

Polyphenols and terpenes in Mediterranean plants: an overview of their roles and possible applications

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Abstract: The Mediterranean basin represents one of the key hotspots in terms of biodiversity and endemic floristic richness in the world (*i.e.*, a reservoir of plant biodiversity). With ongoing climate change, the Mediterranean vegetation is increasingly exposed to different sources of environmental stresses, such as drought, heat, and solar irradiance. To cope with these severe abiotic stresses, beside morpho-anatomical traits, Mediterranean endemic species enhance the production of secondary metabolites, especially terpenes and polyphenols. These compounds have different roles in plants. Terpene and polyphenol compounds play a key antioxidant function (quenching Reactive Oxygen Species) thus improving ozone and drought tolerance, while also acting as pollinator attractors and repellents for dangerous herbivorous insects (contributing to the taste and odour of different plant tissues). In addition to their roles in plants, these bioactive compounds provide multiple health-promoting benefits for humans. Indeed, they can be used in different types of industries, such as pharmaceutical, nutraceutical, green (as supplements to fossil fuel and insecticides) and cosmetic industries. In conclusion, these compounds may be considered as key innovative components in different technological domains.

Keywords: antioxidant activity; environmental stresses; human health; Mediterranean basin; pharmaceutical industry; secondary metabolites.

1. Introduction

Mediterranean plants are rich in secondary metabolites, particularly phenolics (Sardans and Peñuelas, 2013) and terpenes (Ormeño et al., 2007). Many of them have an important physiological and ecological role: improving ozone tolerance, protecting proteins and cell membranes from reactive oxygen species (ROS), quenching ROS (Andre et al., 2010; Di Ferdinando et al., 2014; Griesser et al., 2015), photo-protecting against UV-radiation (Edreva et al., 2008), providing protection against herbivores as well as attracting pollinators (Holopainen et al., 2013).

Secondary metabolite biosynthesis is stimulated by abiotic stress intensification, such as the increase in temperatures and drought waves imposed by global climate change to Mediterranean regions (Akula and Ravishankar, 2011; Tattini and Loreto, 2014). Mediterranean plant species, especially woody evergreens, make a high investment of fresh assimilated carbon in their biosynthesis during the dry season (Di Ferdinando et al., 2013). Recently, Gori et al. (2020) have reported a significant seasonal

and diurnal variation of polyphenol amounts in leaves of several Mediterranean endemic species. These results show that the content of polyphenols presents a monthly variation, with higher amounts in summer rather than spring and autumn, and a clear daily trend, with higher concentrations at midday. This could explain their protective role against UV and drought stress (Agati et al., 2002; Barnes et al., 2016). A similar seasonal trend was reported by Llusia and Peñuelas (2000) for terpenes. Terpene emissions in Mediterranean woody species are prevalently linked with changes in temperature, the maximum emission rate in spring for the least volatile monoterpenes and in summer for the most volatile monoterpenes (Llusia and Peñuelas, 2000). In addition, Tattini et al., (2015) showed an interesting daily orchestration of the different components of the antioxidant machinery of *Platanus × acerifolia* in drought-stressed leaves during summer. It was suggested that a higher isoprene emission early in the afternoon, when the decline in sunlight irradiance is coupled with an increasing air temperature, may complement the antioxidant functions of carotenoids and improve membrane stability.

These organic compounds, in addition to providing the abovementioned benefits to plants, have gained scientific attention for their promising effects on human health. In the last decades, several studies have highlighted the potential applications of secondary metabolites, in particular polyphenols, in pharmacology due to their anti-inflammatory, antioxidant and neuroprotective activities (Finley, 2004; Paduch et al., 2007; Gosslau et al., 2011; Gori et al., 2016). In addition, the link between a polyphenol-based diet and decreased risks of cancer (Soto-Vaca et al., 2012; Hardman, 2014) has been demonstrated as well as their healing effects in chronic pain therapy (Guimarães et al., 2014). Terpenes, instead, are mainly used as natural bio-pesticides and herbicides (Smith et al., 2018).

The main aim of this review is to describe the roles of polyphenols and terpenes in plants and their possible applications for health and human life (Figure 1). Many studies report multiple applications of

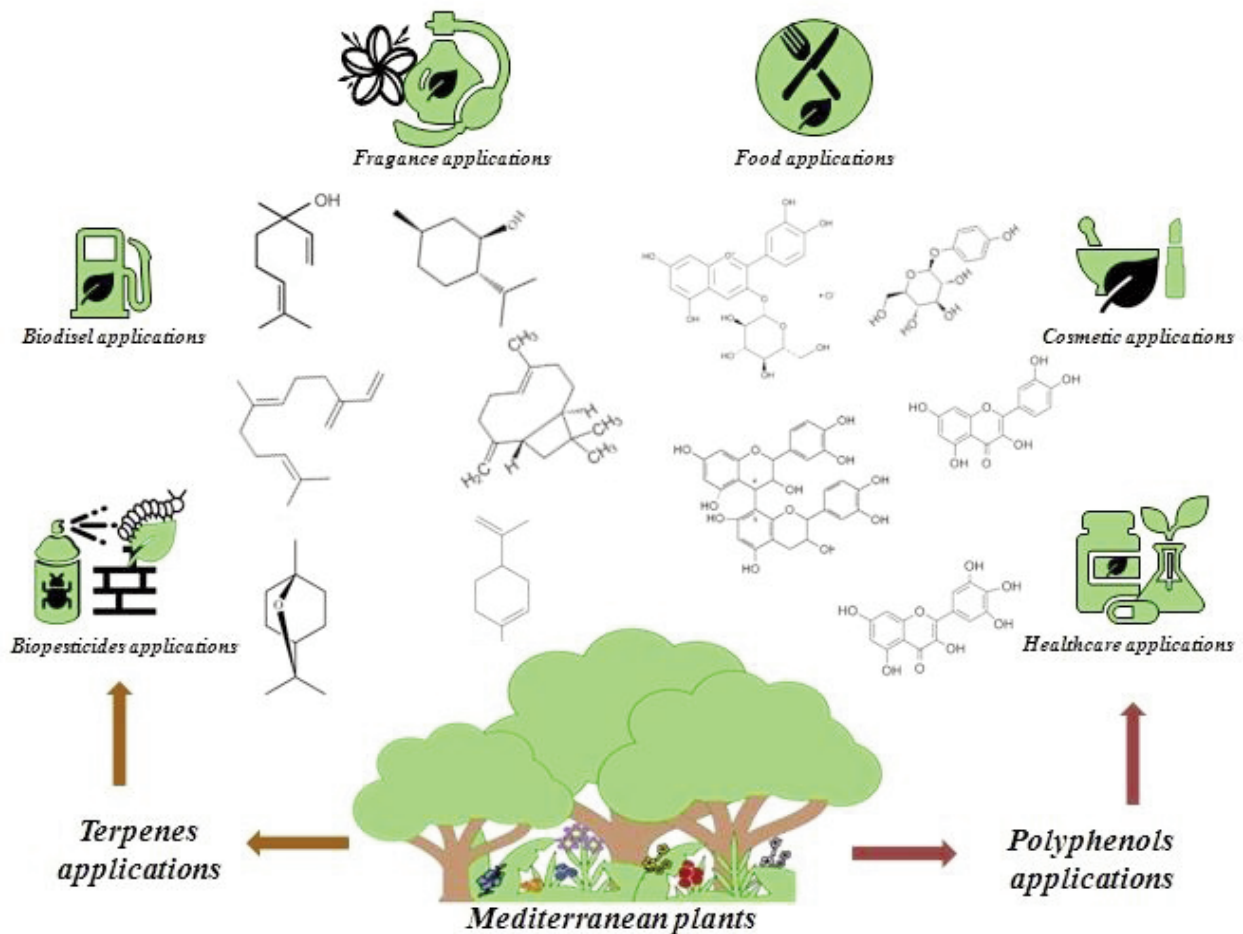


Figure 1. Roles of polyphenols and terpenes in plants and their possible applications for health and human life.

polyphenol enriched extracts obtained from Mediterranean plants; however, the studies are focused on potential applications of terpenes referred to pure isolated molecules. Indeed, most of the reports are mainly focused on aromatic plants utilised for the food and fragrance sectors (Li et al., 2017; Kutyna and Borneman, 2018). Therefore, although several studies report the richness of terpene emissions from Mediterranean woody plants (Loreto et al., 1998; Llusà, and Peñuelasa, 2000; Staudt et al., 2001; Bonn et al., 2019; Bach et al., 2020), only a few of them are related to the possible industrial applications of terpene leaf extracts of Mediterranean woody species.

Thus, given the high importance of these secondary metabolites, it could be crucial to focus on polyphenols and terpenes extracted from Mediterranean plants and their potential health benefits and industrial applications.

2. Polyphenols and their roles in plants

The polyphenols group is the biggest and most variable group of plant secondary metabolites (Scalbert and Williamson, 2000). These compounds can be classified into flavonoids and non-flavonoids (phenolic acids, stilbenes, lignans) (Belščak-Cvitanović et al., 2018). All flavonoids share the basic structural skeleton (C6-C3-C6), consisting of two aromatic rings (ring A and B) and a heterocyclic ring (ring C) that usually contains one oxygen atom (pyran). Due to the hydroxylation pattern and variations of the aromatic rings, flavonoids can be further divided into different subclasses: flavones, flavonols, flavanones, isoflavones, flavan-3-ols and anthocyanidins (Saxena et al., 2012) (Figure 2). In addition, within the flavonoids group, tannins are classified into two main groups: hydrolysable tannins (gallotannins and ellagitannins) and condensed tannins (also called proanthocyanins) (Porter, 1989; Romani et al., 2006; Romani et al., 2012).

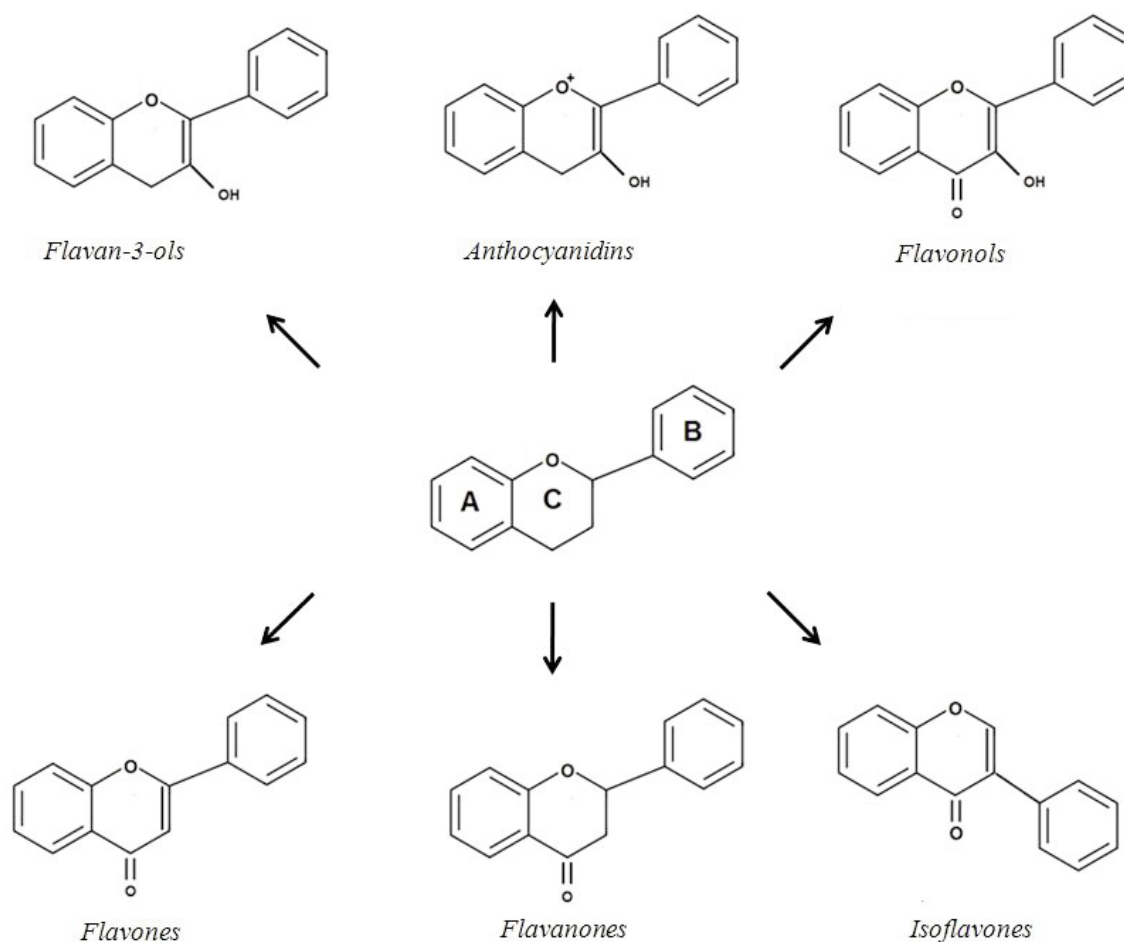


Figure 2: The basic structure of flavonoid subclasses.

Among non-flavonoid compounds, the main group is represented by phenolic acids that can be subdivided into two main types: benzoic acid, constituted by a benzene ring linked to a carboxyl group (C6-C1) and cinnamic acids, derived from a benzene ring linked to a three-carbon side acid chain (C6-C3) (Tsao et al., 2010; Singla et al., 2018).

Polyphenols exhibit a large variety of roles in plants, especially related to growth and development including seed germination and cell division (Tanase et al., 2019). In addition, these compounds act as the major yellow, red, blue, and purple pigments and may act as attractors for pollinators (Crozier et al., 2008; Vinha et al., 2018). Anthocyanins, for example, are water-soluble, are stored in vacuoles and are responsible for the orange to blue colours found in many flowers, leaves, fruits, seeds and other tissues (Tanaka et al., 2008), whereas tannins provide protection against pathogen infection and predator attack (Sieniawska et al., 2017) by conferring bitterness and astringency (Acamovic et al., 2005; Soares et al., 2020). Polyphenols are utilised for many functions within the plant cell acting mainly as defence and protecting molecules against abiotic stresses (Sharma et al., 2019). These compounds play a key role in maintaining the redox balance due to photo-oxidative stress (Caverzan et al., 2016), avoiding the generation of ROS (Reactive Oxygen Species) and quenching ROS, including singlet oxygen (1O_2) and hydrogen peroxide (H_2O_2), once they are formed (Rice-Evans et al., 1997; Agati and Tattini, 2010; Brunetti et al., 2013). For example, vacuolar flavonoids (in conjunction with guaiacol peroxidases) may help in maintaining whole-cell H_2O_2 within a sub-lethal concentration range (Ferrerres et al., 2011).

In addition, polyphenols with their high absorptivity at 250-270 and 335-360 nm act as good UV screeners not only of UV-radiation but also of short-wave visible radiation (e.g., ellagitannins and anthocyanins, Manetas, 2006; Tattini et al., 2007; Hatier and Gould, 2008). The ability to absorb the solar shortest wavelengths is displayed by most polyphenols and it is not a peculiar capacity of hydroxycinnamates and flavonoids (which are well known UV-B and UV-A absorbers, Harborne and Williams, 2000). UV-absorbing flavonoids located in the epidermal cells strongly reduce highly energetic solar wavelengths from reaching ROS-generating cells, and the consequential photo-oxidative stress and damage (Brunetti et al., 2015; Guidi et al., 2016). Furthermore, another important role that they have is the ability to provide heavy metal stress protection by chelation of transition metals (i.e., Fe, Cu, Ni, Zn), which generate the hydroxyl radical via Fenton's reaction (Mira et al., 2002). Kidd et al., (2001) revealed that the chelation of these metals in the soil may be an effective form of defence against the effects of heavy metal concentration toxicity.

2.1. Plant polyphenols and their potential applications

Studies on plant secondary metabolites, especially on polyphenols, have increased over the last decades and have shown that these molecules show an antioxidant function in plants and have been suggested to perform the same reducing functions in humans (Brunetti et al., 2013). As a consequence, in the last few years, there is a renewed interest in medicinal plant-based products and, in this context, many Mediterranean phenolic-rich species may represent unrivalled sources for nutraceutical, cosmetic and pharmacological industries (Gurib-Fakim, 2014).

2.1.1. Polyphenol applications for human healthcare

In recent years, polyphenols have been reported to play key roles as signalling molecules in mammals through their ability to interact with a wide range of receptors and enzymes, which, in turn, are responsible for mediating ROS-induced signalling cascades vital to cell growth and differentiation (Scalbert et al., 2005; Brunetti et al., 2013). Furthermore, some flavonoids (such as quercetin and myricetin derivatives) have been proven to form hydrogen bonds with the Ser212 residue of MAPKs (mitogen-activated protein kinase) through the 3'-OH group, thus showing the capacity to inhibit their activity (Lee et al., 2008). MAPKs can control the expression of antioxidant enzymes, inhibiting cell cycle progression and cell proliferation and the expression and functional activation of oncogenes (Hu and Kong, 2004). Indeed, polyphenols have been shown to modulate cellular signalling processes dur-

ing inflammation, blocking carcinogenesis, and inhibiting tumour growth in both in vitro and in vivo tests (Benvenuto et al., 2016; Clementino et al., 2017). These capabilities, together with an apoptosis-inducing effect, appear to be mostly due to the polyphenolic non-scavenging and antioxidant roles, suggesting their preeminent function in chemoprevention and chemoprotection (Piccolella et al., 2015).

Mediterranean wild species have a long history in ethnic and popular medicine for their health-promoting properties. For example, the medicinal benefit of *Cistus x incanus* L. has been known since the 4th century BC. The leaf extracts of this species were used for treating skin diseases and gastric problems (Riehle et al., 2014). Furthermore, polyphenol-containing aqueous extracts of its leaves have been shown to have anti-bacterial, anti-inflammatory, antioxidant and anti-mycotic effects (Wittpahl et al., 2015; Gori et al., 2016; D'Ambrosio et al., 2020). In addition, the CYSTUS052 aqueous extract derived from *C. x incanus* aerial parts has shown to have a potent anti-influenza virus activity in mice (Droebner et al., 2007) and to inhibit human immune deficiency virus (HIV) in vitro (Rebensburb et al., 2016). Another example concerns *Myrtus communis* L. whose leaf extracts are indicated against diseases affecting the respiratory system such as emphysema or bronchitis (Romani et al., 2012; Jabri et al., 2018). Furthermore, some authors reported the importance of the different compounds found in myrtle extracts, including berry and seed polyphenol extracts, that are used to treat various disorders, such as gastric ulcers and esophageal reflux (Sumbul et al., 2010; Jabri et al., 2016). In a recent study conducted by Ebrahimi (2020), the authors tested the anti-hemorrhagic activity of myrtle leaf extracts that could be attributed also to tannins present in the polyphenolic aqueous leaf extract. Finally, the anti-inflammatory properties of pulp and seed extracts of myrtle were proven in human skin fibroblasts exposed to oxidative stress (Cruciani et al., 2019).

There is a growing interest in plant extracts that could be used as an alternative to current antimicrobial agents with increasing antimicrobial resistance (Ferreira et al., 2012). In this sense, the importance of phenolic compounds and their antimicrobial activity has been well-documented (Cushnie et al., 2003). Some antimicrobial constituents such as tannins, flavonoids and other phenolic acids have been detected in leaf extracts of *Arbutus unedo* L., including arbutin (Tenuta et al., 2020). Indeed, in one recent study, the antimicrobial activity of arbutin and its metabolite hydroquinone against several uropathogenic strains was demonstrated (Jurica et al., 2017). Results of this study showed that the aqueous extract of *A. unedo* leaves could be used as a phyto-therapeutic agent in many clinical applications. Another Mediterranean species that was shown to have antimicrobial properties against a broad range of bacterial and fungal pathogens is the mastic tree, *Pistacia lentiscus* L. (Salhi et al., 2019). Its leaves, rich in polyphenols (representing 7.5% leaf dry weight), including phenolics acids, flavonoids, mostly myricetin derivatives, and hydrolysable tannins (Rodríguez-Pérez et al. 2013; Detti et al., 2020), were shown to possess also anticancer and anti-inflammatory activities. In fact, Remila et al. (2015) demonstrated that the extracts of this species have an anticancer potential against melanoma (B16F10). In addition, Mehenni et al. (2016) demonstrated the hepatoprotective activity against paracetamol-induced hepatic necrosis and the antidiabetic activity against streptozotocin-induced in rats.

2.1.2. Nutraceutical and food industry applications

In the last decades, studies regarding the physiological activities of food-derived bioproducts and food components with functional properties have greatly increased (Erdmann et al., 2008). In fact, the food sector is currently focused in developing functional food additives and food products with improved health promoting benefits (Hernández-Ledesma et al., 2017). Indeed, foods containing bioactive compounds are important for diminishing of risks of important chronic diseases that are becoming the leading causes of global morbidity and mortality (Annuzzi et al., 2014). In this context, polyphenol plant extracts with their properties can be one of the most interesting candidates (Vattem and Maitin, 2015). In fact, after a microencapsulation process, they can be utilised as functional additives in foods (Nazzaro et al., 2012). For example, the enrichment of dairy food products has been recently investigated (Cutrim et al., 2018). The polyphenolic rich aqueous extract of *Rosmarinus officinalis* L., for exam-

ple, was added as a functional ingredient in cottage cheese. The incorporation of the extract increased the antioxidant properties of the cheese. In addition, the nutritional value of cottage cheese was not affected by the introduction of the extract in free and microencapsulated forms (Ribeiro et al., 2016). Moreover, Petrotos et al., (2012) investigated the influence of the application of polyphenolic compounds from olive mill wastewater to yoghurt. In this study, it was observed that the added polyphenols provided a protective effect that avoided an unwanted drop in the pH during storage.

There is an increasing interest in polyphenol plant extracts as potential functional ingredients for improving health in bakery products (Ou et al., 2019; Xu et al., 2019). Cacak-Pietrzak (2019) tested *Cistus x incanus* herbal extracts as functional supplement of food products in bread. The bread sample incorporated with the extract was characterised by significantly higher total polyphenolic concentration, and much higher antioxidant activity, when compared to a control bread sample. Bread with increased antioxidant activity should be consumed because of its role in the prevention and treatment of various chronic and degenerative human diseases (Dziki et al., 2014).

The addition of antioxidants is known to delay or inhibit deterioration of food products and benefit consumers by prolonging their shelf life (Lindley, 1998). Besides, antioxidants also have antimicrobial activities (Babuskin et al., 2014). Primary synthetic antioxidants have been used in the food industry over the last 50 years. Nevertheless, despite their superior efficacy and high stability, there is an increasing concern about their safety because they can have toxigenic, mutagenic and carcinogenic effects (Nanditha and Prabhasankar, 2008). According to Ramarathnam *et al.* (1995) and Kiokias *et al.* (2008), the current trend for consumers requires the utilization of natural antioxidants in the food industry since these compounds are healthier than chemical food preservatives. Galanakis et al. (2018) showed that polyphenols from olive, in a concentration of 200 mg/Kg flour, were able to induce antimicrobial properties in bakery products and subsequently prolong their shelf-life.

Finally, polyphenol plant extracts can also be utilised as colorant agents. In the case of colorants, anthocyanins represent an attractive and natural alternative to the artificial ones (Espín et al., 2000). For example, *Arbutus unedo* fruits, rich in anthocyanins (and in particular of cyaniding 3-*O*-glucoside), were studied to be used as natural colorants with bioactive properties (such as antioxidant, antimicrobial and cytotoxic effects) in wafers (Lopez et al., 2019). Results of this study showed that the polyphenolic extract provided colorant properties without altering the main organoleptic characteristics of the food sample, demonstrating the potential uses of *A. unedo* fruit extracts for industrial applications (Lopez et al., 2019).

2.1.3. Applications in cosmetic industry

The interest in cosmetics prepared with natural products rich in polyphenols is mainly based on the antioxidant action of these compounds against oxidative stress (de Lima Cherubim et al., 2020). In particular, polyphenols have been shown to have a protective function against photoaging (Zillich et al., 2015) and polyphenolic rich extracts are proposed as one of the most effective functional raw material for the production of antiaging cosmetic products (Ratz-Lyko et al., 2012). Indeed, photoaging is caused by overexposure to UV radiations, which increases the production of reactive oxygen species (ROS), causing lipid peroxidation, DNA damage, and protein alterations (Rittié and Fisher, 2002). Moreover, ROS can also contribute to skin ageing by direct activation of enzymes that are responsible for the cleavage of extracellular matrix (ECM) components (Mukherjee et al., 2011). Phenolic compounds can absorb ultraviolet radiation, avoiding penetration of the solar radiation into the skin, and allowing a proven decrease in free radical formation and consequently preventing DNA damage (Petruk et al., 2018). Moreover, it has been shown that the post-treatment of human epidermal keratinocytes after UV exposition with plant polyphenols (such as resveratrol, quercetin and verbascoside) was effective against the overproduction of peroxides and inflammatory mediators (Potapovich et al., 2013). These studies suggested that polyphenolic extracts can be useful ingredients for both sunscreens and after-sun cosmetic products (Zillich et al., 2015; de Lima Cherubim et al., 2020). In this context, some

Mediterranean shrub species such as *Cistus incanus* L. and *Cistus ladanifer* L., naturally rich in bioactive polyphenols, represent a potential source of ingredients for skin protecting cosmetics (Kubica et al., 2016). For example, Gaweł-Bęben (2020) showed that *C. incanus* polyphenol leaf extracts are effective tyrosinase inhibitors (30–70% inhibition at 100 µg/mL). Tyrosinase is a copper containing enzyme catalysing the rate limiting conversion of L-tyrosine to dihydroxyphenylalanine (L-DOPA) and subsequently to dopaquinone. Tyrosinase inhibitory activity is particularly interesting for cosmetic applications due to the increasing problem of hyperpigmentation disorders and thanks to the growing consumer demand for safe and effective skin lightening cosmetics (Pillaiyar et al., 2017). In addition, another Mediterranean wild species, *Pistacia lentiscus* L. has been shown to be a potent elastase inhibitor (74% of elastase inhibitory activity tested at 50 µg/mL) (Chiocchio et al., 2018). Elastase belongs to the chymotrypsin family of proteases and it is responsible for the breakdown of elastin and other proteins, such as collagen and fibronectin, which are fundamental for the elastic properties of ECM (Imokawa and Ishida, 2015). Mis-regulations of this enzyme are involved in skin ageing processes (Korkmaz et al., 2010). In fact, the excessive hydrolysis of the dermal elastin fibre network can lead to the loss of skin elasticity and consequent skin sagging (Thring et al., 2009). For this reason, elastase inhibitors are important for their anti-wrinkle activities, promoting the preservation of skin elasticity (Jadoon et al., 2015).

Finally, polyphenol extracts are important in the cosmetic industry for their antimicrobial activity (Panzella, 2020). Indeed, these molecules can be used to minimise the deterioration caused by microorganisms in order to keep the microbiological purity of cosmetic products during the manufacturing process and also to extend their shelf-life to ensure consumer safety (Herman, 2019; Mellou et al., 2019).

Table 1 summarises all the information about polyphenol compounds present in the plants described in this study. Furthermore, the principal functions carried out by their principal compounds are also included, and the possible applications in different types of industry.

Table 1. List of the main polyphenols extracted from Mediterranean plants and their potential industrial and healthcare applications.

Compounds	Species	Functions	Applications	References
Gallic acid		Anticancer	Human Healthcare	Remila <i>et al.</i> , 2015
Myricetin derivatives	<i>Pistacia lentiscus</i>	Elastase inhibitors	Cosmetic industry	Chiocchio <i>et al.</i> , 2018
Quercetin derivatives				
Hydrolyzable tannins	<i>Myrtus communis</i>	Antiradical activity	Human Healthcare	Romani <i>et al.</i> , 2012
		Anti-hemorrhagic		Ebrahimi <i>et al.</i> , 2020
Arbutin	<i>Arbutus unedo</i>	Anti-microbial	Cosmetic industry	Tenuta <i>et al.</i> , 2020,
Cyanidin-3- <i>O</i> -glucoside		Coloring agent	Food industry	Jurica <i>et al.</i> , 2017
Myricetin derivatives	<i>Cistus incanus</i>	Anti-inflammatory	Human Healthcare	D'Ambrosio <i>et al.</i> , 2020
Quercetin derivatives		Antioxydants	Food Industry	Cacak-Pietrzak <i>et al.</i> , 2019
Epigallocatechin gallate		Tyrosinase inhibitors	Cosmetic industry	
Epicatechin				

3. Terpenes and their roles in plants

Terpenes are a large class of organic compounds and include more than 50.000 molecules (Maimone and Baran, 2007; Mewalal et al., 2017; Keasling and Eiben, 2019). All terpenes are hydrocarbons derived from isoprene, a molecule with five atoms of carbon; for this reason, the terpenes, are classified according to isoprene units: hemiterpenes (C₅H₈), monoterpenes (C₁₀H₁₆), sesquiterpenes (C₁₅H₂₄), diterpenes (C₂₀H₃₂) (Ashour et al., 2010; Mewalal et al., 2017; Tetali, 2019) (Figure 3).

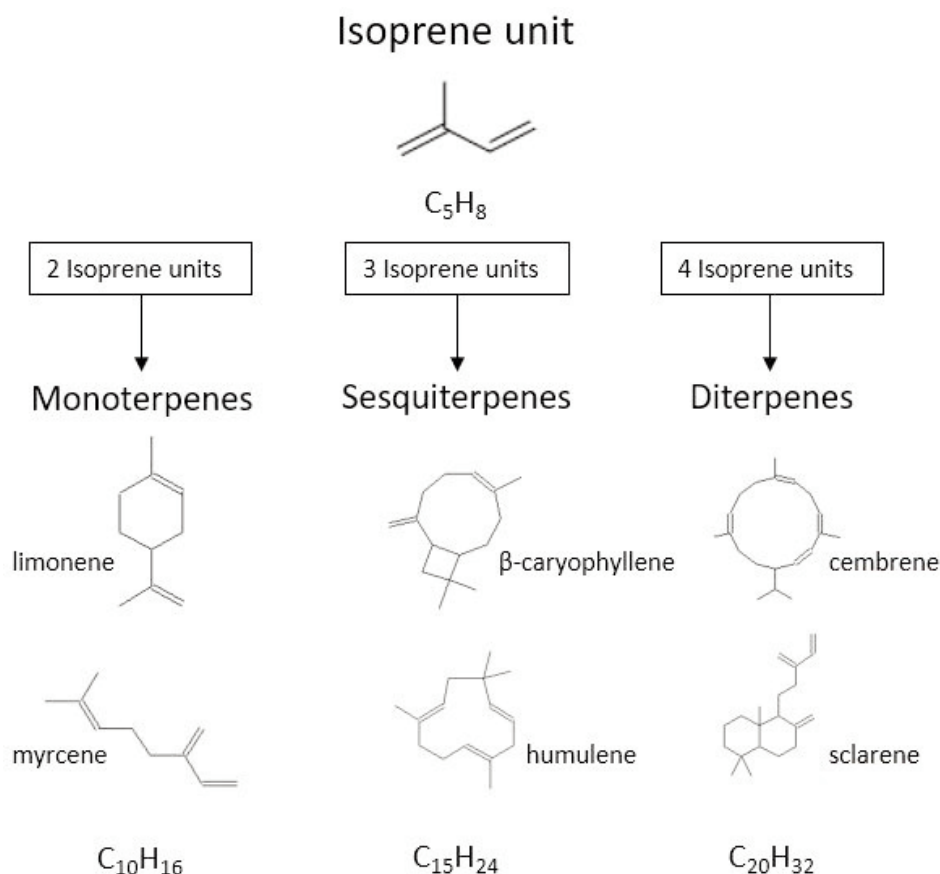


Figure 3. The molecular structure of isoprene and the three classes of terpenes (monoterpenes, sesquiterpenes and diterpenes) deriving from isoprene units with two examples per class.

The primary function of terpenes is their action as signal molecules: plant-plant for allelopathic purposes or to warn neighbouring plants of dangers (Baldwin et al., 2006; Polechońska et al., 2019) and plant-insects to attract pollinators or natural enemies of herbivorous insects (Dicke and Baldwin, 2010). Another important role is related to their antimicrobial and insecticidal activity, for this reason some Biogenic Volatile Organic Compounds (BVOCs) have been defined as “phytoncides” (*phyton* in ancient Greek is “plant”, plus *cide*, which indicates “killing”) (Antonelli et al., 2020). Their emission is linked with abiotic and biotic factors and stresses, such as: high temperature, UV, drought, fire, air pollution and competition, or herbivore attacks (Holopainen et al., 2013; Bonn et al., 2019). The emission mode of these volatile molecules depends on the species: some plants release terpenes directly after their biosynthesis such as *Quercus* spp. (Staudt et al., 2001), while other plants can accumulate them in the foliar tissues, using specific structures such as resin canals and ducts or surface trichomes (Ormeño et al., 2011).

Isoprene emission increases under abiotic stress conditions, such as drought and heat stress. Experimental research shows that isoprene emission can improve photosynthetic performance at high temperatures, stabilizing cells and particularly chloroplast thylakoid membranes (Sharkey et al., 2008; Velikova et al., 2012). Indeed, utilizing an inhibitor of isoprene biosynthesis (fosmidomycin), restored thermotolerance was observed when isoprene was supplied in the airstream flowing over the leaf (Sharkey et al., 2001). Further similar experiments led to the conclusion that thermotolerance of photosynthesis is a substantial benefit to plants that produce isoprene and that this benefit may explain why plants produce isoprene (Sharkey et al., 2008; Tattini et al., 2014; Tattini et al., 2015). In addition, isoprene improves plant tolerance to ozone by quenching reactive oxygen species (ROS) (Loreto et al., 2001; Holopainen et al., 2013). During the Mediterranean dry season,

stomatal closure is the main, early response of plants against drought to avoid tissue dehydration (Gallé et al., 2007), and consequently, a decrease of plant carbon balance (McDowell, 2011). Several authors showed that during drought stress, around 20-50% of the newest photosynthetically assimilated carbon is used to emit isoprene (Sharkey and Loreto, 1993; Brilli et al., 2007). This could be explained by considering the benefits that isoprene, and other secondary metabolites confer to plants (Sharkey et al., 2008; Velikova et al., 2012). In addition, to sustain isoprene production, plants can also use alternative carbon pools, such as xylem-transported glucose from root and stem storage, conferring more resistance against water stress (Genard-Zielinski et al., 2014).

Monoterpene emission allows the plant to reduce ROS induced damages and to improve ozone and thermo-tolerance (Atkinson and Arey, 2003; Jardine et al., 2020). Monoterpenes also play an important role against biotic stresses: to attract natural enemies of herbivores, to defend plants against pathogens and to deter herbivore animals (Sánchez-Osorio et al., 2019). In addition, they have a pivotal function as pollinator attractants and in limiting neighbouring plant's growth due to their allelopathic effects (Holopainen et al., 2013). Some examples of monoterpenes emitted by plants to lure the pollinators are linalool, β -ocimene and β -myrcene (McFrederick et al., 2008), whereas β -ocimene is a signal emitted to warn neighbouring plants of herbivore attacks (Blande et al., 2010).

Finally, sesquiterpenes act prevalently in plant biotic interactions, playing a repellent action against herbivores and neighbouring plants (Ashour et al., 2010; Holopainen et al., 2013). Furthermore, they can also attract pollinators (Raguso, 2016) or natural predators against herbivorous insects (Ashour et al., 2010; Chiu et al., 2017).

3.1. Plant terpenes and their potential applications

Mediterranean plant species produce a wide range of volatile and semi-volatile terpenes (Bonn et al., 2019; Bach et al., 2020). Some species, such as *Rosmarinus officinalis* L., *Cistus albidus* L. and *Pinus halepensis* Mill. (Llusià and Peñuelasa, 2000), store volatile terpenes in specific structures before releasing them to the atmosphere; others, such as *Quercus ilex* L. and *Quercus coccifera* L., release them directly after being synthesised (Loreto et al., 1998; Staudt et al., 2001). Several authors studied the variation of these emissions, for abiotic and biotic influences (Loreto and Schnitzler, 2010; Akula and Ravishankar, 2011) or seasonal trends (Llusià and Peñuelas, 2000; Steinbrecher et al., 2009), focusing mainly on the plant-plant (Baldwin et al., 2006) or plant-insect (Holopainen et al., 2013) interaction and their influences on air quality (Koistinen et al., 2007). Regarding potential applications of terpenes for human health and life, Mediterranean plants have been mainly exploited for the production of essential oils, which constitute an important part of traditional medicinal and food applications (Ali et al., 2015). For example, aromatic and medicinal plants like rosemary, lavender, thyme, and oregano have long been studied for the biological activity of their essential oils (Mancini et al., 2014; Ali et al., 2015). However, considering the growing interest in monoterpenes and sesquiterpenes applications for several industrial and medicinal uses (Tetali, 2019), here we report a summary of the main applications of these compounds even if they are not exclusively extracted from Mediterranean plants.

3.1.1. Terpenes application for human healthcare

Several natural products have been used by mankind as a source of medicinal products since ancient times for their disinfectant and preservative properties. In modern pharmaceutical industry, terpenes are used as active principles for drugs. In 2002, the worldwide sales of terpene-based pharmaceuticals were estimated to US\$12 billion (Guimarães et al., 2014). The recent increasing interest in the clinical application of these compounds is due to the wide range of their biological properties, including cancer chemo-preventive effects, antimicrobial, antiviral, analgesic, anti-inflammatory, antifungal and antiparasitic activities (Paduch et al., 2007; Quintans et al., 2013; Rufino et al., 2014; Ma et al., 2015; Li et al., 2016). For example, α -pinene presents anti-inflammatory activity reducing the production of tumour necrosis factor- α (TNF- α) and interleukin-6, that have pro-inflammatory and anti-inflammatory

functions (Bae et al., 2012; Kim et al., 2015). Moreover, β -caryophyllene and α -phellandrene are used as tumour pre-treatments, causing a reduction of levels of interleukins and TNF- α (Cho et al., 2007; Siquerira et al., 2016). Another bicyclic monoterpene that shows anti-inflammatory effects is borneol (Zhong et al., 2014). Among monocyclic monoterpenes, D-limonene and p-cymene have been shown to reduce allergic lung inflammation in mice (Amorim et al., 2016; Games et al., 2016; Hansen et al., 2016). Regarding the acyclic monoterpenes, linalool inhibits acute lung inflammation by producing IL-6, IL-1 β , IL-8, TNF- α and monocyte chemoattractant protein-1 (MCP-1), which are involved in neuroinflammatory processes and several diseases (Peana et al., 2002; Peana et al., 2003; Sabogal-Guáqueta et al., 2016; Kim et al., 2019). Additionally, after *in vitro* studies, 1,8 cineole (Kahn et al., 2014), D-limonene (Shin et al., 2020) and β -caryophyllene (Hu et al., 2017) show inhibitory actions against neuro-inflammation. A natural sesquiterpene with neuro-protective activity against Parkinson's disease is β -caryophyllene (Ojha et al., 2016) and this sesquiterpene shows reduction of alcohol-induced liver injury (Varga et al., 2018).

Several terpenes show antiparasitic functions, due to their interaction with Fe (II) groups, resulting in the release of free radicals that can kill parasites, as in the case of *Plasmodium falciparum* (Rodrigues Goulart et al., 2004). They present also antimicrobial functions linked to their lipophilic structure. For example, terpinen-4-ol, α -terpineol, 1,8-cyneol and linalool have antibacterial proprieties against Gram-positive and Gram-negative bacteria. Menthol is toxic for *Escherichia coli* (Trombetta et al., 2005), while (4R)-(+)-carvone shows important effects against *Listeria monocytogenes* and *Escherichia coli*, while also showing antifungal properties against *Saccharomyces* (Carvalho and Fonseca, 2006).

The terpenes are also widely used in dermatology and cosmetology as vehicles, because they increase the therapeutic value of drugs, allowing an easier skin penetration through intercellular lipid disruption; thus, improving drug diffusion and action (Moghimi, 1996).

Recently, α -pinene, β -pinene, car-3-ene, borneol, verbenol, pinocarveol and linalool, when inhaled, have shown anti-depressive and anxiolytic functions (Linck et al., 2010; Souto-Maior et al., 2011; Kessler et al., 2014; Guzmán-Gutiérrez et al., 2015; Woo and Lee, 2020).

Some studies have shown the role of terpenes against neuronal diseases and tumours (Crowell, 1999; Legault and Pechette, 2007; Cheng et al., 2014; Sobral et al., 2014; Porres-Martinez et al., 2016). For example, borneol has a free radical scavenging activity, thus performing an important neuroprotective function against Alzheimer's disease (Hong et al., 2011; Liu et al., 2015). Also, β -caryophyllene, myrcene, linalool, 1,8 cineole, α - and γ -terpinene, show neuroprotective functions thanks to their antioxidant effects (Calleja et al., 2013; Cheng et al., 2014), by decreasing the production of ROS, Matrix Metallo-Proteinase (MMP) and Nitric Oxide (NO) (Cutillas et al., 2018; de Christo Scherer et al., 2019). Terpenes have been used as chemotherapeutic agents for treating tumours. They present multiple mechanisms: during the initial phase of carcinogenesis, they prevent interaction of carcinogens with DNA; during the promotion phase, they inhibit cancer cells developing and migrating; in later stages, they allow cancer cell apoptosis (Crowell, 1997) and consequently, tumour regression (Vigushin et al., 1998). Some studies have shown that β -pinene and p-cymene have an acceptable chemotherapeutic potency (Li et al., 2009; Ferraz et al., 2013; Bakarnga-Via et al., 2014). Myrcene shows significant antiproliferative actions in various tumour cell lines such as breast carcinoma (MCF-7), human lung carcinoma (A549) and leukemia (P388) (Silva et al., 2007). One of the most important monoterpenes is D-limonene, well tolerated by humans (Vigushin et al., 1998; Kris-Etherton et al., 2002), it presents protective actions against several tumours: breast, intestine, pancreas, liver and colon by inhibiting the proliferation of cancer cells, thus allowing apoptosis (Lu, 2004).

The important benefits of volatile terpenes in the forest atmosphere for human health are evident in the recent study conducted by Cho et al. (2017), where the authors state that a short trip to the forest is beneficial for humans through showering of biogenic aerosols. This kind of healthy program has been practiced in the United States since 1960 as "forest recreation" (Douglass, 1982). In Germany there is a similar practice called "Kneipp therapy" created by the priest Sebastian Kneipp (Joos et al., 2006;

Spievogel and Spalek, 2012), while in Japan the Japanese Forest Agency introduced the “*Shinrin-yoku*” (*i.e.*, Forest bathing) in 1982, and established the “Therapeutic effects of forest plan” in 2005 (Tsunetsugu et al., 2010). A recent review suggested that even a 2 hour walk in the forest could increase Natural Killer (NK) cells acting against cancer and promoting health (Peterfalvi et al., 2019). It is worth mentioning that inhaling BVOCs in a forest setting does not provide constant effects, as there is a high degree of variability, associated to environmental and individual characteristics. A Japanese study, involving a small group of healthy subjects, measured monoterpene blood concentrations before and after a 60-min visit to the forest (Sumitomo et al., 2015). The authors noticed that blood concentrations of some BVOCs exhibited a marked increase after visiting the forest, and in particular, average plasma levels of α -pinene changed from 2.6 nM (baseline) to 19.4 nM (post-visit). In another toxicokinetic study, the participants were exposed for 2 hours in a chamber with different concentrations of limonene (10, 225, and 450 mg/m³) and the pulmonary uptake was estimated to be up to 70% of the amount supplied, with an increase of plasma concentrations of limonene (Kohlert et al., 2000). Thus, for now, we can only affirm that plasma concentrations of BVOCs tend to rise whenever a subject is exposed to a forest, but it is not possible to quantify the specific beneficial effects for human health.

Additionally, in the last decades, other authors have studied the relationship between human well-being and indoor plants, showing that these plants can play an important role in reducing air pollutants and promoting health and comfort in our houses (Bringslimark et al., 2009; Deng and Deng, 2018). In particular, Yang et al. (2009) suggested that indoor plants can improve the quality of air both removing pollutants and releasing terpenes which have anxiolytic and anti-inflammatory effects.

Lastly, another new use of terpenes is as analgesic drugs. Pain can cause a loss of physical and mental functioning, thus a decrease in life quality and a significant economic damage for society (Guimaraes et al., 2014). Several clinical studies, conducted on human patients, showed an improvement in general health and increased quality of life using drugs with 10-40% of terpenoids (Guimaraes et al., 2014). For example, patients with several types of pain (*i.e.*, headaches, arthritis, muscular aches and back pain) found the use of a combination of natural oils rich in carvacrol, thymol, 1,8-cineol, limonene, α - and β -pinene and cineole very useful (Woolf, 2010; De Sousa, 2011; Guimaraes et al., 2013).

3.1.2. Further industrial application of plant terpenes

Plant-derived terpenes are identified as an alternative, low cost and sustainable source of energy, potentially capable of replacing or supplementing fossil fuel (Mewalal et al., 2017; Tetali, 2019), contributing to decreased CO₂ concentration in the atmosphere and thus climate change. Many qualities of terpenes are appreciated; among them their low hygroscopy, high viscosity, their freezing point, and their high energy density (Melis, 2017). Monoterpenes could be used to replace gasoline (Melis, 2017), while sesquiterpenes and diterpenes could be used as biodiesels (Tippmann et al., 2013). The cyclic forms are preferred because of their higher energy density (*i.e.*, by increasing combustion heat): for example, limonene could be added to diesel fuels (Tracy et al., 2009) and α -pinene could be used as a replacement for fossil fuels (Harvey et al., 2012). Nonetheless, from hydrogenated linalool, myrcene and farnesene (*i.e.*, acyclic terpenes) high-density fuels have also been synthesised (Mewalal et al., 2017). Furthermore, some terpenes are used to obtain adhesive, coating and emulsifier materials in the manufacturing industry (Ashour et al., 2010).

Terpenes and the essential oils containing them are widely used and studied for their applications as flavouring in food and beverages, and in the perfume industry (Ashour et al., 2010). In 2017, the worldwide flavour and fragrance industry was estimated to be of US\$30 billion (Kutyna and Borneman, 2018). The food industry is interested in compounds with antioxidant characteristics, and with a good taste and aroma (Putnik et al., 2019). The most used terpenes are monoterpenes such as limonene, linalool and 1,8-cineole for lemon's aroma (Kutyna and Borneman, 2018); additionally, 3-carene, α -pinene, caryophyllene and β -myrcene are used for the aroma of mango (Li et al., 2017) while woody

Table 2: List of the main terpenes synthesised by Mediterranean plants and their potential industrial and healthcare applications.

Compounds	Species	Functions	Applications	References
1,8-cineole	<i>Hissopus</i> spp., <i>Laurus</i> spp.,	Neuro-protective	Human healthcare	Khan et al., 2014
	<i>Ocimum</i> spp., <i>Origanum</i> spp., <i>Salvia</i> spp.,	Analgesic	Human healthcare	De Sousa, 2011
	<i>Thymus</i> spp., <i>Verbena</i> spp.	Aromatic agent Antiparasitic and toxic for insects	Food industry Insecticide industry	Kutyna and Borneman, 2018 Dambolena et al., 2016
α-pinene	<i>Anethum</i> spp., <i>Mentha</i> spp., <i>Ocimum</i> spp., <i>Origanum</i> spp., <i>Pinus</i> spp., <i>Pistacia</i> spp., <i>Quercus</i> spp., <i>Salvia</i> spp., <i>Thymus</i> spp., <i>Verbena</i> spp.	Anti-inflammatory	Human healthcare	Bae et al., 2012; Kim et al., 2015; Cho et al., 2017
		Anxiolytic	Human healthcare	Woo and Lee, 2020
		Analgesic	Human healthcare	De Sousa, 2011; Guimarães et al., 2013
		Chemotherapeutic	Human healthcare	Silva et al., 2007; Cho et al., 2017
		Replacing fossil fuel	Green energy	Harvey et al., 2012
β-pinene	<i>Anethum</i> spp., <i>Foeniculum</i> spp., <i>Laurus</i> spp., <i>Ocimum</i> spp., <i>Origanum</i> spp., <i>Petroselinum</i> spp., <i>Salvia</i> spp.	Aromatic agent	Food industry	Li et al., 2017
		Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016
		Anti-inflammatory	Human healthcare	Woo and Lee, 2020
		Anti-depressive	Human healthcare	Kessler et al., 2014; Guzmán-Gutiérrez et al., 2015
		Chemotherapeutic	Human healthcare	Li et al., 2009; Bakarrnga-Via et al., 2014
β-caryophyllene	<i>Hissopus</i> spp., <i>Laurus</i> spp., <i>Lavander</i> spp., <i>Mentha</i> spp., <i>Ocimum</i> spp., <i>Origanum</i> spp., <i>Salvia</i> spp., <i>Thymus</i> spp., <i>Verbena</i> spp.	Analgesic	Human healthcare	Woo and Lee, 2020
		Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016
		Anti-inflammatory	Human healthcare	Cheng et al., 2014; Amorim et al., 2016; Cho et al., 2017
		Anti-depressive	Human healthcare	Kessler et al., 2014
		Neuro-protective	Human healthcare	Cheng et al., 2014; Ojha et al., 2016
γ-terpinene	<i>Foeniculum</i> spp., <i>Lavander</i> spp., <i>Mentha</i> spp., <i>Origanum</i> spp., <i>Petroselinum</i> spp., <i>Salvia</i> spp., <i>Thymus</i> spp.	Chemotherapeutic	Human healthcare	Silva et al., 2007
		Chemotherapeutic	Human healthcare	Ferraz et al., 2013
		Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016

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	Anti-inflammatory	Human healthcare	Amorim et al., 2016; Hansen et al., 2016
	Neuro-protective	Human healthcare	Shin et al., 2020
limonene	Chemotherapeutic	Human healthcare	Vigushin et al., 1998; Kris-Etherton et al., 2002
	Analgesic	Human healthcare	De Sousa, 2011
	Antiparasitic and toxic for insects	Food industry	Kutyna and Borneman, 2018
		Insecticide industry	Dambolena et al., 2016
	Anti-inflammatory	Human healthcare	Peane et al., 2003; Sabogal-Guáqueta et al., 2016; Kim et al., 2019
	Anti-bacterial	Human healthcare	Rodrigues Goulart et al., 2004
	Anti-depressive	Human healthcare	Linck et al., 2010; Kessler et al., 2014; Guzmán-Gutiérrez et al., 2015
linalool	Neuro-protective	Human healthcare	Sabogal-Guáqueta et al., 2016;
	Chemotherapeutic	Human healthcare	Silva et al., 2007
	Replacing fossil fuel	Green energy	Mewalal et al., 2017
	Aromatic agent	Food industry	Kutyna and Borneman, 2018
	Antiparasitic and toxic for insects	Insecticide industry	Gallardo et al., 2012; Dambolena et al., 2016
		Chemotherapeutic	Human healthcare
myrcene	Replacing fossil fuel	Green energy	Mewalal et al., 2017
	Aromatic agent	Food industry	Li et al., 2017
	Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016
		Human healthcare	Games et al., 2016; Cho et al., 2017
p-cymene	Chemotherapeutic	Human healthcare	Ferraz et al., 2013
	Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016
	Anti-inflammatory	Human healthcare	Games et al., 2016; Cho et al., 2017
		Human healthcare	De Sousa, 2011
thymol	Chemotherapeutic	Human healthcare	Ferraz et al., 2013
	Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016
	Analgesic	Human healthcare	De Sousa, 2011
	Anti-inflammatory	Human healthcare	Games et al., 2016; Cho et al., 2017
	Chemotherapeutic	Human healthcare	Ferraz et al., 2013
	Antiparasitic and toxic for insects	Insecticide industry	Dambolena et al., 2016

notes are linked to α -humulene, α -bulnesene, γ -cadinene (Campelo et al., 2020). Some terpenes derived from herbs and spices have been commercialised for products like toothpastes, shampoos and soaps (Tetali, 2019).

Another function of terpenes, which is also one of their roles in nature, is their use as insecticides, as they have a short persistence in the environment (Ashour et al., 2010). Terpenes could be considered as an important alternative to chemical insecticides as insects do not seem to develop resistance to them; in addition, terpenes do not contaminate food or the environment (Isman, 2006). Limonene and pyrethrins, that act at the nerve cell membranes level, are a natural insecticide and deterrent for several insect species, while also having low toxicity to mammals (Isman, 2006). Moreover, 1,8-cineole, anisole, β -pinene, linalool, menthone, α -pinene, pulegone, and myrcene have demonstrated fumigant properties against insects (Dambolena et al., 2016), while citronellol and geraniol showed the highest toxicity for lice (*Pediculus humanus capitis*; Gallardo et al., 2012).

Mediterranean plants are very rich in essential oils and for this reason they can be considered very important resources for the above-mentioned sectors. For example, the principal common Mediterranean aromatic species used in food and fragrance industries belong to the *Lamiaceae*, *Verbenaceae* and *Rutaceae* families (Elshafie and Camele, 2017). The *Lamiaceae* family contains several aromatic plants, such as *Lavandula* spp., *Oregano* spp., *Thymus* spp., *Mentha* spp., *Sage* spp. The *Marjoram* spp.; the *Verbenaceae* family hosts *Verbena officinalis*, traditionally used in herbalism and flower remedies (Vohra, 2004). The *Rutaceae* family contains *Citrus limon* with its terpene rich extracts, especially D-limonene, α -pinene, α - and β - phellandrene and sesquiterpene (Price, 1993). The common aromatic compounds synthesised by Mediterranean plants are especially, α -thujene, camphene, myrcene, p-cymene, β -phellandrene, which are all emitted by lavender, marjoram, oregano, and sage. Additionally, γ -terpinene, linalool, limonene, α -pinene are the main compounds all synthesised by mint, thyme, lemon, and vervain (Elshafie and Camele, 2017).

Table 2 summarises all the information about terpene compounds found in the plants described in this study.

4. Conclusions

In the Mediterranean basin, abiotic stresses can pose a serious environmental threat to plants due to increasing aridity and heat waves. Plants adopt various mechanisms capable of ensuring their survival in this harsh environment, such as the ability to synthesise an extraordinary arsenal of secondary metabolites (e.g., terpenes and polyphenols) which act primarily as protective compounds against environmental pressures.

Apart from their role in plants, these bioactive compounds have a wide array of health-promoting benefits. For example, polyphenols, due to their antioxidant effects, can be exploited in different types of industries, such as pharmaceutical, nutraceutical and cosmetic, demonstrating that these compounds are innovation hotspots in the most diverse technological domains. Additionally, as highlighted by recent studies on forest bathing therapy, inhaling BVOCs in forest environments can bring many health benefits, such as the alleviation of mood-related disorders. In particular, the inhalation of some terpenes can reduce mental fatigue by inducing relaxation and increasing cognitive performance (Figure 1).

In conclusion, the Mediterranean region, with its species richness, represents a biological hotspot for the discovery of novel drugs and for developing innovative industrial applications. Furthermore, with its forests and natural parks, it represents a sanctuary where people can obtain physiological and psychological benefits.

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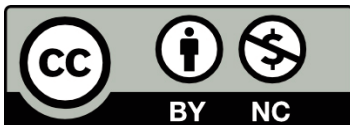
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