



Salt tolerance traits revealed in mandarins (*Citrus reticulata* Blanco) are mainly related to root-to-shoot Cl^- translocation limitation and leaf detoxification processes

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ABSTRACT

Mandarin is an important genetic group in citrus largely used for variety breeding programs and also to generate new rootstocks better adapted to abiotic stress. In this study, 14 mandarin accessions representative of the diversity in this group were analyzed for their salt stress tolerance properties. Physiological parameters such as gas exchange, osmotic pressure, as well as leaf and root chloride contents were measured. Samples were harvested to characterize the presence of hydrogen peroxide and to monitor the activity of enzymes involved in reactive oxygen species synthesis and detoxification processes. Very different physiological behaviors were noted among accessions. Most cultivars that are used as rootstocks such as *Citrus reshni* Hort. ex Tan. ('Cleopatra') or *Citrus depressa* Hayata ('Shekwasha'), were found to be tolerant, with limited root-to-shoot chloride translocation. Also, some accessions used as varieties showed similar tolerance traits. Interestingly some accessions that presented high leaf chloride contents were not always associated with sensitivity traits. Also accessions such as 'Willowleaf' showed quite high leaf chloride contents that were correlated with better detoxification processes. Tolerance traits that we identified are discussed in relation to the known genetic structure in mandarins. Finally, some of the salt stress tolerant accessions that we identified could potentially be used as parents in rootstock breeding programs and others in scion variety breeding programs.

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1. Introduction

Mandarins belong to the *Citrus* genus and are, depending on the accession, used in breeding programs to generate new varieties with good fruit quality traits or rootstocks conferring better adaptation to abiotic stress. However, a very limited number of accessions are used and little is known regarding the properties of adaptation of most mandarin accessions to salt stress. Most mandarins are highly polyembryonic which allows clonal propagation by seedlings. Extensive studies have been carried out in

recent decades to unravel the role of mandarins in citrus cultivar evolution (Nicolosi et al., 2000; Froelicher et al., 2011), while establishing the phenotypic and genetic phylogeny (Mabberley, 1997; Nicolosi et al., 2000; Garcia-Lor et al., 2013). If mandarin germplasm was classified as *C. reticulata* Blanco by Mabberley (1997), classified it in *C. reticulata* and *C. tachibana* (Mak.) and Hodgson (1967) divided mandarins into four species, including *C. unshiu* (satsumas), *C. reticulata* ('Ponkan', 'Dancy', Clementines), *C. deliciosa* ('Willowleaf') and *C. nobilis* ('King'). Tanaka classification (1954) is still commonly used and divides mandarins and related species into five groups that included 36 species. From this classification based on morphological differences in the tree, leaves, flowers, and fruits, we selected for our study different accessions representative of the most important groups. Taking together the different classifications demonstrate the great diversity in mandarins.

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Regarding the cytoplasmic origin, mandarins can be split into two different genotypes (or mitotypes) according to mitochondrial markers: mandarins used as varieties that present a sweet fruit taste and mandarins used as a rootstock the present an acidic fruit taste. 'Nasnaran' presents a particular mitotype because it seems to be an interspecific hybrid between Papeda and mandarin (Froelicher et al., 2011; Ollitrault et al., 2012). Also, Cheng et al. (2005) identified 6 chlorotypes among 10 mandarins using chloroplast markers, which were mostly grouped in a single cluster.

Salinity is one of the major abiotic constraints that affects agriculture, especially in countries where irrigation is required (Flowers, 2004). Citrus species are classified as salt sensitive (Maas, 1993). The impact of salinity on plant growth and development is associated with a decrease in the osmotic potential, accumulation of Cl^- and Na^+ ions to toxic levels, and nutritional imbalances (Byrt and Munns, 2008). In some cases, irrigation using saline water may lead to an increase of salt contents in soils causing a dramatic reduction in plant growth and fruit yields (Maas, 1993; Storey and Walker, 1998).

Plants regulate their osmotic potential after stomata closure and subsequent limitation of photosynthesis, which involves several processes such as K^+ uptake, Na^+ and Cl^- compartmentalization into the vacuole and apoplast, and synthesis of compatible solutes (Ashraf, 1994). In salt stress condition, accumulation of K^+ and compatible solutes will promote the maintaining of subcellular structure and cellular turgor and the increase in the osmotic potential of the cell in plants (Ashraf and Foolad, 2007). Many of these compatible solutes are N-containing compounds, such as amino acids, hence nitrogen content and metabolism in plant is of central importance for salt tolerance (Läuchli and Lüttge, 2002). In addition to salt stress, a secondary effect of the presence of toxic ions is the triggering of oxidative stress leading to Reactive Oxygen Species (ROS) overproduction such H_2O_2 (Gómez-Cadenas et al., 1996; Gueta-Dahan et al., 1997; Tanou et al., 2009). ROS will cause damage by altering cellular components such DNA, proteins and membrane lipids (Mittler, 2002). Plants have evolved efficient antioxidant systems that can protect them from the damaging effects of oxidative stress (Asada, 1999). Among them, antioxidant enzymes are involved in H_2O_2 formation from superoxide (O_2^-) such as superoxide dismutase (SOD, EC 1.15.1.1) or H_2O_2 scavenging such as catalase (CAT, EC 1.11.1.6) and peroxidase (POD, EC 1.11.1.7) can be cited. The adverse effects of salinity on common citrus genotypes have been extensively reported in the literature (Atmane et al., 2003; Lopez-Climent et al., 2008; Saleh et al., 2008; Garcia-Sanchez and Syvertsen, 2009; Hussain et al., 2012) which include leaf injury symptoms, halted growth and decreased fruit yield. Mandarins such as 'Cleopatra' and 'Sunki' (*C. reshni* Hort. ex Tan., *C. sunki* Hort. ex Tan., respectively) are considered to be well adapted to abiotic constraints (Maas, 1993; Moya et al., 2002; Brumós et al., 2009; Gimeno et al., 2009). Moreover, depending on the grafted variety and the cropping site, these rootstocks may enhance the fruit quality (Campbell and Lincoln, 1962; Hardy, 2004). However, these accessions are sensitive to diseases such as *Phytophthora* root rot and/or *Citrus Tristeza Virus* (CTV), which currently limit their use as rootstock. Contrary to most other plants, citrus damage caused by salinity is usually associated with Cl^- accumulation but not sodium uptake (Banuls et al., 1997; Moya et al., 2003; Hussain et al., 2012). Trifoliolate oranges belong to the *Poncirus* genus and their hybrids confer tolerance to CTV and they are considered to be poor Cl^- excluders (Cooper, 1961), although they have a great capacity to exclude Na^+ at low salinity levels (Walker, 1986). 'Cleopatra' mandarin was shown to be a Cl^- excluder (Cooper et al., 1952; Zekri and Parsons, 1992), which explains the salt-tolerant nature of this rootstock. According to Moya et al. (2003), if Cl^- absorption is not limited at the root level, these ions will be translocated to the leaves via transpiration and will cause necrosis and eventually defoliation.

Then, leaf Cl^- content can be considered as a good criterion to evaluate salt stress properties of seedlings and rank genotypes (Hussain et al., 2012). Accessions such as 'Cleopatra' and 'Sunki' mandarins, in association with trifoliolate oranges, are thus widely used in rootstock breeding programs to convey biotic and abiotic traits of tolerance (Forner-Giner et al., 2009; Schinor et al., 2013).

So far, interest in mandarins varieties has mainly been focused on fruit quality criteria and little is known regarding their inherent abiotic stress tolerance properties. Recently, very different sensitivity/tolerance traits were reported in a study dedicated to characterization of salt stress tolerance of citrus genotypes representing different *Citrus* species, as well representatives of *Poncirus trifoliata* and *Fortunella* genera (Hussain et al., 2012). The salt stress tolerance capacity of *Citrus* seems to be strictly dependent on the capacity of the accession to reduce central metabolic processes related to carbon utilization and toxic ion exclusion (Brumós et al., 2009). Our recent studies suggest that tolerance traits are only present in two fundamental species of the *Citrus* genus, mandarins (*C. reshni* and *C. sunki*) and pummelos (*C. maxima*), respectively (Hussain et al., 2014).

In this study, 14 polyembryonic accessions representative of the mandarin diversity were subjected to progressive salt stress for almost 3 months. Seedlings were investigated by measuring fresh root and shoot mass, gas exchanges, Cl^- and H_2O_2 contents and monitoring SOD, CAT and POD activities. The salt stress tolerance properties of the different accessions are discussed on the basis of their parental genetic origin, as well as their potential usefulness as rootstock and in scion variety breeding programs.

2. Materials and methods

Seeds of fourteen mandarin accessions representative of the diversity in this *Citrus* species (Tanaka, 1954) were provided by the INRA-CIRAD station in Corsica, France (Table 1). *C. nobilis* Lour., according to Tanaka classification (1954), ('King' (KioS)) represented group 1; *C. reticulata* Blanco, ('Anana' (Anan), 'Ponkan' (Ponk), 'Sun Chu Sha' (SuCS)) represented the group 2, *C. deliciosa* Ten ('Willowleaf' (WiLe)) and *C. tangerina* Hort. ('Dancy' (Danc) and 'Beauty' (Beau)) represented group 3; *C. erythroa* Hort. ('San Hu Hong Chu' (SHHC) and 'Fuzhu' (Fuzh)), *C. kinokuni* Hort. ('Vietnam à peau fine' (Vipf)), *C. reshni* Hort. ('Cleopatra' (Cle)) represented group 4; and finally *C. depressa* Hayata ('Shekwasha' (Shek)) represented the group 5. To this list, we added two accessions 'Bintangor Sarawak' (BiSa) and 'Nasnaran' (Nasn) [*C. amblycarpa* (Hask.) Ochse] which are known to be mandarin hybrids (Tanaka, 1954; Ollitrault et al., 2012). Plant materials were propagated by sowing seeds in a neutral substrate (perlite). Seedlings were transplanted 4 months after germination into 3 L pots in a mixture of sand, turf and peat (1:1:1), and regular fertilization was applied according to Allario et al. (2011). The ploidy status of seedlings was confirmed by flow cytometry (Partec I) according to Froelicher et al. (2007). For each accession, seedlings with homogenous size and morphology were grown for 8 months in a greenhouse under natural photoperiod conditions.

2.1. Root and shoot fresh weight

One year seedlings were pruned to ensure a homogenous canopy volume. Fresh root and shoot mass were determined at the end of the experiment.

2.2. Salt stress application

The stress experiment was performed from April to July 2012 under natural photoperiod conditions, with day/night temperatures of 19–32 °C/16–18 °C, respectively, with relative humidity

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