi* | Antibiosis<br>Hyperparasitism<br>Competition<br>Antibiosis | Kim et al. (2010)<br>Ashwini et al. (2014)<br>Kim et al. (2014)<br>Sasirekha and Srividya (2016)<br>Boukaew et al. (2018) |
| 6 | *Colletotrichum scovillei* | *Paenibacillus polymyxa* | Antibiosis | Suprapta et al. (2020) |
| 7 | *Colletotrichum truncatum* | *Burkholderia rinojensis*<br>*Trichoderma harzianum*, *Trichoderma asperellum*, *Paenibacillus dendritiformis* | Hyperparasitism<br>Induced systemic resistance | Sandani et al. (2019)<br>Yadav et al. (2021) |
| 8 | *Cucumber mosaic virus* | *Bacillus amyloliquefaciens* | Induced systemic resistance | Lee and Ryu (2016) |
| 9 | *Fusarium oxysporum* | *Pseudomonas aeruginosa*<br>*Bacillus subtilis*<br>*Trichoderma viride*,<br>*Trichoderma harzianum* | Competition/ Antibiosis<br>Competition<br>Hyperparasitism | Perveen et al. (1998)<br>Yu et al. (2011)<br>Dar et al. (2015) |
| 10 | *Fusarium pallidoroseum* | *Trichoderma viride*<br>*Trichoderma harzianum* | Hyperparasitism<br>Hyperparasitism | Wani and Najar (2012)<br>Dar et al. (2015) |
| 11 | *Fusarium solani* | *Pseudomonas aeruginosa*<br>*Bacillus subtilis*<br>*Pseudomonas fluorescens*<br>*Trichoderma viride*<br>*Trichoderma harzianum* | Competition/antibiosis<br>Induced systemic resistance<br>Induced systemic resistance<br>Hyperparasitism<br>Hyperparasitism | Perveen et al. (1998)<br>Sundaramoorthy et al. (2012)<br>Dar et al. (2015)<br>Bhat et al. (2016) |
| 12 | *Leveillula taurica* | *Cephalosporium sp.*<br>*Paecilomyces farinosus*<br>*Ampelomyces quisqualis*<br>*Trichoderma harzianum*<br>*Trichoderma asperellum*<br>*Metarhizium anisopliae*<br>*Pseudomonas fluorescens* | Not known<br>Antibiosis<br>Hyperparasitism<br>Hyperparasitism/Induced systemic resistance<br>Secretion of lytic enzymes<br>Induced systemic resistance/ Secretion of lytic enzymes | Kiss (2003)<br>Brand et al. (2009)<br>López et al. (2019)<br>Anand et al. (2010) |
| 13 | *Macrophomina phaseolina* | *Streptomyces sp.* | Secretion of lytic enzymes and waste products/Plant growth promoting activities | Alaa Fathalla and El-Sharkawy (2020) |
| 14 | *Pectobacterium carotovorum* | *Bacillus vallismortis* | Induced systemic resistance | Park et al. (2013) |
| 15 | *Pepper leaf curl virus* | *Streptomyces sp.* | Plant growth promoting activities | Putri et al. (2019) |
| 16 | *Phytophthora capsici* | *Trichoderma harzianum*<br>*Bacillus licheniformis*<br>*Streptomyces halstedii*<br>*Bacillus megaterium*<br>*Bacillus subtilis*<br>*Trichoderma hamatum*, *Pseudomonas aeruginosa* | Hyperparasitism/induced systemic resistance<br>Secretion of lytic enzymes<br>Hyperparasitism/mycophagy<br>Antibiosis<br>Antibiosis<br>Competition/antibiosis | Sid Ahmed et al. (1999)<br>Ahmed et al. (2000)<br>Sid et al. (2003)<br>Joo (2005)<br>Akgül and Mirik (2008)<br>Lee et al. (2008)<br>Chemeltorit et al. (2017) |

**Table 3** (continued)

| Sr. no. | Pathogen | Bioagent | Suggested mode of action | References |
|---|---|---|---|---|
| 17 | *Pythium aphanidermatum* | *Pseudomonas chlororaphis*<br>*Bacillus subtilis*<br>*Calothrix elenkenii* | Competition/antibiosis<br>Induced systemic resistance<br>Antibiosis | Khan et al. (2003)<br>Nakkeeran et al. (2006)<br>Manjunath et al. (2010) |
| 18 | *Ralstonia solanacearum* | *Bacillus megaterium*<br>*Enterobacter cloacae*<br>*Pichia guilliermondii*<br>*Candida ethanolica*<br>*Bacillus amyloliquefaciens* | Induced systemic resistance<br>Competition<br>Not known<br>Not known<br>Antibiosis | Nguyen et al. (2010)<br><br><br><br>Hu et al. (2010) |
| 19 | *Rhizoctonia solani* | *Pseudomonas aeruginosa*<br>*Bacillus thuringiensis*<br>*Pseudomonas fluorescens*<br>*Pseudomonas putida*<br>*Bacillus subtillis*<br>*Trichoderma viride*<br>*Trichoderma harzianum* | Competition/antibiosis<br>Antibiosis<br>Competition<br>Antibiosis<br>Antibiosis<br>Hyperparasitism<br>Hyperparasitism | Perveen et al. (1998)<br>Mojica-Marín et al. (2008)<br>Abeysinghe (2009)<br><br><br>Dar et al. (2015)<br>Lewis and Lumsden (2001) |
| 20 | *Sclerotium rolfsii* | *Gliocladium virens*<br>*Pseudomonas fluorescens*<br>*Pseudomonas putida*<br>*Bacillus subtillis*<br>*Trichoderma viride,*<br>*Trichoderma harzianum* | Antibiosis<br>Competition<br>Antibiosis<br>Antibiosis<br>Hyperparasitism | Ristaino et al. (1996)<br>Abeysinghe (2009)<br><br><br>Dar et al. (2015) |
| 21 | *Tobacco mosaic virus* | *Bacillus cereus* | Induced systemic resistance and plant growth promoting activities | Damayanti et al. (2007) |
| 22 | *Verticillium dahliae* | *Pythium oligandrum* | Induced systemic resistance | Al-Rawahi and Hancock (1998)<br>Rekanovic et al. (2007) |
| 23 | *Verticillium albo-atrum* | *Pythium oligandrum* | Induced systemic resistance | Rekanovic et al. (2007) |
| 24 | *Xanthomonas campestris pv. vesicatoria* | Lactic acid bacteria | Competition | Shrestha et al. (2014) |

## Indirect antagonism

Indirect modes of antagonism exhibited by BCAs can be either competition for space and nutrition with the pathogen or induction of resistance in the host against the pathogen. Competing for nutrients is generally observed among the species sharing the same ecological niche and having the same physiological prerequisites when resources are constrained. Such competition may lead to reduced proliferation or inhibition of the pathogen (Pal and Gardener 2006). A BCA may limit the growth of the pathogen by competing for host supplied nutrients (exudates, leachates, or senesced tissue), essential soluble nutrients (iron sequestering by producing siderophore) or for colonising root and plant tissues, thus depriving access of the pathogen at the infection site (Vurukonda et al. 2018). When starved of Iron, a *Bacillus* sp. exhibited inhibition of *Fusarium oxysporum* Schl. f. sp. capsici, the causal agent of wilt of *Capsicum annuum* by producing siderophores. This bacterium also did show antagonism against several other plant fungal pathogens, belonging to genus *Fusarium, Colletotrichum, Pythium, Magnaporthe* and *Phytophthora* (Yu et al. 2011). Another study revealed rapid root colonization of chilli plant by Arbuscular mycorrhizal (AM) fungi *Funneliformis caledonium* thus increasing the nutrient acquisition by plant and suppression of *Phytophthora* blight (Hu et al. 2020). Induced systemic resistance is an indirect type of antagonism wherein inoculation with BCAs triggers the induction or enhancement of defence mechanism of plants. This is achieved via production of defence related metabolites (phenolics, reactive oxygen species, phytoalexins, pathogenesis-related proteins) or via activation of pathways (jasmonic acid, salicylic acid) or via formation of physical barriers (modifications of cell walls and cuticles) (Jayapala et al. 2019; Köhl et al. 2019). Suppression of *Colletotrichum truncatum* Anthracnose in Chilli Pepper was observed due to resistance induced by *Trichoderma harzianum*, *Trichoderma asperellum* and *Paenibacillus dendritiformis* in host. The chilli plant exhibited enhancement of the activity of defence-related and antioxidative enzymes, accumulation of phenolic compounds and reactive oxygen species (Yadav et al. 2021). Another study revealed the suppression of disease symptoms caused by *Pectobacterium carotovorum*, *Phytophthora capsici* and *Colletotrichum acutatum* by a *Bacillus* sp. via induction of systemic resistance via a salicylic acid-dependent mechanism (Park et al. 2013). Jisha et al. (2019) reported the induction of defense enzymes peroxidase, polyphenol oxidase and phenylalanine ammonia lyase by *Pseudomonas aeruginosa* in chilli plant. Such induction of host systemic resistance also increased the total phenolic contents in the plant. Thus the strain of *Pseudomonas* proved to be capable of reducing antharcnose disease in chilli.

## Mixed path antagonism

In this type of antagonism BCAs produce secondary metabolites toxic to the target pathogens. This not only include antibiotics, but also lytic enzymes, unregulated waste products and volatile compounds. Such metabolites interfere in the pathogenesis of the target pathogen (Nega 2014). A BCA can also impart the host plant with growth promoting activities which boost the plant growth and help in disease suppression (Beneduzi et al. 2012). Plant growth promoting BCA can confer the host with various attributes like atmospheric nitrogen fixation, solubilisation of unavailable nutrients such as phosphate, potassium, zinc and silicon thus making it readily available to the plant. They also accelerate production of hormones viz. auxins (Indole Acetic Acid), cytokinin and gibberellins (Bhattacharyya and Jha 2012) or of enzymes such as 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, thus helping the plant tolerate various stress conditions (Pourbabaee et al. 2016). A BCA can alternatively secret lytic enzymes like proteases, amylases, lipases, chitinases, glucanases and cellulases which target and degrade the cell wall of pathogens (Subrahmanyam et al. 2020). A *Bacillus* sp. isolated from chilli rhizosphere produced appreciable levels of three mycolytic enzymes chitinase, glucanase and cellulase and showed antagonism against *Colletotrichum gloeosporioides* for management of anthracnose disease of chilli (Ashwini and Srividya 2014). Similar studies were undertaken by Nguyen et al. (2012), who reported increased activity of chitinase and β-1,3-glucanase in roots and surrounding rhizosphere soil of pepper plants treated with *Streptomyces griseus*. This resulted in suppression of Root Rot Disease cause *Phytophthora capsici* in the host plant. Microbial unregulated waste products such as Hydrogen cyanide (HCN) may also contribute to pathogen suppression by effectively blocking the cytochrome oxidase pathway. Volatile metabolite such as ammonia at a particular concentration has also been reported to be toxic to various fungal pathogens (Howell et al. 1988). Whereas other volatiles mainly alkenes, alcohols and ketones, are known stimulate plant growth by enhancing mineral uptake, modifying root structure and modulating hormone signalling. Bacterial volatiles also play important role in functions like bacterial motility, biofilm formation and induction of systemic resistance in the host plant (O'Brien 2017). Most of the times a BCA exhibit several of the above mentioned traits to help the host plant in growth and disease suppression. Treatment of chilli plant with a *Streptomyces* sp. positive for production of protease, chitinase, Indole Acetic Acid (IAA), siderophore, ammonia and HCN and phosphate solubilization activity reduced the percentages of damping-off and root rot severity caused by *Rhizoctonia solani* and *Macrophomina phaseolina* (Alaa Fathalla and El-Sharkawy 2020). Shrestha et al. (2014) reported potential of Lactic acid bacteria (LABs) to colonise roots, produce indole-3-acetic acid (IAA) and siderophores and solubilise phosphate. These LABs showed the inhibition of bacterial pathogens *Xanthomonas campestris* pv. vesicatoria and *Ralstonia solanacearum* which are the causative agents of leaf spot disease and wilt in *Capsicum annuum.* Apart from all these secondary metabolites, the major reason for antagonism is the production of antibiotics by BCAs. These are chemically heterogeneous group of organic, low-molecular weight antimicrobial compounds that hamper the growth or metabolism of the target microorganism at a particular concentration (Thomashow et al. 1997). Table 4 enlists some of the antimicrobial compounds produced by BCAs against pathogens affecting chilli plant. Each of these compounds have a different mode of action, thus some organisms are susceptible to certain antibiotics but others are not, depending on the specific moiety of cellular constituent the antibiotic attacks (Ulloa-Ogaz et al. 2015). Vegetative Catalase protein (KatA) produced by a *Bacillus* sp. induced abnormal conidial swelling and elongation and rupture of hyphae of *Colletotrichum capsici* thus suppressing the anthracnose disease of chili pepper (Srikhong et al. 2018). Wu et al. (2019) suggested that the lipopeptides produced by a *Bacillus* sp. inhibited mycelial growth of *Rizoctonia solani*, thus assisting in the suppression of disease symptoms in chilli plant. Another antimicrobial compound Gliotoxin exhibited anti oomycete activity against *Phytophthora capsici* thus suppressing blight in chilli (Tomah et al. 2020). Whereas the study by Ko et al. (2009) suggested that the inhibition of *Phytophthora capsici* by 4-hydroxyphenylacetic acid produced by *Lysobacter antibioticus* could be due to the deformation, lysis, and bending of hyphae of the fungus. Some antibiotics such as fusaricidin have been also known to induce systematic reistance in host (chilli) to suppress *Phytophthora* blight (Lee et al. 2013). Similar results were reported by Sundaramoorthy et al. (2012) wherein the synthesis of phytolaexins by *Bacillus subtilis* induced systemic resistance against wilt disease caused by *Fusarium solani* in chilli. Cell free supernatant of *Paenibacillus polymyxa* containing 3-hydroxy-2-butanone and 2,3-butanediol showed wrinkles on mycelia of *Colletotrichum scovillei* which causes anthracnose in chilli (Suprapta et al. 2020). Antimicrobial compound Phenazine-1-carboxamide produced by *Pseudomonas aeruginosa* showed deformation of mycelia and inhibition of

Table 4 BCAs producing antimicrobial compounds against phytopathogens infecting chilli crops

| Sr no. | BCA | Antimicrobial compound produced | Target pathogen | References |
|---|---|---|---|---|
| 1 | *Bacillus subtilis*<br>*Pseudomonas fluorescens* | Phytolaexins | *Fusarium solani* | Sundaramoorthy et al. (2012) |
| 2 | *Bacillus subtilis* | Surfactin<br>Iturin<br>Fengycin<br>Bacillomycin | *Rhizoctonia solani* | Wu et al. (2019) |
| 3 | *Lysobacter antibioticus* | 4-Hydroxyphenylacetic acid | *Phytophthora capsici* | Ko et al. (2009) |
| 4 | *Paenibacillus polymyxa* | 3-Hydroxy-2-butanone<br>2,3-Butanediol | *Colletotrichum scovillei* | Suprapta et al. (2020) |
| 5 | *Paenibacillus polymyxa* | Fusaricidin | *Phytophthora capsici* | Lee et al. (2013) |
| 6 | *Pseudomonas aeruginosa* | Phenazine-1-carboxylicacid | *Leveillula taurica, Colletotrichum capsicum* | Rane et al. (2007) |
| 7 | *Pseudomonas aeruginosa* | Phenazine-1-carboxamide | *Colletotrichum capsici* | Kumar et al. (2005) |
| 8 | *Pseudomonas fluorescens* | Pyoluteorin<br>Pyrrolnitrin<br>Orfamide A | *Phytophthora capsici* | Kim et al. (2014) |
| 9 | *Trichoderma virens* | Gliotoxin | *Phytophthora capsici* | Tomah et al. (2020) |
| 10 | *Trichoderma koningiopsis* | Azetidine<br>2-phenylethanol Ethyl hexadecanoate | *Colletotrichum gloeosporioides* | Ruangwong et al. (2021) |

sporulation thus inhibiting the growth of fungal pathogen *Colletotrichum capsici* causative agent of fruit rot in chilli (Kumar et al. 2005).

## Conclusion

Biological control agents (BCAs) have generated great enthusiasm as safe and sustainable plant protection tool but still make up only a small percentage of the chilli crop protection market due to lack of availability of formulated products. There is a need for more extended biocontrol research and better understanding of the mechanisms involved in the antagonistic abilities of microbial BCAs so as to improve its efficacy, stability and consistency in fields. The present review identifies potential microbial BCAs with inhibitory activity against various fungal, bacterial and viral pathogens infecting the chilli crop. This review also gives us insight of how BCAs (single or consortium) employ several mechanisms (direct, indirect and mixed path antagonism) to act as an effective biocontrol agent against target pathogens and trigger different promotional effects on chilli plant growth parameters. Being from a natural source these BCAs are also safe to the environment and thus are a great alternative to replace chemical counterparts which are harmful to environment and ecology. Moreover, the field trials of chilli plants inoculated with these microbial BCAs have also proven its effect *in-vivo*. In conclusion, through thorough understanding of biocontrol activities of such microbes, multiple facets of disease suppression and plant growth promotion is revealed. This will thus aid in the achievement of the objective of commercialization of potential strains against the target pathogens and their implementation in the agriculture industry for protection of chilli plants.

## Declarations

**Conflict of interest** The authors declare that they is no conflict of interest.

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