Chapter 6 Endophytic Fungi of *Baccharis*



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Abstract Endophytic fungi are important mediators in the structure and dynamics of terrestrial plant communities and their relationships with associated fauna. Although endophytic fungi are found in all living plants, only 1% of all *Baccharis* species (*Baccharis artemisioides*, *B. coridifolia*, *B. dracunculifolia*, *B. megapotamica*, and *B. trimera*) have had their endophytic mycota studied. To date, 28 genera of endophytic fungi have been identified in association with species of *Baccharis*. Analysis of the enzymes and metabolites produced by this mycota indicates that these endophytes have numerous properties that may be related to better performance and resistance of their *Baccharis* host to several stressors and natural enemies. Many of these endophytes have properties that can be exploited for the development of beneficial applications in the fields of agronomy, pharmacology, and conservation, making them a particularly important group for the development of biotechnological products.

Keywords Antimicrobial activity · Bioprospecting · Fungal endophyte diversity · Plant performance · Secondary metabolites

1 Introduction

Endophytic fungi are a group of fungi that live inside plant tissues without causing harm to the host (Faeth and Fagan 2002; Hyde and Soytong 2008). They produce a variety of enzymes and secondary compounds, which favor nutrient cycling (Sun et al. 2011; Behie and Bidochka 2014), improve plant performance and resistance to adverse conditions such as droughts and high temperatures (Rodriguez et al.

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G. W. Fernandes et al. (eds.), *Baccharis*, https://doi.org/10.1007/978-3-030-83511-8_6

2004; Hubbard et al. 2014; Bilal et al. 2020), and minimize damage caused by herbivores and pathogenic microorganisms (Breen 1992, 1993, 1994; Fernandes and Price 1992; Hammon and Faeth 1992; Faeth and Hammon 1997; Raps and Vidal 1998; Faeth 2002; Meister et al. 2006; Oki et al. 2008, 2021; Grunseich et al. 2020). These cryptic organisms have been ignored for a long time, and their importance in species interactions and to biodiversity has been rarely studied until recently (Oki et al. 2016). According to a survey of the Web of Science database, it wasn't until the 1990s that scientific articles started to regularly use the term "endophytic fungi" (Fig. 6.1). Although the number of studies on endophytic fungal communities has progressively increased since then, there were still only 557 publications in the first decade of the twenty-first century. Approximately 75% of all the articles about endophytes retrieved by the survey (3043 articles published from 1945 to 2019) were published in the last 10 years (2279 articles between 2010 and 2019). The discovery of the importance of endophytes in nature has captured the attention of researchers and brought a wide prospective for research and applied perspectives.

Although scientific knowledge about these microorganisms is relatively recent, investigations have highlighted their remarkable diversity and wide distribution. Hundreds of species of endophytic fungi may inhabit a given host plant, with their richness being influenced by the phylogeny, ontogeny, and organs, among other factors, of the host species (Arnold et al. 2000; Cannon and Simmons 2002; Arnold and Herre 2003; Arnold and Lutzoni 2007; Banerjee 2011; Oki et al. 2016; Griffin and Carson 2018). The high diversity of endophytes indicates a wide variety of

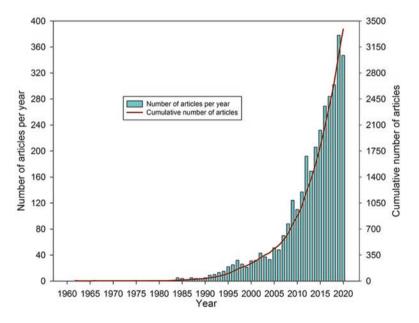


Fig. 6.1 Number of articles found in the Web of Science database (1945 to 2020) published with the term "endophytic fungi" per year and cumulatively

relationships with host plants and possibly a large number of ecological functions as well (Caruso et al. 2020). In this chapter we focus on the diversity and distribution of endophytic fungi found in association with species of *Baccharis*, a genus of shrubs and herbs that occupy many different habitats and ecosystems in their native range in the Americas, and highlight their ecological and economic potential.

2 Distribution and Diversity of Endophytic Fungi of Species of *Baccharis*

Despite there being 422 described species in the genus *Baccharis*, the associated endophytic fungal community is known for only 5: Baccharis artemisioides, B. coridifolia, B. dracunculifolia, B. megapotamica, and B. trimera (Table 6.1) (Heiden and Pirani 2016, see also Chap. 2 in this book). Nevertheless, 31 genera of endophytic fungi have already been reported from these 5 species: Alternaria, Aureobasidium, Acremonium, Aspergillus, Biscogniauxia, Ceratopicnidium, Chaetomium, Cladosporium, Cochliobolus, Colletotrichum, Cercospora, Coriolopsis, Cylindrocladium, Diaporthe, Epicoccum, Eutypella, Fusarium, Glomerella, Myrothecium, Nigrospora, Penicillium, Phoma, Phomopsis, Podospora, Preussia, Rhizoctonia, Talaromyces, Trichoderma, Scopulariopsis, Sporormiella, and *Xylaria* (Table 6.1). Even though none of these fungus genera were reported in all five Baccharis species, there are similarities among these plant species. Baccharis dracunculifolia and B. trimera were found to have the most similar endophytic fungi communities, sharing the following seven genera (Jaccard Index = 33%): Chaetomium, Diaporthe, Nigrospora, Phoma, Phomopsis, Preussia, and Xylaria (Fig. 6.2). Of the genera of endophytic fungi known for species of *Baccharis*, only 24 taxa have been identified to the species level: Aureobasidium pullulans, Aureobasidium melanogenum, Aspergillus versicolor, Aspergillus spinulosporus, Ceratopicnidium baccharidicola, Cladosporium cladosporioides, Cladosporium halotolerans, Cladosporium endophytica, Cochliobolus lunatus, Coriolopsis rigida, Diaporthe phaseolorum, Epicoccum nigrum, Eutypella scoparia, Myrothecium verrucaria, Myrothecium roridum, Penicillium citrinum, Preussia africana, Preussia pseudominima, Talaromyces muroii, Trichoderma reesei, Xylaria adscendens, Xylaria apiculata, and Xylaria venosula. Thus, the possibility exists for the description of unknown fungal species associated with Baccharis spp. and evidence of coevolution events.

Currently, the most studied species of *Baccharis* is *B. dracunculifolia*, with 24 endophytic fungus genera reported in 5 published studies: *Aureobasidium*, *Acremonium*, *Aspergillus*, *Biscogniauxia*, *Cercospora*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Coriolopsis*, *Cylindrocladium*, *Diaporthe*, *Eutypella*, *Fusarium*, *Glomerella*, *Nigrospora*, *Penicillium*, *Phoma*, *Phomopsis*, *Preussia*, *Rhizoctonia*,

Endophytic genera	Endophytic taxa	Host plants	References
Alternaria	Alternaria sp.	Baccharis trimera	Vieira et al. (2014)
Aureobasidium	Aureobasidium pullulans	Baccharis dracunculifolia	Oki et al. (2009, 2020)
Acremonium	Acremonium sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Acremonium</i> sp. strain D5-FB	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Aspergillus	Aspergillus sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Aspergillus</i> sp. strain D2-NC	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Biscogniauxia	Biscogniauxia sp.	Baccharis dracunculifolia	Fernandes et al. (2018)
Ceratopicnidium	Ceratopicnidium baccharidicola	Baccharis coridifolia	Rizzo et al. (1997)
	Ceratopicnidium baccharidicola	Baccharis artemisioides	Rizzo et al. (1997)
Cercospora	<i>Cercospora</i> sp. strain D7-FB	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Chaetomium	Chaetomium sp.	Baccharis trimera	Vieira et al. (2014)
	Chaetomium sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
Cladosporium	Cladosporium cladosporioides	Baccharis dracunculifolia	Oki et al. (2009)
	Cladosporium halotolerans	Baccharis dracunculifolia	Fernandes et al. (2018)
Cochliobolus	Cochliobolus lunatus	Baccharis trimera	Vieira et al. (2014)
Colletotrichum	Colletotrichum sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Colletotrichum</i> sp. strain D4-FB	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Coriolopsis	Coriolopsis rigida	Baccharis dracunculifolia	Fernandes et al. (2018)
Cylindrocladium	Cylindrocladium sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Cylindrocladium</i> sp. strain D8-FB	Baccharis dracunculifolia	Onofre and Steilmann (2012)

 Table 6.1 Taxa of endophytic fungi found among species of Baccharis.

(continued)

Endophytic genera	Endophytic taxa	Host plants	References
Diaporthe	Diaporthe phaseolorum	Baccharis trimera	Vieira et al. (2014)
	Diaporthe sp.	Baccharis trimera	Vieira et al. (2014)
Epicoccum	Epicoccum nigrum	Baccharis trimera	Vieira et al. (2014)
	Epicoccum sp.	Baccharis trimera	Vieira et al. (2014)
Fusarium	Fusarium sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Fusarium</i> sp. strain D3-FB	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Glomerella	<i>Glomerella</i> sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
Myrothecium	Myrothecium verrucaria	Baccharis coridifolia	Jarvis et al. (1987)
	Myrothecium roridum	Baccharis coridifolia	Jarvis et al. (1987)
	Myrothecium roridum	Baccharis megapotamica	Jarvis et al. (1987)
Nigrospora	Nigrospora sp.	Baccharis trimera	Vieira et al. (2014)
	Nigrospora sp.	Baccharis dracunculifolia	Oki et al. (2009)
	Nigrospora sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
Penicillium	Penicillium sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	Penicillium sp.	Baccharis dracunculifolia	Oki et al. (2009)
Pestalotiopsis	Pestalotiopsis sp.	Baccharis trimera	Vieira et al. (2014)
Phoma	Phoma sp.	Baccharis trimera	Vieira et al. (2014)
Phomopsis	Phomopsis sp.	Baccharis dracunculifolia	Oki et al. (2009)
	Phomopsis sp.	Baccharis trimera	Vieira et al. (2014)
	Phomopsis sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	<i>Phomopsis</i> sp. strain D10-NC	Baccharis dracunculifolia	Onofre and Steilmann (2012)
Podospora	Podospora sp.	Baccharis trimera	Vieira et al. (2014)

 Table 6.1 (continued)

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Endophytic	Endonbutio tono	Heat alonta	References
genera	Endophytic taxa	Host plants	
Preussia	Preussia africana	Baccharis dracunculifolia	Oki et al. (2009); Fernandes et al. (2018), Oki et al. (2021)
	Preussia africana	Baccharis trimera	Vieira et al. (2014)
	Preussia pseudominima	Baccharis trimera	Vieira et al. (2014)
	Preussia sp.	Baccharis trimera	Vieira et al. (2014)
	Preussia sp.	Baccharis dracunculifolia	Fernandes et al. (2018)
Rhizoctonia	Rhizoctonia sp.	Baccharis dracunculifolia	Oki et al. (2009)
Trichoderma	Trichoderma sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
	Trichoderma reesei	Baccharis dracunculifolia	Onofre et al. (2014)
Scopulariopsis	Scopulariopsis sp.	Baccharis dracunculifolia	Cuzzi et al. (2012)
Sporormiella	Sporormiella sp.	Baccharis trimera	Vieira et al. (2014)
Xylaria	<i>Xylaria</i> sp.	Baccharis dracunculifolia	Oki et al. (2009)
	<i>Xylaria</i> sp.	Baccharis dracunculifolia	Fernandes et al. (2018)
	<i>Xylaria</i> sp.	Baccharis trimera	Vieira et al. (2014)
	Xylaria apiculate	Baccharis dracunculifolia	Fernandes et al. (2018)
	Xylaria venosula	Baccharis dracunculifolia	Oki et al. (2009), Fernandes et al. (2018), Oki et al. (2021)

Table 6.1 (continued)

Talaromyces, Trichoderma, Scopulariopsis, and Xylaria. The species of endophytic fungi known for *B. dracunculifolia* are Aureobasidium pullulans, Aureobasidium melanogenum, Aspergillus versicolor, Aspergillus spinulosporus, Cladosporium cladosporioides, Cladosporium halotolerans, Cladosporium endophytica, Coriolopsis rigida, Diaporthe phaseolorum, Eutypella scoparia, Penicillium citrinum, Preussia africana, Talaromyces muroii, Trichoderma reesei, Xylaria adscendens, Xylaria apiculata, and Xylaria venosula (Figs. 6.3 and 6.4). Many of these species (e.g., *A. pullulans, P. africana*, and *X. venosula*) play important ecological roles such as improving their hosts' defenses against herbivores and phytopathogens.

All together, these results indicate that the taxonomic diversity of endophytic fungi associated with species of *Baccharis* is enormous and likely underestimated. The array of functions associated with interactions between endophytic fungi and

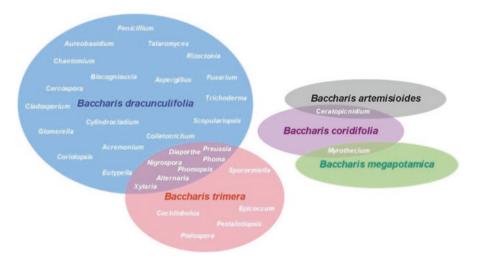


Fig. 6.2 Diagram showing fungal genera associated and shared among *Baccharis dracunculifolia*, *Baccharis trimera*, *Baccharis artemisioides*, *Baccharis coridifolia*, and *Baccharis megapotamica*

Baccharis hosts is also expected to be very large. Thus, there is a broad perspective for future studies to address, besides their biotechnological importance, the phylogenetic relationships of endophytes and hosts and the evolution and stability of associations across species and habitats.

3 Leaf Age, Plant Sex, and the Endophytic Fungus Community

The richness of endophytic fungi found among *Baccharis* spp. varies according to plant organ (Oki et al. 2009; Jia et al. 2016) and organ age (Arnold and Herre 2003; Fernandes et al. 2011; Sanchez-Azofeifa et al. 2012; Nascimento et al. 2015; Christian et al. 2019). For instance, endophytic fungus richness in mature leaves of *B. dracunculifolia* was seven times higher than that of leaves of intermediate age growing at high altitudes of Serra do Cipó, Brazil. No endophytic fungi were found in young leaves (Oki et al. 2008).

Another relevant factor that can affect the composition of endophytic mycota, particularly in the genus *Baccharis*, is host plant gender. The endophytic fungi found exclusively in female plants of *B. dracunculifolia* did not develop from

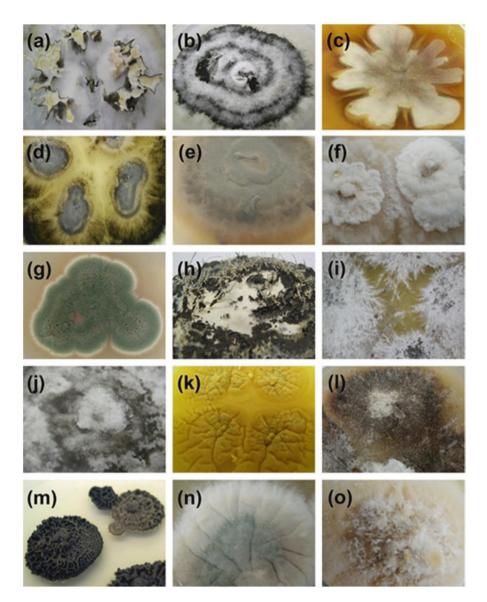


Fig. 6.3 Endophytic fungus genera found for *Baccharis dracunculifolia* (Asteraceae): (a) *Xylaria adscendens* (Xylariaceae); (b) *Biscogniauxia* sp. (Xylariaceae); (c) *Preussia africana* (Sporormiaceae); (d) *Aureobasidium pullulans* (Dothioraceae); (e) *Cladosporium endophytica* (Cladosporiaceae); (f) *Phomopsis* sp. (Diaporthaceae); (g) *Penicillium citrinum* (Trichocomaceae); (h) *Xylaria venosula* (Xylariaceae); (i) *Diaporthe phaseolorum* (Diaporthaceae); (j) *Nigrospora* sp. (Trichosphaeriaceae); (k) *Phoma* sp. (Didymellaceae); (l) *Fusarium* sp. (Nectriaceae); (m) *Aureobasidium melanogenum* (Dothioraceae); (n) *Aspergillus versicolor* (Trichocomaceae); (o) *Acremonium* sp. (Hypocreaceae)

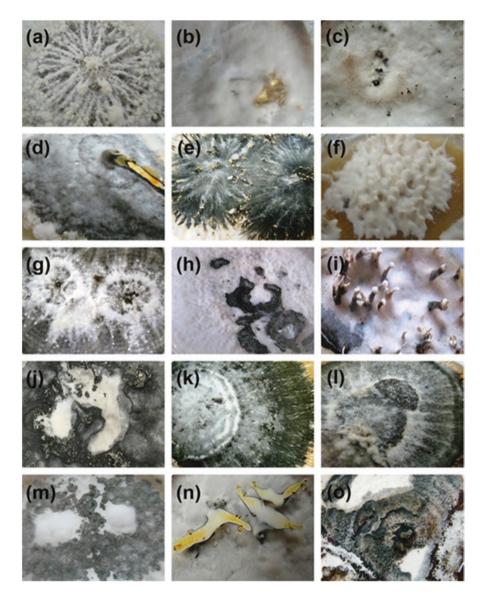


Fig. 6.4 Endophytic fungi of the family Xylariaceae found in leaves of *Baccharis dracunculifolia* (Asteraceae)

extracts from male individuals of the same species (Fernandes et al. 2018). It is likely that chemical differences between female and male plants (Darwin 1877; Wallace and Rundel 1979; Van Etten et al. 2008) determine the endophytic species that are capable of co-inhabiting these plants. Generally, female plants invest less in growth and more in resistance against herbivory than male plants (Wallace and

Rundel 1979; Herms and Mattson 1992; Van Etten et al. 2008) (but see Chap. 4). Nonetheless, these questions remain to be fully addressed in this system.

4 Untapped Potential of Endophytic Fungi: Enzymes and Bioactive Compounds

Enzymes

Despite the high diversity of endophytic fungi found among species of *Baccharis*, knowledge regarding their enzymatic makeup is scarce. This knowledge gap undermines a better understating of the physiological relationships between endophytes and their hosts (Sun et al. 2011) and their potential for industrial application (Côrrea et al. 2014). Endophytic fungi, such as species of the genus *Xylaria*, have a high production of enzymes such as cellulases and ligninases, which can degrade important components of plant cell walls (e.g., cellulose and lignin) (Carroll and Carroll 1978). These enzymes could assist in the decomposition of fallen leaves and promote nutrient cycling in nature. The accumulation of endophytic fungi themselves in leaves as age progresses (e.g., Fernandes et al. 2011; Sanchez-Azofeifa et al. 2012; Nascimento et al. 2015; Christian et al. 2019) seems to be important and in need of further evaluation, as well as the relevance of these fungi to key ecosystem functions such as decomposition.

The endophyte *Aureobasidium pullulans* found in *B. dracunculifolia* can produce lipases that belong to the class of serine hydrolases and do not need the presence of cofactors in order to act, unlike most extracellular enzymes of microbial origin (Nascimento 2010). The biological function of lipases is to hydrolyze triglycerides to form free fatty acids, mono- and diacylglycerols and glycerol (Kwon and Rhee 1986; Berger and Schnelder 1992; Bornscheuer 1995; Carvalho et al. 2003). Currently, lipases are of great interest to food (e.g., aroma improvement, food conservation, reduction of saturated fat), agricultural (e.g., herbicide synthesis), energy (e.g., biodiesel and hydrocarbon production), pharmaceutical (e.g., digestive aid), and cosmetics (e.g., active ingredient in the formulation and synthesis of specific cosmetics) industries, among others (Höfelmann et al. 1985; Cortez et al. 2017). Lipases can also play an important role in plant defense since lipids and lipid metabolites released in plant membranes function as signal molecules in the activation of plant defense responses (Shah 2005).

Recent studies have also indicated that some strains of endophytic fungi, such as *Fusarium* sp. and *Cercospora* sp. in *B. dracunculifolia*, can produce phenoloxidases that are capable of degrading phenolic compounds such as petroleum hydrocarbons and industrial effluents (Onofre and Steilmann 2012). These are important findings for bioremediation initiatives since these contaminants can be found at ca. 35 million metric tons per year in the oceans (Rosenberg and Ron 1996). These contaminants severely impact marine biodiversity over a time span of decades and even

centuries (Goldberg and Bertine 2000; Pinheiro et al. 2019; Magris and Giarizzo 2020). Much of this contamination comes from oil in municipal and industrial waste and runoff, leaks in pipelines and storage tanks, and sewage and ballast water discharge (Telli Karakoç and Ediger 2020; Pokazeev et al. 2021).

Many endophytic fungi have proven to be excellent bioremediators of heavy metals that can harm human health, such as arsenic. Some of these endophytes are resistant to arsenic and arsenate and possess the ability to transform them into volatile arsenic gases (Páez-Espino et al. 2009). *Aspergillus, Cladosporium, Fusarium, Penicillium*, and *Trichoderma* are some of the endophytic fungus genera known for their bioremediation potential. They are frequently found in plants that have tolerance to, or the ability to bioaccumulate, heavy metals (Deng et al. 2014). Coincidentally, these fungus genera are also found among species of *Baccharis,* mainly *B. dracunculifolia. Baccharis dracunculifolia* has been shown to have great phytostabilization potential for areas contaminated with arsenic (Gilberti et al. 2014). This phytostabilization potential is likely associated with the endophytic fungi in this species; however, no studies have evaluated this relationship.

Endophytic Fungi as a Source of Bioactive Compounds

Endophytic fungi represent a promising source of natural bioactive products. Researchers around the world have been intrigued by the diversity of secondary compounds produced by endophytic fungi and by the similarity between the metabolites produced by endophytic fungi and their host plants (Kusari et al. 2013). This similarity in the production of secondary compounds may be due to several factors, including (1) host plant metabolism being induced by the fungus; (2) fungus metabolism being induced by the host plant; (3) fungus sharing specific biosynthesis pathways with the host plant; and (4) host plant being able to metabolize substances of fungal origin or vice versa (e.g., Ludwig-Müller 2015).

Among the best-known examples of bioactive compounds produced by endophytic fungi is palictaxel (commercialized as Taxol) produced by *Taxomyces andreanae* from the medicinal tree *Taxus brevifolia* (Stierle et al. 1993). Palictaxel is one of the most effective chemotherapeutic compounds used in the treatment of various types of cancer (i.e., ovary, breast, and lung) (Stierle et al. 1993, see Chap. 18). Before this discovery, the supply of this diterpenic substance was limited to the slow-growing barks of *T. brevifolia* that grow in moist soils close to lakes and rivers in some regions of the Pacific Northwest (Guchelaar et al. 1994). Thus, the possibility of extracting palictaxel from *T. andreanae* significantly reduced the production costs of this compound and increased its supply and availability. In addition, other species of endophytic fungi have also been reported to produce palictaxel in plant species of the genera *Taxus* and *Podocarpus* and even in *Ginkgo biloba* (Zhao et al. 2010; Naik 2019). One of these endophytic fungi is *Cladosporium cladosporioides* isolated from *Taxus media* (Zhang et al. 2009), which, coincidentally, is also found in *B. dracunculifolia*, although there is no information on whether it produces palictaxel. Future studies could attempt to propagate this fungus species from *B. dracunculifolia* and isolate its products to evaluate if the chemotherapeutic palictaxel is also produced by *C. cladosporioides* when it occurs in different host plant species. Such studies would generate a cascade of interesting and innovative investigations of major economic and medical relevance.

Among the endophytic fungi most frequently found among species of *Baccharis*, the genera Xvlaria and Preussia deserve to be highlighted with regard to their metabolism. Species of Xylaria are known to produce several chemical constituents of the terpene class (Smith et al. 2002), xanthones (Healy et al. 2004), cyclopeptides (Huang et al. 2007), and xyloketals (Lin et al. 2001), among others. Species of this genus are found in other plant species of the family Asteraceae and are known for their inhibitory activity against phytopathogens such as Penicillium expansum (Bleicher and Bernardi 1985; Costa and Veiga 1996) and Aspergillus niger (Lock 1962; Santos et al. 2010). Furthermore, species of the genus Preussia are known to produce the metabolite preussomerin A, which is active against pathogens (Chen et al. 2009). A variety of substances produced by Preussia spp. have been identified in the last 10 years, including coumarins (Gonzalez-Menendez et al. 2017), anthraquinones (Gonzalez-Menendez et al. 2017), chronomes (Zhang et al. 2012; Gonzalez-Menendez et al. 2017), and preussochromones (Zhang et al. 2012). Some preussochromones have shown activity against lung cancer cell lines (Zhang et al. 2012).

Unfortunately, knowledge about the metabolites produced by endophytic fungi of species of *Baccharis* is still incipient and restricted to the endophytes found in *B. megapotamica*, *B. coridifolia*, and *B. dracunculifolia*. For instance, *B. megapotamica* and *B. coridifolia* produce certain macrocyclic trichothecenes, which are also produced by their endophytic fungi *Myrothecium verrucaria* and *Myrothecium roridum* (Jarvis et al. 1987, see Chaps. 14 and 15). These substances have been responsible for causing the death of cattle through necrosis of their ruminal epithelium and some lymphoid tissues (Varaschin et al. 1998, see also Chap. 15). On the other hand, some of these trichothecenes have been reported as effective in the treatment of lymphocytic leukemia (Kupchan et al. 1976; Jarvis et al. 1987, Carvalho et al. 2016, see also Chap. 14).

Among the endophytic fungi found in *B. dracunculifolia*, *A. pullulans* and *Xylaria venosula* stand out for the production of phenols and triterpenes, while *Preussia africana* for fatty acids (Oki et al. 2016, 2021). Chromatographic analysis showed that a group of triterpenes found in extracts from *A. pullulans* was similar to those found in *B. dracunculifolia*.

In addition, host plant metabolism can induce endophytic fungi of different genera and classes to produce similar secondary compounds (Ludwig-Müller 2015). A study with endophytic fungi of species of *Baccharis* revealed that a group of triterpenes present in extracts of *A. pullulans* was similar to those found in extracts of *X. venosula* (Oki et al. 2021). This similarity in the production of secondary compounds between different genera of endophytic fungi from the same plant species indicates a synergistic biochemical relationship between fungus species. Explanations for these findings include (1) endophytes sharing specific biosynthesis pathways with the host plant, and (2) endophytes producing the same secondary compounds as the host plant (see Ludwig-Müller 2015; Stierle and Stierle 2015). *Aureobasidium pullulans* is also used in the production of aureobasidin A, a cyclic peptide substance that has antifungal properties (Takesako et al. 1993). This fungus also releases volatile organic compounds that are capable of suppressing the growth of phytopathogens (Don et al. 2020).

Due to its arsenal of secondary metabolites, *A. pullulans* has been considered an effective biological control agent against several phytopathogenic fungi that affect numerous agricultural crops, including *Alternaria alternata* (Don et al. 2020), *Botrytis cinerea* (Di Francesco et al. 2015; Don et al. 2020; Oki et al. 2021), *Colletotrichum acutatum* (Di Francesco et al. 2015; Oki et al. 2021), *Neofusicoccum parvum* (Rusin et al. 2019), *Penicillium digitatum* (Di Francesco et al. 2015; Oki et al. 2015; Oki et al. 2015; Oki et al. 2021), *Penicillium expansum* (Di Francesco et al. 2015), *Penicillium italicum* (Di Francesco et al. 2015), *Penicillium italicum* (Di Francesco et al. 2015), *and Rhizoctonia solani* (Di Francesco et al. 2020). *Aureobasidium pullulans* is also highlighted for stimulating the growth of beans and soybean (Di Francesco et al. 2020), which may be attributed to improving host plant nitrogen fixation or a greater release of hormones such as auxins, gibberellins, and cytokinins by *A. pullulans* (Ali et al. 2019). Furthermore, this fungus can improve plant resistance in soil with heavy metals through the release of enzymes that assist in reducing metal absorption and enhance the plant's antioxidant system (Ali et al. 2019).

5 Endophytic Fungi-Baccharis-Herbivore Interaction

Some endophytic mycota (i.e., *A. pullulans*, *P. africana*, and *X. venosula*) from *B. dracunculifolia* can produce secondary compounds that reduce the survival of herbivores such as the aphid *Uroleucon erigeronensis* (Oki et al. 2021). On the other hand, a study with *B. dracunculifolia* leaf buds indicated that herbivory can be a gateway for endophytic fungi through horizontal transmission (Fernandes et al. 2018).

Although herbivores often favor the infection of the host plant with endophytic fungi, this was not found to be the case for galling insects on *Baccharis reticularia*. Individuals of *B. reticularia* with and without galls showed no difference in endophytic fungus richness (Formiga 2013). However, a higher richness of endophytic fungi was found in gall samples that had a higher content of nitrogen and potassium (Formiga 2013). Nevertheless, a relationship between endophytic fungus richness and nitrogen and phosphorus content was not observed. These results suggest that endophytes can increase the nutritional status of galled plants by improving plant vigor and reducing the effects of gall infestation (Formiga 2013). This mutualistic relationship has not been reported so far in the literature and certainly needs further studies.

All together, these findings suggest that although endophytic fungi are often imperceptible inside plants, they are important mediators in the relationships between herbivores and their host plants and apparently very important among species of the genus *Baccharis*.

6 Climate Change and Endophytic Fungus Diversity

Growing concerns about the impacts that climate change will have on endophytes have increased research interest in this group with searches for strategies that could mitigate these effects. Recent studies on the endophytes of B. dracunculifolia and Baccharis platypoda grown under increased CO₂ concentration did not find differences in mycota richness (Oki et al. 2020). On the other hand, endophytic community composition changed by 50% when compared to individual plants developed under conditions of ambient CO₂ (Oki et al. 2016). Thus, several species of endophytic fungi that play fundamental roles in plant performance and resistance may disappear or be replaced by other species of unknown functional roles. These changes in species composition are associated with structural and chemical changes (Sanchez-Azofeifa et al. 2012) that may occur in plants under increased CO₂ concentration, such as increased biomass, greater leaf thickness, and higher phenolic content, among other aspects (Oki et al. 2020). Despite these recent studies of endophytic fungi under conditions of predicted climate change, there is still no clear long-term notion of the impacts that increased atmospheric CO₂ concentration might exert on the symbiosis between endophytic fungi and their host plants.

7 Final Considerations and Ways Forward

Despite the limited number of studies on endophytic fungus communities of species of Baccharis, this chapter has shown how relevant these microorganisms are to ecological relationships, as well as their great potential in industrial research and developments involving their bioactive compounds. Further investigations into the diversity of endophytic fungi among species of Baccharis are needed to better understand the phylogenetic, ecological, and metabolic relationships among them, as well as their prevalence under certain environmental conditions. The relationship between endophyte and host attributes is also of major relevance, and the Baccharis system represents an interesting system to be evaluated in this regard. Some of these aspects could be intrinsic to the host plant (e.g., genetics, sex, age, resistant/susceptibility) or of the environment (e.g., seasonality, microhabitat conditions, climate change influence). The association between a host plant and its endophytes may be subject to certain genetic expressions that can vary seasonally and/or spatially (Faeth 2002, Mejía et al. 2014). Another relevant aspect yet to be studied in detail is the ability of endophytic fungi to signal one another triggering silent biosynthetic pathways (Scherlach and Hertweck 2009). Understanding these very interesting relationships and their intrinsic and extrinsic factors would certainly contribute to

solidifying knowledge of endophytic fungi and contribute to better exploration of their potential uses for industrial/pharmaceutical purposes.

Acknowledgments We thank for CNPq, FAPEMIG, Planta and CAPES for grants and scholarships to the authors.

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