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Photochemical performance of *Carpobrotus edulis* in response to various substrate salt concentrations

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ABSTRACT

Substrate salinity is one of the main abiotic factors limiting plant establishment, growth and distribution in coastal habitats. Nevertheless, few studies have investigated the interaction between salt concentration and duration of exposure on the physiology and growth of *Carpobrotus edulis*, an important invasive plant species growing in coastal dune habitats. In this study, four salinity treatment cycles of different length (three, six, twelve and twenty-four days) at salinity of 0 M, 0.1 M, 0.2 M and 0.3 M were imposed. A significant response in plant growth was elicited after 24 days of treatment. The main shoot length (MS_L) and stem biomass (SB_{MS}) increased by 11% and 4%, respectively at 0.1 M and by 25% and 6% at 0.2 M compared with the control. At 0.3 M MS_L did not significantly differ from the control while SB_{MS} was 18% lower. Moreover, *C. edulis* showed a high photoprotection mechanism efficiency resulting in a high carotenoid to chlorophyll ratio increase which was two, three and four times higher than the control at 0.1 M, 0.2 M and 0.3 M, respectively. Photochemically, the quantum yield of photosynthesis (Φ_{PSII}) was 17%, 50% and 52% lower than the control at 0.1 M, 0.2 M and 0.3 M. The Φ_{PSII} decrease was associated with a low leaf nitrogen content (N_L) decrease (16%, 21% lower than the control at 0.1 M and 0.2 M, respectively). By contrast, N_L had the highest decrease (41% lower than the control) at 0.3 M, which constrains the growth capacity. Overall, *C. edulis* was able to modulate its response to salinity. The salt stimulated shoot elongation at low or moderate salt concentrations could confer a competitive advantage making *C. edulis* even more efficient in establishing within the areas which it colonizes. Since the expansion of *C. edulis* may be enhanced by the forecasted increase in soil salinity, it will be of paramount importance to apply effective management practices in areas invaded by *C. edulis* to limit its expansion and preserve the native plant biodiversity.

1. Introduction

Substrate salinity is one of the main abiotic factors limiting plant establishment, growth and distribution in coastal habitats where the salinity substrate level represents the most important threshold, which separates the unvegetated zone from the area colonized by plants (Fenu et al., 2012). Usually, substrate salinity ranges from 0.1% to 3% (Barbour et al., 1985) even though salt concentrations depend on time of year, distance from the sea and sea storm phenomena (Weber and D'Antonio, 1999). For example, substrate salinity varies from 0 after abundant rainfall to 0.5 M NaCl after a sea over-wash in coastal sand dunes of dry areas (Sykes and Wilson, 1989). Moreover, exposure to high soil salinity levels induces detrimental effects on plant establishment and growth causing osmotic stress, which in turn reduces water uptake (Sucre and Suárez, 2011) leading through internal signals to decrease the cell expansion rate in growing tissues (Shabala et al., 2012). Ion toxicity due to Na^+ and Cl^- accumulation in chloroplast and nutritional imbalance contribute to inhibiting plant growth (Greenway and Munns, 1980). At a metabolic level, salt stress restricts the activity of various enzymes (Morais et al., 2012), alters the nitrogen metabolism (Nazar et al., 2011) and reduces carbon assimilation because of stomatal and biochemical limitations (Chaves et al., 2009). Moreover, although the effect of salt stress on photochemistry is not fully understood, there is evidence that Na^+ and Cl^- accumulation in chloroplasts affects electron transport and secondary processes that injure the photosynthetic machinery (Larcher, 2003).

Increase in soil salinity is becoming a serious concern in Mediterranean coastal habitats where climate change is exacerbating the stress conditions (e.g. low soil water-holding capacity). The forecasted decline in rainfall and the concomitant increase in evaporative demand due to warmer air temperature facilitate the substrate salt accumulation from aerosol spray (Greaver and Sternberg, 2007). The Mediterranean Basin could be hit by more extreme climatic events such as sea storm and intense wave episodes accompanied by wind intensification

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(Calvo et al., 2011), which will further lead to intensifying the sea spray phenomena.

On the other hand, the new climatic conditions favor the colonization from non-native species (Davidson et al., 2011). Invasions by alien plant species is a worrisome phenomenon on a global scale because it can seriously compromise the survival of native flora (Chytrý et al., 2008). The threat to native plant species arises through the capacity of alien species to modify ecosystem functioning (Simberloff et al., 2013) through direct competition for abiotic resources, impact on pollination of native species, modification of the soil physical proprieties and by changes in the nutrient cycle (Brown et al., 2002; Ehrenfeld, 2003; Novoa et al., 2014). However, the extent of invasion differs among habitat types depending on different factors such as climate, historical and biogeographical characteristics (Chytrý et al., 2008). Coastal habitats are among those that are most vulnerable to invasion by alien species (García-de-Lomas et al., 2010). The cause of their vulnerability to biological invasions can be ascribed to the high level of disturbance that often characterizes these habitats (Affre et al., 2010). In fact, coastal habitats, especially in the Mediterranean Basin, have been severely degraded over time because of human activities (Fenu et al., 2012, 2013). In addition, the high tourist flux and extent of commercial exchange increase probability of alien plant introductions (García-de-Lomas et al., 2010). The invasiveness of alien plant species relies on specific physiological and morphological traits such as high maximum photosynthetic rate, low shoot/root ratio, high fecundity, high reproductive effort and high growth rate mainly due to clonal growth capacity (Roiloa et al., 2010). Moreover, in coastal habitats the capacity of alien plant species to tolerate the substrate salinity is an important factor affecting their spread (Weber and D'Antonio, 1999).

Few studies have aimed to analyze the ecophysiological response of invasive plant species to stress factors such as high salinity (Morais et al., 2012; Pintó-Marijuan and Munné-Bosch, 2013), although salinity tolerance may have an important role in determining the extent to which an invasive plant species can successfully colonize coastal habitats. Thus, understanding how invasive plant species respond to salinity stress could help to predict what salinity levels might influence future invasion rates.

Carpobrotus edulis (L.) N.E. Br. is a succulent perennial plant species from South Africa (Albert, 1995) introduced to Europe around 1680 (Fournier, 1952) and planted as an ornamental species or used to stabilize dunes and slopes (Traveset et al., 2008). Its growth has become rampant, causing a high impact on diversity, structure and dynamics of native plant communities, sometimes replacing them in many areas such as Southern Europe, California, and Australia, (Roiloa et al., 2010). *Carpobrotus edulis* is now considered to be one of the most harmful and aggressive invasive plant species of the Mediterranean coastal dunes (Sintes et al., 2007; Roiloa et al., 2010). Its clonal growth, which is achieved by the vegetative production of functional individuals (i.e. ramets) produced by the main shoots (i.e. stolons) by rooting at some shoot nodes, has been well studied (Traveset et al., 2008).

By contrast, research aimed at analyzing the physiological response to salinity stress in *C. edulis* is rare (Weber and D'Antonio, 1999; Madawala et al., 2014). Thus, the aim of this study was to analyze growth capacity, biomass production and photochemical functionality in response to a range of salinity levels. Moreover, since coastal habitats are characterized by temporal variations in substrate salinity (Sucre and Suárez, 2011), we hypothesized that the extent of the response of *C. edulis* depended not only on the salt concentration but also on the duration of the stress.

2. Materials and methods

2.1. Plant material

Individual ramets ($n = 40$) were collected at the end of June 2013 from an established sand dune along the Tyrrhenian coast near Rome (41°53′40.99″N; 12°09′45.24″E). This area is characterized by a Mediterranean type climate, with mean minimum air temperature (T_{min}) of 12.0 ± 5.6 °C and mean maximum air temperature (T_{max}) of 23.7 ± 8.5 °C. The total annual rainfall is 822 mm with the majority occurring in autumn and in winter and a dry period in summer from June to August with a total rainfall of 46.3 mm (data from Meteorological Station of Capocotta, SIARL, Arsial, for the period 2004–2013).

Each ramet was transplanted into a pot (68 cm diameter and 60 cm depth) filled with sand from the natural environment. Pots were placed in a glasshouse at the experimental garden of Sapienza University of Rome (41°54′N, 12°31′E; 41 m a.s.l.). During the experimental period (from July 1st to August 18th, 2013) T_{max} was 29.1 ± 1.7 °C and T_{min} was 23.1 ± 1.9 °C, relative air humidity was 40–60% and the photosynthetic photon flux density (PPFD, μmol photons m^{-2} s^{-1}) was 1500–1800 μmol photons m^{-2} s^{-1} in the glasshouse.

2.2. Salinity treatment

Starting from July 1st 2013, plants of the same length (i.e. 14 cm long) were subjected to four salt concentrations (0 M, 0.1 M, 0.2 M and 0.3 M NaCl). To evaluate the effect of the duration of exposure to salinity, plants were exposed to four consecutive cycles (Cycle 1, 2, 3 and 4) of three, six, twelve and twenty-four days, respectively. Salt concentrations in pots were achieved using a mixture of artificial seawater (Instant Ocean®, 3.5% salt content) with a Hogland's nutrient solution (Weber and D'Antonio, 1999). Plants were irrigated with 1 l of salt solution containing 0, 17%, 34% and 50% artificial seawater to achieve the final NaCl concentrations. Control pots (i.e. 0 M NaCl) were irrigated with Hogland's nutrient solution without salt. The reason for using twenty-four days as a maximum duration for the salinity treatment was to ensure substantial but not lethal salinity stress conditions (Zinnert et al., 2012).

Ten pots for each salinity treatment were randomly arranged in four trays and measurements of plant growth, chlorophyll fluorescence, photosynthetic pigment content and leaf nitrogen content were carried out one day after each cycle end (i.e. on July 4th, 11th, 24th and on August 18th, 2013) on six individuals randomly chosen. After measurements had been taken and before the next cycle started, plants were irrigated with tap water to avoid salt increase in the substrate (Weber and D'Antonio, 1999).

2.3. Main shoot elongation and stem biomass

At the beginning of the experiment, ten main shoots (MS) for each salinity treatment (i.e. one MS per pot) were labeled in order to monitor MS length (MS_L, cm) over the entire experiment. MS_L was calculated by summing the length of all internodes produced on a shoot, where internodes are the distance between two nodes, and a node is the point on the shoot at which leaves (one or more) are inserted (Sintes et al., 2007). In addition, at the end of each cycle the number of new shoots was recorded.

Main Stems were harvested at the end of the last salinity treatment cycle (i.e. twenty-four days long) to determine stem biomass. Drying at 90 °C until constant mass was reached preceded stem (excluding leaves) biomass MS (SB_{MS}, g) determinations.

2.4. Chlorophyll fluorescence

Chlorophyll fluorescence measurements, including maximum PSII photochemical efficiency (F_V/F_M), actual quantum yield of photosynthesis of light-adapted leaves (Φ_{PSII}) and electron transportation rate (ETR), were carried out by a portable modulated fluorometer (OS5p, Opti-Sciences, USA) on fully expanded leaves on each MS.

For measurements of F_V/F_M, leaves were first dark-adapted for 30 min by leaf clips then a saturating pulse was applied to measure