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Production of Essential Oil in Plants: Ontogeny, Secretory Structures and Seasonal Variations

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Abstract – Essential oil production in plants is known to play crucial roles in attractive and defensive mechanism responses to environmental conditions. Various factors are known to determine the chemical variability and yields for specific essential oil bearing plants including genetic, physiology and environment. The purpose of this review is to summarize recent publications on the variation of essential oil and its composition with regards to physiological aspects of the plants.

Keywords: Essential oil, ontogeny, physiology, seasonal variations, secretory structures

Introduction

Essential oil (EO) is a valuable natural plant product that has been used in various fields from medicine to flavours and fragrances since antiquity. The extensive applications of EO are largely attributed by a long list of biological properties that are not only functionally important to the plant itself but also beneficiary to human such as anti-oxidants (Adorjan & Buchbauer, 2010; Amorati, Foti, & Valgimigli., 2013; Bakkali et al., 2008), anti-cancer (Sharma et al., 2009), anti-allergic, anti-inflammatory (Passos et al., 2007), antiviral (Astani, Reichling, & Schnitzler, 2011), antibacterial (Bourgou, Rahali, Ourghemmi, & Saïdani Tounsi, 2012; Inouye, Takizawa, & Yamaguchi, 2001), antimicrobial (Gkogka, Hazeleger, Posthumus, & Beumer, 2013), insect repellent (Rajkumar and Jebanesan, 2007) and many more. Historically, the term *essential oil* is derived from the active component of drug preparation called *quinta essentia* by a Swiss physician, Theophrastus Bombastus von Hohenheim, also known as Paracelcus, in the fifteenth century (Guenther, 1948).

The EO components consist of diverse yet complex mixtures of potentially hundreds of chemical constituents with low molecular weights ranging 50 to 200 Da (Rowan, 2011). The active organic compounds can be categorized into four groups defined by chemical structures namely terpenes (mono- and sesquiterpene), terpenoids (alcohols, esters, aldehydes, ketones, ethers, phenols and epoxides), phenylpropenes and other aromatic compounds (sulfur- and nitrogen- derivatives) (Hyldgaard et al., 2012). The odour profile of EO can either be dominated by a single constituent making up about 75% of the EO such as cinnamaldehyde in cinnamon (Alzoreky and Nakahara, 2003; Oussalah, Caillet & Lacroix, 2006) or mixture of constituents such as menthol, menthone, pulegone, 1,8-cineole and terpineol-4 in mint (Hafedh, Fethi, Mejdi, Emira, & Amina, 2010).

Otherwise known as secondary metabolites, most of the compounds are biosynthesized by numbers of metabolic pathways in plant processes designed to interact with the environment. As plant faces immense challenges for being a stationary autotroph, these secondary metabolites are synthesized in response to biotic and abiotic stresses. These include engineering their own pollination and seed dispersal, local fluctuations in the supply of simple nutrients required to synthesize their own food, and coexistence of herbivores and pathogen in their immediate environment (Hermsmeier, Schittko & Baldwin, 2001; Reymond, Weber, Damond, & Farmer, 2000). Generally, it is understood that the roles played by these secondary metabolites mainly as protection (as UV light absorbing and antiproliferative agents), defensive against pests and diseases, and attractive agents (Kennedy and Wightman, 2011).

The production of EO depends on the interaction between genetic, ontogenesis and physiological state of the plant with environmental conditions. In fact, the regulation of the volatile compounds within the plant is further complicated by dynamic differential components of the abiotic factors such as physical-chemical characteristics of the soil, moisture, temperature and light intensity. Over the last 40 years, Croteau's group has made a comprehensive study on the metabolism of EO constituents (Croteau & Hooper, 1978; Srividya, Davis, Croteau, Lange, 2015). The studies made in the perspective of biosynthetic pathways of the natural products have provided insights on how the chemical constituents are derived.

Advances in the biochemistry have contributed huge appreciation at explaining living processes particularly at the cellular level. However, understanding the biosynthesis of EO in relation to the ecophysiology remains elusive due to the multiplex variables involved in the ecosystem. The precise interpretations as to how the volatile compounds are synthesized in association to the physiological state remains to be seen. This review serves to provide summary on the selective recent publications among the many on the biosynthesis of EO and the variation of their components emphasizing on the physiological aspects of the plants.

Physiology of essential oil production

Ontogenesis

According to Gatsuk, Smirnova, Vorontzova, Zaugolnova, & Zhukova, (1980) and Smirnova et al. (1999), the main principle concept of plant ontogenesis is a continuous process of individual plant development that are subdivided into several stages reflecting functional importance. Each stage is defined on the basis of structural indicators such as:

a. presence or absence of embroyonic, juvenile, or mature morphological features
b. ability of an individual to reproduce or to propagate vegetatively,
c. ratio between the living and the dead tissues, and
d. ratio of growing and non-growing plant parts.

Plants synthesize EO only in very young cells which arise from the process of biosynthesis. The accumulation of EO is closely related with leaf ontogeny as the rate of oil release is rapid at the early stage of leaf growth and it remains during the further period of the growth when leaf weight increases significantly (Nurzyńska-Wierdak, Bogucka-Kocka, Kowalski, & Borowski, 2012). In some plant species, the volatile compounds are largely accumulated even before the organ is fully expanded (Figueiredo, Barroso, Pedro, & Scheffer, 2008).

Ontogeny is a depiction of a plant's timeline for growth and development. It has been long considered as one of the most important factors that influence oil accumulation in plants as it also largely determines the proper time for harvesting raw material (Chalchat & Özcan, 2008; Hussain, Anwar, Sherazi, & Przybylski, 2008; Liber et al., 2011; Sangwan, Farooqi, Shabih, Sangwan, 2001; Verma, Padalia, & Chauhan, 2012). As numerous transformations and changes occur inside the cells due to physiological processes, harvesting time is often regarded as critical parameter that can affect chemical compositions of EO (Vekiari et al., 2002).

Variations of EO yield at different developmental stages have been reported in a number of commercially important aromatic plants. The EO yield obtained in the stem bark of *Cinnamomum cassia* of different ages ranged between 0.41 to 2.61%. Twelve years old bark had the highest oil yield (2.61%) compared to five years old bark (0.58%) (Geng et al., 2011).In contrast, EO obtained from young leaf of *Myrtus communis* has the highest yield (0.92% on dry basis) compared to matured leaf (0.48%) (Rowshan, Najafian, & Tarakemeh, 2012). Difference in the trends reported from these two groups of author can be attributed to the plant parts from where the EOs are extracted. Jaafar, Osman, Ismail & Awang (2007) had found a considerable variation in the EO analyzed from different plant parts namely leaves, stems, flowers and rhizomes of torch ginger (*Etlingera elatior*).

Depending on the purposes when the EOs are extracted, Nurzyńska-Wierdak et al. (2012) suggested fully developed inflorescence of *Ocimum basilicum* as an optimal stage of harvest due to higher oil content. In the evaluation between two cultivars of sweet basil, both *Kasia* and *Wala* at the flowering initiation stage had highest oil content (0.90 and 1.03%, respectively). The budding stage had relatively lower oil content (0.83 and 0.65%, respectively) whereas the oil content at the vegetative stage was lowest (0.76 and 0.46 %, respectively). Although basil is usually used as a fresh and aromatic spice, harvesting the herb at the vegetative stage is more preferred.

In tansy (*Tanacetum vulgare*), the highest EO content was reported in the young shoot (0.66%) and as the plant development progressed, oil content continued to decrease until the seed ripening stage (0.14%) (Németh, 2003). According to Msaada, Hosni, Taarit, Hammami, & Marzouk, (2009), the rate of EO accumulation is rapid in newly formed leaves, seeds or fruits compared to later stages. Verma et al. (2014) relate this to describe their findings in the umbels of carrot (*Daucus carota*). The EO yield at the seed initiation stage was highest (1.8%), and then decreased at green seed stage (1.5%), light brown seed stage (1.3%), full bloom stage (1.1%) and finally, the yield was lowest at fully brown seed stage (0.7%). In short, the EO contents decrease with progression of seed development.

There is also a significant correlation between developmental stages and the composition of EO. Li et al. (2013) reported that the juvenile leaf oils of *Cinnamomum cassia* contain more volatile compounds (29) than in the older leaves (21). The study also revealed that developing leaves of two years old yielded highest oil with *trans*-cinnamaldehyde as the major compound. Upon senescence, the *trans*-cinnamaldehyde level in the leaves decreased rapidly. In the inflorescence of *Salvia sclarea*, oil concentration was reported to increase with maturity from stage 1 (bud) to 5 (full bloom). Oil content at bud stage was 0.08% and peaked at full bloom stage. However, the oil content dropped at full maturity (0.07%) when the petals of the florets withered and the seeds were completely brown. Two of the major constituents, linalool and linalyl acetate were also found to increase (17.0 and 40.4%, respectively) from stage 1 to 5 and then decreased at stage 6 (Lattoo, Dhar, Dhar, Sharma, & Agarwal, 2006).

According to Bouwmeester, Gershenzon, Konings, Croteau, (1998), Dudareva and Pichersky (2000), and Dudareva, Pichersky, & Gershenzon, (2004), the process of EO production is developmentally regulated. In leaves and fruits where the volatiles are accumulated whereas emitted in the case of flowers, the process followed similar developmental patterns which increase during the early stages of organ development (i.e. young leaves yet to fully expand, immature fruit, or when flowers are for pollination). After that, the trends either remain relatively constant or decrease over the organ's lifespan. This could be due to the modifications in secondary metabolism associated with growth and development of plants as well as the loss of oil by degradation or evaporation.

Peppermint and sweet basil are two of the most important commercial EO-producing species and have been used best as models of studies especially in biosynthesis pathways. In a detailed study on the developing leaves of peppermint, the total content of monoterpenes increases with leaf age, resulting in significant changes in the monoterpenes composition. Comparative observations on *Mentha* x *piperita* revealed younger leaves were found to contain more menthone than menthol whereas older leaves contained more menthol than menthone (Brun, Colson, Perrin, & Voirin, 1991; Burbott & Loomis, 1969; Croteau & Martinkus, 1979). Generally, compounds that are biosynthesized at the early stages of the pathway mainly present in younger leaves and vice versa. In fact, limonene and menthone are the major monoterpenes present in the young leaves (Gershenzon, McConkey, Croteau, 2000).

In sweet basil, Fischer, Nitzan, Chaimovitsh, Rubin, & Dudai, (2011) discussed the involvement of enzyme in the biosynthesis pathway that contributes to variation in EO composition in relation to ontogeny. It was found that eugenol was the principal component in younger leaves while methyleugenol predominated in older leaves. In fact, Lewinsohn et al. (2000) have demonstrated that there is a net accumulation of EO and estragole during the development of a sweet basil leaf. Enzymatic studies of the chavicol o-methyl-transferase revealed that a substantial level of activity in five-day-old seedlings found resided in leaf primordial of only a few mm in length. Highest activity levels were found in shoot tips of seedlings at four leaf-pair stage while a substantially lower level (45% compared with shoot tips on fresh weight basis) in young leaves. Levels of activity gradually decreased until almost undetectable in fully-developed leaves, indicating that young developing tissues are the primary sites of methyl chavicol biosynthesis.

Secretory structures

Secretory structures are known to be primary sites of production of bioactive secondary products which may function as plant growth regulators and defend the plant against insects, other pathogens and possibly other plants (Wagner, 1991). A common feature of aromatic plants is the specialized structures where the EOs are accumulated and stored (Fahn, 1979). There are multitudes of these structures including oil cells, glands, hairs, ducts and trichomes that are discretely distributed within the plants, from roots to flowers. As such, oil globules are found within the membrane of secretory cell of rhizome in *Zingiber officinale* (Svoboda, Svoboda, & Syred, 2001), peltate gland on leaves of *Lippia scaberrima* (Combrinck et al., 2007), and secretory cavity in peel section of *Citrus* that are responsible for the biosynthesis of EO (Voo et al., 2012).

Interesting findings are noted by Pasqua, Monacelli, & Silvestrini, (2009) where secondary secretory ducts in the pericycle roots of wild celery or garden angelica (*Angelica archangelica*) function as the accumulation site of EO. Several examples of plants with more than one type of secretory structures are also documented. For instance, canals and trichomes are found in young leaves stems and leaves of *Camptotheca acuminata* (Liu, 2004) and *Pittosporum undulatum* (Ferreira et al., 2007), and glandular hairs and secretory ducts in *Matricaria chamomilla* (Andreucci, Ciccarelli, Desideri, & Pagni, 2008).

Glandular trichomes (GTs), categorized as external secretory structures, have been widely and extensively studied over the past forty years and the research is very well documented by Croteau's group. In fact, GTs is the primary secretory organ for many species in Lamiaceae which houses a family of great economic importance such as lavender (*Lavandula pinnata*), sweet basil *(Ocimum basilicum*) and peppermint (*Mentha* x *piperita*). The latter is particularly a notable species having been developed as a model system for the study of monoterpene metabolism (Turner, Gershenzon, & Croteau, 2000). Additionally, the morphology, distribution and frequency of GTs are distinctive characteristics among the Lamiaceae species (Werker, 2000).

Depending on the structure of the secretory head, GTs can be morphologically classified into peltate and capitate (Werker, 1993). Peltate glands consist of four to eight secretory cells attached to the leaf with an oil sac above the secretory cells that are thought to be storage of EO (Bohlmann, Meyer-Gauen, & Croteau, 1998; Gershenzon et al., 1992; McCaskill & Croteau, 1995). Capitate glands, on the other hand, consist of one or two secretory cells that possess only a small oil sac and therefore, limited storage capacity (Ascensão, Marques, & Pais, 1995; Gang et al., 2001; Werker et al., 1985).

Distribution of trichomes varies between different tissues. As such, the peltate GTs in pennyroyal (*Mentha pulegium*) from Portugal are abundantly distributed on the abaxial leaf surface (Rodrigues et al., 2013). In lavender (*Lavandula pinnata*), both capitates and peltate trichomes are randomly distributed on the abaxial surface of fully expanded leaves (Ascensão et al., 1993). The abundant distribution of trichomes on the abaxial surface is in fact a common feature for several other Lamiaceae species (Rodrigues et al., 2006; Rodrigues et al., 2008; Werker et al., 1993). However, different patterns were found on mature leaves of *Origanum*x *intercedens* where peltate GTs was highest on adaxial surface (Bosabalidis & Skoula, 1998).

The development of secretory structures is also often correlated with ontogeny. In a study on distribution of peppermint oil glands, Turner et al. (2000) discovered that continuous initiation of new peltate glands resulted in continuous increase in the gland number throughout the period of leaf expansion. The formation of glands stops upon the completion of leaf growth. Additionally in *Mentha* *pulegium*, the maximum size of glandular secretory head cells was achieved during an earlier stage of leaf development (Rodrigues et al., 2013). Meanwhile, developed roots of previously mentioned *Angelica archangelica* achieved their full capacity of oil biosynthesis in association with increasing numbers of secretory cells as a result of differentiation of the secondary secretory ducts (Pasqua et al., 2009).

Studies by King, Gleadow & Woodrow, (2006) on single glands of *Eucalyptus polybractea* discovered the two factors that determined the total volume of oil glands within leaves: (1) the size of the individual glands and (2) numbers or density of glands across the leaf. Gland density and oil content as well as total gland volume and oil content are positively correlated. On the contrary, gland density and leaf area as well as leaf area and oil concentration per area are negatively correlated. As a result, larger leaves are more likely to have lower gland density, hence lower oil content compared to smaller leaves.

Seasonal variation

There are numerous reports on differences of oil content and composition in aromatic plants due to seasonal variation. Microclimatic factors such as temperature, rainfall distribution and also geographical features especially altitude also contribute to the differences in the chemotype of certain EO bearing plants. The type and nature of the constituents and their individual concentration levels are important attributes particularly in terms of biological activities of the EOs (Batish, Singh, Kohli, & Kaur, 2008).

Vekiari et al. (2002) reported the seasonal variation in the amounts of neryl acetate, geranyl acetate and citronellal observed in the leaves and peel of Cretan lemon variety. Maximum values of the compounds were obtained during the spring season in Greece compared to winter season which is different than that reported by Crescimanno, De Pasquale, Germana, Bazan, & Palazzolo, (1988). On the contrary, high number of compounds (46) was detected in *Cryptomeria fortunei* leaf during winter compared to summer (26). Nevertheless, kaur-16-ene and elemol still predominate as major components harvested in all four seasons (Xie, Huang, & Lei, 2013).

Lakušić, Ristić, Slavkovska, Stojanović, & Lakušić, (2013) analysed the seasonal changes in the composition of EO from Dalmation sage. Throughout the season, constituents of the EO had different dynamics and trends of changes in the concentration which can be categorized into three basic types of change that are attributed to the periods of hot and dry summer and cold autumn-winter months.

a. Decreasing – Concentration of the compounds such as α-humulene, viridiflorol, manool, β-caryophyllene and β-pinene were highest during spring when leaves are at the early stages of development. During the hot and dry summer months, the rapidly decreased and then fluctuated during the wet and cold autumn-winter period.
b. Increasing – Concentration of the compounds such as 1,8-cineole, camphene, camphor, *cis*-thujone, limonene and *trans*-thujone were lowest during spring at the early stages of development. After that, the concentration increased during the summer, autumn and winter period.
c. Fluctuating – Typical compounds such as borneol when the concentration was lowest in developing leaves, then increase sharply in the first summer months. In the warmest period, the concentration fluctuated until winter months when the concentration eventually decreased.

A study involving a perennial, EO-bearing crop is also documented by Sarma, Sarma, Sarma & Handique, (2011). The monthly EO obtained from inflorescence of lemongrass (*Cymbopogon flexuosus*) was observed in north-eastern India. The oil content was found to be comparatively higher during the pre and onset of monsoon season from March to July. The post monsoon and winter period, on the other hand, was termed as low oil content period. The drought season also appeared to have significant influence especially on the oil composition due to the reduction of growth parameters in the case of *Mentha piperita* (Farahani, Valadabadi, Daneshian & Khalvati, 2009) and *Tagetes minuta* (Rahbarian, Afsharmanesh, & Shirzadi, 2010). Leicach et al. (2010), on the other hand, found that drought triggered a significant increase in several oxygenated terpenes production, especially in linalool and 1,8-cineol which are known to repel different defoliator species.

In another investigation, Jordán, Martínez, Goodner, Baldwin & Sotomayor, (2006) studied the seasonal variation of *Thymus hyemalis* harvested at five phonological stages during the entire vegetative cycle. Maximum concentrations of the volatile components (tricyclene, myrcene and limonene) were observed at the beginning of the vegetative cycle. α-terpinene, *(E)*-β-ocimene and valencene, on the other hand, were detected at their greatest concentrations at the full bloom (FB) stage. Meanwhile, the presence of components with less volatility including *(E)*-caryophyllene to δ-cadinene increased between full bloom-beginning of fruit maturation (FB-FR) and fructification (FR) stage. The authors also mentioned about the conversion process of γ-terpinene, being the precursor of *p*-cymene during the phenological stages observed.

In *Calendula arvensis,* quantitative differences in the concentrations of δ-cadinene and α-cadinol were observed between two seasons (winter and spring). Paolini et al. (2010) suggested the reciprocal regulation between the two components as high α-cadinol concentration was associated with decrease in the concentration of the corresponding hydrocarbon (δ-cadinene). Elevated level of the oxygenated sesquiterpene fraction of α-cadinol especially in the spring season might involve the protection role for *C. arvensis*. It is known that terpene metabolites are not only essential for plant growth and development but also interactions between the plants and their environments.

Climatic factors such as temperature and precipitation have also been taken into account in the case of *Porcelia macrocarpa*. Maximum EO yield was obtained in June with lower temperature, while minimum EO was obtained in December/January when higher temperature and precipitation was recorded. da Silva et al. (2013) suggested the inverse proportional relation between EO yields and the temperature and precipitation pattern. EO variations due to rainfall and temperature were also reported on lavender (*Lavandula angustifolia*) during flowering period (Hassiotis, Ntana, Lazari, Poulios, & Vlachonasios, 2014). The EO quality of lavender is characterized by the presence of its major compounds, linalool and linalyl acetate. A relative amount of linalool dropped after the rainfall followed by several days of low temperatures resulting in lower quality of lavender oil. However, the linalool content increased after 15 days, therefore restoring the oil quality. On the contrary, compounds such as α-terpineol, borneol and lavandulyl acetate are characterized by enhanced production after the rainfall.

Conclusion

This review described the contemporary studies on the production of EO emphasizing on the physiological processes of the plant as well as the impact of climatic variations. A major breakthrough was achieved in the metabolic engineering pathways, and transcriptional of the EO constituents have resulted in better apprehension on the regulation of EO in aromatic plants. Recent advances in “omics” technologies, particularly metabolomics, had also helped resolved tremendously in EO research. The sophisticated approach of analytical chemistry has not only allowed the evaluation of the compositions but also to monitor its variations. However, the key challenges remain at interpreting the functional relationships between the metabolic EO components influenced by developmental and environmental factors. Furthermore, understanding their dynamic changes in response to these variables remain to be elusive.

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