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Letter

Do we need a new hypothesis to explain plant VOC emissions?

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Over the past decade there has been considerable debate about the evolutionary significance of the release of volatile organic carbon (VOC) by plants. Several explanations have been advanced to explain why some plants can allocate up to 10% of their carbon to the production of volatile secondary metabolites [1,2]. Recently, Susan Owen and Josep Peñuelas [3] discussed how the 'opportunistic' model of Peñuelas and Llusià [4] might explain isoprene emissions. Peñuelas and Llusià proposed that 'there is not necessarily a specific role for every phytogenic VOC emitted, given that their emission is unavoidable as a result of their volatility…natural selection has worked to take advantage of this volatility'.

An interesting feature of this debate is that it has been largely conducted without reference to a larger but conceptually identical debate about the role of secondary metabolism in general. VOCs should be regarded primarily as secondary metabolites and their volatility as a secondary physiochemical characteristic. Consequently, before devising evolutionary explanations deemed to apply specifically to volatile secondary products, it is necessary to demonstrate that the evolution of VOCs cannot be adequately explained by any of the more general models offering explanations for the chemical diversity found in nature. One model that can explain the production of VOCs is the Screening Hypothesis [5]. The Screening Hypothesis is based on the proposition that because potent biomolecular activity is an inherently rare property for any chemical structure to possess, organisms have to generate substantial chemical diversity for a few compounds to have any likelihood of possessing biomolecular activity. The hypothesis proposed several properties of secondary metabolism that would enhance the production and retention of chemical diversity [6]. One prediction was that some enzymes involved in secondary product synthesis will be promiscuous, a prediction for which there is now a growing body of experimental evidence [7]. Promiscuous enzymes

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will make chemicals with many different physical and chemical properties and it is predictable that some of these substances will be volatile. Hence the production of VOCs, some of which do not individually benefit the producer, is predicted by the Screening Hypothesis.

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Letters Response

Response to Firn and Jones: Volatile isoprenoids, a special case of secondary metabolism

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We thank Richard Firn and Clive Jones for their interest and comments on our recent Opinion article [1] published in the September 2005 issue of *Trends in Plant Science*. They ask if a new hypothesis is needed to explain VOC emissions. Before we respond to the pertinent points in their Letter, we must clarify some definitions. The term 'VOC' (volatile organic compound) includes products and intermediates from many different metabolic pathways. Not all VOCs are strictly secondary metabolites, for example, methanol is a product of primary metabolism and is frequently emitted by vegetation [2]. Our Opinion article [1] refers specifically to the volatile isoprenoids, which form a large sub-group of VOCs. They are indeed secondary metabolites, with important roles in atmospheric, ecological and physiological sciences.

Firstly, we would like to address the comment: 'An interesting feature of this debate is that it has been largely conducted without reference to a larger but conceptually identical debate about the role of secondary metabolism in general'. We approached the hypothesis of 'opportunistic isoprenoid emissions' from almost the opposite end of the research spectrum to Firn and Jones, that is, from atmospheric chemistry and ecophysiology rather than from biochemistry of metabolism. Therefore, it is all the more interesting that we have reached the same conclusion, albeit in a specialized field, and we are happy to support their more wide-ranging screening hypothesis. Naturally, we conducted exhaustive literature searches while we were writing our Opinion article, including a literature search using 'secondary metabolism' as a key-word that resulted in more than 1000 hits. However, we regret not having cited at least some of Firn and Jones's articles (e.g. [3–5]) because they fully support the message we wished to convey in our Opinion article.

This brings us to the next comment in their Letter that we wish to address: '…before devising evolutionary explanations deemed to apply specifically to volatile secondary products, it is necessary to demonstrate that the evolution of VOCs cannot be adequately explained by any of the more general models…'. Volatility is a special trait in these compounds because by being emitted and transmitted to or through the atmosphere they acquire special and specific functions, for example, communication with other organisms such as fungi, microorganisms, other plants, and animals (e.g. herbivores and pollinators [1]), and it is likely that evolution has developed and exploited this trait [6]. Moreover, the thrust of our Opinion article [1] was not intended as an evolutionary explanation 'per se'. It was intended as both a reminder and a suggestion for the active and diverse volatile isoprenoid research community, ranging from molecular biochemists to atmospheric chemists, which has published hundreds of papers since 2000. The reminder was that volatile isoprenoids would not have evolved with a specific role because they are secondary metabolites, and that any role they have now is fortuitous. This is no different from statements of general ecological and evolutionary theory [7] or of Firn and Jones's screening hypothesis for the evolution of secondary metabolism, which we are glad to have a chance of referencing now in conjunction with our work [3–5]. The opportunist hypothesis makes a further innovative suggestion for this group of compounds – given that they are secondary metabolites, volatile isoprenoid synthesis and emissions might be controlled

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to some extent by metabolic, physiological and developmental demands of essential isoprenoid production. Although this is also true for other secondary metabolites (e.g. [8]), this component of the opportunist hypothesis is of particular significance because controlling factors for volatile isoprenoids are important at a wide range of spatial and temporal scales. For example: (i) at the canopy and regional scales, volatile isoprenoids impact on the chemistry of the atmosphere, its oxidizing potential and capacity to form secondary organic particles (e.g. [9,10]); (ii) at the individual plant scale, they have ecophysiological roles involving the defence and propagation of the emitting plant (e.g. [11]); and (iii) at the scale of plant tissue, these compounds might have thermo-tolerance and anti-oxidative functions (e.g. [12]). To date, the volatile isoprenoid research community has not considered that volatile isoprenoids might be controlled in some way by the higher molecular weight essential isoprenoids; we are suggesting that this particular possibility should be addressed. Therefore, the opportunistic hypothesis supports, and is supported by, the screening hypothesis, but it is not the same. The screening hypothesis, as Firn and Jones point out, is a hypothesis of the evolution of all secondary metabolites. The opportunist hypothesis for volatile isoprenoids suggests that their synthesis is opportunistic (supporting theories of general ecological and evolutionary theory, including the screening hypothesis), and, therefore, their synthesis and emissions might be controlled at some temporal and spatial scales in a way that has not yet been considered (Figure 3 in [1]).

In conclusion, we think that the screening and opportunistic hypotheses are indeed mutually supportive. However, because evolution of volatile isoprenoids is affected by volatility-derived traits, because primary isoprenoid metabolism might well exert some control on secondary volatile isoprenoid synthesis, and because of the importance of identifying volatile isoprenoid controls at scales ranging from bio-molecular to global [1,6], we consider that the opportunistic hypothesis is worthy of independent consideration as a useful contribution to volatile isoprenoid research.

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