Essential Oils: A Natural Weapon against Mycotoxins in Food

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Abstract

Essential oils are aromatic liquids that are isolated from plant parts and thus are extremely volatile and scented. These volatile oils are responsible for the different scents that plants emit. The major mycotoxin groups, including aflatoxin, fumonisin, ochratoxin (OT), zearalenone (ZEN), and deoxynivalenol (DON) can induce many harmful health effects, including allergies, cancer, and immunosuppression, owing to the intake of infected food. Currently, it is known that the majority of synthetic chemicals used as preservatives pose a danger to individuals and harm the environment. In this regard, utilizing diverse plant products, particularly essential oils (EOs) and their bioactive constituents, has been considered a green strategy and a safer alternative to synthetic chemicals due to their long-standing traditional use. Essential oils have several modes of action that prevent the growth of fungus and the production of mycotoxin, including changed fungal growth rates, disruption of cell permeability, disruption of the electron transport chain, alteration of gene expression patterns, and metabolic activities. This chapter aims to summarize the different recent studies on the effect of essential oils in inhibiting the growth of mycotoxigenic fungus, eliminating mycotoxins, and their mode of action.

Keywords

Essential oils · Aromatic compounds · Mycotoxins · Aflatoxin, Ochratoxin

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6.1 Introduction

Foodborne diseases caused by consuming contaminated food are a major public health concern around the world. According to the World Health Organization (WHO), 31 foodborne hazards globally contributed to 600 million foodborne illnesses and 420,000 deaths (Havelaar et al. 2015; WHO 2022). Foodborne illnesses are caused by a variety of pathogens, including fungi, viruses, and bacteria. These pathogens can contaminate food at any point during its production, processing, or distribution (Hemalata and Virupakshaiah 2016). Toxins produced by certain fungi cause the most common fungal foodborne diseases. These toxins, known as mycotoxins, can induce diarrhea, abdominal pain, nausea, vomiting, and fever, among other symptoms. In severe cases, mycotoxin poisoning can lead to liver damage, kidney failure, and even death (Dhakal and Sbar 2021). More than 400 different types of mycotoxins have been identified, but the most common mycotoxins that cause foodborne illness are aflatoxins, ochratoxin-A, fumonisin, zearalenone, patulin, and trichothecenes (Ünüsan 2019). Consumption of mycotoxin-contaminated food or feed can cause acute (e.g., turkey X syndrome, human ergotism, stachybotryotoxicosis) or chronic (e.g., cancer induction, kidney toxicity, immune suppression) toxicity in humans and livestock due to their inherent carcinogenic, mutagenic, teratogenic, and immuno-suppressive characteristics (Bennett and Klich 2003; Chaudhari et al. 2021). Mycotoxins are low-molecular-weight (MW ~ 700 Da) secondary metabolites secreted by many filamentous fungi belonging to the genera *Aspergillus*, *Penicillium*, and *Fusarium* that are highly toxic to animals and humans (Liew and Mohd-Redzwan 2018; Alshannaq and Yu 2017). They are grown under favorable conditions (temperature, moisture, water activity, and relative humidity) between 10 to 40 °C and with a pH range of 4 to 8 (Bhat et al. 2010). Depending on the fungal species, mycotoxins can appear in both temperate and tropical climates. These mycotoxins are commonly found in dried fruits, nuts, coffee, oil seeds, cereals, cocoa, spices, beans, dried peas, and fruits, especially apples. Mycotoxins may also be identified in beer and wine due to the use of contaminated raw materials during their production, such as barley, cereals, grapes, etc. (Turner et al. 2009).

To ensure the consumption of toxin-free food with good nutritional values for human health, it is essential to maintain food quality. So, the best approach to maintain the quality of food and stop it from microbial deterioration is to use preservation techniques. Nowadays, there are many different types of preservation techniques available that can be used to preserve food commodities for a very long time, either by using traditional or modern preservation techniques (Sharif et al. 2017). Additional food preservatives, which can be divided into artificial (synthetic) and natural preservatives, are used in some of these preservation methods. Several synthetic preservatives such as sulfur dioxide, sulfites, sodium nitrite, sodium benzoate, benzoates, sorbates, formaldehyde, imidazoles, pyrrolidines, and thiocyanates, etc. have been employed to control microbial contamination of food items (Maurya et al. 2021a, b). A few of them are poisonous, and many others could have fatal adverse effects. Artificial preservatives can lead to major health problems like cancer, hyperactivity, hypersensitivity, allergy, asthma, and other respiratory and

respiratory-related illnesses (Kumari et al. 2019). Customers are generally aware of the health risk posed by the use of artificial preservatives. As a result, the demand for natural food preservatives has significantly increased. In this regard, the use of various plant products, particularly essential oils (EOs) and their bioactive compounds, has been recognized as a green strategy and a safer alternative to synthetic antifungal and mycotoxin treatments (Shukla et al. 2012; Chaudhari et al. 2019).

The word "Quinta essentia" was first used to describe the active component of a drug by Paracelsus von Hohenheim in the sixteenth century. The word "essential" is derived from the Latin essentia (Guenther and Althausen 1948). Essential oils are secondary metabolites produced by many aromatic plant parts, including flowers, buds, leaves, stems, twigs, seeds, fruits, roots, bark, or wood. They are stored in secretory cells, cavities, canals, epidermal cells, or glandular trichomes. They are natural molecules with a complex mixture of chemical structures that are liquid, volatile, rarely colored, soluble in lipids and organic solvents, and have a density often less than that of water (Bakkali et al. 2008; Bouyahya et al. 2019). Essential oils are produced by two natural biochemical processes that involve several enzymatic reactions. The precursors of essential oil biosynthesis, isopentenyl diphosphate (IPP), and its isomer, dimethylallyl diphosphate (DMAPP), are produced in the cytoplasm and plastids via the mevalonic acid (MVA) and methyl-D-erythritol-4-phosphate (MEP) pathways (Rehman et al. 2016). Terpenes (pinene, myrcene, limonene, terpinene, and *p*-cymene), the prominent ingredient of essential oils are hydrocarbons made up of several isoprene (C5H8) units, while terpenoids (oxygen-containing hydrocarbons) are modifications of terpenes with different functional groups and moved or removed oxidized methyl groups at various positions (Masyita et al. 2022). In general, terpenoids possess greater antimicrobial activity than terpenes (Burt 2004). EOs have been widely used successfully in indigenous systems and are thought to have antimicrobial properties. Since the Middle Ages, essential oils have been used for a variety of purposes, including bactericidal, virucidal, fungicidal, antiparasitic, insecticidal, medicinal, and cosmetic ones (Prakash et al. 2015). Due to their natural origin, EOs and their components are regarded as user-friendly, friendly to the environment, and often exempt from the Environmental Protection Agency's standards for toxicity data (Prakash et al. 2010). Cinnamon, fennel, rosemary, oregano, thyme, palmarosa, clove, and eucalyptus have been revealed to be the most efficacious essential oils against mycotoxigenic fungi and their mycotoxins in research published over the past 10 years. Essential oils can prevent the growth of fungi and the production of mycotoxin through a variety of mechanisms, including altered fungal growth rate, extended lag phase, disruption of cell permeability, disruption of the electron transport chain, altering gene expression patterns, and metabolic processes (Mirza Alizadeh et al. 2022). A fungus's ability to produce toxins depends not only on its ability to grow but also on the fungistatic and fungicidal substances that may have an impact on its invasion and colonization. Extensive research publications, reviews, and reports have been written about the fungal species that contaminate food and feed; nevertheless, a large portion of the data is either limited to one type of mycotoxin or the data is fragmented. In light of this, we attempted to provide a thorough overview of essential

oils against the mycotoxigenic fungus, the diversity of mycotoxins, associated health concerns for humans and livestock, etc. in the present book chapter.

6.2 Food Spoiling Mycotoxins and their Types

Mycotoxins are secondary, stable, and physiologically active metabolites that frequently contaminate agricultural goods. Along with significant financial losses, they also represent a long-term, hidden risk to the health of both humans and animals. Currently, more than 400 mycotoxins have been identified and described as toxic, non-volatile, and relatively low-molecular-weight secondary metabolites produced by certain filamentous fungi, such as species of *Aspergillus*, *Alternaria*, *Fusarium*, and *Penicillium* (Gurikar et al. 2022; Venkatesh et al. 2017). Many species of mycotoxins are commonly found in cereals, herbal materials, fruits, and spices (Chaudhari et al. 2021). According to Food and Agriculture Organization (FAO) statistics, approximately one-fourth (25%) of all agricultural products are harmed by mycotoxin-producing fungi worldwide. The most prevalent mycotoxin, aflatoxin, has significant toxicity and carcinogenic potential and is present in a wide range of foods and feeds. Besides aflatoxins, other major toxins are trichothecenes, fumonisins, ochratoxin, and zearalenone, which are present in grains used as food and other agricultural products. Mycotoxins found in contaminated food products and animal feeds can have many harmful effects on human and animal health, including cancer, immunosuppression, gastrointestinal, estrogenic, and kidney diseases (Tola and Kebede 2016; Neme and Mohammed 2017; Gurikar et al. 2022) (Table 6.1).

6.3 Aflatoxins

Aflatoxins are highly toxic secondary metabolites produced by *Aspergillus flavus*, *A. parasiticus*, and *A. nominus* (Rocha et al. 2023). These fungi grow on a wide variety of foods such as wheat, walnuts, and other dry fruits, legume seeds, corn, cotton, peanuts, and tree nuts that cause serious threats to human and animal health through various complications such as hepatotoxicity, teratogenicity, and immunotoxicity (Shukla et al. 2008; Kumar et al. 2017). The four major aflatoxins, B1, B2, G1, and G2, were isolated based on their fluorescence under UV light and identified by thin-layer chromatography (Baranyi 2013). AFTs-M1 and AFTs-M2 are produced by several metabolic processes from animals and animal products. The chemical structure of aflatoxins are shown in Fig. 6.1. The International Agency for Research on Cancer (IARC) classifies AFB1 as a Group 1 carcinogen, with high risks of hepatocellular carcinoma (HCC) in individuals exposed to aflatoxins, whereas AFM1 is classified as a "possible carcinogen" in Group 2B (Alshannaq and Yu 2017). The toxigenic capacities of pathogenic branches within an aflatoxigenic species differ considerably on a mycological and quantitative scale. Cytochrome P450 enzymes convert aflatoxin into reactive 8, 9-epoxide forms that can bind to DNA and proteins. It is generally understood that reactive aflatoxin epoxide

Table 6.1 Mycotoxin production in the food system and its adverse effects

Sr. no.	Mycotoxins	Common fungal sp.	Model foods (common name)	Health effects	Reference
1.	Aflatoxins: AFB1, AFB2, AFG1, AFG2	*Aspergillus flavus, A. parasiticus*, and *A. nomius*	Wheat, walnut, corn, cotton, peanuts, etc.	Teratogenicity, hepatotoxicity, immunotoxicity, etc.	Kumar et al. (2017)
2.	Fumonisins: FB1, FB2, FB3	*Fusarium moniliforme*, *F. proliferatum*, and *F. verticillioides*	Peanut, maize, grape, wheat, rye, barley, maize, oats, millet, etc.	Hepatocarcinoma, nephrotoxicity, adenocarcinoma, etc.	Kamle et al. (2019); Soriano et al. (2005)
3.	Ochratoxins (OTA, OTB, OTC)	*Aspergillus* sp., *Penicillium* sp.	Dry beans, maize, wheat, barley, oats, green coffee beans, etc.	Embryotoxic, teratogenic, immunotoxic, and nephrotoxicity	Reddy and Bhoola (2010)
4.	Zearalenone (ZEA)	*Fusarium graminearum*, *F. equiseti*, *F. cerealis*, *F. culmorum*	Rice, wheat, soybeans, corn, barley, millet, etc.	Genotoxic, teratogenic, immunotoxic, carcinogenic, hemotoxic, and hepatotoxic properties	Rogowska et al. (2019)
5.	Patulin	*Penicillium*, sp., *aspergillus* sp., and *Byssochlamys* sp.	Apple, apricot, black mulberry, corn, figs, pear, peach, pineapple, etc.	Immunotoxicity, gastrointestinal, hepatotoxicity, and neurological problems	Mahato et al. (2021)
6.	Ergot alkaloids: Ergometrine, ergocornine, ergosine, ergotamine, ergocryptine, ergocristine	*Claviceps purpurea*, *Balansia* sp., *Epichloe* sp., *Periglandula* sp., and *aspergillus fumigates*	Cereals like rye, wheat, millet triticale, oats, barley, etc.	Neurotoxicity, hallucinations, abdominal pain, insomnia, burning sensations of the skin, endocrine disruption in animals, convulsions, abortion, suppression of lactation, etc.	Arcella et al. (2017): Mulac and Humpf (2011)

(continued)

Table 6.1 (continued)

Sr. no.	Mycotoxins	Common fungal sp.	Model foods (common name)	Health effects	Reference
7.	Citrinin	*Aspergillus carneus A. terreus*, *A. niveus*, *Penicillium citrinum*, *P. verrucosum*, *P. expansum*, and *Monascus ruber*	Cereals (maize, rye, rice, barley, wheat, corn, oats), oilseeds (e.g., sunflower), and spices (e.g., turmeric, black pepper, cumin, cardamom, fennel, and coriander)	Nephrotoxicity and genotoxicity, teratogenic and embryotoxic effects	Kamle et al. (2022)
8.	Alternario, alternariol monomethyl ether (AME), and tentoxin (TEN)	*Alternaria alternata*, *A. brassicae*, *A. arborescens, A. radicina*, *A. infectoria*, *A. tenuissima*, and *A. brassicicola*	Cereals, cauliflowers, tomatoes, apples, oilseeds, grapes, oil crops, lemons, sunflower seeds, oranges, cucumbers, melons, peppers, and tangerines	Carcinogenicity, mutagenicity, sphingolipid metabolism disruption, induction of DNA strand breaks, and photopho-sphorylation	Escrivá et al. (2017)
9.	Trichothecenes: (T-2 toxin, HT-2 toxin, Neosolaniol (NEO), Diacetoxyscirpenol (DAS), Monoacetoxy-scirpenol (MAS), Verrucarol (VER) and Deoxynivalenol (DON))	*Fusarium culmorum* and *F. graminearum*, *Stachybotrys atra*, *Myrothecium* sp. And *Trichothecium* sp.	Cereals (wheat, corn, oats, and barley) seeds of rye, safflower, and in feed mixtures.	Inhibit the activity of the peptidyl transferase enzyme, as well as the initiation, elongation, and termination of eukaryotic protein synthesis	Polak-Śliwińska and Paszczyk (2021); da Rocha et al. (2014)
10.	Nivalenol/ deoxynivalenol	*Fusarium Graminearum*, and *F. culmorum*	Grains in the field, including corn, wheat, oats, barley, rice, and others	Immunotoxicity, hemotoxicity, edema, diarrhea, headaches, and other symptoms.	Sobrova et al. (2010); Kumar et al. (2022)

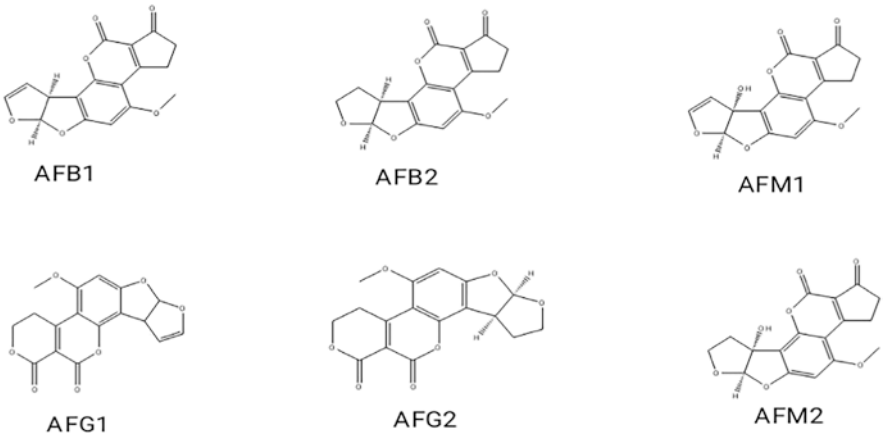


Fig. 6.1 Chemical structures of aflatoxins

interacts with the N7 site of guanines. The cytosol and microsomes contain a reactive glutathione S-transferase system that catalyzes the conjugation of activated aflatoxins with reduced glutathione, resulting in aflatoxin excretion (Bennett and Klich 2003).

6.4 Fumonisins

Fusarium mycotoxins are chemically and thermally stable secondary metabolites produced by *Fusarium verticillioides* (*Fusarium moniliforme*), *Fusarium proliferatum*, and other related species. *Fusarium* species produce mycotoxins such as deoxynivalenol, nivalenol, zearalenone, T-2 toxin, trichothecenes, and fumonisins (Ji et al. 2019; Rheeder et al. 2002). Fumonisins are found in corn, sorghum, millet, and other agricultural products. The Intergovernmental Agency for Research on Cancer (IARC) classified maize-derived toxins as category 2B (possibly carcinogenic to humans) in 1993 due to the typically higher presence of fumonisins in maize. Fumonisin also shows hepatotoxic, nephrotoxic, atherogenic, immunosuppressive, and embryotoxic effects other than its carcinogenic effect (Nair 1998). Since 1988, 28 fumonisin analogs have been identified, and they have been classified into four main groups (A, B, C, and P). The most abundant naturally occurring fumonisins are the FB analogs, which include the toxicologically significant FB1, FB2, and FB3. When cultured on corn, rice, or in a liquid medium, FB1 (Fig. 6.2) predominates and is usually found at higher levels (70 to 80%) than FB2 (15 to 25%) and FB3 (3 to 8%) (Rheeder et al. 2002). In 2014, fumonisin B1 (FB1), FB2, and FB3 were found in 98.1% of corn products collected in Shandong Province, China (Li et al. 2015).

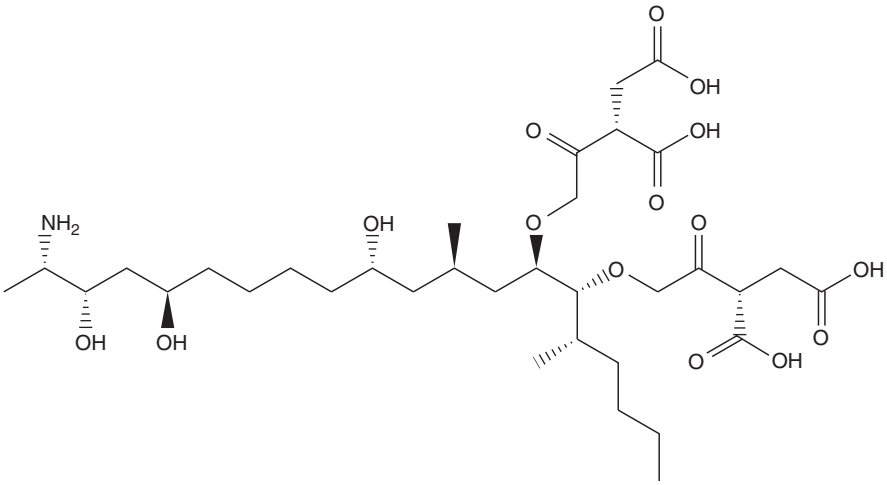


Fig. 6.2 Fumonisin B1

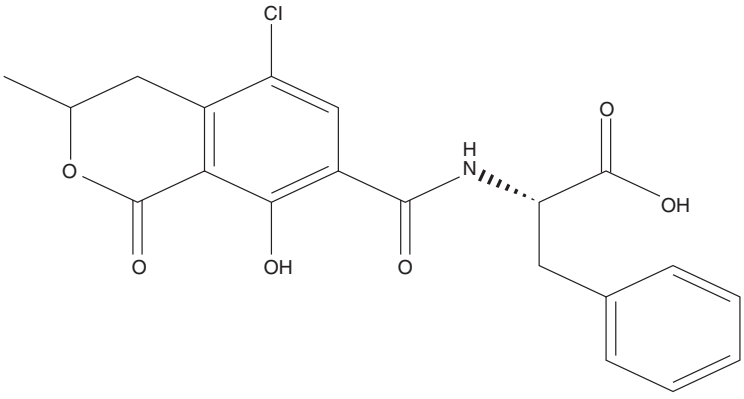


Fig. 6.3 Ochratoxin A

6.5 Ochratoxins

Aspergillus and *Penicillium* species produce ochratoxin as a secondary metabolite. The optimum temperature for the growth of *A. ochraceous* is 24 to 37 °C (pH is 3 to 10), and that of *P. verrucosum* is 20 °C (pH is 6.0 to 7.0) (Reddy and Bhoola 2010). These ochratoxins, ochratoxin A, ochratoxin B, and ochratoxin C, are all present in the environment. Ochratoxin A (Fig. 6.3) is a prominent toxin, and the International Agency for Research on Cancer categorized it as a category 2B likely human carcinogen in 1993 based on evidence that it could cause cancer in animals. Ochratoxin A is a naturally occurring mycotoxin produced by several fungi, including

Penicillium verrucosum, Aspergillus carbonarius, *A. ochraceus*, and *A. niger*. It can be found in a wide range of agricultural commodities worldwide, such as cereal grains, dried fruits, wine, and coffee (Reddy and Bhoola 2010; Bui-Klimke and Wu 2015; WHO,, and IARC 1993, and Kőszegi and Poór 2016). Ochretoxin A can cause a variety of health problems in animals and humans, including nephrotoxic, hepatotoxic, embryotoxic, teratogenic, neurotoxic, immunotoxic, genotoxic, and carcinogenic effects in many species (Malir et al. 2016). Spectroscopy techniques are widely used in the detection of toxic and harmful components in food products (Kumar et al. 2020).

6.6 Zearalenone

Zearalenone is a potent estrogenic mycotoxin produced by the *Fusarium* species, mainly *F. graminearum*, *F. culmorum*, *F. cerealis*, *F. equiseti*, *F. crookwellense*, *F. semitectum*, *F. verticillioides*, *F. sporotrichioides*, *F. oxysporum*, and *F. acuminatum* (Zhang et al. 2018). This mycotoxin is commonly found in cereals such as barley, maize, oats, sorghum, and wheat (Bhat et al. 2010). Zearalenone (Fig. 6.4) is a thermostable (160 °C) weakly polar compound with a molar mass of 318.364 g/mol that dissolves in various alkaline solutions such as benzene, acetonitrile, acetone, or alcohols (Ropejko and Twarużek 2021). McNutt et al. described a typical hyperestrogenism syndrome in pigs in 1928, due to the consumption of spoiled corn. Hyperestrogenism manifests as improper breastfeeding, aberrant udder or mammary gland growth, extended estrus, anestrus, changes in libido, infertility, and a higher frequency of pseudopregnancy. In humans, it can bind to alpha and beta estrogen receptors and disrupt the functioning of the endocrine system (Kuiper-Goodman et al. 1987). Additionally, zearalenone is genotoxic, immunotoxic, toxic to the reproductive system, and toxic to the development of the immune system. The interference with blood coagulation also causes hemato-toxic effects (Zinedine et al. 2017).

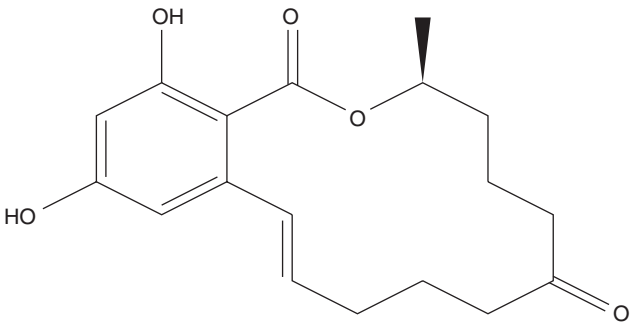
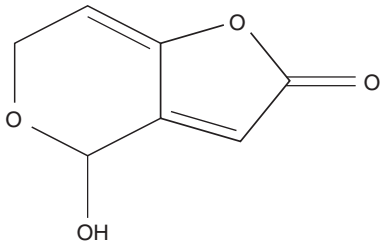


Fig. 6.4 Zearalenone

Fig. 6.5 Patulin



6.7 Patulin

Patulin (PAT) is a mycotoxin discovered in 1940 and produced as a secondary metabolite by numerous fungal species such as *Penicillium*, *Aspergillus*, and *Byssochlamys*. Chemically, PAT [4-Hydroxy-4H-furo(2,3-C)-pyron-2(6H)-1] is a polyketide lactone, which is a colorless, crystalline, water-soluble substance (Sajid et al. 2019; Pal et al. 2017). Patulin toxin was shown to be produced greater, respectively, at pH levels of 2.5 and 4, and storage temperatures of 20 to 25 °C. In most cases, it is associated with food products that have fungal infections. Patulin is generally found on fruits like apples, pears, peaches, and grapes but is mainly produced by the genus *Penicillium* with the species *Penicillium expansum*, which is capable of contaminating pome fruits, especially in apples and apple-based products (Baert et al. 2007). PAT (Fig. 6.5) was classified as non-carcinogenic in Group 3 by the International Agency for Cancer Research (IARC). Initially tested as an antibiotic, patulin was subsequently shown to be dangerous to humans and to produce symptoms including nausea, vomiting, ulceration, and hemorrhage. Glutathione is considered the scavenger of PAT-induced toxicity (Alshannaq and Yu 2017).

6.8 Ergot Alkaloid

The genus *Claviceps* produces the mycotoxins known as ergot alkaloids, which are predominantly produced by one type of fungus and infect a variety of cereals. Alkaloids found in ergot, including ergotamine (Fig. 6.6), ergocrystinine, ergometrimine, ergonovin, and ergocrystin, are toxic. One of the most significant species, *Claviceps purpurea*, mostly affects monocotyledonous plants. The crops infected by Ergot alkaloid (EAs) include rye, barley, wheat, millet, oats, and triticale, with rye having the highest rates of fungal infection (Krska et al. 2008; Agriopoulou 2021). Ergot alkaloids are consumed by humans through food. After consuming foods contaminated with EAs, it can cause ergotism, an illness causing strange hallucinations, convulsions, agalactia, burning sensations, vasoconstriction, and gangrenous loss of limbs, which are some of the symptoms in humans (Gurikar et al. 2022). Purified ergot alkaloids crystallized as translucent compounds that are soluble in organic solvents and buffers as well as inorganic solvents like acetonitrile and methanol. The two types of ergotism are gangrenous and convulsive, respectively.

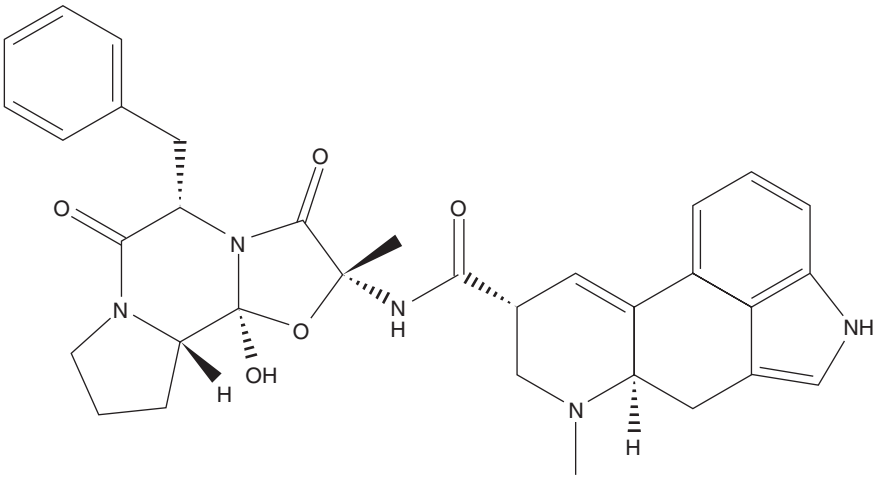


Fig. 6.6 Ergotamine

Convulsive ergotism affects the neurological system, whereas gangrenous ergotism affects the blood supply. Animals are not immune to ergotism, which is a serious threat to veterinarians and can affect a variety of species, including cattle, sheep, pigs, and poultry (Pleadin et al. 2019).

6.9 Effect of Aromatic Bioactive Compounds (Essential Oils) on Mycotoxins

Essential oils are naturally occurring volatile and aromatic compounds produced by aromatic herbs or shrubs for their requirements, such as defense or attracting pollinators, rather than nutrition. Aromatic plants, which are often found in temperate and tropical regions, generate essential oils, a mixture of different constituents. They typically possess a lower density compared to water and are liquid, transparent, sparingly colored, lipid-soluble, and soluble in organic solvents. Essential oils are synthesized by plant parts such as buds (*Syzygium aromaticum*), flowers (*Thymus vulgaris*), leaves (*Eucalyptus globulus*, *Callistemon lanceolatus*), stems (*Cordia trichotoma)*, seeds (*Pimpinella anisum)*, fruits (*Juniperus communis*), root or rhizome (*Acorus calamus*, *Zingiber officinale*), wood or bark (*Santalum austrocaledonicum*) and accumulate in cells, secretory cavities, or glandular hairs of plants (Bakkali et al. 2008; Roh et al. 2011; Shukla et al. 2011; Shukla et al. 2013; Bilia et al. 2014). Essential oils may be extracted using various methods. One of the most popular methods is steam- or hydrodistillation, which allows for the separation of mildly volatile, water-immiscible substances at low temperatures (Chamorro et al. 2012). Essential oils are complex natural mixtures that consist of about 20–60 components at quite different concentrations; two or three major components are present at high concentrations (20–70%) compared to other components that are present in trace

amounts (Chouhan et al. 2017). The main components found in essential oils are typically responsible for their biological effects (Shukla et al. 2009). They have been extensively used as bactericidal, virucidal, fungicidal, antiparasitic, insecticidal, and therapeutic agents (Shaaban 2020). For example, 37 compounds are identified in the oregano essential oil (OEO), of which carvacrol (30.73%) and thymol (18.81%) are the two major constituents (Chen et al. 2022). In the past 10 years, numerous studies have been done on the antimycotic effects of essential oils. These studies have demonstrated the effect of EOs on the restriction or decrease of mycotoxin synthesis. Bocate et al. (2021) investigated the efficacy of garlic essential oil (GEO) to hinder the production of *Aspergillus parasiticus*, *Fusarium verticillioides*, and *Gibberella zeae*, which are responsible for producing the aflatoxins AFB1, ZEA, and, FB1 in stored corn kernels. According to the findings, GEO can prevent the growth of mycotoxigenic fungus. *A. parasiticus*, *G. zeae*, and *F. verticillioides* all exhibiting minimum inhibitory concentrations (MICs) of 0.0086, 0.069, and 0.0086 mg/mL, respectively. *Penicillium verrucosum* and *P. griseofulvum* were discovered in lentils and dry grapes (*Vitis vinifera* L.) in northern Morocco. Chidi et al. (2020) investigated the antifungal activities of *Melaleuca alternifolia* essential oil (EO) against both of these isolates. The results showed that adding *M. alternifolia* EO at various dosages completely decreased the amount of terrestric acid and ochratoxin-A produced by *P. griseofulvum* and *P. verrucosum*. In an in vitro study, Ferdes et al. (2017) investigated the effectiveness of five EOs (sage, rosemary, anise, quinoa, and savory) against *Aspergillus niger*, *Aspergillus oryza*, *Fusarium oxysporum*, and *Mucor pusillus*. Savoury oil treated with a concentration of 20 g/mL was efficient on *A. oryza*, *A. niger*, *F. oxysporum*, and *M. pusillus*. The essential oils of quinoa, sage, and rosemary have fungicidal properties against *A. oryza*, *A. niger*, and *F. oxysporum* at concentrations of 10 and 20 g/mL. Zhou et al. (2018) studied the effects of exogenous essential oil decanal on the growth and patulin production of *P. expansum*. According to the results, 0.12 g/L decanal was considered remarkably to restrict the growth of *P. expansum* in vitro, while 0.24 g/L decanal effectively prevented blue mold rot on apple and pear fruit. According to Ferreira et al. (2013), curcumin and the essential oil of *Curcuma longa* have antiaflatoxigenic properties at concentrations ranging from 0.01 to 5.0%. More than 96% of AFB1 and AFB2 production was suppressed by 0.5% of the essential oils of *C. longa* and curcumin (Table 6.2).

Tian et al. (2011) explored the dill essential oil derived from the seeds of *Anethum graveolens* to access its antifungal activity in vitro and in vivo against toxigenic strains of *Aspergillus flavus*, *A. niger*, *A. oryzae*, and *Alternaria alternata*. They observed that the mycelial growth of *A. flavus* (88.9%), *A. niger* (94.4%), *A. oryzae* (88.9%), and *A. alternata* (83.3%) was significantly reduced by the EO at a concentration of 120μL/mL. Kiran et al. (2016) explore the efficacy of *Cinnamomum zeylanicum* essential oil (CZEO) against *Aspergillus flavus* and aflatoxin B1 secretion, its functional properties, and mode of action. CZEO exhibited absolute fungitoxicity against *A. flavus*, and the MIC of the species fluctuated between 0.25 and 6.0μL/mL. Furthermore, CZEO drastically lowered the generation of aflatoxin B1 and inhibited it at 0.3μL/mL. Li et al. (2016) studied the inhibitory effects of *Litsea*

Table 6.2 Example of some essential oils (EOs) showing inhibitory effect against mycotoxigenic fungi

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Allium sativum	Garlic	Diallyl disulfide,2-vinyl-1,3-dithiane, diallyl trisulfide, Methyl allyl trisulfide	*Aspergillus parasiticus*, *fusarium verticillioide,and Gibberella zeae*	GEO reduces the growth of AFB1, FB1, or ZEA from stored kernels of corn	Bocate et al. (2021)
Cananga odorata	Ylang-Ylang	Linalool, germacrene-D, thymol, limonene, 1,8-cineole, α-phellandrene	*Fusarium graminearum*	2.5 mg/g of COEO limits the growth of *F. graminearum* in stored maize kernels	Kalagatur et al. (2018)
Melaleuca alternifolia	Tea tree	Terpinene-4-ol	*Penicillium griseofulvum*, *Penicillium verrucosum*	EO completely inhibits the growth of *P. verrucosum* and griseofulvin at 2.75%	Chidi et al. (2020)
Callistemon lanceolatus	Bottlebrush	1,8-cineole, γ-terpinene, α-pinene	A. *Absidia ramosa*, *aspergillus*, *fusarium*, *Alternaria*, *Penicillium*, *Dreschelera*, *Chetomium* spp.	CLEO and 1,8-cineole at 0.54 and 0.9 mg/mL, respectively, caused 100% inhibition of AFB1 production	Shukla et al. (2012)
Melaleuca rhaphiophylla	Swamp paperbark	Terpinolene, γ-terpinene, α-terpinene, 1,8-cineole, terpinen-4-ol	*A. flavus, A. niger*, *A. nomius*, *F. graminearum*	EO inhibits the 90% growth of selected fungal strains	Zimmermann et al. (2022)
Cymbopogon flexuosus	Lemongrass	E-citral, α-sinensal	*Aspergillus flavus*	CFEO, citral, geraniol, eugenol, α-pinene, and linlool have respective inhibition of AFB1 at 0.8, 0.4, 0.6, 0.2, and 0.6μL/mL	Kumar et al. (2009)

(continued)

Table 6.2 (continued)

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Xylopia aethiopica	Guinea pepper	α-Pinene, β-Pinene, β-Phellandrene, Z-γ-bisabolene	*Aspergillus Niger*, *fusarium oxysporium*, *A. flavus*, *A. fumigatus and A. versicolor*	Two fungal strains at 300 ppm conc. Of XAEO showed remarkable inhibition	Tegang et al. (2018)
Trachyspermumammi	Carom seeds	Thymol, P-cymene, γ-Terpinene, β-Pinene	*A. flavus*, *A. Niger*, *A. fumigatus*, *C. albicans*, *C. tropicalis*, *C. utilis*	TAEO (11.2 μg/mL) was significantly effective against *Candida* and *Aspergillus* spp.	Dutta et al. (2020)
Illicium verum	Star anise	Trans-anethole, estragole, D-limonene	*Aspergillus flavus*	The growth of *A. flavus* in lotus seeds is inhibited by IVEO at concentrations of 3.6 L/mL in vitro and 6.0 L/g in vivo	Li et al. (2020)
Citrus reticulata	Mandarin	Limonene	*Aspergillus Niger*	*A. niger*'s growth was prevented by the EO concentration of 30.72 mL/L	Abdel-Aziz et al. (2019)
Citrus sinensis	Sweet orange	Dl-limonene	*Aspergillus flavus*	CSEO and dl-limonene completely inhibited AFB1 production at 500 and 250 ppm, respectively	Singh et al. (2010)
Lippia alba	Bushy mat grass	Geranial, Neral	*Mycotoxigenic* fungi (*aspergillus*, *fusarium*, *Penicillium*) and *Rhizoctonia, Trichoderma* spp., etc.	LAEO, and their major components inhibited aflatoxin B1 production at 0.6 to 1.0μL/mL	Shukla et al. (2009)
Zingiber officinale	Ginger	α-Zingiberene, citral	*Fusarium verticillioides*	ZOEO exhibited the inhibitory effect at conc. Of 4000 and 2000μg/mL	Yamamoto-Ribeiro et al. (2013)

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Cymbopogon khasans	Jamrosa	Z-citral, linalyl acetate	*Aspergillus flavus*	CKEO suppressed AFB1 at 0.4μL/mL, whereas, linalyl acetate and Z-citral at 0.7–1.0μL/mL	Mishra et al. (2012a, b)
Pimenta dioica	Jamaica pepper	γ-Terpinene, α-terpineol, β-linalool	*Aspergillus flavus*	PDEO at varying conc. 2.5 μL/mL and 1.5 μL/mL completely retards the growth of *A. flavus*	Chaudhari et al. (2019)
Cinnamomum camphora, *Alpinia galanga*	Camphor and galangal, respectively	Fenchone, camphene, α-thujene, α-pinene	*Aspergillus flavus*	The combination of two EOs completely checked aflatoxin B1 synthesis at 250 ppm	Srivastava et al. (2008)
Mentha rotundifolia	Apple mint	Piperitenone oxide, caryophyllene oxide, cis-cinerolone	*Fusarium culmorum*	MREO effectively inhibits the growth of targeted fungi	Yakhlef et al. (2020)
Melissa officinalis	Lemon balm	P-mentha-1,2,3-triol, P-menth-3-en-8-ol, Pulegone	*Penicillium expansum*, *Botrytis cinerea*, *and Rhizopus stolonifer*	MOEO (10–160μL) obstructs the growth of selected fungal strains	El Ouadi et al. (2017)
Myristica fragrans	Nutmeg	Elemicin, myristicine, thujanol	*Aspergillus flavus*	MFEO observed at 2.75 mg/mL caused a 100% reduction of ergosterol content	Das et al. (2020)
Cinnamomum glaucescens	Sugandhkokila	2-Propenoic, acid1,8-cineole	*Aspergillus flavus*	CGEO inhibited the growth of fungi at 4.5 and 3.5μL/mL	Prakash et al. (2013)
Ocimum gratissimum L.	African basil	Methyl cinnamate, γ-terpinene	*Aspergillus flavus*	OGEO strongly inhibited aflatoxin production at 0.6μL/mL and 0.5μL/mL, respectively	Prakash et al. (2011)

(continued)

Table 6.2 (continued)

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Cinnamomum zeylanicum	Cinnamon	2-methoxy-3-(2-propenyl), caryophyllene	*Aspergillus flavus*	CZEO exhibited inhibition of all test molds at 0.25 to 0.6μL/mL and 0.3μL/mL	Kiran et al. (2016)
Anethum graveolens	Dill	Carvone, limonene, apiol	*Aspergillus flavus*, *A. niger*, *A. oryzae*, and *Alternaria alternata*	AGEO (2.0μL/mL) showed complete growth inhibition of all examined toxin-producing fungi	Tian et al. (2011)
Cinnamomum zeylanicum, *Curcuma longa*, *Zingiber officinale*, *Ocimum basilicum*, and *Cymbopogon martini*	Cinnamon, Turmeric, Ginger, Common basil, Palmarosa, respectively	Cinnamaldehyde, Ar-turmerone, Eugenol, Geranyl, proprionate, Geranyl acetate	*Aspergillus ochraceous*, *Penicillium verrucosum*	CZEO and CMEO inhibited the growth of OTA production at 1500 and 2500 mg/g, respectively	Kalagatur et al. (2020)
Rosmarinus officinalis	Rosemary	1.8 cineole, camphor, α-Pinene	*Fusarium verticillioides*	ROEO at 150μg/mL significantly reduced the growth of fumonisin	da Silva Bomfim et al. (2015)
Curcuma longa	Turmeric	Ar-turmerone	*Fusarium graminearum*	CLEO at 3500 and 3000μg/mL inhibited zearalenone	Kalagatur et al. (2018)
Caesulia axillaris	Pink node flower	Dl-limonene, euasarone	*Aspergillus flavus*	Aflatoxin B1 production was inhibited at 0.8μL/mL of EO	Mishra et al. (2012a, b)
Lantana indica	Shrub verbenas	α-Humulene, delta-3-carene, sabinene	*Aspergillus flavus* and 11 other spp.	LIEO at 0.75 mg/mL caused complete inhibition of AFB1	Kumar et al. (2010)
Carum carvi, *Coriandrum sativum*	Caraway and Coriander	Carvone, Linalool	*Aspergillus flavus*	EOs obstruct the growth of fungal biomass at 1000μg/mL	Lasram et al. (2019)

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Zanthoxylum alatum	Winged prickly ash	Linalool, methyl cinnamate	*Aspergillus flavus*	ZAEO at 1.25μL/mL and 2.5μL/mL protect 86.33% *Piper nigrum* L. fruits against fungi	Prakash et al. (2012)
Ageratum conyzoides	Chick weed	Precocene II, precocene, cumarine	*Aspergillus flavus*	Aflatoxin synthesis was inhibited by ACEO at 0.10 g/mL	Nogueira et al. (2010)
Boswellia carterii	Moxor	Ziranyl-acetate	*Aspergillus flavus*	BCEO protected *Piper nigrum* fruit storage against fungal damage by 65.38%	Prakash et al. (2014)
Matricaria chamomilla	Chamomile	α-Bisabolol, trans-farnesol, α-bisabolol oxide A	*Aspergillus Niger*	The maximal growth inhibition by MCEO was 92.50% at the highest conc. Of 1000 g/mL	Tolouee et al. (2010)
Thymus vulgaris, Satureja hortensis, Syzygium aromaticum	Thyme, summer savory, and clove, respectively	Thymol, carvacrol, eugenol, β-caryophyllene	*Aspergillus flavus*	EOs showed potential inhibition at 350–500 ppm in tomato paste	Omidbeygi et al. (2007)
Illicium verum	Star anise	Trans-anethole, caryophyllene, limonene	*Aspergillus flavus*, *A. parasiticus*, and *fusarium verticillioides*	At 200 ppm, IVEO inhibited all the fungi	Aly et al. (2016)
Rosmarinus officinalis, and Trachyspermumcopticum	Rosemary and carom seeds, respectively	Piperitone, α-pinene, thymol, P-cymene	*Aspergillus parasiticus*	TCEO showed more potency than ROEO against *A.parasiticus* and ROEO slightly inhibited the aflatoxin at 450 ppm	Rasooli et al. (2008)

(continued)

Table 6.2 (continued)

Source plants of EOs	Common name of the plants	Major constituents	Inhibited fungal species	Findings	References
Syzygium Aromaticum, *Rosmarinus officinalis*	Clove and rosemary, respectively	Eugenol, eucalyptol	*Aspergillus Luchuensis*	ROEO inhibited the growth of mycelia 36.6% and SAEO 100% inhibited the fungal mycelia growth at 200 μL/L	Laaziz et al. (2022)
Lippia origanoides	Brazilian lippia	Carvacrol, P-cymene, γ-terpinene	*Aspergillus flavus*, *aspergillus carbonarius*, *aspergillus ochraceus*	LOEO at different concentrations (0.24 L/mL, 0.98 L/mL, 0.98 L/mL) inhibited all fungi	Brandão et al. (2021)

cubeba essential oil (LC-EO) on *Aspergillus flavus* and aflatoxin B1 production in licorice. The minimum inhibitory concentration zone (MIC) and minimal fungicidal concentration (MFC) zone of LC-EO were 0.5 and 1.0μL/mL, respectively. The mycelia growth and aflatoxin B1 accumulation were completely inhibited when licorice was treated with 5.0μL/mL for 20 days. Gemeda et al. (2014) studied the effect of some EOs, viz., *Cymbopogon martinii, Foeniculum vulgare*, and *Trachyspermum ammi*, against toxigenic strains of *Aspergillus* species (*A. niger and A. flavus*). *T. ammi* oil showed the highest antifungal activity and could inhibit mycelial growth at 1 μL/mL. Ozcakmak et al. (2017) compared the effects of mint, garlic, sage, and wild oregano EOs on the growth of *Penicillium verrucosum* and its ochratoxin A production. Sage and mint essential oils reduced considerable toxin production, although wild oregano and garlic essential oils wholly prevented them, at quantities of 0.5 and 0.25%, accordingly. To control four corn fungi, *A. flavus* (CCC116–83 and BXC01), *P. oxalicum* (083296), and *P. minioluteum* (BXC03), which produce mycotoxin in maize, Camiletti et al. (2014) evaluated the antifungal activity of the essential oils of oregano varieties, mint varieties, and rosemary plants grown in Argentina. They noted that oregano EO was most effective against mycotoxigenic fungus, while others had neither antifungal nor toxin inhibitory activity. Pérez-Izquierdo et al. (2022) evaluated the essential oil from hydrodistillation of *Cistus ladanifer* and found a strong antifungal effect on all four species of phytopathogenic fungi (*Rhizoctonia solani*, *Fusarium oxysporum* sub sp., *radicis-lycopersici*, and *Cryphonectria parasitica*) and on oomycete (*Phytophthora cinnamomi*), when tested in vitro. All four species had their sporulation suppressed by EO. Marín et al. (2004) studied the effect of essential oils (cinnamon, clove, oregano, palmarosa, and lemongrass) on zearalenone and deoxynivalenol production by *Fusarium graminearum* in non-sterilized maize grain. The production of ZEA was significantly impacted by all parameters, including essential oils, temperature, a_w, treatment timing, and their interactions. In findings, they noticed that clove, lemongrass, and palmarosa oils reduced ZEA production when compared to the controls at 0.950 a_w/30 °C; however, cinnamon and oregano essential oils had no effect. Lee et al. (2008) explored the efficacy of 11 Myrtaceae essential oils *(Eucalyptus citriodora*, *E. smithii*, *E. globulus*, *E. radiata*, *E. dives*, *E. polybractea*, *Melaleuca dissitiflora*, *M. quinquenervia*, *M. uncinata*, *M. linariifolia*, *and Leptospermum petersonii)* and their components against three phytopathogenic fungi (*Phytophthora cactorum*, *Cryphonectria parasitica*, *and Fusarium circinatum*). As per the report, only three plant species have shown antifungal efficacy in in vitro fungicidal activity. Essential oils from *L. petersonii* had the strongest fungicidal effects (46.2%) in a test against *P. cactorum*, followed by essential oils from *M. quinquenervia* and *E. citriodora* (35.4 and 33.6%). Gakuubi et al. (2017) investigated the antifungal activity of *Eucalyptus camaldulensis* essential oil against maize infecting and fumonisins producing *Fusarium* spp., viz., *F. solani*, *F. verticillioides*, and *F. proliferatum*. After five days of incubation, the EO effectively inhibited fungal growth formation at a dosage of 7–8 L/mL in all of the tested pathogen species. Xing et al. (2014a, b) studied the degradation effect of essential oils on FB1. They found that eugenol oil, eucalyptus oil, cinnamon oil, anise oil, citral, and

camphor oil were quite effective in reducing FB1. Furthermore, the optimal conditions for 94.06% FB1 reduction by EOs were 280 mg/mL on 120 h of incubation at 30 °C. The feasibility of using EOs and natural compounds used against human pathogenic fungal strains using conventional and non-traditional is highlighted by Abd Rashed et al. (2021) in a review. They explained that EOs with high monoterpene content have significant antifungal potential. Several species, including *Cymbopogon* sp., *Thymus* sp., *Lavandula* sp., and *Salvia* sp., were discovered to have excellent antifungal and toxin-inhibitory activity.

6.10 Mode of Action of Essential Oils against Mycotoxigenic Fungi and their Toxins

Aromatic oils extracted from various aromatic herbs or shrubs exhibit intense antimicrobial or antifungal properties. Essential oils are low-molecular-weight, lipophilic molecules that are liquid, lipid-soluble, and volatile (Bakkali et al. 2008; Basak and Guha 2018). Due to the lipophilic nature of essential oils, which enables them to cross the fungal cellular membrane, they may modify how permeable the membrane is to cations like H^+ and K^+. This influences the flow of protons, modifies cellular pH, and has an impact on the chemical components of cells as well as their activity. The interruption of membrane permeability leads to an imbalance in intracellular osmotic pressure, which degrades intracellular organelles including Ca^{2+} ion channels, proton pumps, and ATP (adenosine triphosphate) pools, destroying intracellular organelles, proton pumps, and diminishing membrane potential. The fluidity of plasma membranes could change, which can hamper cytochrome C pathways, affect protein metabolism, and depress calcium ion concentration, among other things. As a result, EOs may damage the protein, lipid, and nucleic acid composition of cells. Permeability of the inner and outer mitochondrial membranes may result in apoptosis or cell death. This leads to harmful morphological and ultrastructural changes that are irreversible i.e., spore germination inhibition, decreased mycelial growth, inhibition of energy release, and changes in gene expression patterns and metabolic processes (Basak and Guha 2018; Swamy et al. 2016; Bakkali et al. 2005; Mani-López et al. 2021; and Andrade-Ochoa et al. 2021). Das et al. studied the mode of action of Myristica fragrans-derived EOs against *A. flavus* and aflatoxin B1 (AFB1) contamination of stored scented rice (*Oryza sativa*) varieties in 2020. They demonstrate that MFEO reduced the ergosterol content of the fungal plasma membrane, increased cellular ion leakage, and decreased the amount of methylglyoxal, the substance that stimulates the production of aflatoxin. Similar studies by Maurya et al. (2021a, b) examine the antifungal mode of action of *Carum carvi* essential oil (CCEO) against the *Aspergillus flavus* (AF-LHP-WS-4) producing aflatoxin B1 strain. CCEO inhibited fungal growth by inducing the efflux of essential cellular ions (viz., K^+, Ca^{2+}, and Mg^{2+}) and inhibiting ergosterol and cellular methylglyoxal (MG) biosynthesis. Under light and scanning electron microscopy, Soylu et al. (2006) investigated the antifungal activities of essential oils extracted from the aerial parts of aromatic plants such as oregano

(*Origanum syriacum* var. bevanii), thyme (*Thymbra spicata* subsp. spicata), lavender (*Lavandula stoechas* subsp. stoechas), and rosemary *(Rosmarinus officinalis*). The images demonstrated significant morphological changes in the pathogen hyphae, including protoplast leakage, vacuolations, hyphal shrivelling, and cytoplasmic coagulation. These changes were found in pathogen hyphae that had been exposed to both the volatile and contact phases of oil. Ramsdam et al. (2021) investigated the ability of five medicinal aromatic plant essential oils, namely *Gaultheria fragrantissima*, *Curcuma longa*, *Zingiber officinale*, *Artemisia nilagirica*, and *Litsea cubeba*, to inhibit the growth of toxigenic *Aspergillus flavus* isolated from stored maize in Meghalaya. They evaluated that *Litsea cubeba* EO had the highest antifungal activity (0.8μL/mL) among the essential oils, and as shown by scanning electron microscopy images, *A. flavus* treated with the oils had damaged hyphae and conidiophores. Ahmad et al. (2013) assessed the in vitro synergistic antifungal activity of thymol and carvacrol with fluconazole against susceptible and resistant *Candida albicans* and also explained the synergistic antifungal effect with the azole antimycotic fluconazole by inhibiting the over-expression of efflux-pump genes CDR1 and MDR1. Both monoterpenes were highly effective at blocking drug efflux transporter pumps (70–90%) in *Candida* spp. Ahmad et al. (2011) elucidated that carvacrol and thymol have strong fungicidal effects against 11 fluconazole-sensitive and resistant *Candida* isolates. These natural isopropyl cresols appear to affect membrane integrity and impair ergosterol production as their primary mode of action (Table 6.3).

According to Rammanee and Hongpattarakere (2011), lime essential oil completely inhibited the growth and aflatoxin production of *A. flavus* at a dosage of 2.25 mg/mL, whereas kaffir and acid lime essential oils significantly reduced the aflatoxin production of *A. flavus* and *A. parasiticus*. The effects of acid lime essential oil on target cell damage were examined using transmission electron microscopy. Essential oil-treated cells had observable alterations to the plasma and nucleus membranes, including loss of cytoplasm, vacuole fusion, and separation of the fibrillar layer. Wang et al. (2018) reported that *A. ochraceus* exposed to 0.4 mmol/L of cinnamaldehyde showed harmful morphological and ultrastructural modifications that were irreversible, including folding of the cell, loss of cell wall integrity, disruption of the plasma membrane, destruction of the mitochondria, and the absence of intracellular organelles. The investigated regulatory and biosynthetic genes, such as pks, laeA, nrps, veA, and velB, were significantly downregulated in the presence of cinnamaldehyde. Singh et al. (2019) reported that chemically characterized nanoencapsulated *Ocimum sanctum* essential oil (OSEO) decreased the ergosterol content, increased the leakage of vital cellular ions, and also decreased the methylglyoxal content (an aflatoxin-inducing substrate). *Boswellia serrata* essential oil was tested in vitro and in a viable maize plant by Venkatesh et al. (2017) to determine its antifungal and anti mycotoxigenic properties. *B. serrata* essential oil completely inhibited the formation of aflatoxin B1 and fumonisin B1, and the ergosterol content fell dramatically as the concentration of essential oil increased. Bennis et al. (2004) exposed yeast cells to thymol and eugenol (phenolic major components of thyme and clove essential oils), which caused lysis as evidenced by

Table 6.3 Mode of action of essential oils against species of mycotoxigenic fungi and their toxins

Targeted fungi/toxins	Essential oils/ constituent	Mode of action/observation	Reference
Aspergillusflavus and AFB_1	*Melaleuca cajuputi*	Preventing the synthesis of AFB1 by inhibiting intracellular methylglyoxal, ergosterol synthesis, leakage of cellular components, and mitochondrial membrane damage potential	Chaudhari et al. (2022)
Aspergillus Niger	*Matricaria chamomilla*	The plasma membrane was damaged and separated from the cell wall, the cytoplasm was entirely depleted and the intracellular organelles were disorganized	Tolouee et al. (2010)
AspergillusNiger	*Thymus x-porlock, Thymus eriocalyx*	Irreversible disruption to the cellular organelles, cell membrane, and cell wall	Rasooli et al. (2006)
Fusarium solani	**Thymol and salicylic acid**	The structure and function of mitochondria were adversely affected, and the integrity and permeability of the cell membrane were degraded	Kong et al. (2021)
Monilinia fructicola	Tea tree oil, lemon oil, rosemary oil, and thyme oil	TTO altered mycelial morphology, intracellular reactive oxygen species (ROS) levels, and membrane permeability in post-harvest peaches	Xu et al. (2021)
Penicillium italicum	**Citral**	Disruption of integrity and permeability of cell membrane, alteration of extracellular pH, the release of cell constituent, and potassium ion leakage, as well as a decrease in ergosterol contents and total lipid	Tao et al. (2014a)
Penicillium italicum, *Penicillium digitatum*	*Citrus reticulata*	Changes in extracellular conductivity and total lipid content, the release of cell components, and cytotoxicity were caused by disruptions in cell membrane integrity and cell component leakage	Tao et al. (2014b)

Table 6.3 (continued)

Targeted fungi/toxins	Essential oils/ constituent	Mode of action/observation	Reference
Fusarium graminearum	*Humulus lupulus* (hop)	Changes in the chitin and total lipid composition of the outer cell membrane, disruption of the cytoplasmic membrane, and prevention of mycelial growth and spore germination	Jiang et al. (2023)
Aspergillus Niger	*Melaleuca alternifolia*	Down-regulation of important genes that are expressed concerning metabolic pathways like glycolysis, pentose phosphate, and phenylpropanoid was significantly induced	Kong et al. (2020)
Candida species	*Ocimum sanctum*	Disruption of membrane integrity and reduction in **ergosterol biosynthesis**	Khan et al. (2010)
Raffaelea quercus-mongolicae, and *Rhizoctonia solani*	*Cinnamomum verum* **and** *Cymbopogon citratus*	Disruption of cell membranes and the generation of reactive oxygen species (ROS)	Lee et al. (2020)
Aspergillus flavus and AFB1	*Caesulia axillaris*	Increased the shelf life of herbal raw materials by reducing lipid peroxidation and biodeterioration	Mishra et al. (2012a, b)
Alternaria alternata	**Cinnamaldehyde**	Loss of cell membrane integrity, reduction in total lipid content, the release of intracellular components, leakage of electrolytes, and reduction in total lipid content	Xu et al. (2018)
Fusarium verticillioides	**Cinnamon oil and cinnamaldehyde**	Irreversible harmful morphological and ultrastructural changes, such as loss of integrity of the cell wall, lack of cytoplasmic contents, destroyed mitochondria, ruptured plasma membranes, and cell folding	Xing et al. (2014a, b)

(continued)

Table 6.3 (continued)

Targeted fungi/toxins	Essential oils/ constituent	Mode of action/observation	Reference
Aspergillus flavus	*Ageratum conyzoides*	Degradation in the surrounding fibrils as well as in the ultrastructure, which was more visible in the endomembrane system, such as in mitochondria	Nogueira et al. (2010)
Candida albicans, *C. tropicalis*, *C. glabrata*, *Saccharomyces cerevisiae*, *Zygosaccharomyces parabailii*, *Debarymyces hansenii*	*Chrysanthemum morifolium*	Cytoplasmic membrane permeability was disrupted, and mitochondrial membrane potential and DNA binding were also affected	Zhan et al. (2021)
Fusarium verticillioides	*Rosmarinus officinalis*	This causes the cell wall to be damaged and the loss of essential cellular elements, which in turn prevents the synthesis of ergosterol and fumonisins	da Silva Bomfim et al. (2015)
Candida spp.	*Laurus nobilis*	Negatively affects *C. albicans* biofilm adhesion and formation by interfering with cell wall production and membrane ionic permeability	Peixoto et al. (2017)
Aspergillus flavus	*Curcuma longa*	Aflatoxin production is suppressed by mycotoxin gene silencing, which disrupts plasma membrane integrity, and mitochondrial dysfunction	Hu et al. (2017)
Geotrichum citri-aurantii	Cinnamaldehyde	Interfering the build of the cell wall and therefore may lead to the damage of cell wall permeability and integrity	OuYang et al. (2019)
Trichophyton. Rubrum, *T. tonsuran*, *Microsporumgypseum T. Mentagrophytes*	*Foeniculum vulgare*	Damages the plasma membrane, and intracellular organelles and also inhibit the activities of a mitochondrial enzyme, such as malate dehydrogenase, succinate dehydrogenase, and ATPase	Zeng et al. (2015)

Table 6.3 (continued)

Targeted fungi/toxins	Essential oils/ constituent	Mode of action/observation	Reference
Aspergillus flavus, *aspergillus ochraceus*	Geraniol and citral	Citral showed antimycotic action mainly by inhibiting the genes involved in sporulation and proliferation. Geraniol inhibited *A. flavus* by increasing intracellular ROS generation, while it exhibited toxicity toward *A. ochraceus* via altering cell membrane permeability	Tang et al. (2018)
Aspergillus flavus and AFB_1	Cinnamaldehyde, citral, and eugenol	Gene transcription levels that are involved in the production of aflatoxin were decreased	Liang et al. (2015)
Candida albicans	Tea tree, thyme, peppermint, and clove oils	Damage to the mitochondria has lethal effects on *Candida albicans*, and also has cytotoxic and genotoxic effects	Rajkowska et al. (2016)

the release of substances that absorb at 260 nm. A scanning electron microscope analysis of the findings revealed significant surface damage in the treated cells. The findings revealed that the antifungal efficiency of both of these components involves modification of the membrane and cell wall of the yeast (Fig. 6.7).

6.11 Conclusion

The essential oils and their bioactive components have significant antifungal and anti-mycotoxigenic properties at the cellular and molecular levels against the major group of fungi responsible for food deterioration. The most commonly used essential oils have an effect on *Aspergillus* spp., *Penicillium* spp., and *Fusarium* spp., which were the most employed genera and species in the last decade for mycotoxigenic fungi, mycotoxins, and their modes of action. In terms of mode of action, various mechanisms involve extending the lagged phase, modifying the fungal growth rate, inhibiting the cell membrane and cell permeability, and disrupting the enzymatic cell system. The current reports suggest that developing aflatoxin-resistant varieties using a green transgenic strategy would be facilitated by their mode of action in AF inhibition via methylglyoxal. Despite the several significant characteristics of essential oils, it should be emphasized that their organoleptic effects can be problematic. In this sense, nanoencapsulation can be a possible approach to dealing with these issues because the process can limit their loss as well as enhance the stability of the antifungal and anti-mycotoxigenic potential of EOs and their bioactive components and may reduce their interaction with food while retaining their original organoleptic properties.

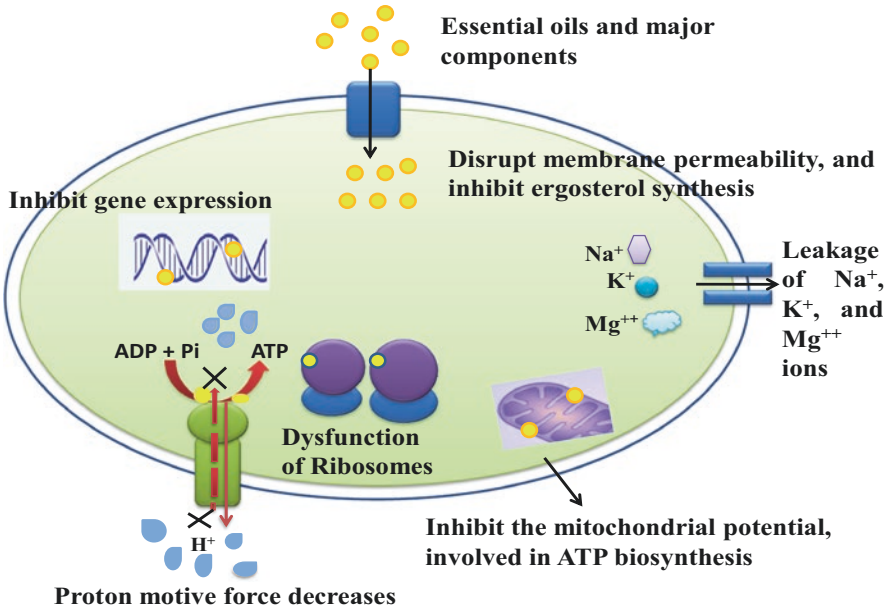


Fig. 6.7 Schematic of essential oil's principle of action against mycotoxigenic fungi

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