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Salvia verticillata: Linking glandular trichomes, volatiles and pollinators

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ABSTRACT

Plants have developed a plethora of signals to interact with other organisms, finally building up a sophisticate language for communication. In this context, we investigated *Salvia verticillata* L. (Lamiaceae), with the primary goal to link secondary metabolites and actual biotic relationships. We specifically analysed the volatile organic compounds (VOC) spontaneously emitted by leaves and flowers and determined the composition of the essential oils obtained from the aerial parts across 2015 and 2016. We merged information of chemical analyses to a micromorphological investigation on the glandular indumentum and to focal observations on the pollinator assemblage.

The VOC profiles were highly variable, with the floral bouquet being the most complex. Flowers and leaves showed 37 and 20 exclusive compounds, dominated by 1,8-cineole (10.4%) and germacrene D (38.4%), respectively. Sesquiterpene hydrocarbons prevailed (83.3% leaves; 73.7% flowers) and 19 common compounds were detected.

The oil profiles proved to be consistent across the two years: sesquiterpene hydrocarbons invariably dominated, with germacrene D, bicyclogermacrene and β-caryophyllene as main compounds.

The whole plant epidermis is thickly covered by two types of glandular hairs: peltates and small capitates, both responsible for the synthesis of terpenes, finally resulting in the VOC emission and in the essential oil production.

S. verticillata attracted mainly bees belonging to two functional groups: medium-sized and large bees, notwithstanding the small size of its flowers. At the site, *Apis mellifera* and different *Bombus* species were recorded, mainly interested in feeding on nectar. The literature survey on the isolated volatile compounds confirmed the hypotheses on the seduction strategies towards Apoidea.

1. Introduction

As stationary organisms, plants use a wide spectrum of sensory signals – *e.g.* blends of volatiles organic compounds (VOCs) – that allows a sophisticated "dialogue" with their mutualists and antagonists.

Current literature provided comprehensive excellent reviews on the functional ecology of such chemicals (Müller and Riederer, 2005; Raguso, 2009; Maffei, 2010; LoPresti, 2015). Anyhow, a whole-plant approach becomes an inescapable perspective to answer the question "What do we know about the vocabulary of this chemical language?"

In this framework, we focused our attention on *Salvia verticillata* L. (Lamiaceae) to investigate and depict the close relationships between the phytochemical productivity and the biotic environmental components.

Salvia verticillata L. (Lamiaceae), commonly known as lilac sage, is a herbaceous perennial native to central and eastern Europe and western Asia, where it grows under semi-arid, continental climatic conditions. Stems are erect and eglandular-hairy (Hedge, 1972) and leaves are mostly simple and ovate-triangular. The pedicellate lilac-blue flowers are clustered in terminal or axillary racemes formed by superimposed verticillasters. The flowers possess a non-functional staminal lever mechanism and the pollination is entomophilous. Two subspecies are currently recognized, based on the colour of the inflorescence axis: *S. verticillata* subsp. *verticillata*, with a wide distribution range in Europe

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and *S. verticillata* subsp. amasiaca (Freyn & Bornm.) Bornm, limited to Turkey and Western Asia.

The current phytochemical literature on *S. verticillata* refers the VOC emission profiles of samples from Polonia and Turkey (Rzepa et al., 2009; Hatipoglu et al., 2016) and to the EO composition of plants with a wide geographic origin ranging from the Balkans to Asia Minor (Sefidkon and Khajavi, 1999; Chalchat et al., 2001; Krstic et al., 2006; Pitarokili et al., 2006; Altun et al., 2007; Yousefzadi et al., 2007; Aşkun et al., 2010; Coisin et al., 2012; Dehaghi et al., 2014; Rajabi et al., 2014; Forouzin et al., 2015). With regards to micromorphological investigations on the glandular indumentum responsible for such productivity, only one work exists (Krstic et al., 2006) and, similarly, a single investigation on the spectrum of pollinators was carried on in Turkey (Celep et al., 2014): therefore, this is the first extensive contribution on *S. verticillata* out of it home range.

We investigated *S. verticillata* growing in Italy, in order to identify the secondary metabolites, to describe the secretory structures and to verify the biotic relationships established in a new environment. We specifically analysed: *(i)* the volatile organic compounds (VOCs) spontaneously emitted from leaves and flowers and the essential oils (EOs) obtained from the aerial parts across two consecutive years; *(ii)* trichome distribution pattern and histochemistry; *(iii)* the pool of pollinators active at the study site, depicting differences in foraging strategies.

The integration of data derived from the results of this multidisciplinary approach finally allowed us to stress how morphological and phytochemical characteristics are decisive in mediating mutualistic relationships with pollinators and to infer the "dialect" of the plant chemical messages.

2. Results

2.1. Morphological investigation

2.1.1. Trichome morphotypes and distribution pattern

Vegetative and reproductive organs of *S. verticillata* are thickly covered by glandular and non-glandular hairs (Fig. SI1). Two main morphotypes of glandular trichomes were recognized: large peltates and small capitates (Fig. SI1 a-b).

The large peltates are made up of a basal cell, a unicellular stalk and a broad head (40–50 μm in diameter) of 4–8 cells (Fig. SI1a). These trichomes occur only on leaf abaxial lamina prevailing on the interveinal regions; they are uniformly arranged on the abaxial sides of both the examined floral whorls while are lacking on the adaxial ones (Fig. SI1).

The small capitates are composed by a basal cell, a short unicellular stalk and a globose or pear-shaped bicellular head (15–20 μm in diameter, Fig. SI1b) surrounded by a thin subcuticular chamber. These hairs are generally scattered among the larger peltates on leaves, calyces and corollas and are the only type of trichome occurring on leaf adaxial side, with a higher density along the midrib and lateral veins in comparison to the interveinal regions (Fig. SI1).

Non-glandular trichomes are multicellular (2–6 cells), uniseriate with an acute and pointed apex; a protruding epidermal crown composed by 4–6 cells surrounds the most basal cell. These trichomes are generally observed along the edges, the veins, and at the proximal portions of the abaxial sides of leaves, and calyces (Fig. SI1 c-f). These hairs may be straight, or longitudinally oriented towards the apex of the organ bearing them, or towards the margins (Fig. SI1 c-f).

An exclusive type of non-glandular hair occurs on corollas: they are multicellular and uniseriate, with a uniform diameter from the base up the rounded apex. They are tightly distributed on the corolla tube, on the adaxial side of the upper lip and on the interveinal regions of the corolla adaxial sides.

Table 1
HS-SPME profiles of the leaves and flowers of *Salvia verticillata.*

	l.r.i.[a]	Compounds	Relative Abundance (%)	
			Leaves	Flowers
1	976	sabinene	tr[b]	–[c]
2	982	β-pinene	0.7	1.1
3	993	myrcene	–	0.2
4	1005	α-phellandrene	0.1	–
5	1009	(*Z*)-3-hexenol acetate	–	0.9
6	1011	δ-3-carene	0.1	–
7	1027	*p*-cymene	0.2	–
8	1031	β-phellandrene	2.0	–
9	1032	limonene	1.2	tr
10	1034	1,8-cineole	–	10.4
11	1062	γ-terpinene	0.1	tr
12	1070	*cis*-sabinene hydrate	–	0.1
13	1071	*n*-octanol	–	0.2
14	1090	*cis*-linalool oxide (furanoid)	–	0.1
15	1101	linalool	–	0.6
16	1102	*n*-nonanal	–	0.3
17	1110	phenylethyl alcohol	–	0.1
18	1139	*trans*-pinocarveol	–	tr
19	1140	nopinone	–	0.4
20	1143	camphor	–	0.4
21	1163	pinocarvone	–	0.3
22	1170	δ-terpineol	–	0.3
23	1178	4-terpineol	–	2.0
24	1187	(*Z*)-3-hexenyl-butyrate	–	1.1
25	1189	α-terpineol	–	0.2
26	1193	myrtenol	–	0.2
27	1199	*n*-dodecane	–	0.4
28	1204	*n*-decanal	–	0.5
29	1205	verbenone	–	0.7
30	1241	methyl carvacrol	0.7	1.0
31	1259	linalool acetate	–	0.8
32	1292	thymol	1.4	–
33	1299	*n*-tridecane	0.4	0.3
34	1340	δ-elemene	1.4	7.4
35	1351	α-cubebene	0.7	0.1
36	1372	α-ylangene	0.2	–
37	1376	α-copaene	2.2	0.4
38	1380	daucene	–	0.3
39	1384	β-bourbonene	5.1	0.7
40	1390	β-cubebene	1.5	0.3
41	1392	β-elemene	–	0.3
42	1399	n-tetradecane	0.4	0.6
43	1409	α-cedrene	0.2	–
44	1414	β-ylangene	0.3	–
45	1415	1,7-*di*-*epi*-β-cedrene	–	0.3
46	1420	β-caryophyllene	21.3	15.5
47	1429	β-copaene	3.1	0.8
48	1432	β-gurjunene	–	0.5
49	1438	*trans*-α-bergamotene	–	0.5
50	1441	aromadendrene	–	0.4
51	1456	α-humulene	–	5.5
52	1460	(*E*)-β-farnesene	–	4.9
53	1462	*cis*-muurola-4(14),5-diene	–	0.3
54	1470	*trans*-cadina-1(6),4-diene	–	1.6
55	1477	γ-muurolene	0.7	10.0
56	1482	germacrene D	38.4	–
57	1485	β-selinene	–	0.1
58	1495	bicyclogermacrene	5.0	21.4
59	1497	epizonarene	–	0.2
60	1498	α-muurolene	0.4	–
61	1500	*n*-pentadecane	–	0.3
62	1507	(*E*,*E*)-α-farnesene	–	0.9
63	1513	*trans*-γ-cadinene	1.5	0.3
64	1515	cycloisolongifol-5-ol	2.5	–
65	1524	δ-cadinene	1.1	0.3
66	1531	(*E*)-α-bisabolene	0.2	1.0
67	1538	α-cadinene	0.2	–
68	1574	dendrolasin	2.3	–
69	1576	spathulenol	0.6	0.2
70	1600	*n*-hexadecane	–	0.6
71	1636	caryophylla-4(14),8(15)-dien-5-ol	0.3	–
72	1643	cubenol	0.2	–

(*continued on next page*)

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