REVIEW

Methyl salicylate as a signaling compound that contributes to forest ecosystem stability

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Abstract

Key message **This review for the first time gathers the current state of knowledge on the role of plant and microbial methyl salicylate (MeSA) signaling processes in forest ecosystems. It aims to establish a basis for the use of high-MeSA-emitting trees as a silvicultural tool aiming to enhance stability and resilience in managed temperate forests affected by climate change.**

Abstract Methyl salicylate (MeSA) is a volatile plant and microbial signaling compound involved in systemic acquired resistance (SAR) and defense against pests and microbial pathogens, and antagonists. MeSA emitted by plants is also believed to trigger SAR in neighboring plant individuals, thus contributing to the resilience of the entire plant community. In this review, we discuss volatile plant-to-plant communication processes with a special focus on MeSA and provide an overview about the occurrence of MeSA in fungi and other microbes. We summarize present findings on the role of MeSA in plants and particularly in birches (*Betula* spp.) and discuss the potential use of MeSA and MeSA-emitting plants in agriculture and forestry. MeSA levels in plant tissues are adjusted by methylation of salicylic acid to MeSA and the reverse process of demethylation. Some plant species possess constitutively high MeSA levels and thus are suitable for experiments of admixture of high MeSA plants, e.g., birches of the subgenera *Betulenta* and *Acuminata* in plant communities such as mixed forests. Furthermore, knowledge of candidate genes and the molecular pathways underlying high MeSA emission is expected to offer a basis for altering MeSA levels and/or the selection of high MeSA mutants.

Keywords MeSA emission · Trees · *Betula* · Salicylic acid · Systemic acquired resistance (SAR) · Biogenic volatile organic compounds (BOVC)

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Volatile compounds and the health of forest ecosystems

Climate change and the spread of invasive phytophagous organisms and disease agents in the course of ongoing biological globalization increasingly affect forests by altering inter-species competitiveness in biocenoses and upsetting the intricate dynamic balances that ensure ecosystem stability and resilience (Gauthier et al. 2015; Roques et al. 2020; Weiskopf et al. 2020).

The warm winter of 2019–2020 and the dry, hot summers of 2018, 2019, and 2020 left forests in large parts of Europe stressed and prone to outbreaks of bark beetle and other pests (Huang et al. 2020; Netherer et al. 2019; Schuldt et al. 2020). This points to a need for a profound understanding of ecophysiological processes at the ecosystem level to be able to adjust management to future environmental conditions.

It is well established that multi-trophic interactions and defense in forest ecosystems are mediated and coordinated by a suite of interlinked signaling mechanisms that depend on biogenic volatiles (Šimpraga et al. 2019; Zemankova and Brechler 2010). These include compounds that are emitted by plants upon exposure to biotic stress factors and induce in others the response to build up resistance ahead of infestation. This leads to a more effective resistance at the community or ecosystem level. Metaphorically speaking, the volatile signals may be described as a warning call or "call to arms" for other plants to be prepared and thus contribute to the stability and fitness of the entire plant community. Alternatively, the interaction was pictured as some plants "eavesdropping" on foreign signals that betray other plant's state of fitness (Baldwin et al. 2006; Karban et al. 2004) to monitor for imminent threats. A classic example of such a plant–plant communication is the famed "talking trees" (Baldwin and Schultz 1983; Haukioja et al. 1985). In the words of Baldwin et al. (2006), the "chemical vocabulary" of volatile organic compounds (VOCs) include ethylene, terpenoids, methyl jasmonate (MeJA), methyl salicylate (MeSA), and a plethora of other compounds. Perception of any of these volatiles alone or in a complex bouquet of other substances may trigger signaling cascades including endogenous hormonal responses via jasmonate (JA), indole-3-acetic acid (IAA), or salicylic acid (SA) signals, leading to the buildup of systemic acquired resistance (SAR). Responses may include accumulation of defense substances or induction of long-distance signaling compounds that attract organisms that act antagonistically to the pest or disease agent. Many compounds appear to fulfill multiple functions, depending on their concentration and the context of other volatiles present and some have signaling functions that reach across kingdoms (Raffa et al. 2005). This versatility and multi-functionality of volatiles contribute to the complexity and dynamic flexibility of the entire system including plant–plant, plant–herbivore, and plant–predator interactions. MeSA, for example, a volatile benzenoid compound, is produced both in fungi and in higher plants and is likely to act as a volatile signal between plants, between fungi, and between plants and fungi. Furthermore, as outlined below, it seems to be part of plant signals directed at insects. MeSA is one of the best-studied biogenic volatile organic compounds (BVOCs) linked to aphid infestation (Blande et. al. 2010; Staudt et. al. 2010). A study of multi-trophic interactions involving MeSA suggests that its role varies depending on plant and insect species (Yangang et al. 2020). It may not only work as a deterrent but also be intricately linked to insect–insect pheromone signaling (Rouyar et al. 2015; Xu and Turlings 2018).

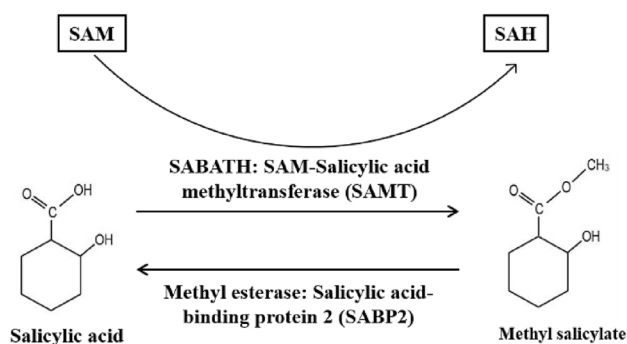The chemical structure of MeSA and its biosynthesis are shown in Fig. 1.

Fig. 1 Structure and biosynthesis of methyl salicylate in plants: *S*-adenosyl-L-methionine (SAM)-dependent methylation of SA into MeSA by salicylic acid methyl transferase, a member of the SABATH gene family. In the process, *S*-adenosyl-L-methionine (SAM) donates a methyl group and is converted into *S*-adenosyl homocysteine (SAH). The reverse reaction is catalyzed by salicylic acid-binding protein 2 (SABP2), a methylesterase (Modified from Singewar 2020c)

MeSA is a beta hydroxy acid that is, via its precursor compound SA, derived from the isochorismate (IC) and phenylalanine ammonia-lyase (PAL) pathways (Lefevere et al. 2020). MeSA was first isolated from wintergreen *Gaultheria procumbens* (Cahours 1843) but is found widely in the plant kingdom. In some cases, it reaches concentrations that make its typical "wintergreen aroma" perceivable to the human nose, such as in the taxa discussed below (Pavlovic et al. 2007; Liu et al. 2013; Ashburner et al. 2013; Singewar et al. 2020b).

Methyl salicylate (MeSA) in fungi and other microbes

Microbial involvement in MeSA emissions has been shown in several cases, and in some instances, the levels of MeSA in connection with disease patterns in woody plants are so high that the scent is easily perceptible. A symptom of elm phloem necrosis caused by phytoplasma is a distinct MeSA odor (Sinclair et al. 2001; Swingle 1942). Wood infested with aspen fire sponge *Phellinus tremulae* (*Hymenochaetaceae*) also exudes a typical wintergreen-like MeSA aroma (Collins and Halim 1972). It remains unclear though, whether the substance emitted is essentially of plant or microbial origin or a result of microbial metabolization of a plant compound. Interestingly also synthetic pathways that do not lead via SA have been described in fungi. MeSA emission causing a noticeable wintergreen smell even independent of a tree host was shown in *P. tremulae* in in vitro culture (Ayer and Cruz 1995; Verrall 1937). In this case, the MeSA emitted most likely originates solely in the fungal metabolism independent of any plant derived SA as substrate.

There are striking differences in MeSA emission levels between individual strains of the same fungal species. Nobles (1948) reported that the MeSA odor of *P. ignariusis* was only faint in some cultures and nonexistent in others. Baxter (1951) found no "wintergreen"–MeSA smell in *P. ignarius nigricans* cultures. Interestingly, *P. ignarius* strains isolated from birch trees were observed to emit MeSA only in small amounts and those isolated from aspen appeared to both emit and tolerate more MeSA in culture (Verrall 1937).

While MeSA synthesis in *Phellinus* is well established, and strains of this fungus are even used industrially to produce this compound (Batt and Tortorello 2014), it is likely that more fungal species possess the ability to synthesize MeSA.

It is possible that MeSA synthesized and emitted by fungi has a role in defense against other microbes. Thus, the emitting fungus itself may be resistant to MeSA or any defense mechanisms it triggers, but fight infection with other competing microbes. Given the volatility of the compound, it may work beyond its immediate habitat and influence competition within larger forest microbial communities. A fungicidal effect of MeSA was shown, for example, with the ascomycetes *Colletotrichum camelliae* (*Glomerellaceae*), which causes anthracnosis in tea shrubs (*Camellia sinensis*) (Zhang et al. 2006).

Depending on the fungal species effects vary dramatically and sometimes not inhibition of growth but rather the opposite is observed. Lin et al. (2017) found that MeSA had a positive effect on both hyphal growth and toxicity of *Lecanicillium lecanii* (*Cordycipitaceae*), an entomopathogenic fungus used to produce biopesticides for applications in horticulture and agriculture.

The presence of MeSA in non-plant organisms (e.g., microbes) suggests a function in the complex signaling networks between individuals of different species and even across different kingdoms (Morath et al. 2012). Notably, SA on its own has antifungal effects (Amborabé et al. 2002; da Rocha Neto et al. 2015) suggesting a microbial conversion of plant SA into MeSA which may enable the fungi to remove SA from host tissue by volatilizing it. In dead tissues, it appears more plausible that saprophytic fungi produce an antimycotic compound to keep other competing fungal species at bay. Metabolizing plant SA into volatile MeSA may yield a double benefit to parasitic fungal organisms that grow on live plants by adjusting SA concentrations in the host tissue to a level they can tolerate and at the same time inhibiting other microbes that compete for the same niche.

Understanding the role of fungal MeSA-signaling requires elaborate in vivo and in vitro studies. It needs extended surveys on MeSA emissions of fungi on both living and dead forest trees, especially birches including high- and low-MeSA-producing species. Such a survey could in a first approximation be performed using the simplest olfactory method: checking whether the fungus smells of "wintergreen" or not.

Role of MeSA in plants

MeSA produced in plants in response to environmental stress acts through its anti-oxidative effects (Ismail et al. 2006), anti-microbial properties (Dai and Mumper 2010), or via SA-dependent signaling pathways (Boba et al. 2017). Its role as a long-distance signaling molecule with a function in SAR has been studied extensively in *Arabidopsis thaliana* and *Nicotiana tabacum* (Shulaev et al. 1997; Vlot et al. 2008) (Fig. 2). It is well established that plants synthesize SA, the precursor compound, as a signal that initiates defense mechanisms upon pathogen infection (Vlot et al. 2009). Earlier, SA was considered to be the mobile signal in the SAR mechanism (Dempsey et al. 1999; Durrant and Dong 2004; Yalpani et al. 1991) since a moving molecule is required to transfer signals from pathogen-affected tissues to distant healthy tissues (Jenns and Kuc 1979). To elucidate the role of SA in SAR Gaffney et al. (1993) expressed the *nahG* gene from *Pseudomonas putida* which encodes a salicylate hydroxylase that converts SA to catechol in tobacco under a constitutive 35S-promoter. Three lower leaves of plants from the same lines were infected with tobacco mosaic virus (TMV) to study the effect of the *nahG* gene transcript on SA accumulation. The concentrations of salicylate hydroxylase protein, *nahG* mRNA, and SA were assayed using leaves that showed lesions amid infection. SA levels in wild-type-treated plants increased to 6000 ng of SA per gram of TMV-infected tissue, which is a 185-fold increase in comparison to controls treated with a virus-free medium. Transgenic lines showed a substantial increase of *nahG* mRNA and salicylate hydroxylase activity resulting in an only two-fold increase in SA upon TMV infection. These lines were used for grafting experiments by Vernooij et al. (1994) who joined wild-type scions with *nahG*-transgenic rootstocks and vice versa. The rootstocks of grafted plants were inoculated with TMV and the infection allowed to progress for seven days. Plants with transgenic rootstocks were still able to transmit a signal across the graft junction into the wild-type tissue which was thus protected from pathogen attack (Vernooij et al. 1994). The results suggest an involvement of a vascular-mobile molecule in long-distance signaling and the establishment of SA-dependent SAR (Vernooij et al. 1994).

Li et al. (2018) showed a rise in both SA and MeSA levels in *Populus tomentosa* after infection with the fungal pathogen *Botryosphaeria dothidea* (*Botryosphaeriaceae*). The SA level was found to be elevated after 6 h and remained steady between 12 and 72 h. The MeSA level in contrast began to rise 48 h after inoculation. The chronological sequence and
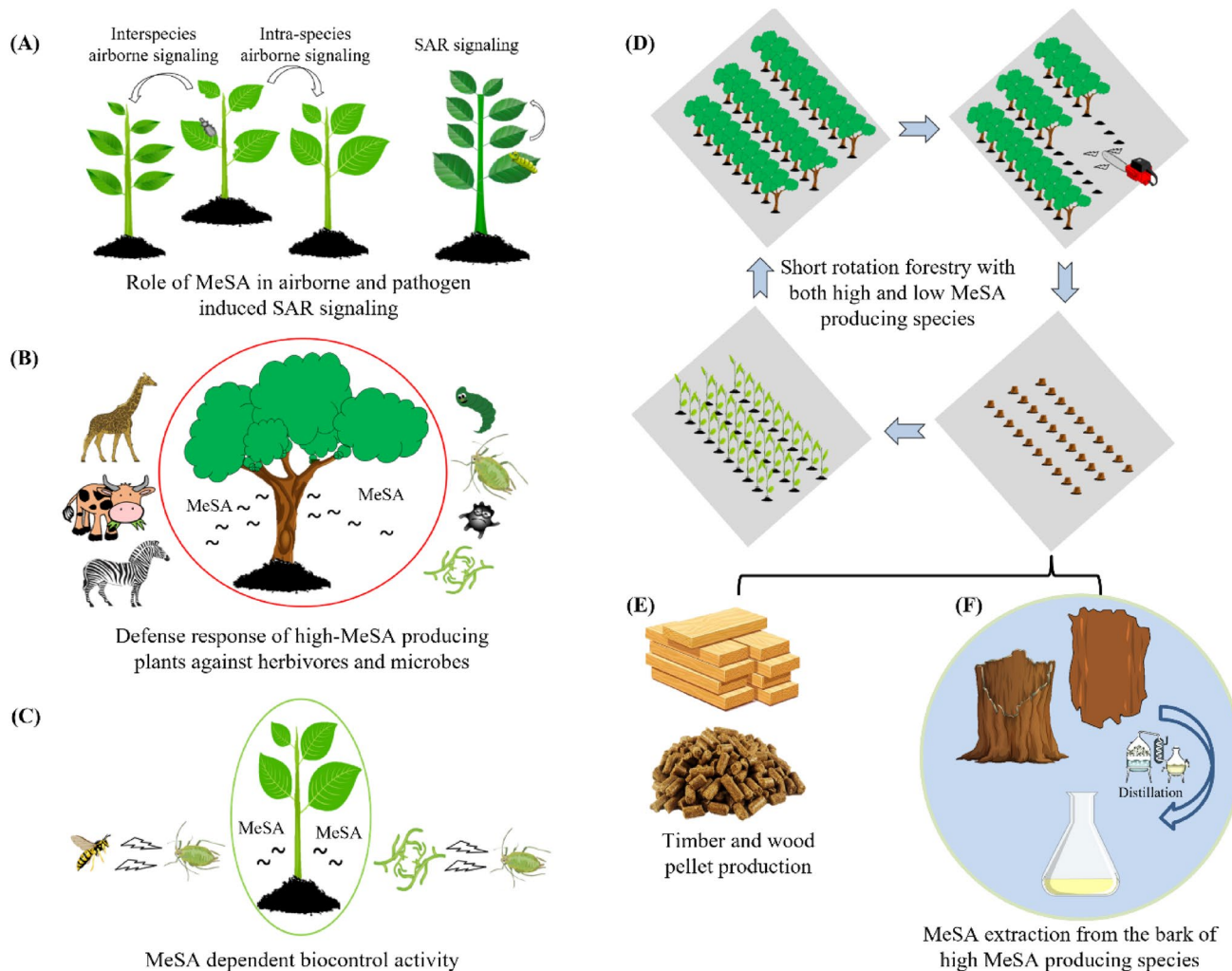
Fig. 2 Ecological and economic advantages of MeSA signals in managed forest ecosystems: as a signaling element between multiple organisms MeSA contributes to maintaining ecological stability. **A** Involvement of MeSA in SAR and airborne signals "warning" against pathogen attack. **B** High MeSA emission by plants protects them from herbivores and microbial damage. **C** MeSA helps to activate the biocontrol activity by attracting predatory arthropods of aphids that harm the plants. **D** Short rotation forestry with high- and low-MeSA-producing forest tree species. **E** Traditional economic use of forest trees for timber and fuelwood production. **F** Production of organic MeSA from the bark of high-MeSA-emitting tree species

the molecules' chemical structure suggest that SA may be converted into MeSA, giving rise to a mobile signal. Thus, MeSA is a candidate molecule for signaling that initiates responses in the healthy tissues of the plant. Furthermore, MeSA levels declined under the same condition after a further 48 h suggesting its short-term signaling activity and subsequent conversion of MeSA back to SA. ^{14}C labels were recovered in SA after treating tobacco plants with ^{14}C-MeSA which demonstrated that MeSA signals can be modified by demethylation and conversion into SA suggesting MeSA signals can be regulated by demethylation to SA (Shulaev et al. 1997) (Fig. 2). Detailed analysis of pathogen-induced MeSA production in poplar revealed accumulation of SA and MeSA near the site of infection, providing strong

evidence for the role of MeSA in induced defense mechanisms (Li et al. 2018).

Kumar and Klessig (2003) downregulated the expression of salicylic acid-binding protein 2 (SABP2), a methylesterase involved in MeSA biosynthesis, in tobacco by means of RNA interference (RNAi) and found suppression of SAR development. In grafting experiments using the same lines wild-type scions were grafted onto rootstocks with silenced SABP2 expression, and vice versa (Park et al. 2007). Small lesions occurring after TMV infection at the rootstock suggested that SAR was induced in the wild-type scion grafted on either SABP2-silenced or wild-type rootstocks. In contrast, larger lesions were observed in SABP2-silenced scions grafted onto wild-type or SABP2-silenced rootstocks,

indicating a failure of SAR in the plants. The results suggest, although MeSA esterase is not required to trigger SAR, it is vital for transmitting the SAR signal in distal tissues (Park et al. 2007).

Furthermore, a function of airborne MeSA in long-distance signaling promoting resistance against TMV was shown by Shulaev et al. (1997). In TMV-infected 5-week-old tobacco plants 185 µg MeSA was collected from total volatiles, compared to only 23 µg collected from non-infected plants (Shulaev et al. 1997).

MeSA emission is also an element in an indirect defense mechanism that is activated upon herbivore attack to attract these herbivores' natural enemies (Van Den Boom et al. 2004; Mallinger et al. 2011; Ghirardo et al. 2012). Here, volatile compounds like MeSA are referred to as herbivore-induced plant volatiles (HIPV) (Gadino et al. 2012). Predatory arthropods are attracted by HIPVs suggesting that these compounds indicate the presence of potential prey (Fang et al. 2015). Aphids were shown to move away from plants treated with an exogenous dose of 10 µl MeSA per plant, suggesting that the potential prey also perceives the signal (Coppola et al. 2018). Measurements of seasonal emissions of BVOC from *Pseudotsuga menziesii* (*Pinaceae*) by gas chromatography–mass spectrometry (GC–MS) showed that MeSA emission was elevated not only in response to biotic stress but also rose in the summer heat and fell with the temperatures in winter (Joó et al. 2011) (Fig. 2).

In response to pathogen attack, almost all plant species produce MeSA as a long-distance mobile signal-inducing SAR (Chen et al. 2019; Liu et al. 2011; Shine et al. 2019). Therefore, we denote species that synthesize MeSA mostly when needed in defense as "low-MeSA-producers". In contrast, species that have constitutively high MeSA levels are referred to as "high MeSA-producers" (Singewar et al. 2020b).

In some species, concentrations reach a level sufficient for the characteristic aroma to be well perceivable to the human nose such as in species of the genera *Polygala*, *Gaultheria*, *Filipendula, Primula,* and *Betula* (Pavlovic et al. 2007; Liu et al. 2013; Joshi and Subedi 2014; Joshi 2015; Bijttebier et al. 2016; Olennikov et al. 2016; Singewar et al. 2020b). Also, some ferns such as *Asplenium lamprophyllum* (*Aspleniaceae*) or *Polypodium vulgare* (*Polypodiaceae*) contain MeSA (Briggs and Taylor 1947).

The MeSA odor is colloquially referred to as "wintergreen" after *Gaultheria procumbens* (Ericaceae), the eponymous American wintergreen. *Gaultheria* species of the Himalayas and South India are known as Eastern Teaberry. Most of the approximately 134 species in the genus contain high MeSA levels and were historically used to produce wintergreen oil for numerous applications (Liu et al. 2013).

The compound is, as noticeable by the wintergreen scent, also emitted from crushed roots of *Polygala* species, e.g., the perennial White Milkwort (*Polygala alba, Polygalaceae*) or the biannual Candy Root *P. nana*. GC–MS analyses showed MeSA to be the main constituent of essential oils extracted from roots of *P. paniculata* (89.1%) and *P. cyparissias* (97.8%) (Pizzolatti et al. 2009). Several species of the genus are linked to a rich native North American ethnobotanical heritage (Moerman 1986).

Trees of the genus *Parkia* (*Mimosaceae*) have been reported to emit a MeSA aroma from their bark (Hopkins 1986). There appear to be no studies exploring whether the MeSA emission, is possibly age dependent or triggered by specific environmental factors since it not constitutively high in all individuals of the species. Also, high levels of MeSA were found in trees of the neotropical genus *Pouroma* (*Urticaceae*) (Lopes et al. 2002). The intensity of the MeSA scent differs among species in the genus with a weaker odor being found for instance in *P. bicolor* and *P. villosa* and a stronger one in *P. cecropiifolia*, *P. guianensis*, and *P. myrmecophila*. The odor emanates from all parts of the trees. A particularly strong scent not only comes from bark and branches (Gaglioti 2015) but also leaves and fruit harbor a wintergreen aroma (Lopes-Lutz et al. 2010). In the woody liana *Ampelozizyphus amazonicus* (*Rhamnaceae*) from Amazonia, high MeSA content is not only obvious from the interior cortex emitting a MeSA smell but is also reflected in its ethnopharmacological significance (Ducke 1935).

Likewise, some *Betula* species (specifically, of the subgenera *Aspera* and *Acuminata*; Section *Lentae*) produce a high amount of MeSA in their leaves and bark (Ashburner et al. 2013; Singewar et al. 2020b). MeSA synthesized and emitted by birch species may be of significance for interspecies signaling in forest ecosystems. MeSA in the genus *Betula* is discussed in a separate section below.

MeSA appears also to have another role that is rather different from putative functions in defense, namely in pollinator attraction. This is suggested by the observation that in some taxa, MeSA is contained in the bouquet that makes up the floral scent. The Tiaré flower *Gardenia taitensis* (*Rubiaceae*), traditionally used to make perfume and anti-inflammation medicine, contains MeSA (Claude-Lafontaine et al. 1992) and its scent has a note of "wintergreen". Some *Plumeria rubra* (*Apocynaceae*) selections also have that note in their floral bouquet (Goswami and Chauhan 2016). Several orchids, e.g., species of the genera *Catasetum* (Chandra et al. 2014) or *Anguloa* have floral aromas with an "overwhelming scent of oil of wintergreen" (Oakeley 1991,2005), e.g., *A. clowesii*, the Tulip orchid (Seaton 2020). Besides, some fruit, e.g., the pineapple guava *Acca sellowiana* (*Myrtaceae*), have a faint wintergreen aroma (Harrison 1967), which may be hypothesized to be part of an olfactory attractant for frugivorous mutualists involved in the plant's dispersal strategies.

In the process of ripening, various fruits produce MeSA which, as one element in a large suite of compounds, contributes to the flavor (Paul and Pandey 2014; Baldwin et al. 2000; Amoore 1952). A selection of high MeSA-producing taxa are listed in Table 1.

Betula species with high MeSA contents

The genus *Betula* is a major group of trees and shrubs in the *Betulaceae* family. Birches are widely distributed in the Northern Hemisphere (Shaw et al. 2015), especially in temperate and boreal ecosystems. The genus encompasses between 30 and 120 species (Furlow 1990; Koropachinskii 2013; McAllister and Rushforth 2011) and some new species were recently discovered (Jie et al. 2014; McAllister and Rushforth 2011). Hybridization between different *Betula* species gives rise to natural hybrids some of which are considered species by some authors (Koropachinskii 2013; McAllister and Rushforth 2011; Zeng et al. 2008). The rapid growth, comparatively short life cycle, and abundance of seed are typical for pioneer species that play an important role in the regeneration of forests for example after forest fires (Fischer et al. 2002). Within the wide geographical distribution of the genus *Betula*, there are species adapted to various climatic and edaphic conditions (Hemery et al. 2010; Hynynen et al. 2009). Wind pollination helps birches to maintain high genetic variability to survive in a range of

environmental conditions (Yasaka et al. 2009; Aspelmeier and Leuschner 2004). Birch can readily establish on a given site and create ideal conditions for other non-pioneer tree species (Prévosto and Curt 2004; Rosenvald et al. 2014). Thus, birches significantly contribute to the recovery of temperate and boreal forests after disturbances (Dubois et al. 2020). Birch enhances soil porosity and water infiltration improves soil quality and thus contributes to biodiversity (Perala and Alm 1990).

Among trees of relevance to forestry, several American and Asian birch species contain high concentrations of MeSA, which is perceptible upon scratching young twigs (Singewar et al. 2020b). Among the North American species, Sugar birch (*B. lenta*), the rare Virginia round-leaf birch (*B. uber*) (described by some authors as *B. lenta* var. *uber*) and Yellow birch (*B. alleghaniensis*) contain high MeSA levels, as noticeable by the scent of wounded bark (Singewar et al. 2020b). *B. lenta* was historically an important source of *Oleum betulae*, birch oil, or oil of wintergreen, aromatic oil with a high MeSA content. For both *B. lenta* (Gilmore 1933) and *B. alleghaniensis* (Tantaquidgeon 1942), a medicinal use by Native Americans is well documented.

Among the Asian birches, the Japanese species *B. grossa*, *B. corylifolia*, and *B. globispica* have a high MeSA content and accordingly the "wintergreen" smell emanating from young twigs when scratched (Ashburner et al. 2013; Singewar et al. 2020b). The East-Asian species *B. insignis*, the Chinese endemite *B. austrosinensis*, and the Caucasian

Table 1 Genera that were reported to emit high levels of MeSA. There appears to be a predominance of woody and perennial species that produce high MeSA

Genus/species	Family	Plant parts	Plant habit	References
Acca sellowiana	*Myrtaceae*	Fruit	Shrub, tree	Harrison (1967)
Ampelozizyphus amazonicus	*Rhamnaceae*	Bark	Woody liana	Ducke (1935)
Anguloa spp.	*Orchidaceae*	Floral	Perennial	Oakeley (1991), Oakeley (2005) and Seaton (2020)
Betula spp.	*Betulaceae*	Young bark	Tree	Ashburner et al. (2013) and Singewar et al. (2020b)
Catasetum spp.	*Orchidaceae*	Floral	Perennial	Chandra et al. (2014)
Filipendula spp.	*Rosaceae*	Leaves, roots	Perennial	Bijttebier et al. (2016), Joshi (2015), Olennikov (2016) and Pavlovic et al. (2007)
Gardenia taitensis	*Rubiaceae*	Floral	Shrub	Claude-Lafontaine et al. (1992)
Gaultheria spp.	*Ericaceae*	Leaves	Small shrub	Liu et al. (2013) and Joshi and Subedi (2014)
Parkia spp.	*Fabaceae*	Bark	Tree	Hopkins (1986)
Plumeria rubra	*Apocynaceae*	Floral	Shrub, tree	Goswami and Chauhan (2016)
Polygala spp.	*Polygalaceae*	Roots	Perennial and biannual	Pizzolatti et al. (2009)
Pouroma spp.	*Urticaceae*	Ubiquitous, esp. bark	Shrub, tree	Lopes et al. (2002), Gaglioti (2015) and Lopes-Lutz et al. (2010)
Primula spp.	*Primulaceae*	Roots	Perennial herbs	Steinegger and Hänsel (2013) and Wyk and Wink (2018)
Securidaca longepedunculata	*Polygalaceae*	Roots	Tree	Belmain et al. (2001), Jayasekara et al. (2002, 2005) and Nébié et al. (2004)

B. megrelica and *B. medwediewii* also belong to the "wintergreen" birch group characterized by their unmistakable aroma. *B. alnoides,* the alder-leaf birch from South East Asia, and *B. maximowicziana*, the monarch birch from the Caucasus, have lower MeSA contents, but the scent is still perceptible (Dũng et al. 1995; Nath et al. 1991).

The latest phylogenetic evolutionary analysis of birches showed absolute clustering of high MeSA producers, *B. grossa*, *B. alleghaniensis,* and *B. lenta* suggesting their progressive evolutionary relationship (Singewar et al. 2020b). These results were consistent with previous studies that suggest the subgenus *Betulenta* (including *B. grossa*, *B. alleghaniensis*, and *B. lenta*) be among the oldest (Bina et al. 2016; De Jong 1993). Various evolutionary and population studies in the genus *Betula* (Bina et al. 2016; Li et al. 2005; Wang et al. 2016) along with the most recent network analysis (Singewar et al. 2020b) gave rise to the hypothesis that the diploid *B. lenta* is one of the ancestors of the genus *Betula* which constitutively produces high MeSA. This hypothesis is also supported by an earlier network analysis which yielded evidence that *B. lenta* including *B. lenta* var. *uber* forms the oldest clade (Bina et al. 2016). These results suggest that the ancestral ability of high MeSA production was passed on to some of the later evolving *Betula* species, while others lost their MeSA-producing potential (Singewar et al., 2020b; Hughes 2012; Bina et al. 2016).

Several natural or garden-origin hybrids between "wintergreen" birches and sympatric "low MeSA" species of other subgenera have been described. *Betula × purpusii*, is a hybrid between *B. alleghaniensis* and *B. pumila* var. *glandulifera* (Dancik and Barnes 1972) and *B. murrayana* is a back–cross between *B. × purpusii* and *B. alleghaniensis* (Barnes and Dancik 1985). Natural hybrids of *B. alleghaniensis* and *papyrifera* were also described (Barnes et al. 1974). *Betula × jackii* is a hybrid of *B. lenta* and *B. pumila* (Jack 1895), of which different lines display a varying intensity of the scent.

Besides, historical breeding trials produced various hybrids of "high–MeSA" 'wintergreen' birches and "low–MeSA" birches of other subgenera, such as crosses of *B. turkestanica* and *B. alleghaniensis* (Hoch et al., 2002). Hybrids between *B. lenta* and *B. alleghaniensis* are also published (Sharik and Barnes 1971). High-MeSA-producing birches are listed in Table 2.

Candidate genes of MeSA biosynthesis and metabolism in low- and high-MeSA-producing birches

Several studies confirmed that salicylic acid methyltransferase (SAMT) and salicylic acid-binding protein 2 (SABP2) enzymes mediate the biosynthesis of MeSA in many plant

Table 2 *Betula* species reported to contain high levels of MeSA according to Ashburner et al. (2013) and Singewar et al. (2020b)

Betula species	Native range	Plant habit
B. alleghaniensis	North America	Tree
B. alnoides	Southeast Asia	Tree
B. alnoides spp. *luminifera*	Southeast Asia	Tree
B. corylifolia	Japan	Tree
B. austrosinensis/insignis	China	Tree
B. globispica	Japan	Tree
B. grossa	Japan	Tree
B. lenta	North America	Tree
B. lenta var. *uber*	North America	Tree
B. medwediewii	Caucasus	Tree
B. megrelica	Caucasus	Tree, shrub
B. maximowicziana	East Asia, China	Tree

MeSA is present in the young bark of all species listed

species (Chen et al. 2003; Clarke et al. 2000; Effmert et al. 2005; Zhao et al. 2009, 2016) (Fig. 1). The enzymes were functionally characterized through gene expression studies and biochemical analyses in various plant species such as *Vitis vinifera*, *A. thaliana*, *Clarkia breweri*, *N. tabacum,* and *Populus trichocarpa* (Chen et al. 2003; Kumar and Klessig 2003; Ross et al. 1999; Zhao et al. 2008, 2009, 2016). However, very little is known about SAMT and SABP2 at gene and enzyme levels in birches (Singewar et al. 2020a).

MeSA is produced by methylation of SA catalyzed by SAMT, utilizing *S*-adenosyl-L-methionine (SAM) as a cofactor. SAM is the most common methyl donor for methyl transfer reactions (D'Auria et al. 2003; Ross et al. 1999) (Fig. 1). Upregulation of *SAMT* at the infection site increases MeSA synthesis and MeSA is transported to uninfected sites of the plants as a long-distance signaling molecule (Li et al. 2018), prior to being reverted to SA (Forouhar et al. 2005; Li et al. 2018). SABP2, possessing esterase activity, catalyzes the conversion of MeSA to SA by demethylation (Kumar 2014; Park et al. 2007) (Fig. 1). Silencing and overexpression of *SAMT* and *SABP2*, respectively, resulted in lower MeSA levels and a weakened SAR, indicating MeSA synthesis to be mediated by *SAMT* and *SABP2* (Kumar and Klessig 2003; Zhao et al. 2009). One function of MeSA production may be to lower SA concentration to non-cytotoxic levels (Manthe et al. 1992; Vlot et al. 2009).

In a recent study, the *SAMT* and *SABP2* genes were cloned from four high (*B. lenta*, *B. alleghaniensis*, *B. grossa*, and *B. medwediewii*) and four low (*B. utilis*, *B, pendula*, *B. nana,* and *B. alnoides*) MeSA-producing birches (Singewar et al. 2020a). In bark tissues, *B. alleghaniensis* and *B. lenta* showed higher relative expression of *SAMT* than low-MeSA-producing species. The higher expression of *SAMT* in bark tissues of constitutively high-MeSA-producing birches

supports its significance for MeSA synthesis (Singewar et al. 2020a). In contrast, high *SABP2* expression in the bark of low-MeSA-producing species *B. utilis* and *B. pendula*, appears consistent with a high rate of reversion of MeSA to SA, resulting in lower MeSA levels.

Extensive genomic analysis revealed that SAMT and SABP2 enzymes belong to the SABATH and MES families, respectively (D'Auria et al. 2003; Yang et al. 2008). Both families were recently studied in silver birch (*Betula pendula*) (Singewar et al. 2021). Plant SABATH and MES family members catalyze methylation and demethylation of many hormones, signaling molecules, and floral scent metabolites, including SA, JA, and IAA. The name SABATH is an acrostic based on the three genes that were first isolated and characterized; **S**alicylic **a**cid methyltransferase, **B**enzoic **a**cid methyltransferase, and **Th**eobromine synthase (D'Auria et al. 2003). The resulting methyl esters of SA (MeSA), JA (MeJA), and IAA (MeIAA; methyl IAA) are demethylated by methyl esterases (MES) that belong to the α/β hydrolase superfamily.

MeSA in folk medicine, food, and cosmetic industry

MeSA is a major constituent of essential oil extracted from birch bark (Başer and Demirci 2007; Nath et al. 1991; Angmo et al. 2012; Ashburner et al. 2013; Singewar et al. 2020b). It was used as a herbal medicine in various parts of the world (Clark 1999). Indigenous Native American and Canadian First Nation communities used plants with high MeSA content, including birch, for pain relief, antipyretic, and treatment of gastrointestinal ailments (Anderson et al. 2017; Clark 1999). MeSA is frequently used as a fragrance ingredient and for its anti-inflammatory activity for muscle and joint pain and rheumatic conditions (Mason et al. 2004). Similar to North America, various species of "wintergreen" birches have been used in the folk medicine of different cultures in Asia. *B. insignis*, for example, finds use as an antiseptic in Chinese medicine, and *B. alnoides* bark is used in Asia to treat fever, inflammations, and sprains (Quattrocchi 2012).

In Southern Brazil, no less than 19 species of the genus *Polygala* (*Polygalaceae*) are known to be used in folk medicine for topical anesthesia (Pizzolatti et al. 2009; Wurdack and Smith 1971). In Eastern Africa, *Polygala* species are used to treat fever, cough, cold and other ailments (Ajali and Chukwurah 2004). Extracts of *Polygala campestris, P. cyparissias, P. paniculata, P. pulchella,* and *P. sabulosa* showed a strong effect against the opportunistic fungal species *Cryptococcus gattii* (*Filobasidiaceae*) and *Sporothrix schenckii* (*Ophiostomataceae*) (Johann et al. 2011). High MeSA contents appear to be a trait shared by other genera of the *Polygalaceae* (milkwort family). Dried powdered roots of the African violet tree *Securidaca longepedunculata* (*Polygalaceae*) that contain high MeSA levels are used as traditional medicine or for storage pest control (Belmain et al. 2001; Jayasekara et al. 2002, 2005).

Various species of the genus *Gaultheria* have been used in traditional medicines (Joshi and Subedi 2014; Liu et al. 2013; Sievers 1947), and over-the-counter preparations in both Western and Asian medicine and dentistry, e.g., heat ointments and sports massage oils, antiseptic mouthwashes, or toothpaste (Elvin-Lewis 1983). It also found use as a fragrance and flavoring agent, e.g., for chewing gum or soft drinks such as "Birch beer".

MeSA has been commonly used in the postharvest management of fruit since it delays senescence through upregulating the activity of alternative oxidase (AOX) (Valverde et al. 2015). The treatment of freshly harvested sweet peppers, pink tomatoes (Fung et al. 2006), and sweet cherry trees with MeSA was found to reduce free radicals that could damage the cells resulting in fruit spoilage (Valverde et al. 2015). The red color development and ethylene production of tomatoes (*Lycopersicon esculentum*, *Solanaceae*) were delayed when 0.5 mM MeSA was applied to mature green fruit. The treatment lowered transcript levels of *LE-ACS2* and *LE-ACS4,* ACC synthases that are upregulated in response to ethylene and that are linked to fruit ripening (Ding and Wang 2003).

Use of MeSA and MeSA-emitting plants in agriculture and forestry

The anti-microbial and insect-deterring effects mentioned above make MeSA a suitable tool to protect stored seeds from insects, as used for example by applying root bark extracts or powders of the Violet tree *Securidaca longepedunculata* (*Polygalaceae*) in grain storage (Jayasekara et al. 2002).

Kalaivani et al. (2016) found that treatment of rice seeds with MeSA significantly reduced bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae* in the seedlings. Furthermore, they found that treatment also enhanced germination and seedling growth, suggesting an influence on plant hormone metabolisms. An increase in seed germination upon MeSA pretreatment was also observed in different crops including wheat (Dolatabadian et al. 2009), maize (Khodary 2004), barley (Almeida 2012), and pea (McCue et al. 2000). In addition, MeSA has been applied as an artificial spray in various crops to attract beneficial insects (De Boer and Dicke 2004).

Effects observed with the artificial application of MeSA suggest that MeSA emitted by plants may also have comparable effects in the context of their ecosystem. Natural

emissions of volatiles from plants play a role in horticultural "companion planting". The volatile compounds can either overlay and mask the insect-attracting emissions of the actual target plant, attract predators, or possibly act directly as repellents. For example, it was shown that interplanting *Tagetes patula* (Asteraceae) between tomato plants in greenhouses protected against whitefly infestation by limonene emissions (Conboy et al. 2019). In experimental agroforestry systems, similar observations were made using "aromatic" trees. For example, potatoes growing between rows of citrus trees showed less insect damage (Mousa and Ueno 2019).

The use of companion planting in silviculture to manage emissions of volatiles as a protective mechanism is a new concept. Intermediate planting of *Cedrela odorata* and *Azadirachta indica* (both *Meliaceae* and both rich in aromatic compounds), in stands of West African Iroko (*Milicia excelsa*, *Moraceae*) resulted in higher seedling survival rates and a lower infestation with *Phytolyma lata* (Homoptera; Psylidae) (Ugwu et al. 2017).

Emission of MeSA by birch foliage following infestation with harmful insects has been proven (Blande et al. 2010). The effect of the substance may also extend well beyond the immediate crown space of the emitting plant and benefit neighboring individuals of the same and other species.

Jactel et al. (2011) showed that MeSA lowered attractivity of pheromone traps to pine processionary moths in maritime pine (*Pinus pinaster, Pinaceae*) stands suggesting either a repellent function or lowered pest population densities. In *Tortix viridana* larval-feeding experiments with tolerant ("T-oaks") and susceptible oaks ("S-oaks"), HIPV emissions profiles were followed before, during, and after larval feeding for 2.5 days (Ghirardo et al. 2012). Most relevant to larvae feeding, besides mono-, sesqui-, and homoterpenes also MeSA emission was induced. However, no difference could be detected between the S- and T-oaks (Ghirardo et al. 2012). Attack by pine processionary moth (*Thaumetopoea pityocampa*, Thaumetopoeidae) on *P. pinaster* also decreased when the trunks were surrounded by cut birch branches (Jactel et al. 2011)–an effect to which MeSA emission may have contributed. Also, maritime pine *P. pinaster* suffered less infestation by pine processionary moth when associated with birch (*B. pendula*). However, the protective effect weakened over time (Castagneyrol et al. 2020).

The use of birch as an accompanying tree species could therefore be particularly effective in the early phases of forest development. Such use would then correspond to the classical forestry use of birch as a "nurse crop" or "nurse stand" that can be established on open areas to be newly afforested, for example by sowing on snow (Sieber 1929; USFS 1948), prior to the stand of target species. Trees suitable for nurse stands may also be introduced as an element in a temporary mixture to facilitate the establishment of more long-lived tree species that do not grow well on an open field. Today, nurse stands

have virtually disappeared from the management strategies in European forestry. Birches, therefore, are mostly of importance in the natural regeneration of forests and unmanaged stands undergoing natural succession dynamics.

Historically, a change from mixed forests with uneven age structure and different stages of regeneration to even-aged coniferous monocultures must have equaled a significant change in atmospheric chemistry and the bouquet of volatile signaling compounds wafting through the stands. As climate change alters inter-species competition in trees and shifts optimum sites of individual species, volatiles in forests will likely change accordingly, and therefore, changes in the dynamics of pests and pathogens may be observed. Šimpraga et al. (2019) suggest that "Future forestry practices should consider the importance of BVOCs in attraction and repulsion of attacking bark beetles, but also take an advantage of herbivore-induced BVOCs to improve the efficiency of natural enemies of herbivores".

Understanding such processes of change and developing approaches for enhancing resilience requires integrated work that spans from the molecular base of resistance and development to physiological and ecological studies that explore interactions between species.

Future perspectives

Variations in MeSA emission by *Phellinus* strains collected from birch and other woody plants were shown using American birch trees, including the high-MeSA-emitting *B. lenta*. It remains to be investigated whether this early finding (Verrall 1937), which was based solely on the olfactory perceptibility of the substance, can be confirmed with European birches and *Phellinus* strains, as well as with European *Phellinus* strains on *B. lenta* and other wintergreen birches and using modern analytical methods. Various birches have been extensively used to produce MeSA for decades; still, a comprehensive analytical examination is needed to evaluate their MeSA-producing ability. Initial phylogenetic and expression analysis with birches have defined the candidate genes mediating high and low-MeSA production (Singewar et al. 2020a, b). These selected candidate genes could be subjected to further functional studies like targeted mutagenesis and genetic modifications through CRISPR/Cas technology generating gain and loss of function mutants to modify MeSA levels (Kalaivani et al. 2016).

Fieldwork with short rotation copies and MeSA distillation from birches could give rise to the mass production technology of organic MeSA (Fig. 2).

Conclusions

Silvicultural practices that change the bouquet of volatile compounds by altering species composition may offer a way to engineer the complex and dynamic "safety net" made of volatile signaling compounds. Birch species are the only high-MeSA forest trees known to the authors to be hardy in the temperate zone. They are, therefore, promising for starting research in silvicultural systems that make use of volatile emissions and inter-species communication to enhance these managed ecosystems' stability and resilience to pest and pathogen attacks.

It appears likely that MeSA is only one element in highly complex signaling pathways and networks. It is, however, a compound that is not only accessible to research with current analytical methods but also can be modified in forest stands without applying any transgenic methods. Nature offers a suitable tool in high- and low-MeSA birches, and the range of species and hybrids that fall in between. Baldwin et al. (2006) speak of "mute" and "deaf" plants that allow studying the interactions utilizing VOCs. Plants that have especially high natural MeSA emissions and are, therefore, to stay with the simile used by Baldwin et al. (2006), particularly "VOCal", are ideal for such studies.

Further work requires close monitoring of ecosystem dynamics, pathogenesis, and insect populations and, therefore, calls for long-term, multi-disciplinary projects. It requires thorough knowledge of ecosystem dynamics in natural stands of high-MeSA birches in North America and Asia and existing ex situ collections or plantations of such species. Data from forest ecosystems possibly also open perspectives for advanced studies of agricultural intercropping and agroforestry systems.

Understanding the interplay of methylation and demethylation, glucosylation, and deglucosylation in altering and adjusting endogenous pools of MeSA and its active and inactive forms at a molecular level provides a basis for the search for natural high-MeSA–emitting mutants of birches that are in their nominate form low-MeSA producers—and the reverse, low-MeSA mutants of e.g., *B. lenta* and other high MeSA species.

Successful identification of such mutants would allow comparative studies with higher precision. It also allows studies and larger scale experiments in regions where no high MeSA-birch species are native without a need to introduce a non-native tree-crop that possibly alters native forest ecosystems. Such work is a contribution to developing a new silviculture to make forests healthy and stable for an age of climate change and biological globalization.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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