What shapes our knowledge of the relationship between water deficiency stress and plant volatiles?

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Abstract

In this review, we attempt to highlight the issues related to plant volatile and essential oil studies in connection with drought stress. Our literature search included all publications on drought stress related to either the biosynthetic context of volatiles, or the ecophysiology and environmental interactions of species via these compounds. In addition, we surveyed publications on practical questions, such as the optimization of cultivation techniques of essential oil bearing plants. Emphasis was placed on theories explaining regularities in the detected symptoms of test plants and discrepancies of other results. Carbon allocation from primarily metabolism to secondary one, competition of parallel terpenoid pathways and the surplus of reductive power are the main theories that are discussed around. During evaluation, the main question was: which principles have already been justified in the biosynthesis/accumulation/emission of plant volatiles due to drought stress? What are the strengths and limitations of the theories? In discussing results from different scientific fields, the intention is to reveal logical connections that are yet to be addressed in the future co-operative multidisciplinary research. The simple question—whether drought stress increases the biosynthesis/accumulation/emission of plant volatiles—is not adequate any more. According to current scientific knowledge, the fine-tuning of all related variables is the challenge of next generation studies, especially for MAP species.

Keywords Drought stress · Volatile isoprenoids · Essential oil · Carbon allocation · Opportunistic emission · Over-reduced state

Introduction

Stress in plant life is defined as any external factors or deviations from optimal conditions that adversely affect plant homeostasis (Lichtenthaler 1996). *Water deficiency stress* occurs when the amount of water decreases to a level limiting plant life (growth, reproduction or survival) and impairing plant metabolism (Tardieu 1996; Kulak et al. 2019). A synonym term is the category of *drought stress*, but sometimes *water stress* is used in the literature with the same meaning, excluding flooding from the interpretation (Lewitt 1980; Simon et al. 1992; Munné-Bosch and Alegre 1999; Said-Al Ahl et al. 2009; Ahmadian et al. 2011;

Azhar et al. 2011; Debnath et al. 2011; Chrysargyris et al. 2016; Morshedloo et al. 2017; Kulak et al. 2019). As an experimental implementation, the amount of water inducing water deficiency must be defined by the *wilting point* (Furr and Reeve 1945; Said-Al Ahl et al. 2009; Asadi et al. 2012). However, several definitions are present in the literature, depending on the aim of the study. Subcategories such as *mild*, *moderate* and *severe* drought stress are frequently found in publications (Llusià and Peñuelas 1998; Bettaieb et al. 2009; Laribi et al. 2009; Nowak et al. 2010; Selmar and Kleinwächter 2013a; Bloem et al. 2014; Yadav et al. 2014; Kleinwächter et al. 2015; Saeedfar et al. 2015; Griesser et al. 2015; Chrysargyris et al. 2016; Németh-Zámbori et al. 2016; Radácsi et al. 2016; Morshedloo et al. 2017; Caser et al. 2018, 2019). This approach suggests a continuously induced change at cellular level in response to decreased water availability, while the strict definition of wilting point evidently implies a certain point in water availability where stress begins.

Metabolites produced by plants are usually categorized in two main groups. *Primary* metabolites include all basic,

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constructive, essential molecules of plant life. They are primary products of photosynthesis and basic biosynthetic pathways. A metabolite is considered *secondary*, when its formation is not strictly indispensable for plant life. Its biosynthesis is based on primary metabolites. Their specificity is often restricted to a certain taxonomic category (Pott et al. 2019).

Among secondary compounds, vascular plants have a wide array of *volatile secondary compounds*. They have great ecological usefulness in the communication with the surrounding flora and fauna (Rosenkranz and Schnitzler 2016). The term *plant volatiles* covers chemical compounds produced by plants that can spread in the air at environmental temperature. Plant volatiles are typically grouped into four main sections depending on their biosynthetic origin: terpenes (isoprene, monoterpenes such as linalool or geraniol and sesquiterpenes such as β -bisabolene or β -caryophyllene), fatty acid derivatives (short-chain derivatives with different functional groups, furthermore a distinct group of green leaf volatiles (GLVs) released upon mechanical damage), amino acid derivatives (volatile amines, indoles and sulfur compounds) and phenylpropanoid compounds (eugenol, methyleugenol, chavicol, and methyl chavicol) (Dudareva et al. 2004; Rosenkranz and Schnitzler 2016). From the viewpoint of atmospheric pollution, the term biogenic volatile organic compounds (*biogenic VOCs*) is defined as atmospheric volatile molecules originating from biological sources except carbon dioxide and monoxide (Kesselmeier and Staudt 1999). Biogenic VOCs significantly affect atmospheric chemistry and climate. Their emission is influenced by environmental factors—among them drought—, therefore

they have strong relevance in drought related surveys (Bertin and Staudt 1996; Llusà and Peñuelas 1998). While the expression of volatile organic compounds (VOCs) in plant research studies is mainly applied in the context of interaction with the surrounding environment, there is a significant group of plant secondary metabolites—namely the constituents of essential oils—where their volatility is especially utilized by humans (Fig. 1).

Essential oils (EO) are defined as products of extraction after a process such as distillation or, in the case of citrus rinds, the mechanical processing of natural materials (ISO 9235: 2014). The term essential oil can be used properly only in research studies where the content of volatile compounds of a species is measured with methods complying with the ISO standard. The ISO definition of essential oils expresses clearly one main aspect of all publications dealing with essential oil content and composition changes of species as a consequence of drought stress: results can only approximate the *in planta* situation.

The separated terminology of different scientific fields (VOCs and EO) predetermines the compartmentation of research ideas and thinking. Emission studies show isoprene and monoterpenes as the most prominent compounds within VOCs (Kesselmeier and Staudt 1999; Dudareva et al. 2004; Rosenkranz and Schnitzler 2016). Therefore, the two terms, plant volatiles and essential oils, should be connected somehow when the *theoretical background* of drought stress reactions of essential oil bearing plants is addressed.

Drought is receiving rising attention in the literature because of the effect of climate change and all its ecological consequences, but it is equally crucial in the optimization

Fig. 1 Overview of subjects related to water deficiency and plant volatiles

of secondary metabolite production/cultivation techniques of medicinal and aromatic plant (MAP) species. Both in nature and in experimental designs, drought stress highly *differs* in its *timing*, *length of time* and *severity*; furthermore, *test species/genotypes* are never the same. This fact results in great variations in consequences that have been detected in experiments, which hinders generalization (Szabó et al. 2017).

Therefore, in the following sections, the research results on plant volatile isoprenoids in drought stress experiments were evaluated *in the light of different theories explaining the link* between drought stress and production of volatile compounds. Ideas of different researchers are connected in a *logical flow* to find regularities or identify knowledge gaps for studies of next generations.

The contrast of different theories

Carbon allocation theory

Drought stress limits the operation of photosynthetic apparatus in plants as a consequence of stress induced stomata closing. A frequently cited hypothesis (Kreuzwieser et al. 2002; Turtola et al. 2003; Delfine et al. 2005; Šimpraga et al. 2011) is, that the decreased CO₂ uptake and fixation somehow is compensated by the altered *carbon allocation* to maintain/increase secondary metabolite synthesis for the protection of plants under stress circumstances.

According to Delfine et al. (2005) the water deficit stress increased the monoterpene concentration (µg/g DW) by the allocation of carbon to terpenoid biosynthesis rather than by maintaining the biomass production in a drought stress experiment with *Rosmarinus officinalis* and *Mentha spicata*.

However, when carbon allocation is suggested, it is not enough to express terpene or EO concentration on a dry weight basis. In these cases namely the question arises: whether the increase of secondary metabolites among stress circumstances is on the basis of a real increase via biosynthesis or just attributable to a change in reference numbers (e.g. smaller biomass production with the same rate of biosynthesis) (Kleinwächter et al. 2015; Paulsen and Selmar 2016). To demonstrate the importance of this aspect, some data extracted from the literature are presented in Table 1. In this table, the changing ratio of EO production expresses the relative decrease of carbon use for primary and secondary metabolisms compared to the control conditions as benchmark (100%). It shows also the difference in conclusions when either the theoretical background or the practical questions of drug quality/quantity changes are in focus.

The examples presented in Table 1 show the different situations. Increased accumulation, but without significant decrease of biomass can be read in the publication of Ahmadian et al. (2011). They recorded slightly less seed

and biological yield/biomass (kg/ha) for *Cuminum cyminum*, while the EO contents (%) were significantly higher at reduced watering. As it is shown, the biomass and seed yield resulted in 80 and 86% of the control data, but the essential oil yield is 93% when compared with the control, therefore the increase in EO % may be a drought stress related genuine increase of secondary metabolism. Carbon allocation allowed a lower level of decrease in secondary metabolism compared to the primary metabolism used for plant dry matter production (Table 1).

In a similar example, Khalid et al. (2006) demonstrated a significant and parallel elevation of EO content of *Ocimum basilicum* due to drought stress. However, the yield of the EO (ml/plant) decreased in consequence of the severely reduced biomass production. When the rate of decrease in biomass versus the rate of decrease in EO yield are compared, a drought stress connected genuine increase of EO production is detected contrary to the unsatisfactory result for the practical aspects of cultivation (e.g. lower drug and EO yields). As for the aspect of drug quality enhancement, the increase in EO content due to water deficiency stress presents an advantageous potential (Table 1).

The next example is about *Dracocephalum moldavica* (Said-Al Ahl and Abdou 2009). Due to water deficiency, both the biomass (fresh mass g/plant) and EO (% and ml/plant) decreased. Following the same calculation, we can recognize that in this experiment no carbon allocation can be interpreted from the data. The biomass of the plants in the water deficiency treatment reached 77%, while the essential oil yield (ml/plant) reached only 60% of that of the control plants (Table 1).

Lower soil water content (40% SWC in contrast to the control 70% SWC) resulted in both significantly lower biomass production and EO content in the case of four *Lamiaceae* species: lemon balm, thyme, peppermint and marjoram (Németh-Zámbori et al. 2016). Similarly to the former trial, percentage data of changes in biomass and EO yield for all species prove, that presumably no carbon allocation was present in the species under drought stress, since the rate of decrease in EO yield (ml/plant) is bigger than the relative decrease in biomass production (Table 1).

Most papers do not mention the relative decrease of EO/plant versus biomass for the different treatments. However, following the calculation of Paulsen and Selmar (2016) as an example, one can easily calculate if the values of EO content under drought stress represent a genuine increase or even a decrease in biosynthesis. Based on this analysis it can be concluded that the *carbon allocation in the examples discussed is not always present, therefore generalization of the carbon allocation theory cannot be supported*.

There are limited references where carbon allocation have been directly quantified, just as it was made for *Fagus sylvatica* young trees under drought stress (Šimpraga et al. 2011).

Table 1 Examples for calculation of the rate of biosynthesis in relation to the biomass as reference value, based on Paulsen and Selmar (2016) and further extracted data from references

Reference	Species	Parameters	Results of treatments and ratios to each other			
			Control	In %	Stress treatment	In %
Paulsen and Selmar (2016)	<i>Thymus vulgaris</i>	Biomass	17.45 g/plant	100	11.63 g/plant	67
		Concentration of terpenes	6.42 mg/g DW	100	7.44 mg/g DW	116
		Total amount of terpenes	112 mg/plant	100	87 mg/plant	78
Reference	Species	Parameters	Results of treatments and ratios to each other			
			3 irrigations	In %	2 irrigations	In %
Ahmadian et al. (2011)	<i>Cuminum cyminum</i>	Biological yield	775 kg/ha	100	624 kg/ha	80
		Seed yield	402 kg/ha	100	349 kg/ha	86
		EO content	2.6%	100	2.8%	107
		EO yield	10,452 ml/ha	100	9772 ml/ha	93
Reference	Species	Parameters	Results of treatments and ratios to each other			
			75% Field water capacity (FWC)	In %	50% FWC	In %
Khalid (2006)	<i>Ocimum basilicum</i>	Fresh yield	2773 g/plant	100	1393 g/plant	50
		Dry yield	554 g/plant	100	279 g/plant	50
		EO content	0.33%	100	0.38%	115
		EO yield	1.83 g/plant	100	1.10 g/plant	60
Reference	Species	Parameters	Results of treatments and ratios to each other			
			80% Soil water capacity (SWC)	In %	40% SWC	In %
Said-Al Ahl and Abdou (2009)	<i>Dracocephalum moldavica</i>	Fresh mass	36 g/plant	100	28 g/plant	77
		EO content	6.2%	100	5.2%	83
		EO yield	23 ml/plant	100	14 ml/plant	60
Reference	Species	Parameters	Results of treatments and ratios to each other			
			70% SWC	In %	40% SWC	In %
Németh-Zámbori et al. (2016)	<i>Majorana hortensis</i>	Fresh biomass	41 g/plant	100	21.3 g/plant	52
		EO content	2.134 ml/100 g DW	100	1.755 ml/100 g DW	82
		EO yield	0.87 ml/plant	100	0.37 ml/plant	42
	<i>Mentha piperita</i>	Fresh biomass	52.6 g/plant	100	11.3 g/plant	21
		EO content	3.166 ml/100 g DW	100	2.685 ml/100 g DW	85
		EO yield	1.66 ml/plant	100	0.30 ml/plant	18
	<i>Thymus vulgaris</i>	Fresh biomass	40.4 g/plant	100	12.0 g/plant	30
		EO content	4.758 ml/100 g DW	100	4.223 ml/100 g DW	89
		EO yield	1.92 ml/plant	100	0.50 ml/plant	26
	<i>Melissa officinalis</i>	Fresh biomass	236.8 g/plant	100	58.0 g/plant	24
		EO content	0.298 ml/100 g DW	100	0.107 ml/100 g DW	36
		EO yield	0.70 ml/plant	100	0.06 ml/plant	9

Woody, non-storing, VOC emitting species are suitable subjects to follow the consequences of drought stress, since they react to water deficit with differences in radial stem growth rather than just wilting. If the production of volatiles can be followed simultaneously with registering growth parameters for a longer period by measuring emission in a

closed system without cutting and distilling the plant material, then the dynamics of both parameters allow us to study the consequences of drought on isoprene/VOC emission. In this experiment, authors continuously evaluated the status of water deficiency stress in a young *F. sylvatica* via changes in radial stem growth together with simultaneous assessment

of biogenic VOC emissions and extend of photosynthetic activity. It was confirmed that depending on the severity of drought stress beech shifts its carbon allocation to VOC production or radial stem growth. Increase in monoterpene emission was detected parallel to drought stress until the stem growth was reduced (mild stress). Emission started to drop from the phase the beech stem ceased growing (severe stress). Beyond recording the pattern in monoterpene volatile emission, the authors disclosed an abrupt outbreak in emission of a volatile compound when drought stress was acute and the trees showed pronounced negative stem growth. A similar outcome for the same species was published by another group, too (Wu et al. 2015).

Due to species' specificities the knowledge gained above cannot be transferred to non-woody, volatile-storing species. However, these experiments seem to demonstrate a continuously induced change as response to decreased water availability rather than a certain point in water availability when stress reaction begins, therefore *validity of carbon allocation theory could be restricted to a certain period in the homeostatic processes*.

A slightly different interpretation of carbon redistribution can be seen in the publication of Turtola et al. (2003). According to the authors, the increase of monoterpenes concentration ($\mu\text{g/g DW}$) in woods of *Pinus sylvestris* and *Picea abies* seedlings is a result of the reduced plant growth from water deficiency stress, so the carbon built in during the photosynthesis can be employed for the synthesis of monoterpenes. This approach must assume that the reduced plant growth does not mean proportionally reduced photosynthetic activity and/or proportionally reduced chlorophyll content. This logic could be derived mainly from the characteristics of these woody species, where reduced plant growth primarily means less stem thickening. However, the generation of reactive oxygen species due to stress is likely to cause chlorophyll destruction (Foyer et al. 1994). The few papers dealing with this aspect provide contradictory results.

The chlorophyll content (SPAD index values) increased significantly while the biomass decreased due to water deficiency in *Satureja hortensis* (Radácsi et al. 2016) and in *Melissa officinalis* (Németh-Zámboi et al. 2017, Zámboiné et al. 2017). However, the presumed higher photosynthetic rate could not be manifested in the consequent increase of the EO content in either case. In Greek sage (*Salvia fruticosa*), drought stress induced a severely reduced biomass production in parallel with a significant increase of EO percentage, however, total chlorophyll content (mg/g FW) showed fluctuations (Chrysargyris et al. 2016). This latter study also calls attention to the fact that there might be differences among species. In the same experiment, lavender (*Lavandula angustifolia*) did not show any changes in the parameters which were measured (Chrysargyris et al. 2016). According to Shairat et al. (2018) 40% reduction in

total leaf chlorophyll content (mg/g FW) was identified in drought stressed *Satureja rechingeri* compared to the control plants. At the same time, the production of several phenolic and monoterpene compounds increased within the 12-day drought stress treatment, indicating that secondary metabolism of this species was improved—either by carbon allocation or the decrease of chlorophyll content rate was not proportional to the loss of fresh biomass.

Carbon allocation approached from the viewpoint of plant anatomy

Confirming or disproving carbon allocation, investigations may include the *context of plant anatomy* (e.g. carbon allocation between plant parts or between different tissues, possibility of accumulation of the secreted VOCs in different secretory structures, etc.). Searching among the publications, one can also find examples evaluating the carbon allocation theory based on this approach.

The possibility of the carbon allocation theory is supported (albeit indirectly) by the results of Asensio et al. (2012). In this experiment, the symbiotic arbuscular mycorrhiza colonization increased the demand for carbon in the roots of tomato, inhibiting carbon allocation to non-essential isoprenoids. This resulted in the decrease of root volatile terpenes compared to non-mycorrhizal plants. This study underlines that volatile accumulation/emission of different plant organs may react differently; therefore, *validity of the carbon allocation theory could be restricted by physical distance between the sites of carbon demand and terpene synthesis within an individual*.

Studies of isoprene and monoterpene-emitting *Quercus ilex* tree species in pot experiments proved that volatile terpenoid emission is inhibited under progressing/severe drought (Staudt and Seufert 1995; Loreto et al. 1996; Llusà and Peñuelas 1998; Wu et al. 2015). Some authors explain their deduction *exactly because of this species does not store isoprenoids* (Staudt and Seufert 1995; Loreto et al. 1996). According to the accumulated knowledge on this species, terpenes emitted by *Q. ilex* leaves are not raised from a storage supply, but are synthesized just before emission from currently fixed carbon. Therefore this proves that the emission is directly regulated by the presence of photosynthesis intermediates (Staudt and Seufert 1995; Loreto et al. 1996). As emission is directly inhibited by water deficiency, it can be concluded that the *volatile terpene syntheses are not modified by carbon allocation* to maintain or even enhance terpene synthesis. Change in monoterpene emission in this species is a response to a shortage of water.

The possibility of carbon allocation between tissues was studied by Kreuzwieser et al. (2002), who found that under conditions of limited photosynthesis the role of xylem-transported carbohydrates may also become

important for biosynthesis of secondary compounds via carbon allocation. The results of *Q. robur* demonstrated that xylem-transported glucose or its related carbohydrates are further possible carbon sources for leaf isoprene synthesis. At the same time, the authors emphasize that their results were gained on cut twigs, and the experimental results must be affirmed in *in vivo* plants to prove unequivocally the carbon allocation from xylem to terpene biosynthesis.

Since the aim of this review is to recount the connections among the different ideas, attention must be drawn to the following gap. As far as we know, only sporadic data are available on the possibility, magnitude and importance of *in vivo* terpene emission parallel to essential oil accumulation of essential oil bearing plants (Dement et al. 1975; Kesselmeier and Staudt 1999). Terpene emission in this case would influence the equation when genuine synthesis is examined. Generally, sampling and collecting of VOCs are carried out in a short time-frame via the headspace technique (Tholl et al. 2006), while drought stress experiments extend to days, weeks or even months. To the best of our knowledge, only a few publications on MAP species (*Helicrysum petiolare*, *Salvia sinaloensis*, *Salvia dolomica*) deal with EO accumulation and VOCs emission within the same experimental design, although biogenic VOCs were sampled only once, while the stress treatments were sustained for a total of 34 days (Caser et al. 2016, 2018, 2019).

Emission and/or evaporation of accumulated and stored volatiles from the plant tissue largely depends on the accumulation structure. In species where EO is accumulating in *glandular hairs*, recent research indicates the presence of mechanisms providing transport of VOCs to the subcuticular space but restraining their subsequent outward emission. The cuticle and cell wall covering the subcuticular space in glandular hairs seem to be the key to withhold volatiles, although their precise structure and the relevant molecular mechanism are mostly unexplored (Tissier et al. 2017). These glandular hairs are not uniform either, but two main types have been detected in plants, which differ in their potential to withhold the secreted and accumulated volatile molecules (Werker 1993).

Considering the co-occurrence of terpene emission and the accumulation of EO in *inner ducts*, the example of the *Eucalyptus* species is the most prominent one. While these trees increase isoprene emission rates during drought, the reaction follows a species-specific threshold for drought tolerance. Accumulation of the EO in these trees shows variable responses to reduced water availability depending on the experimental design and the species used as a test plant in the studies (McKiernan et al. 2014, Dani et al. 2015).

Carbon allocation within the cell

The hypothesis of carbon allocation requires further considerations and studies about how the allocation takes place *within the cell*.

Rodríguez-Calcerrada et al. (2013) proved that the increased concentration of soluble sugars in the cytosol due to the applied drought stress, played little role in sustaining isoprene synthesis and emission of *Quercus pubescens*. This result suggests that in this species there is no import of cytosolic carbon (sugars) into chloroplasts (2-C-methyl-D-erythritol 4-phosphate (MEP) pathway—biosynthesis of isoprenes in *Q. pubescens*, based on the authors' explanation) under severe water deficiency. It also implies the importance of co-occurrence of biosynthetic pathways *within the same cell organelle to enable carbon allocation* between biosynthetic pathways, mentioned by Dani et al. (2015).

However, in plants, a terpenoid biosynthetic pathway can be found both in cytosol [Mevalonate pathway (MVA)], and chloroplast (MEP) (Lichtenthaler 1999) and terpenoids (including isoprene) as VOCs can be produced by both, depending on the species. Until now, the mechanism of an eventual natural crosstalk (metabolic flow) between the two pathways in case of shortage of precursors [isopentenyl diphosphate (IPP), dimethylallyl diphosphate (DMAPP)] in planta still remains to be fully unravelled. At the same time the increasing number of *in vitro* outcomes is pointing towards the possibility of such a metabolic flow of precursors to some degree (McCaskill and Croteau 1995; Dudareva et al. 2005; Bartram et al. 2006; Vranová et al. 2013).

While reflecting on these ideas, the role of both pathways in the synthesis of volatile compounds should be considered. It is generally accepted, that sesquiterpenoids are synthesized via the MVA pathway, while isoprene, hemi- and monoterpenoids are the products of the MEP pathway (Vranová et al. 2013). Therefore, in those experiments on MAP species where water deficiency increased the concentration of sesquiterpenes in the EO, the carbon allocation theory within the same cell organelle seems to be verified, however indirectly. The quality changes within the EO could possibly originate in *carbon surplus-reuse within the cytosol*.

There are several reports indicating similar changes. The amount (absolute/relative) of sesquiterpenes increased in the EO of *Carum carvi* (µg/g DW, Laribi et al. 2009), *Salvia officinalis* (µg/g DW, Bettaieb et al. 2009), *L. angustifolia* (%), Chrysargyris et al. 2016), *Mentha piperita* (%), Charles et al. 1990), *Artemisia annua* (%), Yadav et al. 2014) under water deficit, while for *Ocimum basilicum* the amount of total sesquiterpenes in the EO (µl/g DW) decreased (Simon et al. 1992). In many reports other characteristic tendencies could be registered. In *S. sinaloensis* the accumulation of oxygenated monoterpenes (%) (Caser et al. 2018), and in

Salvia dolomitica and *Helichrysum petiolare* the accumulation of oxygenated sesquiterpenes was induced by drought stress (Caser et al. 2016, 2019). In the case of *Origanum vulgare*, the relative percentage of total oxygenated compounds decreased due to increasing water deficiency (Said-Al Ahl et al. 2009). In the chemotaxonomic evaluation of Hungarian *O. vulgare* subsp. *vulgare* populations a clear shift towards the oxidized molecules was detected: the ratio of β -caryophyllene oxide increased significantly due to the unseasonably dry summer (Cserháti et al. 2013). Both in thyme and marjoram, water shortage seemed to increase the synthesis of end products (thymol, carvacrol, sabinenes, linalool) at the expense of their precursors in the same pathway (Németh-Zámboi et al. 2016; Hussein et al. 2019). According to Mohasseli and Sadeghi (2019) this is true only in the case of mild (60% field capacity) water deficiency stress for two thyme species (*Thymus serpyllum* and *Thymus vulgaris*).

Opportunistic emission of volatile isoprenoids theory

Terpenoid biosynthesis includes not only the volatile hemi-, mono- and sesquiterpenoids, but also isoprenoids with higher carbon atom numbers synthesized from the same five-carbon-atom units. Somewhat similar to the carbon allocation theory or even as a side aspect, a competition between isoprenoid compounds under water shortage conditions might be presumed. *The hypothesis of opportunistic emissions of volatile isoprenoids* emphasizes the terms of essential versus non-essential isoprenoids. According to Owen and Peñuelas (2005) VOCs are not essential in all plants, although in certain species their emission provides eco-physiological advantages and therefore has been evolved and maintained through the evolution. The opportunistic hypothesis suggests that circumstances modifying the synthesis of higher isoprenoids (abscisic acid, gibberellic acids, tocopherol, sterols and carotenoids) are responsible indirectly for the amount of non-essential isoprenoids. Their synthesis may be primarily depending on the remaining surplus precursors (IPP and DMAPP).

Nevertheless, contradicting results have been published on this issue as well. An example of this is *A. annua*, which resulted in decrease of total carotenoid content (mg/g FW) as a higher isoprenoid, while the ratio (%) of sesquiterpenoids increased parallel to the upregulation of sesquiterpene cyclase enzyme (*SQC*) under mild or moderate water stress treatments (Yadav et al. 2014). Additionally, carotenoids (mg/g FW) in *S. sinaloensis* and *S. dolomitica* were not affected by different water regimes (Caser et al. 2018, 2019), while the biogenic VOC and EO profiles altered. Severe water deficiency dramatically reduced the carotenoid content (mg/g FW) of *H. petiolare*, and the amount of VOC

and EO was not affected, although both spectra were modified. Finally, a completely different tendency was measured in *O. vulgare*. The carotenoid content (mg/g FW) increased with increasing water deficiency level and the EO content (%) decreased significantly when severe water deficit was maintained (Khalil and El-Noemani 2015).

The difference among species in this context suggests that *the validity of this theory might be restricted to certain plant taxa*.

The question of the phenylpropanoid pathway

In numerous species, essential oil compounds include also volatile *phenylpropanoid molecules* (Iijima et al. 2004; Mandoulakani et al. 2017). Various papers indicate that enhanced accumulation of polyphenols (anthocyanin, flavonoid, etc.) may be a stress response resulting from initiation of the phenoloid pathway by the (drought) stress effects (e.g. Chalker-Scott 1999; Alishah et al. 2006; Yuhang et al. 2011; Yuan et al. 2012; Nakabayashi et al. 2014; Griesser et al. 2015; Shairat et al. 2018). According to the findings of Németh-Zámboi et al. (2017) on four EO accumulating species, it was concluded that in some of them the parallel decrease of biomass and elevation of the content of total phenolic content might allow the latter to function as an adequate marker in predicting the lack of appropriate water supply.

Interestingly, only a few attention has been given to the volatile phenoloids in studying drought stress responses of EO accumulating species. As they are products of a pathway basically different to the one of the isoprenoids, they could represent new *pros and cons* in ascertaining the theories we have discussed.

Scientists believe that with increasing understanding of these pathways it will be possible to select genotypes with better adaptation characteristics (Wang et al. 2003; Witcombe et al. 2016). *Indeed, genotype dependence and its manifestation in secondary metabolism is another emerging issue in drought tolerance*. Results about genotype dependent drought reaction were published in the case of *Melissa officinalis* (Szabó et al. 2017) and *Petroselinum crispum* (Petropoulos et al. 2008) cultivars, in two closely related species as *Thymus vulgaris* and *Thymus serpyllum* (Moradi et al. 2017) and for two subspecies of *O. vulgare* (subsp. *virens* and subsp. *gracile*) (Morshedloo et al. 2017).

The surplus of reductive power theory

Another hypothesis behind the elevated level of secondary metabolites in case of stress reactions is *the surplus of reductive power theory* (Selmar and Kleinwächter 2013a, b; Kleinwächter and Selmar 2015). According to this idea, the notable decrease of available CO₂ due to drought finally eventuates in oxidative stress with an oversupply of

reduction equivalents. To cope with the excess NADH plants shift their metabolism towards reactions employing reducing agents, such as the synthesis of isoprenoids, phenols and alkaloids, even without altering the relevant enzyme activity. This theory is supported by further data on the decline of over-reduced status and accumulation of monoterpene compounds in consequence of elevated CO₂ concentration (Nowak et al. 2010).

However, the same logical questions arise here as well; namely, how the relocation of NADH is taking place within the cell to reach all the different biosynthetic pathways in different organelles; how the regulation of flux is involved; and are there any limiting obstacles in intracellular transport? This is especially interesting, since cellular compartmentalization in plant metabolism is highly complex (Heinig et al. 2013), which certainly brings to light the export of excess NADH to different secondary metabolic pathways in different organelles. So far, mitochondria seem to play a major role in ensuring the removal of excess redox equivalents from chloroplasts under both limiting and optimal conditions (Raghavendra and Padmasree 2003). Studies in different bacteria indicate the role of secondary metabolism to maintain cellular homeostasis by regenerating intracellular NAD⁺ concentrations (Price-Whelan et al. 2007; Dietrich et al. 2008); however, *the direct assessment of secondary metabolites for MAPs in these processes has yet to be carried out.*

Molecular tools in support of discoveries

Following gene expressions under different water supplies can certainly provide clues to whether the increase in any terpenoid biosynthesis is only an exhaustion of stress-related surplus reducing agents, or an active biosynthetic change due to upregulation of certain genes involved in terpenoid synthesis. However, it is difficult to capture the right time for sampling, since the phenotypical response is generally delayed compared to the gene expression level; this is due to post-transcriptional regulation, protein synthesis and terpenoid production. This approach was followed in MAPs by Caser et al. (2019) in *S. dolomitica*, by Morshedloo et al. (2017) in *O. vulgare*, by Shairat et al. (2018) in *S. rechingeri* and by Yadav et al. (2014) in *A. annua*. In all of these cases, the up- or down-regulation of key genes detected was positively related to changes in the EO of corresponding species indicating a transcriptional regulation of the synthesis.

A completely new level of analysis in gene expression can be seen in the publication of Zhang et al. (2019), where the gene expressions of *Populus deltoides* were followed under water deficiency stress conditions. The global transcriptome survey of the RNA-sequence data could facilitate tracking of all expression patterns of genes engaged in both terpenoid pathways (MVA and MEP/DOXP), giving a complex insight which

requires equally high investment from the technical and financial points of view. These possibilities are not readily available for most of the scientists involved in drought response studies.

It is now commonly agreed, that MVA and MEP pathways are regulated at both transcript and protein levels to control precursor supply (Vranová et al. 2013). In general, less information is available on the changes in the biosynthesis rate due to translational and posttranslational regulations of MVA and MEP/DOXP pathway enzymes. Differences in expression or accumulation level of isozymes in plants regulated by environmental events is now emerging. Future trend in research will presumably focus on these questions, too.

Conclusion and outlook

Plant taxa exhibit significant differences; therefore, evaluation of their reactions to drought is even much more challenging. For the most part, drought stress experiments have been focusing on selected partial questions, which inevitably are reflected in both the methods used and throughout the interpretation of data.

Considering the principal outcome of this review, we can conclude that the simple question—whether drought stress increases the biosynthesis/accumulation/emission of plant volatiles—is not adequate any more. Generalization to such an extent distorts reality. According to current scientific knowledge, *the fine-tuning of all related variables is the challenge* of next generation studies, especially for MAP species.

According to the available references one of the basic uncertainties may derive from improper definition of drought. Definition of water supply levels (e.g. mild, moderate, severe) for water deficiency stress studies should reflect the ecological requirements of test species instead of mechanically copy the experimental design of earlier publications on other species. Optimum water demand is rarely given as SWC %/FWC % or wilting point in botanical-coenological descriptions or in cultivation guidelines, therefore *translation of this knowledge into water supply setting* is essential. It only makes sense to follow any indicator of drought stress if this very first step is defined properly. Definitions of mild, moderate or severe drought stress should reflect changes in plant physiological data (from water potential changes to membrane damage). Publications of MAP species dealing with drought stress rarely explain the correlation of different water supply settings with the water demand of test species.

Limits of all kind of studies must be understood when outcomes are listed. Theoretical background explanations (not proved but assumed) should not be expected and included in studies with practical aim and experimental design such as the case in drug quality optimization. Applying rules of population

genetics when dealing with sampling is crucial. Molecular biological studies rarely could cover the representative number of individuals in an accession to examine properly the reaction of a population/variety to water deficiency. Furthermore, mass sampling of several individuals due to limited sample size is implausible. The small sample size usually taken for molecular studies could further limit the portrayal of an individual, because it cannot represent the necessary plant organs for volatile (essential oil) accumulation measurement within the same experiment.

Focusing primarily on MAP species, the following issues were outlined by this joint assessment of publications. In the future, *measurement of both* emission and accumulation of volatiles for the whole period of water deficiency stress could result in deeper understanding of drought reactions. Next generation research must focus on the *interrelation of different coping mechanisms* (shift in secondary metabolism and/or initiation of other carbon sources as a substitute for photosynthesis), *their correlation to* timing, duration and severity of drought stress; *their dependency on* species specificities, plant anatomical constitution and aspects of secondary metabolite pathway.

Probably a degree of drought stress exists in which a desired essential oil accumulation or even an altered essential oil composition is achievable. Trials on endless variations of factors in a complex net of interactions (species/genotype/water deficit treatments/other stress and environmental effects) will always have a limited applicability without deep understanding how the different water supply affects volatile production. Therefore, more research is required to reveal the molecular and biochemical mechanisms that allow for fine-tuning in cultivation. It would be necessary, that co-operative multidisciplinary studies with an omics approach should be given high priority to change the perspective of discoveries in drought stress experiments.

Author contribution statement KS reviewed the literature and wrote the article. PZ took part in literature search and general brainstorming on the subject. ÉNZ discussed the manuscript with K Szabó with several good suggestions, additional parts and corrections.

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