

Multiple functions of inducible plant volatiles

Jarmo K. Holopainen

Department of Ecology and Environmental Science, University of Kuopio, PO Box 1627, FIN-70211 Kuopio, Finland

A considerable amount of the carbon fixed by plants is emitted back into the atmosphere as volatile organic compounds (VOCs). Novel inducible VOCs released from plants after biotic or abiotic stresses temporarily increase total emissions of carbon substantially. As well as having a role in attracting the natural enemies of herbivores, inducible VOCs are also involved in plant-to-plant signalling, pathogen defence and ozone quenching, as well as tropospheric ozone and fine-particle aerosol formation. To relate these diverse observations to active plant defence, a conceptual framework of four functional levels (plant cellular interspace, leaf boundary layer, ecosystem and atmosphere) of inducible VOCs is proposed to aid understanding of the evolutionary role of inducible plant volatiles.

The evolution of plant secondary compounds is often considered to be tightly associated with defence against herbivores and other parasites, but recently it has been proposed that plant chemical defence could be primarily aimed at abiotic stresses, such as photodamage and climate changes [1,2]. Volatile organic compounds (VOCs) emitted by plants show a puzzling diversity. VOCs can form as by-products of plant processes and can be emitted to the atmosphere owing to their volatility with no apparent function [3]. However, as a result of natural selection, some volatile compounds have become signals for plant protection and communication. A specific group of VOCs related to herbivory are called herbivore-induced plant volatiles (HIPV) or 'inducible volatile organic compounds' (IVOCs) and are emitted from plant foliage after herbivore damage [4,5]. There is substantial evidence that these novel compounds act as an indirect plant defence by repelling conspecific herbivores [6,7] or by attracting predators and parasitoids of herbivores [8,9]. However, the scenario that plants started to produce volatiles to attract enemies of herbivores is questionable [10] because it would require a simultaneous change in the plant (to produce) and in predators and parasitoids of the plant (to respond) to these volatiles. Furthermore, HIPV emissions are inducible by ozone (O_3) [11] and fungal pathogens [12]; mould infection might even increase the attraction of parasitoids to herbivore-damaged plants [8]. Do these observations suggest that the attraction of parasitoids is only a secondary event, perhaps a function acquired later in the evolution of these compounds? How

can such diverse biotic and abiotic factors induce the production of similar volatile compounds? What could be the primary function of these compounds in plant evolution? These specific questions will be addressed here by evaluating our current knowledge of IVOCs and their function in different spatial scales. This information is needed to estimate the potential environmental effects of genetically engineered plants that have enhanced IVOC production capacity [13].

Inducible volatile organic compounds

The difference between constitutive and inducible VOCs is ambiguous. Most of the constitutive VOCs normally released from healthy intact plants become inducible volatiles (IVOCs) after foliar damage, which is when these compounds are produced in larger quantities or in different ratios [5,14,15]. In contrast to the constitutive VOCs, novel compounds are produced only by damaged plants after induction. The advantage of novel IVOCs is that they are *de novo* synthesized only when needed and therefore they are more economical in terms of carbon usage and do not reduce plant fitness [9]. There is a broad diversity of known IVOCs, including alkenes, alkanes, carboxylic acids and alcohols, but the dominating compounds tend to be terpenes and C6 green leaf volatiles (GLVs) [15] (Box 1). IVOCs can be split into two classes of compounds. One class of compounds is released from mechanically damaged leaves immediately (0–5 min) after damage (GLVs) [16]; a second class of novel compounds (mainly terpenes) is synthesized after damage but only released a few hours after the initial damage took place. The compounds are released from damaged and undamaged leaves of the wounded plants.

GLV emissions from damaged plant organs can occur as a result of mechanical tissue damage independently of any influence from biotic organisms [16]. In response to the damage, some GLVs such as (*Z*)-3-hexenyl acetate are also released from younger intact leaves of herbivore-damaged plants, indicating that the lipoxygenase (LOX) pathway, which oxidizes catabolic products of fatty acids, has been activated [17]. Most of the GLVs are not specific to any plant taxon. Some of these compounds elicit the production of jasmonic acid and the emission of novel homo- and sesquiterpenes in intact receiver plants as well as the behavioural response of parasitoids of herbivores [18].

Monoterpene-storing species have a special structure for storing, but non-storing species synthesize and emit these compounds in a light and temperature-dependent

Corresponding author: Jarmo K. Holopainen (jarmo.holopainen@uku.fi).

Box 1. Main inducible volatile compounds emitted by plants

Green leaf volatiles

C6 compounds produced via the lipoxygenase (LOX) pathway, called green leaf volatiles (GLVs), can account for >50% of the emissions from damaged plant parts. Chemically, GLVs are mostly saturated or monounsaturated aldehydes, alcohols and esters, and they can have different configurational isomers with different sensory properties [48]. GLVs are typically released only from damaged plant organelles within 1–2 s of the mechanical damage occurring [16], but some GLVs are released from younger undamaged leaves of herbivore-damaged plants, indicating that the LOX pathway can be activated in intact leaves.

Terpenes

The biological precursors to terpenoids are isopentenyl pyrophosphate (IPP) and its isomer dimethylallyl pyrophosphate (DMAPP). C5 isoprene (2-methyl-1,3-butadiene) is a hemiterpene synthesized from DMAPP. It is the simplest terpenoid emitted by plants. There are two biosynthetic routes to IPP, the precursor of terpenoids, the classical mevalonic acid (MVA) pathway in the cytosol and the methylerythritol (MEP) pathway in plastids [17]. It is proposed that C10 precursors of monoterpenes are predominantly synthesized within plastids by the MEP pathway, whereas precursors of sesquiterpenes are produced via the classical MVA pathway. However, there is evidence that a small amount of cross-talk between the two pathways might occur, implying that the pathways are not completely autonomous [17].

Highly volatile monoterpene molecules (C10) have two isoprene units. These compounds are stored in specific structures. However, some of the monoterpenes, for example, oxygenated compounds such as linalool are *de novo* synthesized after herbivore damage and released systemically from the whole plant.

Sesquiterpenes (C15) have three isoprene units and they are typical flower fragrances [19], but considerable amounts of sesquiterpenes are emitted from the herbivore-damaged foliage of plants. Among the most typical inducible sesquiterpenes emitted by herbivore-damaged plants are β -caryophyllene and α -farnesene.

Homoterpenes, acyclic C11 homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and C16 homoterpene (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMNT) are the most typical compounds related to herbivore feeding. In herbivore-damaged plants, biosynthesis of DMNT proceeds via the conversion of sesquiterpene alcohol, (*E*)-nerolidol from farnesyl diphosphate, the universal precursor of sesquiterpenes [49].

way. Monoterpenes form nearly 100% of the total VOC emissions from intact cabbage plants, whereas in herbivore-damaged plants, total monoterpene emission increases but the relative proportion drops below 60% because of novel induced compounds such as homoterpenes and sesquiterpenes [5].

Sesquiterpenes are emitted from flowers [19]. However, considerable amounts of sesquiterpenes can also be emitted from the foliage of herbivore-damaged plants [5], whereas in intact plants the concentrations emitted are lower [14]. High levels of sesquiterpene are produced in O₃-resistant tobacco immediately after O₃ exposure; in O₃-sensitive tobacco, sesquiterpene emissions peak the following day [20]. Compared with, for example, monoterpenes [21], sesquiterpenes are highly reactive with atmospheric O₃ and are often completely reacted in the atmosphere before their detection for analysis [22]. Homoterpenes (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMNT) are among the most typical compounds emitted after herbivore feeding as well as from O₃-damaged plants [11].

Functional levels of IVOCs

The plant physiological and atmospheric functions proposed by Manuel T. Lerdau and Lawrence B. Slobodkin [23] for all biogenic VOCs are more distinctive among IVOCs, which are highly reactive with O₃ and OH⁻ radicals [21] and have several functions in intra- and interspecific communication. The four functional levels proposed and the potential progress of IVOCs is summarized in Figure 1.

Plant tissue level

The production of the volatile plant hormone ethylene is associated with herbivore [24] and O₃ damage [25] in plants. If ethylene perception is chemically blocked, O₃-induced cellular damage in plant leaves increases [26]. Ethylene seems to have a role as a switch by reducing the production of constitutive defence compounds such as nicotine after herbivore damage and stimulating the production of jasmonic acid and IVOCs [23].

Jasmonic acid, methyl jasmonate (MeJA) and GLVs are oxidation products derived from the catabolism of fatty acids. They are released from damaged plant tissue immediately after biotic and abiotic stress [16]. Pre-treating an O₃-sensitive *Arabidopsis* ecotype with MeJA decreased O₃-induced H₂O₂ content and salicylic acid concentrations and completely abolished O₃-induced cell death. Furthermore, jasmonic acid-deficient *Arabidopsis* mutants are sensitive to O₃ [26]. These results suggest that O₃ resistance in plants is linked to jasmonic acid-induced pathways and the possible production of several IVOCs that quench O₃. Isoprene [27] and some monoterpenes [28] quench ozone and reduce reactive oxygen species (ROS) such as hydrogen peroxide (H₂O₂) and hydroxyl anions (OH⁻) in cellular interspaces of plants. At the cellular and tissue level, IVOCs might have a similar antioxidant role.

Analogously to O₃ resistance, direct and indirect anti-herbivore plant defence is dependent on the jasmonic acid pathway. Herbivore-damaged wild-type *Arabidopsis* plants induce a greater production of IVOCs (primarily the sesquiterpene β -caryophyllene and the monoterpenes) than do damaged jasmonate-deficient plants [29], whereas in jasmonate-deficient plants treated with exogenous jasmonic acid both the direct and indirect defence capabilities are restored. Furthermore, an *Arabidopsis* mutant with decreased sensitivity to MeJA is unable to attract parasitoids after damage by leaf-chewers [30].

Plant surface level

The leaf boundary layer is ~5 mm thick – the microclimate here is more humid than in the air surrounding the plant and the many small herbivores and fungal hyphae on the plant surface can be kept under surveillance [31]. Plant pathogens [8,32] induce the production of IVOC, which because of their antimicrobial activities probably inhibit the spread of the pathogen into plant tissues. In addition, tomato mutants deficient in the biosynthesis of the octadecanoid pathway are highly susceptible to small leaf-feeding mites and thrips whereas MeJA treatment restores resistance [33].

Leaf boundary layer thickness is dependent on laminar and turbulent air flows as well as on leaf size and

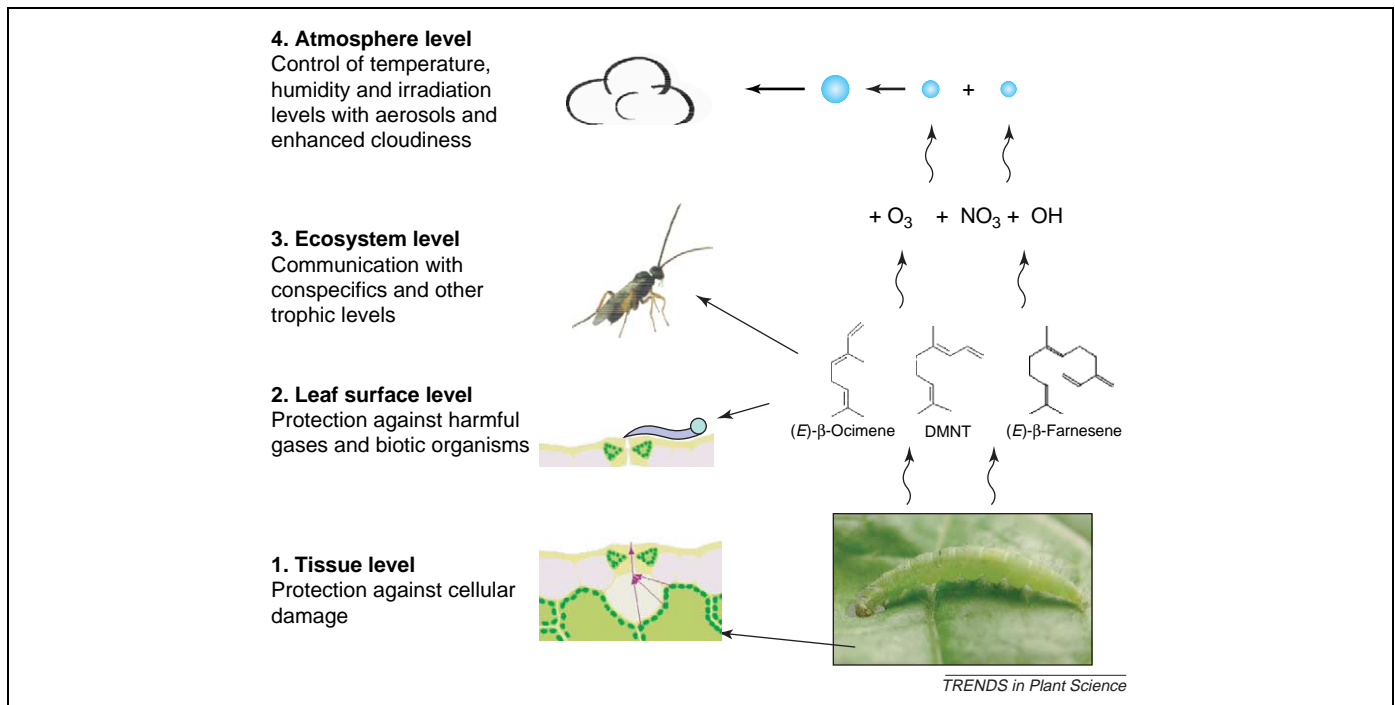


Figure 1. A model of four functional levels of phytogetic, inducible volatile organic compounds (IVOCs). (Level 1) In leaf cellular interspace, monoterpenes and IVOCs act as internal antioxidants against oxidative stress induced by ozone [28] and herbivory [50]. (Level 2) On the leaf boundary layer, IVOCs depress growth of plant pathogens and deter feeding of herbivores [7]. (Level 3) Ecological interactions of phytogetic IVOCs are diverse, including attracting natural enemies of herbivores [4,47], inducing IVOC production in nearby intact plants [37] and repelling female insects from laying eggs on plants where eggs were laid earlier by the same species [6]. (Level 4) Atmospheric reactions of IVOCs with air pollutants induce novel fine-particle formation leading to growth of aerosol particles by clustering of smaller particles and development of cloud condensation nuclei [42]. The image of the stomatal cavity is adapted from Ref. [34].

structure. The concentration of monoterpenes is probably high in the leaf boundary layer because of emissions through the cuticle even when stomata are closed [34]. Isoprene [27] and monoterpene [28] emissions quench O_3 within the leaves or in the leaf boundary layer and reduce oxidative stress caused by O_3 , particularly in a humid atmosphere. When monoterpene synthesis is blocked, reactive oxygen species such as hydrogen peroxide (H_2O_2) rapidly accumulate in the foliage [28].

Many less volatile monoterpenes and sesquiterpenes are more reactive with ozone than with isoprene in the atmosphere [21,22]. In some plant species, induced production of monoterpenes [11,20,28], sesquiterpenes [20] and homoterpenes DMNT [11] starts after exposure to high concentrations of O_3 . The advantage of O_3 quenching outside the tissue could be a reduction in the level of phytotoxic organic peroxide formation [28] in the liquid phase of the plant apoplast in O_3 -exposed plants. Many of the IVOCs are compounds that are released from flowers. It has been suggested [19] that the floral volatiles of self-pollinating *Arabidopsis* could also play a variety of other roles. One role could be to protect the reproductive organs and their valuable germ line cells from pathogens or oxidative damage caused by O_3 instead of, or in addition to, attracting pollinators.

Ecosystem level

The most thoroughly investigated aspect of IVOCs is their induction by herbivore damage and their role as semiochemicals for natural enemies of herbivores [9]. The components such as volicitin in saliva and regurgitates [35] of insects are the inductors of the IVOC, whereas

ethylene is a volatile plant hormone [24] in herbivore-damaged plants that stimulates the production of IVOCs. The direct response of predators and parasitoids to ethylene is poorly understood. However, herbivores induce specific IVOC emission profiles and these signatures are used by natural enemies of herbivores as signals to distinguish between herbivores and to recognize the host species [9].

Communication between damaged plants and conspecific and heterospecific plants using emissions of IVOCs is a well-known phenomenon when using charcoal-filtered air in laboratory experiments [36] but observations of this kind in nature are limited [4]. Under laboratory conditions, IVOCs released after herbivore damage induce the production of IVOCs in nearby healthy plants [37] or activate genes responsible for the production of these compounds [36]. To date, the IVOC receptors in receiver plants have not been identified [37]. Plant-to-plant signalling in the field might fail over distances > 10 cm [38], although signals attracting predators and parasitoids are known to occur over distances greater than 10 cm in nature. *Nicotiana attenuata* plants [4] growing in the desert and treated with elicitors are able to reduce herbivore damage by 90% by attracting predators when the plants are grown 3–5 m apart, but herbivore damage is reduced by only ~20% when the plants are grown > 20 m apart.

The IVOC signals of individual plants might become less attractive to parasitoids and predators beyond a few meters from the plant because the gases are diluted or because the chemicals degrade in chemical reactions with atmospheric contaminants [21]. Therefore, analysing the

atmospheric reactions of IVOCs will be important to understanding how different air pollutants might disturb their signalling role. However, IVOC molecules that have only a short lifetime in the atmosphere might guide parasitoids and predators more efficiently towards damaged plants than more stable molecules that persist in the atmosphere even after the death of the herbivores.

Atmospheric level

About 80% of plant-emitted VOCs are chemically reactive and therefore can regulate the oxidative capacity of the troposphere as well as carbon monoxide, O₃ and aerosol budgets [2]. Total VOC emission from herbivore-damaged plants can be nearly 2.5-fold higher than emissions from intact plants [5]. This observation suggests that local herbivore-induced VOCs might have substantial role in tropospheric processes.

In sunlight, together with the high concentration of nitrogen oxides from urban sources, some IVOCs can participate in forming phytotoxic O₃, particularly in urban areas. The highest peaks of O₃ concentrations are in rural areas close to urban centres as a drift, whereas in urban areas reversible atmospheric processes will destroy O₃ formed during sunshine hours [39]. Although O₃ phytotoxicity is a disadvantage for plants, the precipitation of nitrogen [40] during O₃ formation could compensate for the cost of O₃-induced tissue damage. By contrast, when NO_x levels are low, oxidation of VOCs removes O₃ from the troposphere [40] and produces novel aerosol particles [22].

During atmospheric processes the balance between OH radicals, O₃ and plant-emitted terpenes varies. Boris Bonn and Geert Moortgat [22] proposed that the low-volatile sesquiterpenes emitted from plants are probably mainly responsible for the reactions between VOCs and O₃ and for fine-particle aerosol formation in remote areas. Aerosols are an effective protection against excessive UV-B radiation [41], although the aerosol formation processes related to VOC emissions are still poorly understood in nature [42]. There is some evidence that plants might actively promote aerosol formation to reduce UV-B radiation because monoterpene emission from vegetation increases under enhanced UV-B radiation [43] and also LOX genes related to jasmonic acid and GLV production are activated in plants grown at elevated UV-B radiation [44].



Evolution of IVOCs

It seems that inducible VOC emissions are typically emitted from plants of younger plant clades such as angiosperms that have not faced the harsh growth conditions of pioneering terrestrial plants. Among early land plants, such as mosses and ferns, constitutive isoprene emissions are typical. Gymnosperms such as conifers store and emit high concentrations of monoterpenes, which might be evidence of the use of VOC compounds as exogenous protection against ozone [27,28] in these old plant clades. Protection against harmful UV-B radiation has been a strong selective force in the evolution of terrestrial plants [45]. Oxygen was released to the atmosphere from the seas of the Cambrian and Ordovician periods (590–438 million years ago) by photosynthesizing

cyanobacteria and green algae. The oxygen concentration in the atmosphere reached ~2% 410 million years ago, which is estimated to be a sufficient concentration of oxygen [46] to start filtering out UV rays by gradually forming an ozone layer. This created less hostile environments for the first pioneering terrestrial plants [45]. Unfortunately, we do not know what concentration of ozone the early terrestrial plants faced and how important ozone resistance was as a selective force in early terrestrial plant evolution.

Conclusions and future prospects

It is still open to debate whether IVOCs are just by-products of various plant processes [3] or if they are actively produced and used as a sophisticated 'language' by plants to have a dialogue with other organisms [37]. The high diversity of IVOCs activated by various biotic and abiotic inducers suggests that plants are capable of disseminating information to their environment by using IVOCs and that plants can actively change the growth conditions using reactive IVOCs. Engineered or mutant plants with altered rates of IVOC emission and composition [13] will be the tools of the future to increase our understanding of the ecological impacts of IVOCs. However, breeding crop plants with higher IVOC emissions to attract natural enemies of herbivores [13] is an approach that must be used cautiously to avoid negative effects on plant growth and on local air quality as a result of aerosol formation. With the current trend of rising CO₂ and O₃ levels in the atmosphere, elevated IVOC signals might become a less efficient way of attracting natural enemies [47]. Finally, non-destructive metabolic profiling of IVOC emissions using modern mass-spectrometry [16] is a promising tool for quickly detecting the physiological status [35] of crop plants as well as for identifying the initial phase of pathogen and herbivore infections.

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