



Polar lipidome profiling of *Salicornia ramosissima* and *Halimione portulacoides* and the relevance of lipidomics for the valorization of halophytes

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ABSTRACT

Some halophytes are currently used as gourmet plant ingredients for human consumption. The polar lipidome of the succulent organs of *Salicornia ramosissima* (fresh branch tips) and *Halimione portulacoides* (leaves) were characterized in-depth, with more than two hundred lipid species being identified in both halophytes. The lipid species identified were distributed over five classes of phospholipids, three classes of glycolipids and one class of glycosphingolipids. Despite the existence of some species-specific differences between the polar lipidome, phospholipids and glycolipids show a high content of *n*-3 fatty acids in both *S. ramosissima* and *H. portulacoides*. These results highlights the advantage of employing mass spectrometry based lipidomic platform towards the valorization of halophytes as a source of valuable nutrients and bioactives, fostering potential applications in the fields of healthy and functional food products, and for nutraceutical and pharmaceutical uses.

1. Introduction

Plant lipidomics is an emerging field that aims to address a diverse range of topics related to, for example, lipid identification, quantification and structural adaptation to biotic and abiotic conditions. Plants, in general, display a remarkable variety of lipids with important biological functions involving plant metabolism. Also these lipids have significant structural and signaling roles in the metabolic regulation, protection, and homeostasis of the cell. Consequently, the same genotype may display specific phenotypic signatures to a given spatio-temporal environment (Hou et al., 2016). With current advances in mass spectrometry (MS) platforms coupled to liquid chromatography, it is now possible to perform high resolution, high throughput analysis of complex lipidome and to determine the molecular profile of numerous individual lipid species present in plant tissues (Barh et al., 2015; Hummel et al., 2011). Nonetheless, the lipid composition, at a molecular level, of specialized vast number of plant groups, such as halophytes, remains mostly unknown. (Maciel et al., 2016).

Halophytes, such as *Salicornia ramosissima* (Hook. f.) J. Woods ex W. A. Clarke & E. S. Marshall and *Halimione portulacoides* (L.) Aellen [Syn. *Atriplex portulacoides* L.], popularly known as green samphire and sea purslane, respectively, belong to a group of plants that have the ability

to cope with saline environments, i.e., halophytes (salt-tolerant plants). Halophytes have evolved some unique physiological traits that enable them to thrive under conditions of high salinity. This adaptation is an essential advantage considering the rate of salinization of soils formerly used for agriculture worldwide, with salt stress being one of the most severe environmental factors limiting the productivity of conventional crop plants (Fita et al., 2015). The halophytes included in this study have a wide geographical distribution. The genus *Salicornia* L. occurs in temperate and subtropical habitats, with the exception of South America and Australia (Kadereit et al., 2007). The genus *Halimione* Aellen is one of the most abundant and productive plant species in European salt marshes, and can be found along the Atlantic coast of Europe and along the Mediterranean coast (Bouchard et al., 1998). With the decline of saltworks commercial activity in several countries, namely those in southern Europe and the Mediterranean basin (Fita et al., 2015), the sustainable production of autochthonous halophytes can be a solution to reverse the eco-decline of these unique habitats. Moreover, the growing shift towards a more sustainable and healthier diet may open new markets for halophytes with high nutritional value (Ventura et al., 2015). Both *Salicornia* and *Halimione* halophytes are already traded in gourmet markets for human consumption, with their succulent organs, namely the fresh branch tips of *Salicornia* and the

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leaves of *Halimione*, fetching premium slots in the value chain. Despite their increasing use for human consumption, halophytes still appear to be a largely untapped reservoir of bioactive compounds, namely antioxidants (Jang et al., 2007) and lipid components with high nutritional value, such as essential fatty acids (*n*-3 and *n*-6) (FA) (Isca et al., 2014). In addition, it is also known that lipids from halophytes, namely glycolipids (GL) and phospholipids (PL), can have bioactive properties (Cortés-Sánchez et al., 2013; Holdt and Kraan, 2011). Their ecological relevance and increasing range of applications for food, feed, cosmeceutical and pharmaceutical industries foster the need to gain more detailed knowledge of their lipidome. To the best of our knowledge, the complete polar lipidome profile (i.e., the lipid molecular signature) of halophyte plants has yet to be described. This approach may reveal new opportunities for their valorization. Our current knowledge on halophyte lipids is restricted to the characterization of non-polar lipids (Sui and Han, 2014a; b; Sui et al., 2010) and sterols (Ksouri et al., 2009, 2012, 2013). Recently, liquid chromatography–mass spectrometry (LC–MS) based techniques was used to characterize the lipidome of macrophytes, thus confirming the importance of this omics approach in plant phenotyping (da Costa et al., 2015; Melo et al., 2015; Wang et al., 2016; Zhou et al., 2014).

Overall, detailed knowledge of the chemical diversity of halophytes may contribute to their valorization as highly-valued products for human consumption or other high-end applications. To achieve this objective, the polar lipidome of *Salicornia ramosissima* (*S. ramosissima*) fresh branch tips and *Halimione portulacoides* (*H. portulacoides*) leaves were determined using a lipidomic approach. LC–MS using a Q–Exactive mass spectrometer was employed to identify the polar lipid molecular species, and gas chromatography–mass spectrometry (GC–MS) was used to confirm the identity of methyl ester fatty acids. Results are discussed in the scope of the nutritional value and potential applications in nutraceutical and pharmaceutical industries.

2. Results

In this work, we determined the polar lipid profile of the halophyte plants *S. ramosissima* and *H. portulacoides* using mass spectrometry-based approaches. Esterified fatty acids were analyzed by GC–MS, while the polar lipid profile was determined using hydrophilic interaction liquid chromatography (HILIC) coupled to high resolution mass spectrometry in MS and MS/MS modes. Both halophyte plants had a very complex lipidome, which included more than 200 molecular species. Lipid molecular species were distributed over five different classes of phospholipids (PL): phosphatidylcholine (PC), phosphatidylethanolamine (PE) phosphatidylglycerol (PG), phosphatidylinositol (PI) and phosphatidic acid (PA); three classes of glycolipids (GL): sulfoquinovosyldiacylglycerol (SQDG), monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG), and one class of glycosphingolipid, the hexosylceramide (HexCer).

2.1. Lipid profile of *Salicornia ramosissima*

Seventeen different fatty acids (FAs) were identified in the lipid extracts of *S. ramosissima* (Table 1). Results obtained indicate that *S. ramosissima* had a high content of long chain FA, with a length between 16 and 18 carbons and a high level of unsaturation (e.g., polyunsaturated fatty acids (PUFA)) up to 61.3%. PUFA included mainly *n*-3 and *n*-6 FA. The most abundant FAs were α -linolenic acid (C18:3*n*-3, ALA), which correspond to with nearly 40% of the total pool of FAs, followed by linoleic acid (C18:2*n*-6, LA), which contributed with 20% of the total pool. Saturated fatty acids (SFA) were the second most abundant group of FAs, whose content was estimated to be ~30% of total FAs present in *S. ramosissima*. The main saturated FA was palmitic acid (C16:0, PA) (22.1% of the total pool of FAs). Monounsaturated fatty acids (MUFA) were less abundant than PUFA and SFA, only accounting for approximately 6% of the total pool of FA. Oleic acid

Table 1

Fatty acid composition of total lipids in leaves of two halophytes: *Halimione portulacoides* and *Salicornia ramosissima* (% of total FA).

Fatty acid	<i>S. ramosissima</i>	<i>H. portulacoides</i>
C14:0	0.29 ± 0.03	0.55 ± 0.17
C16:0	22.14 ± 0.55	19.18 ± 1.62
C16:1 ⁽⁷⁾	0.11 ± 0.02	0.32 ± 0.04
C16:1 ⁽¹¹⁾	1.46 ± 0.14	0.60 ± 0.19
C16:2 ^(7,10) (<i>n</i> -6)	nd	0.34 ± 0.06
C16:3 ^(7,10,13) (<i>n</i> -3)	nd	1.40 ± 0.05
C17:0	0.23 ± 0.03	0.26 ± 0.05
C18:0	5.53 ± 1.37	3.91 ± 1.53
C18:1 ⁽⁹⁾	3.97 ± 1.76	10.39 ± 0.43
C18:1 ⁽¹¹⁾	0.34 ± 0.05	nd
C18:1 ⁽¹³⁾	nd	0.97 ± 0.02
C18:2 ^(9,12) (<i>n</i> -6)	20.02 ± 0.98	14.21 ± 0.71
C18:3 ^(9,12,15) (<i>n</i> -3)	39.60 ± 0.63	43.53 ± 1.66
C20:0	0.69 ± 0.03	0.52 ± 0.12
C20:1 ⁽¹¹⁾	0.17 ± 0.01	0.27 ± 0.03
C20:2 ^(6,11)	0.14 ± 0.01	0.36 ± 0.11
C20:3 ^(11,14,17) (<i>n</i> -3)	0.13 ± 0.01	0.15 ± 0.01
C22:0	1.17 ± 0.13	1.24 ± 0.32
C23:0	0.37 ± 0.02	0.16 ± 0.05
C24:0	2.78 ± 0.03	1.09 ± 0.13
SFA	32.44 ± 0.24	26.91 ± 2.89
MUFA	6.24 ± 0.21	12.56 ± 0.60
PUFA	61.32 ± 0.08	59.63 ± 2.19
<i>n</i> -3	40.44 ± 0.08	45.08 ± 1.65
<i>n</i> -6	20.74 ± 0.04	14.54 ± 0.64
<i>n</i> -6/ <i>n</i> -3 ratio	0.51 ± 0.01	0.32 ± 0.01

The values shown are the means ± standard deviation (*n* = 3). SFA, saturated fatty acids; MUFA mono-unsaturated fatty acids; PUFA polyunsaturated fatty acids. The three measurements were performed from the same homogenized plant sample.

(C18:1*n*-9) was the most abundant MUFA, although it only accounted for 5% of the total pool of FAs.

The polar lipidome was determined in crude lipid extracts using HILIC coupled to a high resolution and accurate mass spectrometer. Over 200 molecular species were identified in *S. ramosissima* lipid extracts, distributed by five different classes of PL, three classes of glycolipids and one glycosphingolipid, as described above. The MS profiles are shown in supplementary information (Figs. S1 and S2).

MS/MS data allowed the identification of 62 PC, 43 PE, 30 PA, 15 PG and 9 PI molecular species, with different fatty acyl moieties ranging from 15 to 24 carbon atoms and containing from 0 to 6 double bonds. FA distribution was found to be class dependent (Table 2). The main PC molecular species were found at *m/z* 756.551 (PC 16:0/18:3), *m/z* 758.567 (PC 16:0/18:2), *m/z* 780.550 (PC 18:2/18:3), *m/z* 782.566 (PC 18:2/18:2 and PC 18:1/18:3) and *m/z* 870.666 (PC 18:2/24:0). The PC profile of *S. ramosissima* was characterized by the presence of polyunsaturated PC species, odd-chain FA and very long FA, such as C24:0. These FA were also detected using GC–MS analysis (Table 1). In the case of PE class, the molecular species were composed of a combination of acyl groups ranging from 15 to 24 carbon atoms containing 0 to 3 double bonds (Table 2). The most abundant PE molecular species was found at *m/z* 714.490, corresponding to PE 16:0/18:2, followed by PE 18:2/18:2 at *m/z* 738.505. Similar to the PC class, some species with very long chain FAs, such as 24:0 were identified in PE class, namely at *m/z* 824.614, *m/z* 826.630, *m/z* 858.584 and *m/z* 872.600. PE molecular species esterified with odd-chain FA were also found such as the FA C15:0, C19:2 and C21:0. PA class included molecular species carrying fatty acyl groups ranging from 16 to 19 carbon atoms and the major PA molecular species were identified at *m/z* 669.448 (PA 16:0/18:3 and PA 16:1/18:2), *m/z* 671.464 (PA 16:0/18:2), *m/z* 693.448 (PA 18:2/18:3) and *m/z* 695.463 (PA 18:2/18:2 and PA 18:1/18:3). Species with odd-chain fatty acids (C19:0, C19:1, C19:2, C19:3, C17:0 and C21:0) were also identified. In the case of PG class, the most abundant molecular species were found at *m/z* 719.484 and

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