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Unlocking the potential of *Cannabis sativa* L. – interactions with microorganisms for growth, protection and cannabinoid production: A review

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ABSTRACT

Cannabis sativa L., also called hemp, is a plant of the Cannabaceae family that originates from central and southwest Asia. Over time, the genetic diversity of cannabis has expanded, leading to the emergence of numerous distinct genotypes characterized by varied phenotypes and a wide range of secondary metabolites. These metabolites exhibit diverse biological properties and are utilized in human medicine and the pharmaceutical industry. *Cannabis sativa* L. includes different genetically distinct biotypes, notably industrial hemp and recreational cannabis. It has been used for its fiber, oil, food, and medicinal properties, as well as for recreational and religious purposes. It contains various bioactive substances such as alkaloids, flavonoids, terpenoids, and cannabinoids. The concentrations of these secondary metabolites vary significantly depending on the plant genotype and environmental factors, whether abiotic or biotic. Microorganisms associated with *Cannabis sativa L.*, whether residing on the surface, within tissues, or in cultivated soils, exhibit significant genetic diversity. They provide benefits, such as promoting plant growth, protecting against pathogens, improving mineral absorption, and influencing the production of secondary metabolites. The use of beneficial microorganisms, such as PGPR bacteria, endophytic fungi, or their bioactive molecules, could play a key role in enhancing cannabinoid production in cannabis plants. Although the chemistry of cannabis has been extensively studied, further research is needed to understand the influence of biotic and abiotic factors on the variation in synthesized cannabinoid levels. This review provides a comprehensive overview of *Cannabis sativa L.*, specifically focusing on its associated microorganisms and their interactions with the plant. It also explores opportunities for the optimal utilization of this plant, particularly focusing on its microorganisms, to enhance growth, protect against bio-aggressors, and promote cannabinoid biosynthesis. This paper also reviews current investigations and suggests various opportunities for further research perspectives.

Keywords: Cannabis plant, cannabinoid, associated microorganisms, genotype, biostimulant, biopesticide.

INTRODUCTION

Cannabis sativa L. is a multipurpose plant of significant economic, pharmaceutical, and industrial interest due to its rich repertoire of bioactive compounds. Among these, cannabinoids and terpenoids are the most prominent, with applications spanning the pharmaceutical, cosmetic, and agrochemical sectors (Morales et al., 2017; Aliferis and Bernard-Perron, 2020; Nelson et al., 2020; LaVigne et al., 2021). The plant's therapeutic potential is also influenced by secondary compounds like cannabigerol (CBG) and cannabichromene (CBC), in addition to the primary cannabinoids Δ-tetrahydrocannabinol (THC), cannabidiol (CBD), and cannabinol (CBN) (Flores-Sanchez and Verpoorte, 2008; Aliferis and Bernard-Perron, 2020). With their antimicrobial and antifungal properties, these metabolites – which are mostly produced in the glandular trichomes of female flowers – not only contribute to plant defense but also serve as the foundation for the pharmacological value of the plant (McPartland, 1984; Taura et al., 2007; Happyana et al., 2013; Elsohly et al., 2017; Ahmed and Hijri, 2021).

However, cannabinoid yield and composition are highly influenced by genetic, environmental, and biotic factors, including pathogenic microbes and insect pressures (Meijer et al., 2003; Ahmed and Hijri, 2021). Traditional chemical synthesis of cannabinoids remains costly and inefficient due to the complexity of their molecular structures (Wang et al., 2024). Therefore, the use of beneficial microorganisms, including microalgae, endophytic fungi, and plant growth-promoting rhizobacteria (PGPR), to increase cannabinoid biosynthesis in plants is gaining popularity as a biotechnological alternative (Carvalho et al., 2017; Gorelick and Bernstein, 2017; Pagnani et al., 2018; Luo et al., 2019; Kakabouki et al., 2021).

Several studies have highlighted the efficacy of such microbial inoculants. For instance, Pagnani et al. (2018) reported increased accumulation of CBD, CBN, and THC in the "Finola" hemp variety following PGPR treatment. Similarly, Kakabouki *et al.* (2021) demonstrated enhanced CBD content and biomass upon inoculation with *Trichoderma harzianum*. Ahmed et al. (2023) further expanded this concept by applying a microbial consortium, including *Rhizophagus irregularis*, *T. harzianum*, *Bacillus subtilis*, *Dictyosphaerium chlorelloides*, and native forest soil microbes, resulting in significant cultivar-specific changes in cannabinoid profiles. In parallel, advances in microbial biosynthesis, such as the expression of cannabinoid synthase genes in engineered microorganisms like *Komagataella phaffii*, offer a controlled and scalable alternative to traditional plant extraction (Zirpel et al., 2015; Poulos and Farnia, 2016).

Despite these promising developments, the cannabis-associated microbiome, or phytomicrobiome, remains underexplored due to long-standing legal restrictions in many countries. A recent bibliometric study by Laaboudi et al., 2024 analyzing several publications between 2012 and 2022 revealed a research bias toward medical and biochemical aspects, with limited focus on beneficial microbiota, particularly in regions like Morocco. To overcome this gap, a more comprehensive understanding of the structure and function of cannabis microbial communities is crucial.

OVERVIEW OF THE PLANT

According to Clarke and Merlin (2016), the oldest known plant, *Cannabis sativa L.*, was initially domesticated in Southeast Asia after being found more than 12,000 years ago in Central Asia (India and China), namely in the area surrounding the Altai Mountains (Halioua et al., 2020). Due to the high-value natural components in their fiber, grain, and flower, cannabis plants have been grown for a variety of purposes, including the production of textile fiber and food for humans and animals, the treatment of various illnesses and symptoms (Benkhnigue et al., 2010; Salhi et al., 2010; Chaachouay et al., 2021, 2022a, 2022b 2023; Amallah et al., 2024), and religious and recreational purposes (Russo et al., 2008; Piluzza et al., 2013; Amaducci et al., 2015; Clarke and Merlin, 2016; Calzolari et al., 2017; Zhang et al., 2020; Santos and Romao, 2023).

Cannabis research has been of interest for a long time, and the first document listed in Scopus is a correspondence by William Ley, dated 1844, entitled 'The medicinal properties of Indian hemp' published in The Lancet. This was followed in 1845 by a publication by M. Donovan in The Dublin Journal of Medical Science, entitled "On the physical and medicinal qualities of Indian hemp (*Cannabis Indica*), with observations on the best methods of administration and cases illustrating its effects" (Laaboudi et al., 2024).

Cannabis is an annual herbaceous plant that belongs to the *Cannabaceae* family, order *Urticales*. More than 600 varieties of cannabis are currently available in the global market, growing at varying altitudes, soil, and climate conditions (Rahn et al., 2016; Clarke and Merlin, 2016; Aliferis and Bernard-Perron, 2020).

The name *Cannabis sativa* L. is used to designate the species or varieties of the genus Cannabis, although the exact number of species is debated (Figure 1). Some authors recognize a single species, which is C. sativa L., while others identify up to seven species, including *C. ruderalis, C. sativa* ssp. *sativa, C. sativa* ssp. *spontanea, C. indica* ssp. *kafiristanica, C. indica* spp. *indica, C. indica* ssp. afghanica *and C. indica ssp. chinensis,* based on geographical, chemical and

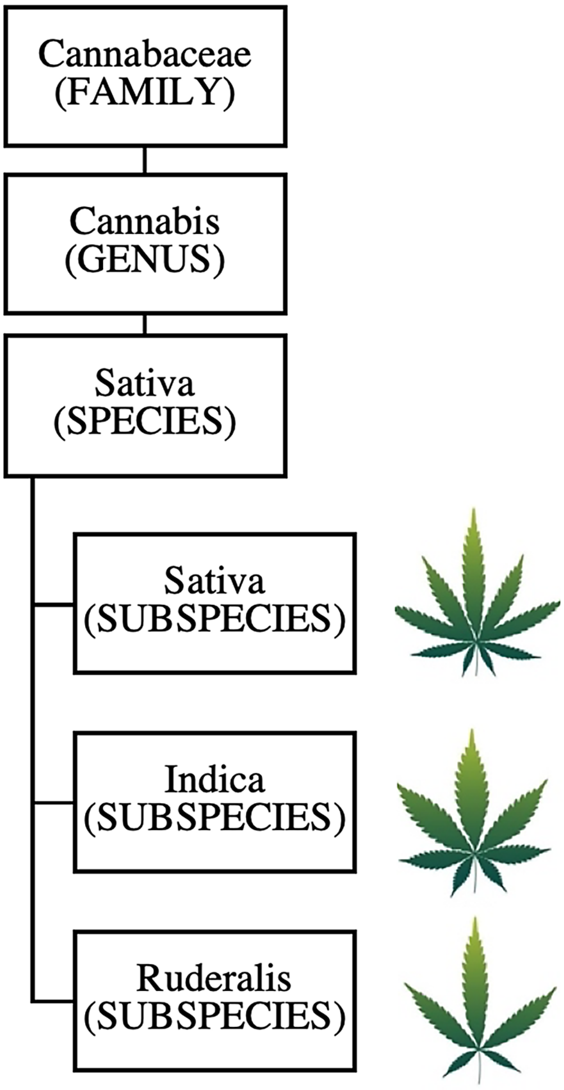

Figure 1. Classification of *Cannabis* plant

phenotypic criteria (Linnaeus, 1753; McPartland, 1984; Clarke and Watson, 2000; Hillig, 2005).

The two main chemical groups of cannabis (*Cannabis sativa* L.), a complex, polymorphic plant species that produces a wide range of bioactive metabolites (Chaachouay et al., 2023), are cannabinoids and terpenoids. However, the psychoactive cannabinoid tetrahydrocannabinol (Δ9-THC), which is used as a recreational drug as well as to treat pain and other medical conditions, and the non-psychoactive cannabidiol (CBD), which is used as a source of fiber for textile production and oil seeds, are the two main cannabinoids that have monopolized research interest (Russo, 2011; Carvalho et al., 2017; Aliferis and Bernard-Perron, 2020).

According to Lewis et al. (2018), cannabis strains are divided into three types: Type I, which has a high Δ9-THC content; Type II, which has varying Δ9-THC to CBC ratios; and Type III, which has a high CBD content. Nonetheless, the bioactivity of other cannabis metabolites, especially terpenoids, has led to the proposal of a chemovar classification that takes into account the entirety of its bioactive components, which probably offers a more thorough explanation of their characteristics (Hazekamp and Fischedick, 2012; Hazekamp et al., 2016; Fischedick, 2017; Aliferis and Bernard-Perron, 2020).

GENETIC DIVERSITY

The genetic diversity of cannabis has grown throughout time, resulting in a large range of genotypes with unique phenotypic traits and secondary metabolites (Ahmed et al., 2023). In both human health and the pharmaceutical sector, these metabolites exhibit a variety of biological functions (Taghinasab and Jabaji, 2020).

Molecular typing of cannabis based on DNA fingerprinting makes it possible to identify its variety with certainty and to pinpoint regions of production and distribution (Miller Coyle, Palmbach et al., 2003). Currently, a large number of molecular biology techniques are used to analyze DNA extracted from *C. sativa* L. plant material (seeds, leaves, and stems). These include AFLP (Amplified Fragment Length polymorphism) and sequencing (Kojoma, Seki et al., 2006), ISSR (Inter Simple Sequence Repeats) analysis (Seyit Ali Kayis, 2010) and STR (Short Tandem Repeats) microsatellite analysis. The first STRs for *C. sativa* L. were developed by Gilmore and Peakall (2003) identified 15 microsatellites in Australia. In the same year, 11 additional STRs were discovered by a different group of researchers (Alghanim and Almirall, 2003; Hsieh, Hou et al. 2003). According to the validation standards of the Scientific Working Group on DNA Analysis Methods (SWGDAM), the first STR multiplex created by Gilmore (Gilmore and Peakall, 2003) was approved for use in standard forensic analysis. All these techniques provide the possibility of exploring genetic variability between cannabis plants based on their genetic profiles and represent a powerful investigative tool.

Despite advancements in cannabis breeding, factors like parent plant sex, genotypes, growing techniques, and exposure to environmental stressors can all have a substantial impact on cannabinoid levels, especially those of CBD and Δ9-THC. (Saloner and Bernstein, 2020; Danziger and Bernstein, 2021a, 2021b; Backer et al., 2019).

The plant genotype is also critical in influencing the microbial communities, which are vital for plant health and are often referred to as the plant's "second genome" (Ahmed and Hijri, 2021).

Numerous investigations have demonstrated that particular microorganisms, such as bacteria and fungi, can activate the host plants' biosynthetic and signaling pathways, resulting in the synthesis of metabolic chemicals that are significant for pharmacological or agronomic purposes (Ryffel et al., 2016; Pascale et al., 2020). Associated bacteria are also essential to the manufacture of cannabinoids in cannabis (Ahmed and Hijri, 2021). They are still underutilized and mainly untapped for the production of cannabis, nevertheless.

ASSOCIATED MICROORGANISMS AND DIFFERENT INTERACTIONS WITH CANNABIS

The link between various plant parts and one or more microorganisms, such as bacteria or fungi, is referred to as plant-microbiome interaction (Albatnan et al., 2025). For example, rhizospheric soil is a potential source of beneficial microbial diversity that positively affects plant health (Weller et al., 2002; Philippot et al., 2013; Berendsen et al., 2012; Errifi et al., 2024a, 2024b).

Bacillus, Azospirillum, Streptomyces, Pseudomonas, Azotobacter, Alcaligenes, Arthrobacter, Burkholderia, and *Enterobacter* are among the bacteria that can enhance the growth of vegetative plants and fight off phytopathogens (Lugtenberg et al., 2009; Borriss, 2011; Santoyo et al., 2012; Berg et al., 2014; Qessaoui et al., 2019; Wei et al., 2019; Elbouazaoui et al., 2022a, 2022b). Bacteria generally work by producing antibiotics and phytohormones, solubilizing minerals, inducing host defenses and immunity through parasitism, competition, quorum sensing, induced systemic resistance (ISR), and parasitism (Rascovan et al., 2016; Eljounaidi et al., 2016; Win et al., 2018; Cordovez et al., 2019).

Plant growth-promoting rhizobacteria (PGPR) isolated from the rhizosphere of *Cannabis sativa L.* cultivated in the Rif plains were the subject of a 2019 study by Nafis et al. Five actinobacterial strains were found by the researchers; four of these were from the Streptomyces genus and one was from the Nocardioides species. These strains demonstrated the ability to fix nitrogen and solubilize potassium. Similarly, microbial communities known as endophytic fungi are essential to the growth and development of plants (Hardoim et al., 2015; Msairi et al., 2023; Laanaya et al., 2025). These microbes have different ways of working (Elouark et al., 2025). By generating phytohormones, obtaining nutrients (Soufiani et al., 2022), solubilizing phosphate (Kribel et al., 2019a, 2019b; Ourras et al., 2025; Kerroum et al., 2025), fixing nitrogen, and assisting plants in surviving a variety of biotic and abiotic stress conditions (Maheshwari et al., 2019; El Aymani et al., 2023), they support plant growth (Qostal et al., 2020; Mouden et al., 2023; El Kaissoumi et al., 2023, 2023; Sellal et al., 2024).

By inducing resistance to host pathogen defenses through systemic acquired resistance and ISR (Van der Ent et al., 2009; Busby et al., 2016; Taghinasab et al., 2018), or by antibiosis and mycoparasitism (Silva et al., 2019), endophytic fungi serve as a systemic boost of the plant immune system in the event of pathogen attack.

Like any plant species, cannabis harbors a diverse microbial community in terms of its genetic diversity. This microbiome rhizospheric, phyllospheric and endospheric plays several roles, including stimulating plant growth, improving mineral uptake, protecting against pathogen attack, and contributing to the production of certain phytocannabinoid compounds (Turner et al., 2013; Alegria et al., 2016; Jacoby et al., 2017; Taghinasab and Jabaji, 2020; Kakabouki et al., 2021; Ahmed and Hijri, 2021; Singh et al., 2022; Ahmed et al., 2023), especially in plants with limited root systems, such as *Cannabis.*

Kusari et al. carried out the first investigation into endophytic fungi associated with *Cannabis sativa L.* in 2012. 30 strains of Ascomycota, belonging to species like *Aspergillus, Eupenicillium, Penicillium,* and *Paecilomyces,* were found in a variety of plant tissues. Gautam et al. (2013) expanded on this work by reporting six more genera that were isolated from leaves, stems, and petioles: *Cladosporium, Phoma, Colletotrichum, Rhizopus* and *Curvularia*. Later research, such as that conducted by McKernan et al. (2015), discovered other fungus genera from cannabis petioles, including *Aspergillus, Penicillium, Alternaria, Cladosporium,* and *Cryptococcus.*

In 2018, Scott *et al.* identified Aureobasidium and Cochliobolus strains in hemp leaf tissues and seeds cultivated in Canada. More recently, Punja and Scott (2023) isolated additional endophytic fungi from stems and rootsincluding *Acremonium alternatum, Lecanicillium aphanocladii, Metarhizium anisopliae, Trichoderma harzianum,* and *Humicola.*

At the same time, Msairi et al. (2023) investigated arbuscular mycorrhizal fungi (AMF) in the rhizosphere of Taounate-grown *Cannabis sativa L.* They identified a diverse assemblage of endomycorrhizal fungi associated with two hybrid varieties, Critical and Khardala, including the genera *Rhizophagus, Acaulospora, Glomus, Funneliformis, Gigaspora, Dentiscutata and Scutellospora.*

A variety of parameters, including cultivar type, plant tissues, soil type, and development stage, affect the microbial composition of cannabis, which varies in terms of abundance, distribution, and diversity (Winston et al., 2014; Comeau et al., 2020, 2021; Ahmed and Hijri, 2021). The dominant bacteria were Norcardiodaceae and Streptomycetaceae of the phylum Actinobacteria, while the dominant fungi were identified as *Aspergillus, Fusarium, Burkholderiaceae* and *Zopfiella* of the phylum Proteobacteria (Ahmed and Hijri, 2021).

Microbes may colonize epiphytes (plant surfaces) or cannabis (plant tissues) (Scott et al., 2018; Comeau et al., 2020; Ahmed and Hijri, 2021). By boosting development, defending against biotic and abiotic stressors, and releasing nutrients for plants, they can serve as plant growth-promoting bacteria (PGP) regardless of how they colonize (Deng et al., 2022).

According to a study by Comeau et al. (2021), inoculating *Cannabis sativa L.* with a combination of Bacillus and Pseudomonas species resulted in a notable 70% increase in production. According to genomic study, Pseudomonas species are closely linked to the stimulation of plant growth, while Bacillus species are important in regulating the richness of the rhizosphere microbiome (Comeau et al., 2020, 2021).

In order to prevent the growth of the pathogen *Fusarium oxysporum*, a recent study by Corredor-Perilla et al. (2023) showed the advantageous qualities of Bacillus strains isolated from the rhizosphere of *Cannabis sativa L.*, including improving seed germination, increasing phosphorus availability, and controlling pathogenic growth. In a related work, Hu et al. (2023) inoculated cannabis roots with strains of *Metarhizium* and *Pochonia chlamydosporia.* The findings showed notable gains in shoot length, stem weight, and root weight as well as improvements in vegetative development.

Diseases and epidemics caused by bacteria, fungi, viruses, and insect pests represent major challenges for cannabis cultivation. Among these attacks, fungi and oomycetes are the most frequent, whereas those caused by viruses and bacteria are less common (Punja, 2021). According to previous studies, *Fusarium* and *Pythium* species are the most destructive to cannabis cultivation, with losses of up to 30% in production (Punja, 2021; Gwinn et al., 2022).

Numerous bacteria, such as *Pseudomonas orientalis, Pseudomonas fulva* and *Panibacillus* sp., as well as fungal endophytes, such as *Paecilomyces lilacinus, Alternaria niger* and *Penicillium copticola* have proven to be effective biocontrol agents in cannabis, exhibiting potential against a range of pathogens, such as *Botrytis cinerea, Trichothecium roseum, Curvularia lunata, Fusarium solani, Fusarium oxysporum* and *Aspergillus niger* (Kusari et al., 2012; Gautam et al., 2013; Qadri et al., 2013; Afzal et al., 2015; Scott et al., 2018).

According to recent research, using strains of *Gliocladium catenulateum, Trichoderma harzianum, Trichoderma virens, Trichoderma asperellum,* and *Bacillus amyloliquefaciens* decreased the severity of *Fusarium oxysporum* in cannabis by 30–56.3% during the vegetative and flowering stages (Gwinn et al., 2022; Scott et al., 2018). To investigate other bioproducts for disease control in cannabis, more investigation is necessary.

Research on cannabis-associated microorganisms is an emerging field that requires further attention. Understanding their beneficial roles in plant nutrition, pest and disease defense, and stress resilience is needed to unlock their potential as biostimulants and biopesticides, which could enhance plant health, boost productivity, reduce external inputs, and minimize environmental impacts (Figure 2).

CANNABINOID BIOSYNTHESIS

Cannabinoids and terpenoids are the two main chemical groups that comprise the diverse range of bioactive substances found in *Cannabis sativa* L. These substances are mostly used in the agricultural, cosmetic, and pharmaceutical sectors

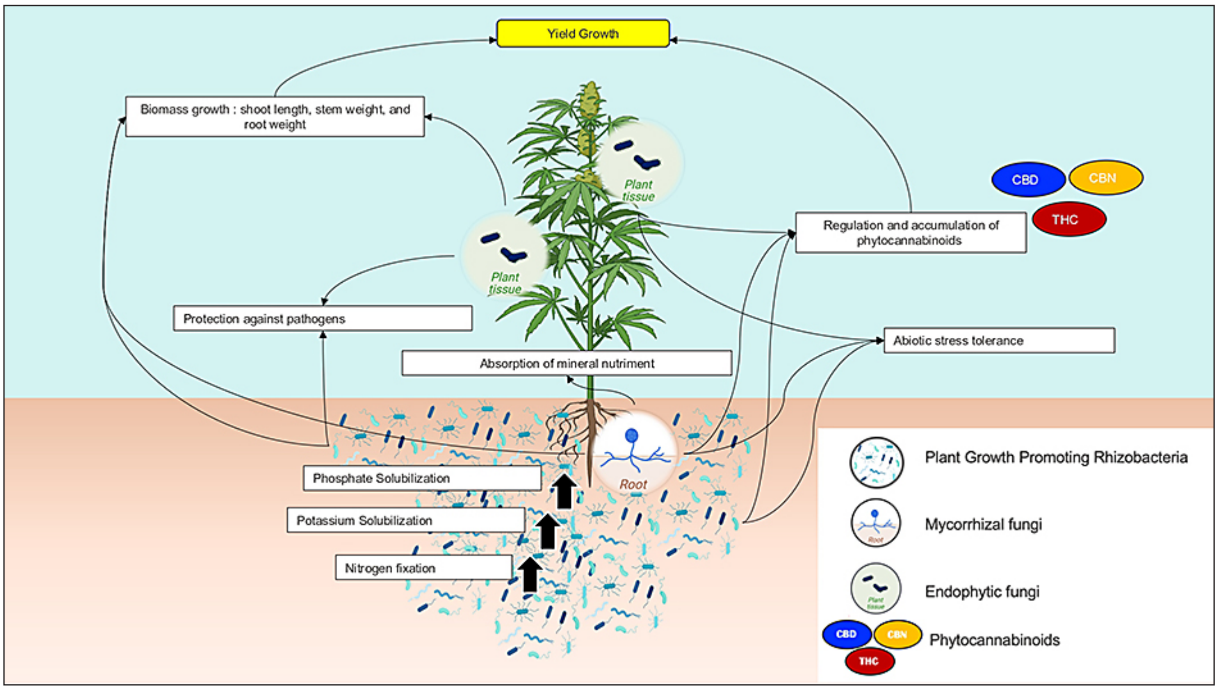

Figure 2. Potential modes of action of beneficial microorganisms in cannabis plant

(Morales et al., 2017; Aliferis and Bernard-Perron, 2020; Nelson et al., 2020; LaVigne et al., 2021). According to Flores-Sanchez and Verpoorte (2008) and Aliferis and Bernard-Perron (2020), the primary cannabinoids that are created are Δ9-tetrahydrocannabidiol (Δ9-THC), CBD, and cannabinol (CBN). These are followed by cannabigerol (CBG), cannabichromene (CBC), and other trace amounts. According to McPartland (1984), Δ9-THC and CBD help cannabis plants fight against infections, whereas CBG and CBD have modest antifungal effects (Elsohly et al., 2017). The secretory head cells of glandular trichomes, particularly the capitate-stalked glandular hairs of female flowers, are the primary site of cannabinoid production (Taura et al., 2007; Brenneisen, 2007; Happyana et al.2013, Aliferis and Bernard-Perron, 2020; Ahmed and Hijri, 2021).

As noted by Meijer et al. (2003) and Ahmed and Hijri (2021), the genotype of the plant, cultivation practices, biotic (such as the presence of pathogenic microbes and insects), and abiotic (such as temperature, day length, soil pH, and nutrient levels) factors all have a significant impact on the production of these secondary metabolites.

The intricacy of cannabinoids makes their chemical synthesis expensive and ineffective. It is currently possible to obtain Δ9-THC and CBD through chemical synthesis or extraction from cannabis (Wang et al., 2024). A different strategy is to use beneficial biostimulant microorganisms, including endophytic fungi or PGPR bacteria, or their bioactive compounds to biosynthesize cannabinoids (Carvalho et al., 2017; Gorelick and Bernstein, 2017; Pagnani et al., 2018; Luo et al., 2019; Kakabouki et al., 2021).

Pagnani et al. (2018) conducted the first investigation on the application of PGPR and found that a group of PGPR (*Gluconacetobacter diazotrophicus, Herbaspirillum seropedicae, Azospirillum brasilense* and *Burkholderia ambifaria*) boosted the accumulation of CBD, CBN, and Δ9-THC in C. sativa "Finola." Kakabouki et al. (2021) showed in another study that inoculating hemp with *Trichoderma harzianum* enhanced its biomass and CBD content.

The potential of microbial inoculants to increase phytocannabinoid synthesis in *Cannabis sativa* L. was highlighted in a recent study by Ahmed et al., (2023). The microalga *Dictyosphaerium chlorelloides*, *Bacillus subtilis, Trichoderma harzianum, Rhizophagus irregularis*, and a microbial solution from forest soil dominated by Planctobacteria spp. were among the inoculants that were evaluated. According to this study, depending on the kind and cultivar, these inoculants may have a considerable impact on phytocannabinoid profiles.

There is a substitute for cannabis biosynthesis. Microbial biosynthesis of cannabinoids is one of these; it provides a more regulated and effective substitute for conventional plant-based extraction techniques, which are frequently constrained by environmental conditions and the supply of high-quality cannabis plants. THCA synthase expression in the yeast *Komagataella phaffii* enabled the bioconversion of CBGA to Δ9-tetrahydrocannabinolic acid (Δ9-THCA), as Zirpel et al. (2015) showed. The microbial production of cannabis in genetically modified microorganisms was the subject of a 2016 patent application submitted by Poulos and Farnia.

Such innovations are important for scaling up cannabinoid production, particularly in the pharmaceutical and medical industries where the demand for cannabinoids such as Δ9-THC and CBD is increasing. These developments could potentially lower production costs, enhance the consistency and purity of cannabinoids, and reduce reliance on plant cultivation, which face challenges related to land use, climate, and crop management. Progress in microbial biosynthesis represents a promising area for future research, with the potential to revolutionize the cannabinoid industry by providing an alternative to traditional plant extraction methods while ensuring sustainable and efficient production processes.

CONCLUSIONS

This literature analysis highlights the considerable potential of plant–microbe interactions in enhancing the culture and metabolic yield of *Cannabis sativa* L. The evidence collected indicates that plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and endophytic microorganisms can significantly affect plant development, resilience to biotic and abiotic stresses, and the quantitative and qualitative profiles of cannabinoids, including CBD and THC. The consequences are very different depending on the plant genotype, the type of microbes involved, and the environment. This illustrates the complexity and specificity of these symbiotic relationships.

Moreover, recent advances in synthetic biology and microbial engineering have paved the way for the heterologous biosynthesis of cannabinoids in microbial platforms, presenting new opportunities for controlled, scalable, and sustainable production systems. However, the cannabis-associated microbiome's diversity, structure, and functional activities are still not well understood, notably in ecological zones where microbial biodiversity associated with cannabis remains understudied due to legal restrictions on cannabis cultivation and the complexity of microbial communities in diverse agroecological contexts.

Further multidisciplinary investigations are required to describe the microbial communities linked to various cannabis cultivars, clarify their functions in the manufacture of secondary metabolites, and create targeted bioinoculants that satisfy the expanding needs of this rapidly evolving industry.

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