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C0725 ***Cakile maritima*, a promising model for halophyte studies and a putative cash crop for saline agriculture**

Delphine Arbelet-Bonnin^a, Ibtissem Ben-Hamed-Louati^{a,b},
Patrick Laurenti^a, Chedly Abdelly^b, Karim Ben-Hamed^b,
François Bouteau^{a,*}

^aUniversité Paris Diderot, Laboratoire Interdisciplinaire des Energies de Demain (LIED), Paris, France

^bLaboratoire des Plantes Extrêmophiles, Centre de Biotechnologie de Borj Cedria, University of Carthage-Tunis, Hammam Lif, Tunisia

*Corresponding author: e-mail address: delphine.bonnin@univ-paris-diderot.fr

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Abstract

Agricultural intensification necessary for global food security as well as changes in temperature and precipitation patterns expected from climate change are likely to cause further deterioration irrigated lands in various part of the world. Salinization is spreading particularly in arid and semi-arid regions and urban sprawl is forcing agricultural production into marginal areas. Many salted marginal areas could support biomass production if halophytes able to tolerate high salinity were used. This chapter presents general data on *Cakile maritima*, a halophyte, concerning its ecological characteristics, diversity and distribution, adaptation to environment and its potential uses as medicinal plant, for oilseed production or phytoremediation. In a second part we present what have been uncovered in *C. maritima* in term of mechanisms and physiological adaptations to salinity when compared to other plants.

Cakile maritima appears worthy of attention since it meets numerous criteria for being a good genetic model of halophyte. It has a small diploid genome, a short life cycle and produces large amount of seeds. Furthermore *Cakile maritima* represents a promising species owing its large geographical and ecological amplitude, its economic potential because of its ability to produce numerous secondary compounds and as an oilseed and energy crop. This renders the cultivation of this plant on salted marginal soil of practical significance in the context of the necessary development of biosaline agriculture in the future.

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1. Introduction

Salinization is a problem associated to agriculture, both as a constraint and as the result of inappropriate practices. In addition, agriculture intensification, as well as changes in temperature and precipitation patterns expected from climate change, is likely to cause further deterioration of irrigated lands in various part of the world (Panta et al., 2014). Salinization affects 15–23% of the world's total land area (Rozentsvet et al., 2017) and is spreading particularly in arid and semi-arid regions. Moreover, the amount of arable land lost due to urban sprawl is forcing agricultural production into marginal areas (Shabala, 2013). Most agricultural plants are sensitive to the presence of salinization in the soil that is one of the main environmental constraints threatening global crop biomass production and thus food security. At the same time many areas could support biomass production if plants available could tolerate high salinity. Hence halophytic species are currently widely studied in world because of their value for the development of saline agriculture. Halophytes are a small group, estimated at 5000–6000 species, or ~2% of all angiosperms (Le Houérou, 1993). Flowers and Colmer (2008) have defined “euhalophyte” species as those with a high level

of salt-tolerance and able to complete their life cycle in conditions equivalent to >200 mM NaCl (approximately half the salinity of seawater). Halophytes have a range of highly efficient and complementary morphological, physiological and anatomical adaptations that enable them to combat and even benefit from saline environments (Flowers et al., 1977, 2015; Flowers and Colmer, 2008; Shabala and Mackay, 2011). Halophytes might be used as vegetables and developed as oilseed crops (Debez et al. 2018; Rozema and Schat, 2013; Weber et al., 2007). A better understanding of how halophytes tolerate saline soils could also allow plant breeders and molecular biologists to increase the salt tolerance of conventional crop plants (Glenn and Brown, 1999). The two major families of halophytes are the *Amaranthaceae* with over 380 halophytic species and the *Poaceae* with over 140. *Brassicaceae* is also a family of well-known halophytes like *Eutrema* or *Thellungiella* (*T. salsuginea*, *T. parvula*), *Cochlearia* and *Lepidium*. Despite the intensive work on unraveling salt tolerance mechanisms in plants that has been done, much remains to be known. In this review, we provide a summary of the current uses of *Cakile maritima* for human food consumption, as an oilseed and energy crop, for phytoremediation purposes, for use in medicine, and we provide some information on its ecological characteristics and physiological behavior. We further propose this coastal halophyte as a model to examine salinity tolerance and as a putative crop.

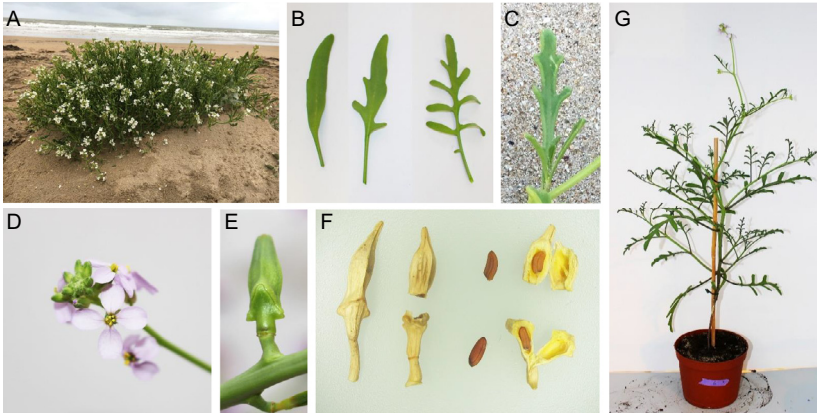
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2. *Cakile maritima*

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2.1 Description

p0020 Sea rocket *Cakile maritima* Scop., *Brassicaceae* (Fig. 1A and D), is a succulent annual diploid species ($2n=18$) with a C3 pathway of photosynthesis. It is closely related to *Arabidopsis thaliana* (Bailey et al., 2006) with a ~ 719 Mb genome size (4.5-fold that of *A. thaliana*). Leaf shape could be variable during development (Fig. 1B), among regions (Cousens et al. 2013) and ecological conditions (Ciccarelli et al. 2010; Davy et al. 2006), the leaves being more pinnatifid in arid climate in comparison to those originating from humid climates (Davy et al. 2006). It is mainly an obligate outbreeder, and is insect-pollinated but low rates of selfing have been recorded (Rodman 1974). It has a short life cycle (3 months from seed to seed) and can produce up to 10,000 seeds per plant. The average plant height in green house for Raoued accession coming from Tunisia is around 100 cm (Fig. 1G). It is thus easy to grow *C. maritima* plants under controlled laboratory conditions, which makes *C. maritima* suitable as a model halophyte for physiological research.



f0010 **Fig. 1** *Cakile maritima* morphological details. (A) *C. maritima* in its natural environment (Noirmoutier, Vendée, France), (B) entire leaf and pinnatifid leaf, (C) succulent leaf, (D) inflorescence, (E) maturing fruit, (F) dry fruit and seed and (G) *C. maritima* in green house (D).

p0025 The fruit is a two-segmented and asymmetric silique as you can see in the Fig. 1E and F (Rodman, 1974) that contains two seeds that disperse differently. The distal segment is readily detached (Fig. 1F) and allow dispersal over considerable distances in seawater. Plant dispersal is aided by the ability of fruits to float and be transported by the action of wind and waves (Barbour & Rodman, 1970; Maun & Payne, 1989). The lower fruit segment remains attached to the parent plant, thereby forming clumps of seedlings in a productive habitat (Barbour, 1972). A further dimorphism was reported for seed size in relation to their position on the fruit (Barbour, 1972). Seed heteromorphism is known for many halophytic species and is generally considered to be an adaptive strategy that enables plants to escape from competition and to tolerate a changeable environment (Yao et al., 2010). For *C. maritima* the seeds from lower fruits have a significantly lighter mass than upper seeds (Barbour, 1972). Fruit dimorphism may be of adaptive significance mainly for seedling establishment and seed dispersion. With respect to dispersal, *C. maritima* seeds can survive up to 4 months immersed in sea water and may float for up to a year on sea water (Gandour et al., 2008).

s0025 2.2 Ecological characteristics

p0030 In its natural habitat, *Cakile maritima* is confined to maritime strandlines on sand (Fig. 1A), where it can initiate foredune formation and dune succession (Clausing et al., 2000; Davy et al., 2006; Kadereit et al. 2005). It has a root

system that cans growth to 40 cm depth, with extensive lateral roots (Davy et al., 2006). The habitats of species are characterized by non-constant environmental stresses such as salt spray, low nutrient and water availability, high temperatures, substrate instability and sandblasting (Hesp, 1991; Maun, 1997; Rozema et al., 1985). *Cakile maritima* is naturally tolerant to salt spray and transient seawater inundation (Ciccarelli et al., 2010; Debez et al., 2006). It even requires moderate salinities (50–100 mM NaCl) to express maximal growth and seed production and can survive at salinities close to seawater (500 mM NaCl) while also accumulating large amounts of Na⁺ in the leaves (Ben Hamed-Laouti et al., 2016a; Debez et al., 2004). Such conditions will cause substantial decreases in the plant growth, but *C. maritima* is able to maintain growth, flowering and produce seed at up to 500 mM NaCl.

p0035 Nutritional factors may also contribute to differences in the performance of *C. maritima* in strandline and foredune habitats (Pakeman and Lee, 1991a,b). A difference in growth was observed depending on their habitat. Large, rapidly growing plants are associated with sand containing macro-algal litter, whereas small stunted plants are found on foredunes above the limit of tidal inundation. Pakeman and Lee (1991a) did not conclude about the phosphorus growth involvement due to variability data even if they observed a weaker concentration in foredune leaves. Actually, the observed differences in performance are not associated with water or potassium availability, but with nitrogen availability which is much higher in the strand habitat compared with the foredunes. In accordance the concentration of nitrogen in sand and in the plant leaves growing in the strand environment is higher than that measured for foredune plants and sand (Pakeman and Lee, 1991a,b). The difference in performance is exacerbated by the emptying on plant nitrogen by the synthesis and accumulation of compounds for osmotic adjustment in strandline *Cakile maritima*.

s0030 **2.3 Dispersal and environmental adaptation**

p0040 *Cakile maritima* is an annual species, and is wholly dependent on seed dispersal and recruitment for survival. Therefore populations of *C. maritima* exist as often ephemeral and shifting populations that depend on short range dispersal of proximal segment fruit and long range dispersal of distal segment fruit by wind onto water and then by sea currents on tides. The seeds of *C. maritima* require cold stratification. Germination is not affected by a concentration up to 200 mM NaCl (Debez et al., 2006, 2012; Westberg and

Kadereit, 2009). Although *C. maritima* appeared to be equipped with proteins encoded by constitutively expressed genes in its saline environment supposed to allow the seed to cope successfully with salinity (Debez et al., 2012), a delay in the degradation of seed storage proteins was observed when germination takes place under salinity. This may explain the slower germination rate observed. At higher concentrations of NaCl a secondary dormancy could be induced and the germination process can be impaired. Interestingly, non-germinated seeds remained viable and they show high germination percentage and faster germination than the control seeds after their transfer on distilled water (Debez et al., 2018). Thus if high salinity seems to impact germination of the halophyte *Cakile maritima* it may have a priming-like effect allowing rapid germination upon stress release. Priming of *C. maritima* seeds with H₂O₂ was also shown to improve *C. maritima* tolerance to both osmotic stresses and ameliorate growth and antioxidant content when plants are later exposed to stress (Ellouzi et al. 2017). Light does not alter the final germination percentage of upper or lower fruit segments, but inhibit the rate of germination.

p0045 The potential for long-distance dispersal means that species can be exposed to a wide-range of climatic conditions. The upper fruit segments do not differ significantly in floating ability from lower fruit segments, but seedling establishment and survival may be affected by seed mass because germination rates increase with seed size (Cordazzo, 1994, 2006; Maun and Payne, 1989). The fruit and seed sizes also depend on the region, smallest fruits and seeds being produced in arid zones when compared to humid and sub-humid areas (Barbour, 1972; Maun and Payne, 1989). It was suggested that seed and fruit variability improve the adaptation capacities of halophytes to their natural environment (Mandak and Pysek, 2001). Accordingly, population genetic studies of Mediterranean populations show that natural populations of *C. maritima* in Tunisia are characterized by a moderately high fixation index (F_{ST} ; Gandour et al., 2008), a statistics that measure genetic diversity at neutral loci (Wright, 1951). As a high F_{ST} is awaited for outbreeding insect pollinated plants, the moderate F_{ST} of *C. maritima* reveals a long distance gene flow that have been shown to be due to long range seed dispersal by sea currents (Gandour et al., 2008). Therefore long range dispersal of distal segment fruit confers a great genetic diversity and a high potential of adaptability to these *C. maritima* populations. However, it should be noted that in recent years the genetic diversity of Mediterranean populations trends to decrease due to anthropic fragmentation of natural populations (Gandour et al. 2008). *Cakile maritima* displays an

additional remarkable genetic feature that makes it a successful invader: its capability to hybridize with congeneric species such as *Cakile edentula*. Usually, invading populations fail to establish because they are small and therefore suffer of severe Allee effects (i.e., a fitness decrease at low population density). Strikingly, *C. maritima* replaced the earlier, inbreeding, colonizer *C. edentula* within the period of European human expansion in North America, New Zealand and Australia (Cousens and Cousens, 2011; Rodman, 1986). Mesgaran et al. (2016) have shown that this quick invasion was favored by transient hybridization of *C. maritima* with the earlier colonizer *C. edentula* that overcame pollen limitation and therefore reduced Allee effects.

s0035 2.4 Diversity and distribution

p0050 *Cakile maritima* has diversified across a wide range of latitudes, naturally occurring as far north as northern Norway and as far south as the southern coasts of the Australia (Fig. 2). It is thus widely distributed throughout the



f0015 **Fig. 2** Worldwide distribution of *Cakile maritima*. Data were compiled from Global Biodiversity Information Facility website (<http://www.gbif.org/species/3048831>), Clausing, G., Vickers, K., Kadereit, J.W., 2000. Historical biogeography in a linear system: genetic variation of Sea Rocket (*Cakile maritima*) and Sea Holly (*Eryngium maritimum*) along European coasts. *Mol. Ecol.* 9, 1823–1833; Cousens, R.D., Cousens, J.M., 2011. Invasion of the New Zealand coastline by European sea-rocket (*Cakile maritima*) and American sea-rocket (*Cakile edentula*). *Invasive Plant Sci. Manage.* 4, 260–263; Cousens, RD, Ades, PK, Mesgaran, MB, Ohadi, S. 2013. Reassessment of the invasion history of two species of *Cakile* (*Brassicaceae*) in Australia. *Cunninghamia* 13, 275–290.

world with climates ranging from arid to humid *Cakile maritima* shows great phenotypic plasticity of form, within and between subspecies, especially in fruit morphology and leaf shape (Ciccarelli et al., 2010; Cousens et al., 2013; Gandour et al., 2008). This can be correlated with adaptation strategies to heat, high light intensity and drought (Ciccarelli et al., 2010). The better salt tolerance of an arid climatic area accession compared to a humid climatic area accession is related to its capacity to maintain leaf water status even at 400 mM NaCl (Megdiche et al., 2007). Using the technique of amplified fragment length polymorphisms, a remarkable differentiation between Atlantic and Mediterranean populations of *C. maritima* was also found in Europe (Clausing et al., 2000; Westberg and Kadereit, 2009). Flow cytometry analysis showed that the Tunisian populations have a smaller genome than Atlantic populations from Brittany (Debez et al., 2013). Thanks to this latitudinal range, *C. maritima* is an ideal system to study phenological adaptation to climate. However, *C. maritima* is subdivided into a number of controversial subspecies based primarily on morphological characters, the shape of the distal segment, and leaf shape. The most recent subdivision of the species recognizes four subspecies: ssp. *baltica*, ssp. *maritima* (*integrifolia*), ssp. *aegyptiaca* and ssp. *euxina*. The ssp. *integrifolia* is found in northern Norway, on the shores of the Atlantic and the Mediterranean coast. It is largely replaced by ssp. *baltica* in most Baltic areas and completely replaced by ssp. *euxina* along the Black Sea. In northern Europe, it shares part of its distribution with ssp. *Islandica*, and in the Mediterranean region and southern Portugal with ssp. *aegyptiaca*. A population genetic analysis conducted on nine Mediterranean subpopulation of *C. maritima* in Tunisia have shown that phenotypic divergence between populations from different regions are likely due to independent local adaptation through divergent selection (Mhemmed et al., 2012). As mentioned above genetic variation could be measured by F_{ST} (or by an analogous statistics G_{ST} ; Nei, 1972) at neutral loci. Genetic differentiation could also be measured for quantitative traits thanks to Q statistics (Q_{ST} , Spitze, 1993). Models predict that Q_{ST} and G_{ST} should be equal when population divergence is driven by neutral genetic drift, as it is the case for natural populations of *Arabidopsis thaliana*, for instance (Kuittinen et al., 1997). In contrast, stabilizing selection leads to $Q_{ST} < G_{ST}$ whereas diversifying selection leads to $Q_{ST} > G_{ST}$. Mhemmed et al. (2012) found a significantly higher genetic difference in almost all quantitative traits, such as leaf length, leaf morphotype, flower emergence, petal color, or fruit size, than at neutral loci, indicating occurrence of phenotypic plasticity and independent local adaptation.

s0040 **2.5 *Cakile maritima* and fungal interactions**

p0055 *Cakile maritima* does not seem to form mycorrhizal association (Giovannetti and Nicolson, 1983). This could be explained by large amount of glucosinolates in the tissues, which may also be responsible for the limited ranges of herbivores and fungal pathogens affecting *C. maritima* (Merchaoui et al. 2016). However, glasshouse fungal inoculation experiments of fungal species, *Fusarium culmorum*, *F. oxysporum*, *Phytophthora* sp. resulted in reduced biomass in comparison to controls. On temperate beaches in Australia and New Zealand *C. maritima* was also shown to be attacked by the fungal pathogens *Alternaria brassicicola* or *A. alternata* which form necrotic lesions on all aboveground parts, *A. brassicicola* being the more effective pathogen (Oliver et al., 2001; Thrall et al., 2001, 2005). A field survey showed that 30% of the seeds could be infected with *A. brassicicola*. Glasshouse inoculation trials demonstrated that infection could occur either through the flowers or fruits. Then seedlings were found to emerge with infections. This suggests a vertical transmission in addition to the horizontal disease transmission (Oliver et al., 2001). The closely related species *C. edentula* (tight inbreeder) is also attacked by *Alternaria brassicicola*, making *C. maritima* (outbreeder) a good system to investigate the evolution of resistance in individual host populations with contrasting recombination constraints (Cousens and Cousens, 2011).

s0045  **3. Potential uses of *Cakile maritima***

p0060 The potential use of this plant as a food or in industry is frequently discussed due to its production of oil seeds and its possible nutrient and therapeutic utilizations (Casal and Casal, 2004; Ksouri et al. 2007; Zarrouk et al., 2003).

s0050 **3.1 Traditional uses**

p0065 Although *C. maritima* could be a nutrient food due to its edible leaves (Merchaoui et al., 2016), it has a bitter taste and was till now mainly used in time of scarcity. However, it was also used in traditional medicine for treatments of a wide range of ailments; e.g., antidiuretic, antiscorbutic, headaches, purgative due to its high and diverse content in secondary metabolites notably in antioxidant molecules (Aboul-Enein et al., 2012; Ben Hamed-Laouti et al. 2016b; Merchaoui et al., 2016). *Cakile maritima* is effectively able to synthesize number of secondary metabolites, flavonoids with antioxidant properties (Radwan et al., 2008), polyphenols (Ksouri et al., 2007;

Meot-Duros et al., 2008) or glucosinolates (Radwan et al., 2008). A series of hydrocarbons, cholesterol, campesterol, sitosterol and the triterpen, amyrin were also identified from the aerial parts (Radwan et al., 2008). Compared to others *Brassicaceae* species moderately tolerant to salt stress (*Brassica oleraceae* and *B. napus*), *C. maritima* effectively presents a high level of sterols (Chalbi et al. 2015). This halophyte has relatively strong total antioxidant activities, notably a strong ascorbate pool (Ksouri et al., 2007; Meot-Duros et al., 2008). *Cakile maritima* extracts have antimicrobial activities against various bacterial and yeast strains (Elbashiti et al., 2011; Meot-Duros et al., 2008). They also have significant molluscicidal activity probably due to the presence of phytoalexins and glucosinolates (Radwan et al., 2008). As many halophytes *Cakile maritima* is thus a promising source of pharmaceuticals due to their high contents of bioactive compounds (Ksouri et al., 2011).

s0055 3.2 Oilseed halophyte

p0070 In addition *C. maritima* is considered as a promising crop with regard to its seed-oil; the seeds contain 30–40% oil (Fresh matter basis) (Zitouni et al., 2016). To place this in content, two other halophytes (*C. edentula* and *Crambe abyssinica*) could have higher oil contents (50% and 60%, respectively, Mandal et al., 2002; O’Leary et al., 1985), and a range of other oleaginous species (*Carthamus tinctorius* and *Sesamum indicum*) have similar oil contents (Karleskind, 1996), and some rapeseed genotypes (Bhardwaj & Hamama, 2003). Triacylglycerols (TAG), diacylglycerols (DAG), monoacylglycerols (MAG), free fatty acids (FFA), and polar lipids (PL) have been identified in *C. maritima* seeds, TAG representing the main form of reserve lipids. *Cakile maritima* also presents a high ratio of unsaturated fatty acid (Chalbi et al. 2015) since they represent 86.7% of total fatty acids. Erucic acid, an unsaturated fatty acid (22:1), is the most abundant fatty acid, accounting for about 30% of the total fatty acids (Zarrouk et al., 2003). Erucic acid is considered as anti-nutritional for animals (Rajcan et al., 1999, Zitouni et al., 2016) and a potent inhibitor of mammalian vasculature and heart functions (Christophersen and Bremer, 1972). However it is a valuable industrial feedstock (Domergue et al., 1999; Kaushik and Agnihotri, 2000) with a large number of applications in the chemical industry thanks to its technological characteristics, such as high lubricity, cold stability and fire resistance (Merchaoui et al., 2016; Zanetti et al., 2012). Moreover, high erucic acid seed oils can be processed enzymatically to produce biodiesel (Nath et al., 2016; Tao and He, 2006). Thus, as for other

Brassicaceae, the high lipid content of *C. maritima* seeds may also be useful for biofuel production (Papini et al., 2010). Saturated, mono-unsaturated and poly-unsaturated fatty acids have all been identified. An intra-specific heterogeneity was observed (Ghars et al., 2006), possibly due to environmental factors, such as precipitation (Pannelli et al., 1994; Rana & Ahmed, 1981), temperature (Champolivier & Merrien, 1996) or salinity (Zarrouk & Cherif, 1983). More, *C. maritima* seeds content a high proportion of phosphatidylcholine (56% of the total glycerophospholipids), a potential pharmaceutical ingredient especially in the treatment of neurological and liver diseases (Zitouni et al., 2016). The phospholipids molecular composition highlights the presence of linoleic and alpha-linolenic acids which are involved in human liver metabolism and promotion of gastrointestinal functions.

s0060 **3.3 Potential plant for phytoremediation and biosampling**

p0075 Halophytes are ideally suited for remediation of salt-affected soils and the revegetation of salinized land (Hasanuzzaman et al., 2014; Nouri et al., 2017; Shabala, 2013). Some halophytes also have a great potential for phytoremediation with respect to reducing the levels of toxic metals from saline soils (Lutts and Lefèvre, 2015). To our knowledge the capacity of *C. maritima* in the remediation of soils containing toxic metals has not been tested but it has been shown to tolerate high concentrations of cadmium and even accumulate it without altering physiological parameters (Ellouzi et al., 2013; Taamalli et al., 2014). Recent proteomic and metabolomic investigations allow observing up-regulation of thiol compound anabolism which allows an intracellular chelation of Cd^{2+} and its compartmentalization into the vacuole by a significant up-regulation of vacuolar transporters. These studies also allowed observation of the up-regulation of the PPP, Calvin cycle (both at the enzyme and metabolite level) and antioxidant system, and as a result it was more efficient in coping with heavy metals stress than common plants. Metabolomic results confirmed proteomic and previous physiological evidences, indicating that osmoprotectants, betaine and proline, together with plant hormones, methyl jasmonate and salicylic acid, might be involved in mediating responses to Cd^{2+} -induced stress (Taamalli et al., 2015). Concerning nickel *C. maritima* appears less tolerant than other halophytes such as *Sesuvium portulacastrum* (Fourati et al. 2016). *Cakile maritima* is also a potentially good candidate for polycyclic aromatic hydrocarbon phytoremediation (Shiri et al., 2015).

p0080 *C. maritima*, as a coastline plant species, is used as an indicator of the air trends around coastal areas. In this way, [Ribeiro et al. \(2017\)](#) found an accumulation of emerging contaminants revealing the level of these target emerging pollutants in the environment. Compared to others coastal plant species, *C. maritima*, thanks to its high water content, accumulates preferentially synthetic musk compounds and makes it a good biosampler.

p0085 All the above mentioned data are of practical significance in the context of biosaline agriculture using domesticated halophytes, since they point to the economic potential and the feasibility of cultivating *C. maritima*. Moreover *C. maritima* is also a suitable halophytic model to identify molecular mechanisms that regulate tolerance to salt stress in plants.

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4. Mechanisms and physiological adaptations to salinity

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Sodium is generally regarded as being toxic to the metabolism of plants, glycophytes and halophytes, at the concentrations required for the osmotic adjustment. Despite their polyphyletic origins, to regulate internal salt levels, halophytes have developed three main strategies: (i) salt exclusion at the root level, (ii) salt excretion through foliar glands and/or (iii) salt accumulation in their cells and tissues ([Hasanuzzaman et al., 2014](#); [Maathuis et al., 2014](#)). These mechanisms are not mutually exclusive, and a particular plant may use several of these different strategies depending on the circumstances ([Roy et al., 2014](#)). Not surprisingly, *C. maritima* also shows many of the typical halophytic responses.

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4.1 Na⁺ exclusion from the cell

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Ion homeostasis in the cytosol can be maintained by the restriction of Na⁺ accumulation which minimizes Na⁺ toxicity. The best described system in Na⁺ exclusion is the Salt Overly Sensitive (SOS) system, which is involved in the exclusion. Actually, the SOS system is also involved in the exclusion of Na⁺ by roots and in the loading of the xylem. The SOS system is composed of SOS1, SOS2 and SOS3 components. SOS3 is a myristoylated calcium binding protein, calcineurin B-like 4 (CBL4) which perceives the increase in cytosolic Ca²⁺ triggered by salt stress. This protein is able to interact and activate a serine/threonine protein kinase, the CBL-interacting protein kinase 24 (CIPK24, also called SOS2). This complex finally activates the SOS1 Na⁺/H⁺ antiporter ([Ji et al., 2013](#)). SOS1 mediates Na⁺ efflux to the apoplast against the electrochemical potential using secondary active

transport driven by the H^+ gradient across the plasma membrane established by H^+ -ATPase. The activity of SOS1 is required for the resistance of salinity for halophytes and the loss of 50% of this activity causes a loss of halophytism in *Thellungiella salsuginea* (Oh et al., 2009). Cosentino et al. (2010) highlight the SOS1 activity in *Mesembryanthemum crystallinum*, a facultative halophyte. In this species there was no increase of the expression of SOS1 during a salt stress to the roots, but there was in the leaves. This observation suggests that SOS1 has not a major role in xylem loading but rather in the maintenance of low cytosolic Na^+ . The expression of SOS1 in roots, stems and leaves was shown to be induced by salt stress in the glycophyte *Salicornia oleracea*, whereas in the halophyte *Salicornia dolichostachya* SOS1 has a high (up to 100-fold more) and constitutive expression (Katschnig et al., 2015). In *C. maritima*, our data highlights the presence of SOS-like genes *CmSOS1* (accession number KY286433), *CmSOS2* and *CmSOS3* (Arbelet-Bonnin et al. 2018). These SOS-like genes present constitutive expressions that could be regulated according to the NaCl concentrations as highlighted in Fig. 3 and as observed for *S. dolichostachya* (Katschnig et al., 2015). Moreover the SOS system activation during salt stress seems to be dependent on a 1O_2 production, then an intracellular calcium increase allowing the initiation of SOS system toward survival (Arbelet-Bonnin et al., 2018) (Fig. 4).

s0075 4.2 Na^+ excretion from leaves

p0100 Halophytes frequently have specialized morphological structures that they use for an external sodium sequestration. The most famous structure present in 50% of the halophytes is the salt bladder. Salt bladders have not been observed in *C. maritima*. However Ciccarelli et al. (2010) studied two morphotypes of *C. maritima* in Italy that have different leaf morphological adaptations. Indeed, one morphotype had pennatifid leaves and not the other one. Actually large vesicular cells turned outward are present on the pennatifid leaves surface whereas the other morphotype has very small one and slightly turned outward. But, in the two cases, the vesicular cells presents salt crystals localized in the wall pore on the upper and lower sides. The authors suggest that these specific cells are involved in salt excretion like epidermal bladder cells (Ciccarelli et al., 2010) (Fig. 4).

s0080 4.3 Na^+ accumulation in leaves and cells

p0105 The control of intracellular sodium concentration for plants coping with salinity may also be achieved by compartmentalization of Na^+

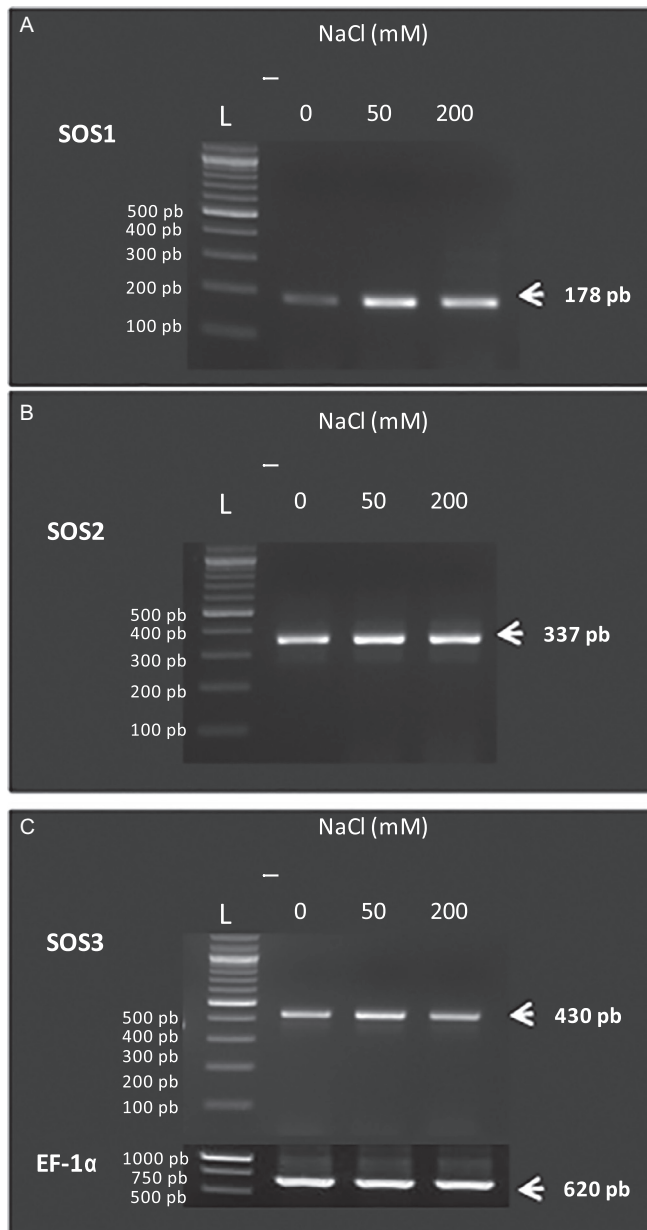


Fig. 3 Relative expression of *CmSOS1*, *CmSOS2* and *CmSOS3* according the NaCl treatment. (A, B and C). EF1 α gene expression as control (C). Total RNA was extracted from cell culture of *Cakile maritima*. The extraction was made with Trizol/chlorophorm method. DNA contaminations was removed from RNA samples to use kit DNase I amplification grade (SIGMA-Aldrich) and 1 μ g of RNA was then reverse transcribed

predominantly in vacuoles (Fig. 4), thereby maintaining Na^+ concentrations in the cytoplasm within tolerable levels (Flowers and Colmer, 2008; Shabala et al., 2013). Sequestration of Na^+ in the vacuole is possible thanks to: (i) the presence of $\text{NHX Na}^+/\text{H}^+$ antiporters in the tonoplast which can increase in activity under salt stress (Zhang et al., 2008) and (ii) V-H^+ -ATPases which create the pH gradient between cytoplasm and vacuole allowing transport Na^+ against its electrochemical gradient into the vacuole (Flowers and Colmer, 2008, Hasegawa 2013, Shabala, 2013; Zhu, 2001). The combined stimulation of both these transporters seems to be important in the adaptation of halophytes to salt stress (Qiu et al., 2007). The compartmentalization of Na^+ in the vacuole contributes not only to ion homeostasis and cell turgor, but also protects the metabolic enzymes from salt toxicity (Aharon et al., 2003). The accumulation of Na^+ and Cl^- in the vacuole also increases stem or leaf succulence. The succulence in leaves, or stems characteristic of numerous halophytes, is associated with an increase in cell size, a decrease in surface area per tissue volume and a high water content per unit surface area (Short and Colmer, 1999).

p0110 In *C. maritima* cultured cells, the Na^+ accumulation is dose dependent but fourfold less important than in *A. thaliana* cultured cells (Ben Hamed-Laouti et al. 2016b). The authors highlighted the involvement of non-specific-cation-channels (NSCC) in Na^+ influx (Fig. 4). In *C. maritima*

with the Superscript II RT kit (Life technologies). The cDNAs were amplified with PCR reaction with the appropriate primers (below). Primers were designed thanks to the blast and comparison of SOS1, SOS2 and SOS3 cDNA sequences already known in other plant species (*Arabidopsis thaliana*, *Camelina sativa*, *Thellungiella halophila*, *Capsella rubella* for SOS1; *Arabidopsis thaliana*, *Camelina sativa*, *Eutrema salsugineum*, *Brassica napus* for SOS2; *Arabidopsis thaliana*, *Brassica napus*, *Brassica oleracea*, *Camelina sativa* for SOS3). The temperature of annealing is 50 °C with 30 s of extension. The amplification products were separated by electrophoresis on 1.5% agarose gel.

t0010

Name	Primer reverse	Primer forward	Length (bp)
CmSOS1	CCT TTG AAT GCT GTC CTT GC	TGT CTC GGT TCT TTG GCT CA	178
CmSOS2	TCA AGW GTT TCA CCA GCA GC	TTG AGG GVA GTT ATG TAG CG	350
CmSOS3	CCT TTA GAT ANG GCA ANG TCA TG	GAN GGT CTT ATT CAT AAG GAA GA	430

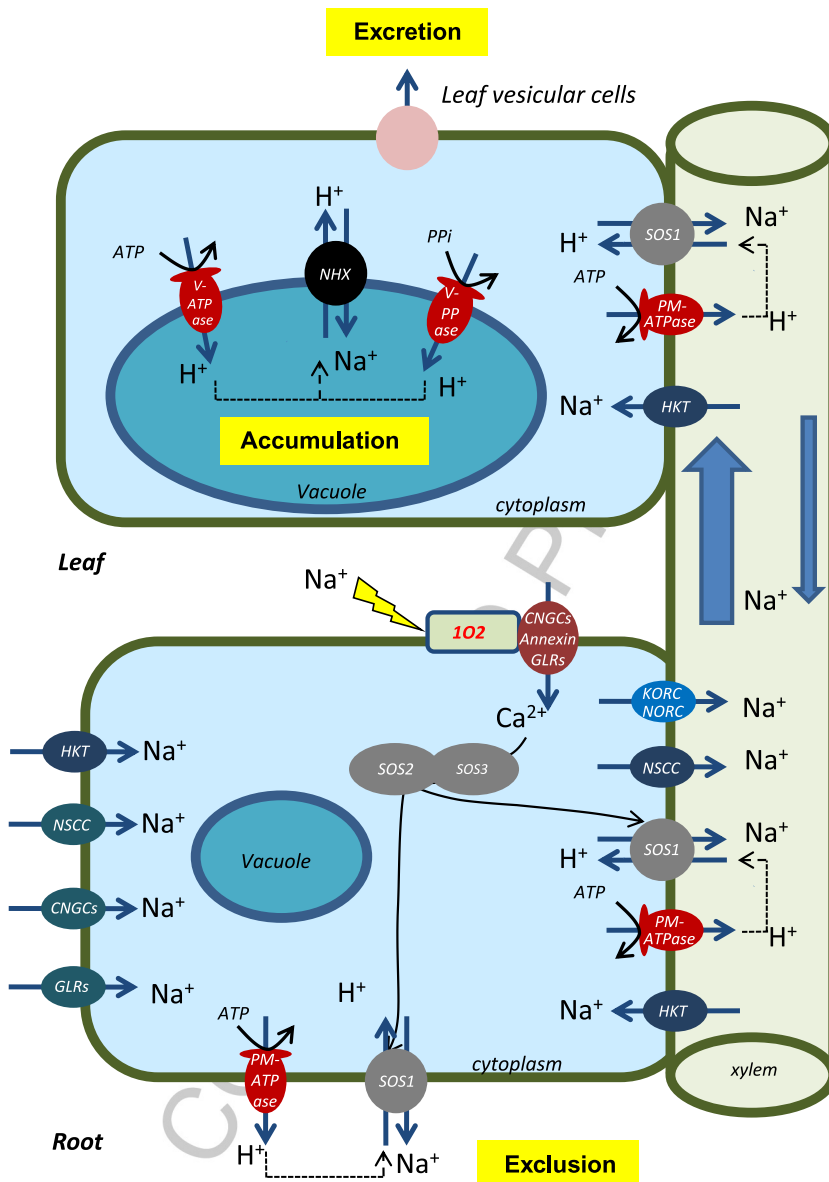


Fig. 4 Overview of the Na⁺ fluxes recently described in plant cells and their role the tissue-specific regulations. Some mechanisms are still debated and/or concerned a limited number of halophytes.

leaves the Na^+ concentration increased with increasing Na^+ concentrations in the medium (Ben Hamed-Laouti et al. 2016a; Debez et al., 2004) and no salt-related toxicity symptoms were noted. Moreover high leaf Na^+ concentration was associated with increased leaf thickness and succulence (Debez et al., 2006; Fig. 1B) suggesting the existence of mechanisms for compartmentalization of Na^+ in these organs. The increased succulence being correlated with the water status of the leaves could be interpreted as an adaptation in terms of conservation of internal water and dilution of accumulated salts (Koyro and Lieth, 2008). Moreover the increased activity of V-H^+ -ATPases since 300 mM NaCl in *C. maritima* leaves has been reported (Debez et al., 2006). This activity could provide the necessary proton driving force triggering sodium transport toward the vacuole. These are typical adaptations of plant halophyte includer (Fig. 4).

s0085 **4.4 Sodium and potassium homeostasis**

p0115 The K^+ homeostasis at the whole plant and cellular levels plays a crucial role in salt adaptation of plants and some studies (Shabala and Cuin, 2008) present an approach of salt tolerance involving targeting K^+ homeostasis in plant tissues. An important concentration of Na^+ in soil triggers a water exit out of the cell and at the same time a reduction of cell turgor. This osmotic reaction impacts the leaf and root elongation until the organism adjusts its osmotic condition thanks to the K^+ . The same compartment is observed for cells individually. The retention of K^+ in the cytosol to ensure an optimal K^+/Na^+ ratio was observed in *Quinoa* (Bonales-Alatorre et al., 2013). Thus the ability to regulate Na^+ and K^+ uptake and transport to the shoot seems crucial for salt tolerance in plants (Munns, 2005; Tester and Davenport, 2003). The sodium regulation in the organism of the plant implies its transport along the xylem. The halophytes have the capacity to use Na^+ as an osmoticum to maintain the cell turgor and create a gradient into the xylem to drive the water to the shoot (Shabala, 2013). If the transport system in the parenchyma-xylem interface is not yet totally understood, the outward-rectifying K^+ channels KORC and NORC could effectively be involved in the xylem loading of K^+ but also of Na^+ (Deinlein et al. 2014). There are also hypotheses on the involvement of non-selective Na^+ channels; active pump or co-transporters (Fig. 4). In *Salicornia dolichostachya* the role of the SOS1 transporter into the roots to assure a xylem loading toward the shoots was reported (Katschnig et al., 2015). More, the Na^+ tolerance depends on the rapid regulation of the xylem loading. The recirculation

of sodium from the shoot to the root seemed to be mediated by the high affinity K^+ transporter (HKT) which has an important role in salt tolerance. HKT class 1 (HKT1) proteins exhibit high Na^+ selectivity, while class 2 (HKT2) proteins are more selective for K^+ than Na^+ or are non-selective (Hasegawa, 2013).

p0120 In *C. maritima*, salt treatments (100 to 500 mM) decreased the net uptake rates of K^+ and caused a reduction in the K^+/Na^+ ratio compared with no salt treatment. However the K^+ use efficiency is proportional to the external salinity and may offset the lower nutrient uptake to contribute to the halophyte survival (Debez et al., 2008). The K^+ could be replaced by Na^+ for osmotic adjustment by accumulation in the shoot vacuoles. Ellouzi et al. (2011) observed an increase in K^+ concentration in shoots with time but it didn't change in roots. This result is possible thanks to the absorption of K^+ even in salt condition because *C. maritima* exhibited a higher selectivity for K^+ over Na^+ . Although the translocation of Na^+ through xylem seems obvious in *C. maritima* in view of the leaves accumulation, and the presence of SOS system now verified (Arbelet-Bonnin et al., 2018), no research elucidates at the molecular level the xylem role on the Na^+ regulation.

s0090 4.5 Osmotic stress tolerance

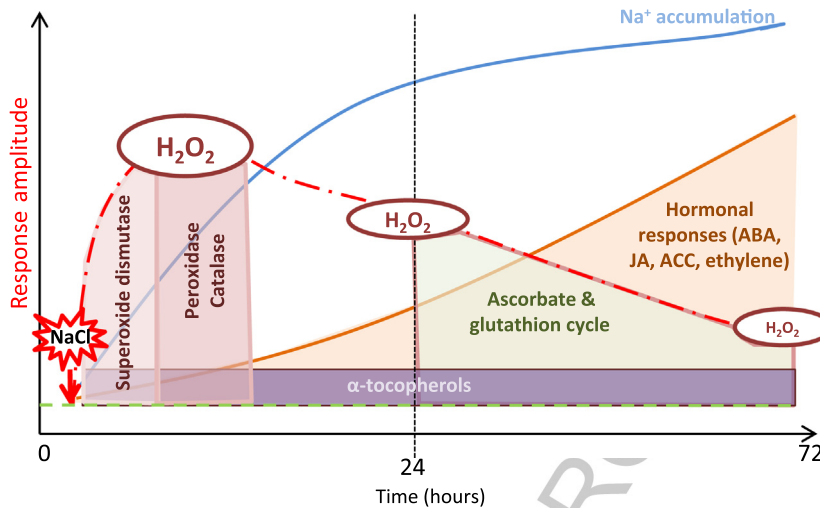
p0125 To grow in saline soil halophytes need to adjust osmotically to maintain a positive turgor pressure. The K^+ homeostasis as the accumulation of high concentrations of Na^+ and Cl^- are thought to be achieved by intracellular compartmentalization within vacuoles (Flowers and Colmer, 2008, Flowers et al., 2015). However, the accumulation of glycine-betaine and proline two important organic osmotica is also involved in osmotic adjustment in response to low external water potential (Flowers and Colmer, 2008). The halophytes have effectively the capacity to control the catabolism of the proline and greatly accumulate it in the cell compare to the glycophytes after a salt stress (Duarte et al., 2014; Sanada et al., 1995). It is further noteworthy that glycine-betaine as proline accumulation could play a role in ROS homeostasis in halophytes (Katschnig et al., 2013) and serve in preservation of the structural and functional integrity at the cellular level (Jdey et al., 2014). The leaves and roots of *C. maritima* have a proline pool similar to *A. thaliana* under non-saline conditions, but after 72h of salt stress, *C. maritima* had two- and threefold higher concentrations of proline in leaves and roots, respectively, than in *A. thaliana* (Ellouzi et al., 2014). Thus

C. maritima could use organic osmotic in addition to compartmentalize Na^+ for osmotic adjustment. It is further noteworthy that the decrease of sterols percentage and the increase of sitosterol/stigmasterol ratio could be important for the membrane flexibility and resistance and improves the water permeability in the roots of *C. maritima* treated with 200mM NaCl (Chalbi et al. 2015). In their natural habitat, the sand dune *C. maritima* presents a sap osmotic pressure above the others halophytes present in the same environment. They also can accumulate more Na^+ than species with the same osmotic pressure (Storey et al., 1977).

s0095 **4.6 Regulation of reactive oxygen species (ROS) in response to salinity**

p0130 Reactive oxygen species are important in the cell for all organisms in their signaling pathway, but, large accumulation of ROS in the cell can trigger an oxidative stress. This can induce lipid peroxidation that cause damage to DNA and denature proteins for examples. Plant sensitivity to ROS seems to differ between glycophytes and halophytes. Actually, halophytes endure a higher level of ROS since high salinity can lead to the formation of ROS. Scavenging of ROS is thus critical in plant salt tolerance, and accordingly halophytes are equipped with powerful antioxidant systems, including enzymatic and non-enzymatic components to regulate the level of ROS in the cell (Bose et al., 2013). Halophytes have the capacity to regulate the superoxide dismutase (SOD) activity to tolerate oxidative stress due to salinity (Jithesh et al., 2006; Ozgur et al., 2013). This enzyme converts the O_2^- in H_2O_2 , a more stable ROS that can be transformed to H_2O using catalase (CAT) and peroxidase (POX). *Cakile maritima* contains a total of 10 SOD isozymes: 2 Mn-SODs, 1 Fe-SOD, and 7 CuZn-SODs, where the Fe-SOD is most prominent isozyme in the different organs analyzed (Houmani et al. 2016). The activity of these SOD isozymes is modulated during development and under high long-term salinity (400mM NaCl) stress conditions (Ellouzi et al., 2011; Houmani et al. 2016). Actually *C. maritima* also increased the activity of the CAT and the POX at the same time and with the same kinetic (Fig. 5). Those effective activities of SOD, CAT and POX allow reducing the H_2O_2 level in the *C. maritima* leaves and for a long time (72h after the salt treatment) (Ellouzi et al., 2011).

p0135 The presence of *C. maritima* in different places in the world or in the same country shows different antioxidant activities according to the humidity or aridity of the climate. In Tunisia, for example, higher polyphenol content and antioxidant activity partly explained the better salt-tolerance of



f0030 **Fig. 5** Coordination of the overtime physiological responses of *C. maritima* to salt stress. Dotted line: response in absence of salt.

C. maritima accession from arid region (Ben Amor et al., 2006; Ksouri et al., 2007, 2008) even if the lipid peroxidation after a drought stress did not change according to the provenance (Jdey et al., 2014).

p0140 In addition to the enzymatic system to scavenge ROS, halophytes have a great system of non-enzymatic antioxidants. The most common antioxidant system in plants is the ascorbate and glutathione cycle. Actually, the salt treatment induces an increase of reduced ascorbic acid and glutathione in halophytes (Cao et al., 2015). In *C. maritima*, the reduced ascorbate is four-fold more important than in *A. thaliana* without a salt stress in the leaves and comparable in roots (Ellouzi et al., 2011) (Table 1). In addition during a salt stress, the reduced ascorbate increases up to threefold the starting rate in the whole plant. About glutathione, the proportion of reduced glutathione increases only under the salt stress and is three- to fourfold more important after 72 h of treatment (Fig. 5). The antioxidant mechanisms took place early following salt exposure in *C. maritima* when compared to *A. thaliana* (Ellouzi et al., 2011). Those data suggest a rapid intrinsic capacity to *C. maritima* to deal with a salt stress and to boost its metabolism to detoxify its organism (Ellouzi et al., 2014).

p0145 Plants also use tocopherols, types of vitamin E containing α -, β - and γ -tocopherols, which have a great antioxidant power. They detoxify lipid peroxy radicals and singlet oxygen (1O_2) during an abiotic stress like salt stress in both glycophytes and halophytes (Bose et al., 2013). *Cakile maritima*

Table 1 Variations of *Cakile maritima* metabolite content in salt conditions compared to *A.thaliana*.

Metabolism	Metabolite	Response to salt treatment	Part of plant	Level compared to <i>A. thaliana</i>	References
Photosynthesis	Chlorophylls	↑ up to 300 mM NaCl	Leaves	=	Debez et al. (2008), Ellouzi et al. (2014)
Antioxidant pathways	Polyphenol content	↑ up to 100 mM NaCl then ↓	Leaves (Jerba accession)		Ksouri et al. (2007)
		=	Leaves (Tabarka accession)		
	Dehydroascorbate		Leaves	Threefold more	
	Ascorbate	↑	Cell culture	Fourfold more	Ben Hamed Laouti et al. (2016b)
		↑	Leaves	=	Ellouzi et al. (2014)
	Glutathione		Roots	Twofold less	Ellouzi et al. (2014)
		↑	Leaves	=	Ellouzi et al. (2014)
	Tocopherols	↑	Roots	Twofold more	Ellouzi et al. (2014)
		=	Leaves	=	Ellouzi et al. (2014)
Osmoregulation	Proline	↑	Root/leaves		Ellouzi et al. (2014)
Hormonal pathways	Acide abscisique	↑	Leaves	Sevenfold more	Ellouzi et al. (2014)
		↑	Roots	Twofold less	
	Jasmonic acid	↑	Leaves	Fourfold less	Ellouzi et al. (2014)
		↑	Roots	Fourfold less	
	Aminocyclopropane-1-carboxylic acid	↑	Leaves	Twofold more	Ellouzi et al. (2014)
		↑	Roots	=	

Continued

Table 1 Variations of *Cakile maritima* metabolite content in salt conditions compared to *A.thaliana*.—cont'd
Level compared to *A. thaliana*

Metabolism	Metabolite	Response to salt treatment	Part of plant	References
Fatty acids	Palmitoleic (16:1)	=	Leaves and roots	Chalbi et al. (2015)
	Oleic (18:1)	=	Leaves and roots	Chalbi et al. (2015)
	Linoleic (18:2)	=	Leaves and roots	Chalbi et al. (2015)
	Linolenic (18:3)	=	Leaves and roots	Chalbi et al. (2015)
Sterols	Brassicasterol	↑ up to 100mM NaCl then ↓	Leaves	Chalbi et al. (2015)
		↓	Roots	Chalbi et al. (2015)
	Campesterol	↑ up to 100mM NaCl then ↓	Leaves	Chalbi et al. (2015)
		↓	Roots	Chalbi et al. (2015)
	Stigmasterol	↑ up to 100mM NaCl then ↓	Leaves	Chalbi et al. (2015)
		↓	Roots	Chalbi et al. (2015)
	Sitosterol	↑ up to 100mM NaCl then ↓	Leaves	Chalbi et al. (2015)
		↓↓	Roots	Chalbi et al. (2015)

has a large pool of α -tocopherols (two- to fivefold more than *A. thaliana*) that is not increased upon 100mM salinity treatment (Ellouzi et al., 2011). In contrary, the pool of γ -tocopherols is less important when compared to *A. thaliana* (10-fold minus) and no change was observed during salt treatment. γ -tocopherols seem to respond to osmotic stress but not to salt induced oxidative stress unlike the α -tocopherols. Polyphenols are another group of powerful antioxidants, scavenging the majority of ROS in the cell (Bose et al., 2013). Ksouri et al. (2007) showed that *C. maritima* regulates its phenols content according to its environment. So, an extreme climate triggers a significant increase in phenols content to deal with extreme conditions as important salt concentrations in soil (Ksouri et al., 2008). Others non enzymatic antioxidants mechanisms known in halophytes such as polyols, iron-binding proteins, carotenoids and sulphated polysaccharides have not yet been described in *C. maritima*.

p0150 In *C. maritima*, the oxidative stress could be reduced with calcium treatment improving the salt tolerance and consequently the growth. Effectively the addition of moderate calcium (3,5 mM) increases the activity of antioxidant enzymes in presence of 100mM NaCl; 300% for POX, 200% for SOD, 183% for ascorbate peroxidase, 150% for monodehydroascorbate reductase, 180% for dehydroascorbate reductase and 200% for glutathione reductase (Ben Amor et al., 2010).

p0155 Recent researches use *C. maritima* to describe the ROS and reactive nitrogen species (RNS) signals through the plant in response to a mechanical wounding (Houmani et al., 2018). Indeed, the injury of the seedlings hypocotyls triggered a local oxidative stress response noticeable by H_2O_2 content increase and lipid peroxidation. More, the authors noticed a higher SOD activity in the roots and in the green cotyledons. This study on *C. maritima* reveals ROS and RNS propagated signals in the whole plant due to a local injury beyond to its salt resistance research. Since NaCl was shown to induce action potentials in sunflower seedlings (Stolarz and Dziubinska, 2017) further studies would be needed to search for a putative role of NaCl-induced ROS in systemic electrical signaling in *C. maritima*.

s0100 4.7 Hormonal responses to salt stress

p0160 The main plant hormones involved in response to salt stress are abscisic acid (ABA), jasmonic acid (JA) and ethylene. They are strongly cross-linked with ROS regulation and life/dead scale under salt stress (Ismail et al., 2014; Kazan, 2015; Zhang et al., 2016). ABA is synthesized in roots and

transported to the others part of plant including leaves to control the stomatal closure and the transcription of genes involved in abiotic stress response. In *C. maritima*, a salt stress triggered an increase of ABA 6–16-fold more important than in control after 4 h of treatment in the leaves and 72 h in the roots, respectively (Table 1). An increase of 10–35-fold in the roots and leaves, respectively, for both JA and 1-aminocyclopropane-1-carboxylic acid (ACC, the precursor of ethylene) production, was reported 72 h after the beginning of the treatment (Ellouzi et al. 2014). In leaves of *C. maritima* the increases of JA and ACC were strongly correlated (Fig. 5) and the abundance of the ethylene response factor1 (ERF1) transcripts, a transcription factor that mediates the expression of a number of defense genes (Solano et al. 1998), was very high under salt stress. Although, ethylene seems regulated differently in accordance to the plant organ, these regulations could improve *C. maritima* performance against salt stress (Ellouzi et al. 2014).

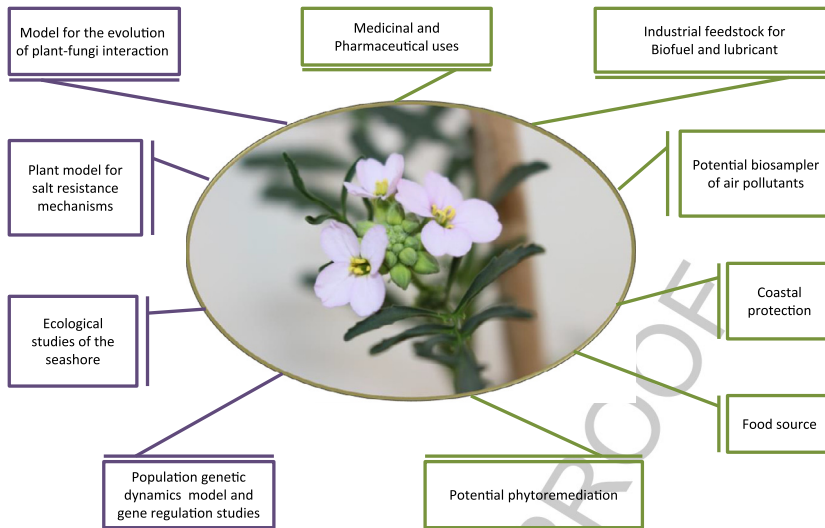
s0105 **4.8 Na⁺ impact on photosynthesis**

p0165 Salinity also has an impact on photosynthesis which is directly linked with biomass production. For photosynthesis to occur, the plant must contain adequate chlorophyll, in intact chloroplasts, and the stomata must be open. These physiological parameters are important clues to determine the photosynthetic activity. In *T. Nitratia*, the structure of seedling leaf chloroplasts was observed during 7 days at 500 mM NaCl. The treatment affects the granum thylakoids through the apparition of osmiophilic bodies, thus possibly the function of chloroplasts. The photosynthesis rate and the stomatal conductance decrease by 3 days of treatment. Combined with a diminution of the transpiration rate, this suggests a stomatal closure. The reduction of stomatal aperture in response to salt stress is a characteristic response of salt-adapted plants and may prevent water loss through transpiration. But, even if the stomatal conductivity decreases, the intracellular CO₂ is not affected. Moreover, the efficiency of PSII photochemistry increased during the salt stress. These results suggest a significant regulation of photosynthesis during salt stress (Cheng et al., 2015). In *C. maritima*, Debez et al. (2008) showed that the pigment content increased during the salt stress (chlorophyll and anthocyanin) (Table 1). In addition the increase in stomata number triggers the water use efficiency increase. Finally, both the CO₂ uptake and the specific activity of Rubisco rise of 75% at the optimum salinity for the growth (Debez et al., 2006, 2012). Comparative proteome analysis of leaf tissue upon salt-exposure of *C. maritima* to 100 mM NaCl for 1 month revealed

44 proteins with different abundance changes, most of which being involved in energy metabolism (Debez et al., 2012). A significantly higher abundance of several proteins involved in photosynthesis was reported (Debez et al., 2012). At 100 mM NaCl PSII maximum quantum efficiency was not significantly different from the control but decreased largely at high salt concentrations (300 and 500 mM NaCl) (Ellouzi et al., 2014). It thus seems that the photosynthetic activity was significantly improved in *C. maritima* at an optimal salinity of 100 mM NaCl, followed by a decline at higher salinities mainly due to stomatal closure (Debez et al., 2008).

s0110 4.9 Na⁺ impact on programmed cell death

p0170 Apart from death due to Na⁺ and Cl⁻ toxicity, possibly through insufficient osmotic adjustment, diversion of energy, toxicity to metabolism and damage from ROS (Flowers et al., 2015), several studies reported NaCl-induced programmed cell death (PCD) process in plants (Huh et al., 2002; Lin et al., 2006; Monetti et al. 2014; Wang et al., 2010; Yang et al. 2014). Na⁺ influx effectively triggers a cell depolarization followed by mitochondrial dysfunction, ROS generation and caspase-like activation participating in PCD processes observed in glycophytes as tobacco and *A. thaliana* (Ben Hamed-Laouti et al., 2016a, b; Lin et al. 2006, Monetti et al. 2014) and halophyte as *Thellungiella halophila* (Wang et al. 2010). The retention of K⁺ in the cytosol observed in *Quinoa* leaves (Bonales-Alatorre et al., 2013) could be essential to maintain the activity of metabolic enzymes and inhibits the caspase-like activity triggered the cell death (Shabala, 2009). Although the role of such PCD is not clearly known, such process could be regarded as a salt adaptive mechanism; e.g., PCD-mediated elimination of the primary root in response to salt could be a mechanism that facilitates the production of most capable roots to cope with a saline environment (Huh et al., 2002; Katsuhara and Shibasaka, 2000). Using *C. maritima* cultured cells, the same signaling events leading to PCD were reported (Ben Hamed Laouti et al., 2016b). However, interestingly, upon salt stress a larger part of the cell population was allowed to survive in *C. maritima* cultured cells when compared to *A. thaliana* cultured cells. Furthermore this behavior seemed to be correlated to the cell ability to repolarize rapidly upon the salt stress. So salt stress seems to induce two distinct pathways with their own physiological responses; one toward death and another one to survive that succeeded to cope with salt (Ben Hamed Laouti et al., 2016b; Arbelet-Bonmin et al., 2018).



f0035 **Fig. 6** Potential and confirmed uses of the halophyte *Cakile maritima*. Research uses in green and others in purple.

s0115

5. *Cakile maritima*, a halophyte model for future research and a putative crop

p0175

Although, knowledge on molecular responses of *C. maritima* toward salinity are limited at the moment, this plant is worthy of attention, because it meets all the criteria for being a good genetic model of halophyte (Fig. 6), since it has developed several physiological and morphological adaptations to cope with salt stress (e.g., putative succulence and leaf exclusion of Na^+ ; use of Na^+ for osmotic adjustment and efficiency of selective K^+ uptake, in spite of high Na^+ concentration in the medium allowing maintenance of cellular integrity and water status or preservation of the functional integrity of the photosynthetic apparatus).

p0180

Furthermore, the species has a small diploid genome closely related to those of *Arabidopsis thaliana* that will facilitate genetic analysis thanks to its sequenced genome. It has a short life cycle and it produces a large amount of seed. The recent establishment of a suspension culture which preserves its salt resistance (Ben Hamed et al., 2014) should provide an opportunity to gain insights into the cellular biology of *C. maritima*. Moreover, thanks to its great genetic diversity and a high potential of adaptability, *Cakile maritima* populations have a large geographical and ecological distribution.

This makes it an ideal model to study phenological adaptation to climate. In addition, its ability to produce numerous secondary compounds and oilseed could be very valuable for its development as a putative crop for biosaline agriculture in the future.

st0130 Acknowledgments

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Non-Print Items

Keywords: *Cakile maritima*, Halophytes, Salinity, Plant model, Alternative crop

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