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1 **Emission of volatile organic compounds from plants shows a biphasic pattern**
2 **within an hormetic context**

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13
14 **Abstract:** Biogenic volatile organic compounds (BVOCs) are released to the atmosphere from
15 vegetation. BVOCs aid in maintaining ecosystem sustainability via a series of functions,
16 however, VOCs can alter tropospheric photochemistry and negatively affect biological
17 organisms at high concentrations. Due to their critical role in ecosystem and environmental
18 sustainability, BVOCs receive particular attention by global change biologists. To understand
19 how plant VOC emissions affect stress responses within a dose-response context, dose responses
20 should be evaluated. This commentary collectively documents hormetic-like responses of plant-
21 emitted VOCs to external stimuli. Hormesis is a generalizable biphasic dose response
22 phenomenon where the response to low doses acts in an opposite way at high doses. These
23 collective findings suggest that ecological implications of low-level stress that may alter BVOC
24 emissions should be considered in future studies. This commentary promotes new insights into
25 the interface between biological systems and environmental change that influence several parts

26 of the globe, and provide a base for advancing hazard assessment testing strategies and protocols
27 to provide decision makers with adequate data for generating environmental standards.

28

29 **Keywords:** dose-response; hormesis; risk assessment; U-shape curve; volatile organic
30 compounds

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32 **Capsule:** The emission of volatile organic compounds (VOCs) from plants displays a biphasic
33 pattern within a hormetic context.

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Introduction

Volatile organic compounds (VOCs) are abundant in the Earth's atmosphere as a result of natural (e.g. vegetation) and anthropogenic emissions. Recently, VOCs received particular attention due to their contribution in the formation of ground-level ozone (O₃). Such O₃ levels can be significantly elevated in the Northern Hemisphere, posing risks to animals and vegetation (Agathokleous et al., 2016; Kampa & Castanas, 2014; Li et al., 2017).

Despite their potential to affect the formation of O₃, VOCs help to maintain ecosystem sustainability (Peñuelas & Staudt, 2010; Tumlinson, 2014). For example, VOCs are part of an external communications network which transfers plant-to-plant signals (Peñuelas & Staudt, 2010; Tumlinson, 2014). A further crucial role is mediating interactions between plants and (a)biotic factors (Peñuelas & Staudt, 2010; Tumlinson, 2014). For instance, when a plant is attacked by herbivores or other organisms such as fungi, it releases a complex VOC blend which will be transferred to neighboring plants preconditioning against potential threats within a defined time window (Himanen et al., 2010; Piesik et al., 2017). Plant-emitted VOCs can be of profound significance to insects which rely on them for tracing their route to host plants (Piesik et al., 2014); plants may also rely on VOCs to attract insects as is the case of the Venus flytrap (*Dionaea muscipula*) which relies on food smell mimicry to attract prey. In addition to VOC utilization by animals to trace host/prey, animals utilize VOCs for sexual communication, i.e. pheromones (Tumlinson, 2014). VOCs, therefore, are relevant to a variety of scientific disciplines, including agriculture, behavioral science, biology, chemistry, earth and planetary sciences, ecology, engineering, environmental science, and physiology.

Within the context of global change, it is necessary to understand how plant VOC emissions affect stress responses in a dose-response framework. Three common dose-response models are the threshold, linear-non-threshold (LNT) and hormetic (Fig 1). The threshold and LNT models have dominated the literature throughout the 20th century (Calabrese 2017a,b).

99 mechanical wounding (Harren & Cristescu, 2013; Piesik et al., 2013), drought (Jubany-Marí et
100 al., 2010), or light (Rasulov et al., 2009, 2011).

101 In addition to the time-dependent biphasic VOCs responses, concentration-dependent
102 biphasic VOCs responses to external stimuli were also reported (Carriero et al., 2016; Rasulov et
103 al., 2009, 2011). For instance, the response of isoprene emission rate to CO₂ levels was biphasic
104 in aspen (*Populus tremula* × *P. tremuloides*) leaves (Fig 2A); isoprene emission rate was closely
105 related to the chloroplastic DMADP pool (Rasulov et al., 2009). In the same aspen hybrid, signs
106 for a biphasic dose response of isoprene emission rate to CO₂ (Fig 2B), O₂ (Fig 2C), and leaf
107 temperature (Fig 2D) were observed (Rasulov et al., 2011). Biphasic emission of isoprenoids is
108 supported by further studies, particularly in response to O₃ (Calfapietra et al., 2009; Tani et al.,
109 2017; Yuan et al., 2016). Emission rates of several compounds (α -pinene, β -pinene, limonene,
110 ocimene, hexanal and DMNT) from birch (*Betula pendula* Roth) plants exposed to O₃ and 10, 30
111 or 70 kg N ha⁻¹ yr⁻¹ consistently indicate the occurrence of hormesis (Carriero et al., 2016),
112 however, unlike isoprene, with reduced emission in the low-dose region (Fig 2E,F,G,H).
113 Interestingly, the latter results (Carriero et al., 2016) raised the question that some biphasic dose
114 responses may have two maxima, in agreement with results from other studies (Jiang *et al.*,
115 2017). Reduced emission potential of sesquiterpenes in the low-dose region has been also
116 reported for Norway spruce (*Picea abies* (L.) H. Karst.) which displayed typical hormetic dose
117 response of sesquiterpenes to O₃ (Bourstsoukidis et al., 2012). Similarly, evidence for O₃-
118 induced hormesis in the emission rate of several VOCs was revealed in tobacco (*Nicotiana*
119 *tabacum* L. ‘Wisconsin’) plants which were exposed to 0, 400, 600, 800, and 1000 ppb for 30
120 min and their VOCs emission rates were measured at 0.5, 3, 10, 24, and 48 h (Kanagendran et al.,
121 2018).

122 Biphasic isoprene emissions, with maximum in the low-dose zone (Fig 2A,B,C,D), are
123 particularly important to air quality and environmental health as isoprene is non-specifically

124 stored in the plants and has the largest emission rate among VOCs thus being the major biogenic
125 VOC affecting tropospheric photochemistry. Hence, higher emissions under low-level stress
126 would result in more isoprene in the atmosphere. However, biphasic emissions of VOCs
127 specifically stored in plant tissues are also important to ecological health because reduced
128 emission in the low-dose zone may have implications for plant tolerance against environmental
129 stress and to the interactions among plants, herbivores, and other organisms, therefore with
130 potential consequences to ecosystem sustainability (Ormeño et al., 2011).

131 The biphasic dose responses of plant-emitted VOCs as noted above reveal hormesis, a
132 highly generalizable dose response phenomenon (Agathokleous, 2018; Calabrese & Blain, 2009;
133 2011; Calabrese & Mattson, 2011, 2017). The evolutionary basis of hormesis (Agathokleous,
134 2018; Calabrese & Mattson, 2017; Kim et al., 2018) suggests that plants/VOCs biology and
135 accompanying VOC emissions have evolved within the context of enhancing communication,
136 conditioning, protection, and defense functions.

137 **Conclusions & Perspectives**

138 This commentary promotes new insights into the interface between biological systems
139 and environmental change that influences several parts of the globe, by collectively documenting
140 hormetic-like responses of plant-emitted VOCs to stimuli. Hormetic acting VOCs challenge the
141 environmental pollution research community to consider the ecological implications of low-level
142 stress that may alter VOC emissions. The blend of VOC emissions also warrants further
143 examination within the context of their evolutionary adaptations and how these may be mediated
144 within a dose response framework.

145 The study of hormetic dose responses will be challenging, requiring stronger study
146 designs with more doses, especially in the low dose zone, and probably with repeat measure-time
147 components. However, the continued ignoring of the possibility of hormesis in ecological system

148 responses by inadequate hazard assessment testing strategies and protocols will provide decision
149 makers with inadequate data upon which to base environment standards. With the use of more
150 rigorous and demanding protocols that permit an evaluation of the entire dose response
151 continuum, preferably over time, the scientific and policy rewards should be substantial.

152
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163

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272 **Captions**

273

274 **Fig 1.** Hypothetical hormetic, threshold, and linear non-threshold (LNT) dose-response models.

275 The five-point star indicates the no-observed-adverse-effect-level (NOAEL) for the threshold
276 and hormesis models. The LNT model assumes that response increases linearly with increasing
277 dose.

278

279 **Fig 2.** Typical preliminary examples of hormetic-like emissions of volatile organic compounds
280 (VOCs) from plants. Dose and response data presented only in figures in the reviewed articles
281 were estimated using image analysis software (Adobe Photoshop CS4 Extended v.11, Adobe
282 Systems Incorporated, CA, USA).

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