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Review

Floral volatile organic compounds: Between attraction and deterrence of visitors under global change

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ABSTRACT

Plants produce and emit a large variety of volatile organic compounds that play key roles in interactions with abiotic and biotic environments. One of these roles is the attraction of animals (mainly insects) that act as vectors of pollen to ensure reproduction. Here we update the current knowledge of four key aspects of floral emissions: (1) the relative importance and interaction of olfactory signals and visual cues, (2) the spatial and temporal patterns of emission in flowers, (3) the attractive and defensive functions of floral volatiles and their interference, and (4) the effects of global change on floral emissions and plant–pollinator interactions. Finally, we propose future lines of research in this field that need to be addressed or investigated further.

Contents

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Introduction

Previous reviews on floral emissions have provided a good basis on the biochemical processes involved in the interactions of flowers with their flower visitors (Dudareva et al., 2000; van Schie et al., 2006), their action over pollinators' behaviour (Riffell, 2011) and the ecological processes that drive their evolution (Raguso, 2008b). Here we update previous reviews on floral BVOCs and address diverse complementary and less considered ecological aspects of floral volatile emissions. We review their coexistence and association with visual signals, their patterns of emission and their underlying causes, their attractive and defensive functions and their interference, and finally we discuss the potential effects of global change on plant–pollinator interactions through the induction of changes in these floral emissions.

Plants produce and emit a large array of biogenic volatile organic compounds (BVOCs) that are useful in their interactions with their immediate environment. BVOCs include terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and amino acid derivatives (Dudareva et al., 2004, 2006). These emissions of BVOCs to the atmosphere have significant biological effects on the relationships of plants with other organisms and also environmental effects on atmospheric physicochemical properties (Peñuelas and Llusia, 2003; Peñuelas and Staudt, 2010). These volatile substances serve diverse functions in plants, including interactions with both abiotic (Sharkey and Singsaas, 1995; Peñuelas and Llusia, 2002; Peñuelas and Munné-Bosch, 2005; Niinemets, 2009) and biotic factors (Dudareva et al., 2006; Pichersky and Gershenzon, 2002; Seco et al., 2011; Kegge and Pierik, 2010; Peñuelas et al., 1996). As sessile organisms, plants do not have the capacity to move to escape from detrimental organisms and conditions to which they are exposed. Plants have therefore evolved a great diversity of chemicals to deal with those detrimental factors. BVOCs, and especially terpenoids, are among the most relevant compounds used by different tissues of the plant to interact with their abiotic and biotic environments (Peñuelas and Llusia, 2004; Schiestl, 2010). Benzenoids are ubiquitous in floral scents (Knudsen et al., 2006) and they are similarly important and abundant than terpenes (van Schie et al., 2006).

This capacity to chemically interact with their environment emerged early and diversified extensively in the evolution of the plant kingdom (Chen et al., 2011; Paul and Pohnert, 2011). The protection of plant tissues from its consumption by other organisms (herbivory) might be one of the first needs that the ancestors of terrestrial plants had to cope with (Van Donk et al., 2011). One of the mechanisms that plants have evolved to resolve this need was the production and eventual release of deterrent compounds from their tissues. Also competition has been one of the most common biotic interactions experienced by plant ancestors, and in response to this they have evolved allelopathic substances (Rasher et al., 2011). Primitive BVOCs may have served diverse other functions related to the interaction with abiotic agents, as primitive plants have been exposed to diverse environmental stresses. With the appearance of terrestrial plants and phanerogams, diverse plant lineages developed other biological interactions, like those established with pollinators (Bronstein et al., 2006). The establishment of these interactions is mediated at least in part by chemical communication channels (Negre-Zakharov et al., 2009). At this point, the large array of pre-existing chemical substances may have assumed new biological functions, such as the attraction of pollinators (Pellmyr and Thien, 1986; Armbruster, 1997; Schiestl, 2010), which is one of the most relevant functions of BVOCs (Dudareva et al., 2006). The evolution of these compounds experienced a new impulse with the radiation of flowering plants, as it has been stated that biotic pollination has contributed to the diversification of flowering plants and their floral traits (Grimaldi, 1999; Niet and Johnson, 2012).

More than 85% of the species of flowering plants depend on insects for pollination (Ollerton et al., 2011). Pollinators see communities of flowering plants as "biological markets" that offer a wide variety of flowers from which they can choose those with the best rewards (Chittka and Raine, 2006). The distribution of visitors among flowers is strongly affected by competition between plants, mechanisms of facilitation for the attraction of pollinators (Ghazoul, 2006; Duffy and Stout, 2011), and competition between pollinators for the exploitation of floral resources (Pleasants, 1981). Plants need to attract and compete for the attention of pollinators to receive their services. At this point, floral recognition by pollinators plays a key role in plant–pollinator systems.

Olfactory vs. visual cues

Floral recognition is mainly mediated by colour vision and olfaction (Chittka and Raine, 2006). The visual and olfactory display of flowers includes thus the floral traits that play the most important roles in the attraction of pollinators (Kunze and Gumbert, 2001). Plant–pollinator relationships have been historically regarded to be mostly mediated by vision. The study of communication between plants and pollinators has therefore focused mostly on visual traits; little consideration has been given to the contribution of the chemical traits of floral phenotypes (Raguso, 2008a). Visual cues, though, may act in concert with olfactory cues to allow pollinators to find plants (Burger et al., 2010; Leonard et al., 2011a,b). The presence of floral odours may enhance the discrimination of colours by improving attention towards visual cues, and the combination of chromatic and aromatic cues may enhance the formation and retrieval of memories in pollinators (Kunze and Gumbert, 2001). The relative importance of each sense may vary in the various plant–pollinator interactions. Olfactory signals are particularly important in plants that bloom at night when visual characteristics are less important for their pollinators (Jürgens et al., 2002; Carvalho et al., 2012); however, some nocturnal pollinators may rely in both visual and olfactory cues to locate and feed on night-blooming flowers (Raguso and Willis, 2005). In fact, investment in the production of scent as an advertisement of reward provides a net fitness benefit to plants (Majetic et al., 2009a). Olfactive signals can constitute a more reliable signal for pollinators to detect the presence of rewards and find them than visual traits (Raguso, 2004a). Ample evidence shows that pollinators such as bees are able to detect pollen and nectar in flowers via olfactive cues (Wright and Schiestl, 2009, and references therein). Floral scents thus occupy a relevant place in the hierarchy of stimuli that drive floral selection (Parachnowitsch et al., 2012); honey bees and bumble bees learn odours faster and with a higher retention than colours, and odours evoke a stronger discrimination between flowers (Kugler, 1943; Menzel, 1985; Dobson, 1994; Leonard et al., 2011a,b). Many pollinators learn the particular scents of different species of plants to recognise those flowers offering the highest quality rewards (Chittka et al., 1999). The learning of olfactory cues in pollinators strongly contributes to forming the networks of interactions established in plant–pollinator communities, which are dynamic in time and space (Riffell, 2011), and represents an important component of the selective environment determining the evolution of floral signals through their impact on plant fitness (Wright and Schiestl, 2009).