BIOLOGIA PLANTARUM 44 (4): 481-487, 2001

REVIEW

The complexity of factors driving volatile organic compound emissions by plants

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Abstract

The emissions of volatile organic compounds, VOC, from plants have strong relevance for plant physiology, plant ecology, and atmospheric chemistry. We report here on the current knowledge of the many internal (genetic and biochemical) and external (abiotic – temperature, light, water availability, wind, ozone, and biotic – animal, plant and microorganisms interactions) factors that control emission rates of different VOC by altering their synthesis, vapour pressure or diffusion to the atmosphere. The complex net of these factors, their interactions and the different responses of the different VOC produces the large qualitative and quantitative, spatial and temporal variability of emissions and the frequent deviations from current standard emission models. The need for a co-operative multidisciplinary multiscale research to disentangle this complex and important issue of plant VOC emissions is reminded.

Additional key words: controlling factors, biogenic emissions, isoprene, terpenoids, VOC.

Physiological, ecological and atmospheric importance of plant VOC emissions

A great amount of the volatile organic compounds (VOC) in the atmosphere comes from plants (Lerdau *et al.* 1997, Seufert 1997) showing that the composition of the Earth's atmosphere is largely a product of biological activity. VOC are very diverse, including isoprene, terpenes, alkanes, alkenes, alcohols, esters, carbonyls or acids. The major classes, their estimated emission rates, their reactivities and their atmospheric concentrations are summarised in Table 1.

VOC are produced in many different plant tissues and in diverse physiological processes. Some of them (*e.g.* methyl salicylate, hexenal or terpenes) may act as defence compounds against pathogens and herbivores, and others (*e.g.* methyl jasmonate, alkenes, (E)-3-hexen-1-ol or terpenes) as signals between different parts of the same plant, between plants, and between plants and animals and micro-organisms (Farmer and Ryan 1990, Langenheim 1994, Peñuelas *et al.* 1995, Lerdau *et al.* 1997, Shulaev *et al.* 1997). Other potential functions of VOC such as isoprene and terpenes are the stabilisation and protection of plant membranes against high temperatures or the alteration of flowering in nearby plants (Tingey *et al.* 1991, Sharkey and Singsaas 1995, Terry *et al.* 1995, Loreto *et al.* 1998). Terpenes may also be involved in vegetation fire development (Owens *et al.* 1998).

Biogenic VOC substantially contribute to the hydrocarbon load on the atmosphere, and significantly affect atmospheric chemistry and climate, through ozone and aerosol formation, methane oxidation or the carbon monoxide budget (Chameides *et al.* 1988, Guenther *et al.* 1995, Andreae and Crutzen 1997, Lerdau *et al.* 1997, Kavouras *et al.* 1998, 1999).

Received 7 December 2000, *accepted* 12 March 2001.
Acknowledgements: Supported by grant CLI99-0479 and REN-2000-0278/CLI from the CICYT (Spain), grant IMMPACTE from the DURSI and DMA (Generalitat de Catalunya), and a grant from Fundació Territori i Paisatge (Caixa de Catalunya). We thank I. Filella, F. Lloret, F. Rodà, and J. Terradas for comments on the manuscript.
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Table 1. The major categories of volatile organic compounds emitted by plants. Data are derived from Guenther *et al.* (1995), and from the reviews of Bonsang and Boissard (1999), Kesselmeier and Staud (1999) and Fall (1999).

Species	Annual global emission [Tg C]	Atmospheric lifetime [h]	Atmospheric concentrations	Example
Isoprene	175-503	4.8	pmol mol^{-1} to several nmol mol^{-1}	
Monoterpenes	127-480	2.4-4.8	pmol mol^{-1} to several nmol mol^{-1}	α-pinene, β-pinene, limonene
Other reactive VOC	~260	< 24	1-3 nmol mol^{-1}	2-methyl-3-buten-2-ol, hexenal, acetaldehyde
Other less reactive VOC	~260	>24	2-30 nmol mol^{-1}	methanol, ethanol, formic acid, acetic acid, acetone
Ethylene	1-20	45.6	pmol mol^{-1} to several nmol mol^{-1}	

Emission rates and controlling factors

Measurements conducted during the last two decades at the leaf and branch levels with enclosure techniques, and more recent measurements at the canopy level with micrometeorological methods such as eddy covariance, flux-gradient and relaxed eddy-accumulation, and at the landscape and regional levels with aircraft-borne techniques (Guenther *et al.* 1996, Valentini *et al.* 1997, Greenberg *et al.* 1999) have provided important advances in quantification of biogenic VOC emissions under different environmental conditions. Total VOC emission rates are very variable in time and space and among species; usually ranging from 0 up to *ca.* 100 $\mu g\ g^{-1}\ h^{-1}$ (Kesselmeier and Staudt 1999), which is intriguing because they may represent a significant portion of carbon fixed by a plant, from 0 to 8 % or even more under stressful conditions (Monson and Fall 1989, Staudt and Bertin 1998, Peñuelas and Llusià 1999, Llusià and Peñuelas 2000). The global annual emission rate is roughly estimated to range between 800 and 1500 Tg C (Table 1).

The large quantitative and qualitative, temporal and spatial variability of biogenic VOC emission rates and the consequent inaccuracy of their global estimation are due to the great complexity of controlling factors, which also hinders the understanding of their biological function. This complexity increases at the landscape and regional levels, especially in regions with very diverse vegetation. Recently, good success is being achieved in understanding these controlling factors of emission, especially for isoprene and terpenes, which represent the major share (> 50 % of the total, Guenther *et al.* 1995, Kesselmeier and Staudt 1999) and are the most intensively studied groups of biogenic VOC. There is much less information on the other biogenic VOC because many of them have been identified only recently thanks to new techniques overcoming problems of sampling and analysis.

Emissions essentially result from diffusion of VOC along a vapour pressure gradient from cellular compartments of relatively high concentrations to the air surrounding the leaf, where there are relatively low concentrations as a consequence of the extreme reactivity and brief lifetime of most VOC (Fall 1999). Emissions will thus be controlled by VOC volatilities and those internal (genetic and biochemical) and external (abiotic and biotic) factors that alter, at long or short term, *1*) plant VOC concentration, *2*) VOC vapour pressure or *3*) the resistance to VOC diffusion to the atmosphere.

Genetics and biochemistry

Knowledge of internal genetic and biochemical factors is improving especially for isoprene, monoterpenes, ethylene, C_6 aldehydes and C_6 alcohols, acetaldehyde and ethanol (Fall 1999). Isoprene emitting species exist among bryophytes, ferns, conifers and angiosperms (one third of the 122 families examined) (Harley *et al.* 1999). There is production of terpenes in most plant families (Hatanaka 1993, Lerdau *et al.* 1997), and of C_6 aldehydes and C_6 alcohols. Detailed biochemistry of production of these VOC is increasingly being elucidated. For example, recently the enzymes involved on isoprene synthesis have been localised both in the stroma and at the thylakoids, with important implications for its function (Wildermuth and Fall 1998). Also recently ^{13}C-labelling evidence has indicated that the isoprene and terpene precursor isopentenyl pyrophosphate may also be produced *via* another pathway in higher-plant chloroplasts and independent of mevalonate (Zeidler *et al.* 1997). This pathway originated from pyruvate is also known as the Rohmer pathway (Rohmer *et al.* 1993, 1996). The metabolisms of other VOC such as methanol, formic acid and acetic acid or methyl butenol are less known. In any case, it is clear that genetics strongly determines VOC production, making emission highly species-specific (Guenther *et al.* 1995, Kesselmeier and Staudt 1999) or even ecotype-specific as a consequence of species evolutionary differences in different regions (Peñuelas and Llusià 1999a). A recent overview on emission rates for the different VOC and for the different species can be found in Kesselmeier and Staud (1999).

Storing and non-storing species

VOC are produced throughout different plant structures and cellular compartments, which is relevant for VOC emissions because of the different influences on diffusive processes. However, for many VOC apart from isoprene and some monoterpenes, the diffusion coefficients through cell membrane, cell walls, leaf air spaces, cuticles or stomata are not well known. Moreover, there is an additional complexity in the control of VOC emissions. It comes from the fact that once produced, these VOC may be stored or not in specialised structures depending on the compounds and on the species. For example, terpenes are stored in the glandular trichomes of mints or the resin ducts of pines, and their total concentration often ranges between 1 and 3 % of dry mass, but in some cases it can reach up to 15 - 20 % (Farmer and Ryan 1990, Langenheim 1994, Peñuelas *et al.* 1995, Shulaev *et al.* 1997). The stored quantity may depend more on species genetic traits than on environmental conditions altering the carbon source-sink balance (Peñuelas and Estiarte 1998). Interestingly, it has been discovered during this decade that there are plant species such as the Mediterranean tree *Quercus ilex* that produce and emit monoterpenes without significantly storing them (Pio *et al.* 1993, Stauld and Seufert 1995, Loreto *et al.* 1996, Peñuelas and Llusià 1999a,b, Llusià and Peñuelas 2000). The storage or absence of storage, apart from affecting the concentration and vapour pressure, importantly affects the diffusive resistance for VOC species. This resistance depends primarily on leaf anatomy: it is larger in internal pools such as resin ducts than in external structures such as glandular trichomes. It is, of course, smaller in non-storing species. Very often, however, both storing and non-storing species present a similar range of emission rates, with maxima in spring-summer under high temperatures and irradiances (Peñuelas and Llusià 1999a, Llusià and Peñuelas 2000). Precisely, temperature and light are the best described external factors responsible for a primary control over most VOC emissions.

Temperature and light

Temperature increases the emission rates of most VOC exponentially up to an optimum by enhancing the synthesis enzymatic activities, raising the VOC vapour pressure, and decreasing the resistance of emission pathway (Tingey *et al.* 1991, Loreto *et al.* 1996). Even for non-stored VOC such as α-pinene in *Quercus ilex*, emission has been found to increase three times when temperature raises from 20 to 30 °C (Loreto *et al.* 1996). However, there are differences in the response depending on the compound volatility and biochemistry. Terpenes with high volatility seem to be more responsive to ambient temperatures than less volatile ones (Peñuelas and Llusià 1999a, Llusià and Peñuelas 2000). Moreover, there are acyclic terpenes such as cis-β-ocimene whose emission might be more light dependent and temperature independent than for most other terpenes (Kesselmeier *et al.* 1997, Loreto *et al.* 1998).

Irradiance influences long term VOC pool size by providing biosynthetic energy, regulating the synthesis and controlling growth (Tingey *et al.* 1991, Langenheim 1994). Moreover, irradiance influences on a short time scale of minutes and hours the emissions of non-stored VOC such as terpenes that need photosynthetic products for their biosynthesis (Kesselmeier *et al.* 1996, Loreto *et al.* 1996, Bertin *et al.* 1997, Peñuelas and Llusià 1999a,b, Llusià and Peñuelas 2000). On the contrary, usually there is not such instantaneous light influence on terpene emissions in the case of terpene-storing species (Peñuelas and Llusià 1999b, Llusià and Peñuelas 2000) (Fig. 1), even though a part of the emission may be derived from recently synthesised terpenes (Kesselmeier and Staudt 1999). Again, different compounds present slightly different emission responses: *e.g.* the least volatile terpenes seem more responsive to irradiance and photosynthetic rates than the most volatile terpenes (Peñuelas and Llusià 1999a, Llusià and Peñuelas 2000). Other nonterpenoid VOC such as some oxygenated compounds also show a light-triggered emission (Kesselmeier *et al.* 1997, Harley *et al.* 1998, Staudt *et al.* 1999).

Other abiotic and biotic factors

Current standard modelling of most VOC emissions is based on the genetically determined species-specific emission factors and on these two external environmental factors, temperature and light (Guenther *et al.* 1995).

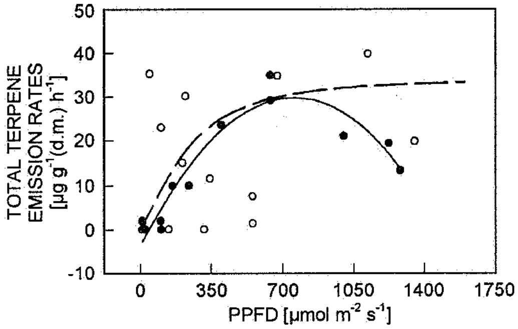

Fig. 1. Total terpene emission rates in a storing (*empty circles*, *Pinus halepensis*) and a non-storing (*full circles*, *Quercus ilex*) species as a function of photosynthetic photon flux density (PPFD) in Mediterranean hot and dry summer field conditions (data are from Peñuelas and Llusià 1999b). There was no relationship for the storing species, whose emissions were temperature-dependent, whereas the non-storing species presented a relationship that did not follow the response expected by standard models (Guenther *et al.* 1995) (*dashed line*). Emissions started to decrease at highest PPFD when net photosynthetic rates and stomatal conductance decreased under summer drought (*continuous line*).

However, emissions are very variable and their short-term, diurnal and seasonal responses have often been found to deviate from the standard light and temperature algorithms (Sharkey *et al.* 1996, Guenther *et al.* 1995, Staudt and Bertin 1998, Harley *et al.* 1999, Peñuelas and Llusià 1999b) (Fig. 1), which were mainly developed for shade-grown greenhouse temperate plants. Recent studies have shown that these standard algorithms can significantly underestimate the isoprene emissions under the high light and high temperature conditions that experience the sun leaves from tropical and temperate forests (Sharkey *et al.* 1996, Harley *et al.* 1997, Keller and Lerdau 1999). These algorithms can instead largely overestimate terpene emissions under the dry conditions of the Mediterranean summer (Staudt and Bertin 1998, Llusià and Peñuelas 2000, Peñuelas and Llusià 1999b). Under these conditions, there are significant reductions in emissions (Bertin and Staudt 1996, Llusià and Peñuelas 1998, 2000). They seem to be linked to water limitation generating a lack of carbon substrate and ATP, and stomatal closing, and to low relative humidities decreasing the permeability of the cuticle to gas exchange (Tingey *et al.* 1991, Bertin and Staudt 1996, Llusià and Peñuelas 1998, Llusià and Peñuelas 1999). Moreover, other seasonal and phenological factors such as budding, leaf development, flowering, fruiting or senescence also generate deviations from the standard light and temperature algorithms (Tingey *et al.* 1991, Llusià and Peñuelas 2000, Peñuelas and Llusià 1999a). They entail changes in VOC concentrations and composition and in permeability of the cuticle, and therefore alter VOC vapour pressure and cuticle diffusive resistance.

The complexity of factors deviating emissions from standard algorithms does not stop with high PPFD, high temperature, water availability, developmental stage or phenology. Physical disturbance by wind, rain, hail or harvesting induces production of VOC in tissues in proximity to the wound site, disrupts storing structures allowing direct volatilisation of stored VOC, and leads to long-lasting increased emission (Tingey *et al.* 1991). Wind also facilitates emission by decreasing diffusive resistance. And there is another factor that could be added to this long list. Ozone, which is a VOC atmospheric secondary product when NO_x are present, and similarly to other stressor factors, could itself favour VOC emission in response to the stress and injury it produces. Recent results of fumigation experiments in open top chambers have shown an order of magnitude increase in emission of VOC by tomato plants when ozone concentrations were increased by 40 nmol mol^{-1} (Peñuelas *et al.* 1999). Although other results show different responses depending on the species or the conditions (Lindskog and Potter 1995, Peñuelas *et al.* 1999, Heiden *et al.* 1999), this phenomenon deserves further investigation because if several other species respond similarly as tomatoes, there would be a positive feedback on tropospheric ozone formation.

Biotic external factors also determine VOC emissions. Certain intra- and inter-specific neighbour interference in terpene emission between plant species such as pines and holm oak has recently been described (emission rates increased when the neighbour was a pine), but this exciting issue also needs further study and confirmation (Peñuelas and Llusià 1998). There is much more evidence for the production and emission of VOC as a result of plant interactions with animals and other organisms. Many of these compounds possess a defence capacity by acting as direct chemical weapons or feeding deterrents, but there are also others that attract pollinators (Harborne 1987, Farmer and Ryan 1990, Bergström 1991, Langenheim 1994, Peñuelas *et al.* 1995, Shulaev *et al.* 1997). Other VOC are emitted during phytophagous attack to attract and recruit the herbivore natural enemies, predators and parasites (Dicke *et al.* 1990, Turlings *et al.* 1990, Turlings and Tumlinson 1992, Bruin *et al.* 1995). Moreover, not only the infested leaves but the whole plants, and even neighbour non-infested plants, seem to emit VOC as signals in response to phytophagous attack (Dicke *et al.* 1990, Turlings *et al.* 1990, Turlings and Tumlinson 1992, Bruin *et al.* 1995). Phytopathogenic attacks can also have multiple short- and long-term impacts on VOC emission by plants that have been reviewed by Gershenson and Croteau (1991), Langenheim (1994) and Kesselmeier and Staudt (1999), among others. They emphasize the defensive role attributed to VOC emission. The ecological importance of these biotically-driven emissions is evident, but the evaluation and modelling of their importance for tropospheric VOC fluxes is even more difficult than for most of the above mentioned abiotic factors, since these herbivore and pathogenic attacks may be rather localised or temporary. Moreover, the emission rates of some of these defensive and signalling compounds such as methyl jasmonate (Farmer and Ryan 1990) seem too low to play an important role in the chemistry of the atmosphere (Lerdau *et al.* 1997).

Concluding remarks

Since the action of most of the abiotic and biotic factors remains to be wholly elucidated, since they have different effects on different VOC, and since most of them covary and are intimately related in a complex net of interactions (Fig. 2), it is still difficult to evaluate their relative importance and to correctly incorporate them in improved algorithms that accurately model the large variability of biogenic VOC emissions. With these aims, and also to improve measurement techniques and knowledge of biological functions, further co-operative studies of biologists, chemists, physicists, ecologists and modellers are needed. These studies should include models and actual VOC emission measurements, accompanied by simultaneous genetic, physiological (*e.g.* photosynthetic rates, water relations), ecological (*e.g.* herbivores) and physico-chemical (meteorology, O_3 and atmospheric chemistry) measurements not only in temperate regions but also in less studied regions such as the tropical or the arid ones. Their approach should be multidisciplinary and integrate the several processes and scales of VOC emissions: from genes and metabolic pathways, across cells, tissues and canopies, to landscapes, regions and the whole biosphere. The fruits would be greatly worthy for plant physiology, plant ecology and atmospheric chemistry. They would give light to the very important and still mostly enigmatic VOC emission by plants.

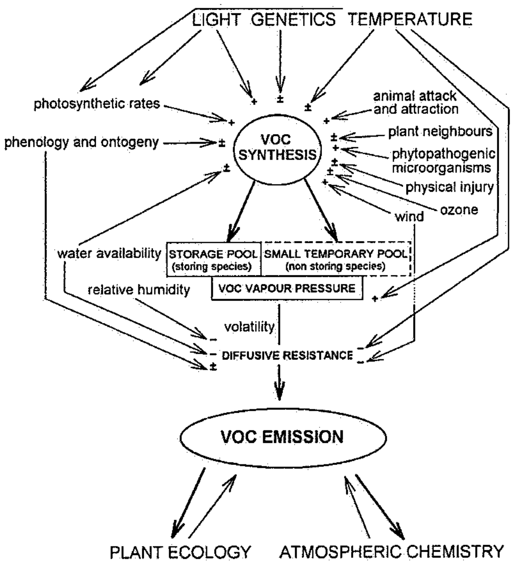

Fig. 2. Net of factors controlling VOC emissions by plants. The main steps of VOC production and emission and the major and best known controlling factors used in current standard modelling (Guenther *et al.* 1995) are depicted in bold type. The other factors have less known, more temporary, more local or lower effects, and are not implemented in current standard algorithms. The resulting complex net of interactions explains the large spatial and temporal variability of biogenic VOC emissions measured in the field and the short-term, diurnal and seasonal deviations from current standard algorithms (+ enhancing effect, - decreasing effect).

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