***INT. J. BIOL. BIOTECH.*, 18 (3): 499-507, 2021.**

SALT TOLERANCE OF A LEAF SUCCULENT HALOPHYTE *SALSOLA IMBRICATA* FORSSK – GROWTH AND WATER RELATIONS PERSPECTIVE

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ABSTRACT

Salsola imbricata Forssk is a leaf succulent halophyte of coastal and inland salty soils. This study was carried out to evaluate the salt tolerance range of *S. imbricata* and on the effects of moderate (100 mM NaCl) and high (600 mM NaCl) salinity treatments in comparison with non-saline control treatments. Shoot fresh and dry biomass increased under saline conditions indicating high salt tolerance. Root fresh biomass decreased in the high salinity treatment while root dry biomass remained unchanged with increasing salinity treatment. Leaf succulence remained unchanged while root succulence decreased under high salinity treatment. Electrolyte leakage decreased transiently in moderate salinity indicating improved ROS management at optimal conditions. Constitutively low water and osmotic potentials under saline conditions indicated its osmoregulator strategy to maintain water balance. Chlorophyll content remained unchanged while carotenoids increased progressively. Leaf light absorbance also remained unaffected with rise in salinity however, leaf reflectance increased with parallel decrease in transmittance. Relative electron transport rates peaked in non-saline control but decreased under increasing salinity treatments. Lowest photochemical quenching was coupled with highest non-photochemical quenching under 100 mM NaCl treatment. *S. imbricata* tended to achieve a balance between water relations, electron transport and protective energy dissipation mechanisms (higher NPQ and carotenoids) under saline conditions.

Key words: Leaf light responses; Membrane integrity; Photo protection; Photo inhibition; Water uptake.

INTRODUCTION

Many arid and semi-arid saline regions of the world are faced with difficulties in growing conventional crops due to scarcity of water and high salt content (Nerd and Pasternak, 1992). Such areas could still be used to grow halophytic plants as fodder (Khan *et al*., 2009; Hasanuzzaman *et al*., 2014) due to their high nutrient value and palatability as cattle fodder (Koyro *et al*., 2014; Nikalje *et al*., 2018). It is imperative to study the ecophysiology of salt tolerance of indigenous halophytes to utilize their potential benefits from growing them in saline lands.

In most of the dicotyledonous halophytes, physiological parameters such as decreased water and osmotic potential, turgor maintenance and succulence are considered important growth determinants (Khan *et al*., 2000ab; Aziz and Khan, 2003; Aziz *et al*., 2005). A number of plants in which growth is stimulated under moderately saline conditions are regarded as ‘obligate halophytes’ (Ungar, 1991) which usually accumulate salts in their foliage through increased succulence (Manousaki and Kalogerakis, 2011). Under saline conditions salt accumulating plants tend to partition salt in their vacuoles to protect cytosolic metabolism however, high salt flux across cytoplasm could cause disruption of cellular structure and metabolic functions (Chaves *et al*., 2009). Salt toxicity could affect membrane integrity and ion transport across membranes (Lu *et al*., 2002). Increased salinity is also known to induce changes in leaf morphology and pigment content (Tarchoune *et al*., 2015). As a first line of defense, induction of non-photochemical quenching (NPQ) mechanisms helps to avoid photoinhibition by heat dissipation of light energy in excess of that required for photosynthesis (Taiz and Zeiger, 2006; Yamori and Shikanai, 2016). Many C_4 halophytes show resilience to CO_2 fixation under salt stress by achieving a balance between electron transport and effective energy dissipation mechanisms (Bose *et al*., 2017; Maricle *et al*., 2007; Moinuddin *et al*., 2017).

Salsola imbricata Forssk., is a leaf succulent perennial halophyte belonging to the family Amaranthaceae (formerly Chenopodiaceae), distributed all along the desert areas of Saharan Africa, the Arabian Peninsula, Afghanistan, Iran and Pakistan (Khan and Qaiser, 2006). *Salsola imbricata* is economically important as animal fodder besides being used as vegetable, production of soda ash, soap and medicines (Qureshi *et al*., 1993; Gilani *et* *al*., 2010). *Salsola imbricata* is reported as a salt includer species that may be effectively cultivated on saline lands (Mujeeb *et al*., 2020). However, little is known about growth characteristics, water relations and photosynthesis of this plant in saline conditions.

The current study was designed to understand growth and water relations ecophysiology of *S. imbricata* under moderate and high salinity. Following hypotheses were tested: 1) Moderate salinity will help in promoting growth of *S. imbricata* plants by improving water relations and photosynthesis and 2) High salinity will decrease plant growth and photosynthesis due to increased water stress, at the cost of energy dissipation by non-photochemical quenching.

MATERIALS AND METHODS

Growth conditions

Seeds of *Salsola imbricata* were taken from its population growing at Clifton (Latitude: 24^o 45' 38.56"; Longitude 67 05 ^{o} 30'.649"), Karachi. Seeds were cleaned and stored in dry condition and subsequently placed in plastic pots (12 cm diameter) filled with sandy soil, water from holes drilled underneath the pots using half-strength modified Hoagland's nutrient solution (Epstein, 1972). Three salinity regimes were provided i.e., non-saline (0 mM NaCl) controls, moderately saline (100 mM NaCl) and highly saline (600 mM NaCl) treatments. Plantlets were initially grown in moderate light (PAR ~500-600 µmol photons m^{-2} s^{-1}) with mean day temperatures and relative humidity of about 32-35^{o}C and 50-65% respectively, in a netted green house for 8 weeks. Plants were then placed in high light (PAR ~1500-1800 µmol photons m^{-2} s^{-1}) in an open screen house with average day temperatures of 36-40^{o}C with 45-50% relative humidity for about 4 weeks. Plants were finally harvested for growth, water relations, plant pigments and chlorophyll fluorescence.

Growth

Plants were harvested for growth parameters (shoot and root fresh and dry weights) and other water related parameters such as succulence and relative water content (RWC). Plants were washed with distilled water and carefully blotted and their fresh weights taken immediately. Roots and shoots were spread on blotting paper for surface drying and finally placed in oven at 60 °C until constant dry weight (DW) was obtained.

Water relations Leaf succulence was measured with the help of following formula:

Succulence (g H_2O g DW^{-1}) = (FW - DW) / DW

Leaf relative water content (RWC) was determined gravimetrically according to Barrs and Weatherly (1962) on five twigs of each treatment. The relative water content of plants were calculated by using following formula

RWC = [(FW − DW) / (TW − DW)] x 100

where, FW = fresh weigth; TW = turgid weight and DW= dry weight.

Plant shoots (approximately 5 mm diameter) with five replicates from each salinity treatments were taken for determining water potential using a dew point micro-voltmeter (Wescor Inc. USA). Leaf osmotic potential was determined in freeze killed samples with the help of an osmometer (Vapro, 5520, Wescor Inc. USA). Difference between water and osmotic potentials was taken as the turgor potential.

Chlorophyll and carotenoid content

The photosynthetic pigments were estimated by the method of Ritchie (2006) on fresh leaves by extracting samples in dark with pure ethanol and stored at 4^{o}C for 3 days before chlorophyll extraction. Samples were spun down at 4000*g* for 10 min at 4°C, light absorbance was measured at 470, 648.6 and 664.2 nm on a spectrophotometer. Pigment content were determined with the help of Lichtenthaler and Buschmann (1987).

Chlorophyll fluorescence

Chlorophyll fluorescence parameters were noted with a fluoremeter (PAM 2500, Walz, Germany). on dark adapted plants prior to determination of minimal fluorescence.Leaves were lluminated with stepwise pulses of 0 to 1857 $mmolm^{-2}$ s^{-1}. The relative electron transport rates (rETR) of PSII, photochemical quenching (qL) and non-photochemical quenching (NPQ) were measured (Genty *et al*., 1989).

Electrolyte leakage (EL%)

To determine leaf electrolyte leakage, fresh tissues was taken, rinsed with distill water, blotted dry and weighed. Electrical conductivity EC) of samples were measured before and after one hour of autoclaving at 121^{o}C. with an

EC meter (CM-115, Kyoto Electronics, Japan). Electrolyte leakage (EL%) was measured according to Pinhero and Fletcher (1994) method with the formula:

Electrolyte leakage (%) = [E1 / E2] * 100

where E1 = electrical conductivity before autoclaving and E2 = electrical conductivity after autoclaving leaf tissues.

Statistical analyses

All statistical analysis were carried out by using SPSS for Windows, Ver. 16 (SPSS Inc., Chicago, Ill., USA). One-way analyses of variance (ANOVA) test was used to find out the significant differences among salinity treatments whereas, the post hoc Bonferroni test ($P < 0.05$) was used to determine differences between individual treatment means.

RESULTS AND DISCUSSION

Shoot fresh and dry weights in *S. imbricata* increased with increasing salinity however, root fresh biomass was reduced in 600 mM NaCl (Fig. 1). Plants maintained shoot relative water content (% RWC) as well as succulence in salinity treatments (Fig. 2). A significant decrease in root biomass ($p < 0.05$) may be related to a decrease in root succulence (Fig. 2). Contrasting results on growth parameters indicates that *S. imbricata* may have compromised its root growth for shoot as observed in other halophytes (Khan *et al*., 2000ab).

Most of the dicotyledonous halophytes adjust osmotically by rapidly decreasing shoot water potential with the introduction of salinity in growing medium (Khan *et al*., 2000b, Aziz and Khan, 2014, Munns, 2002). Osborne and Sack (2012) suggested a strong link between evolution of C_4 photosynthesis and improved water relations in the face of increasing environmental pressures such as decreased [CO_2] and water availability resulting in high water use efficiency compared to their C_3 counterparts. In *S. imbricata*, shoot water and osmotic potentials decreased ($p < 0.05$; Fig. 3) progressively with salinity increments which may be related to an increased solute uptake required to maintain cell expansion for growth (Munns and Tester, 2008). *S. imbricata* appeared to follow an osmoregulator strategy (Khan *et al.*, 2000a; Aziz and Khan, 2001). Although, turgor potential decreased abruptly in 600 mM NaCl, no changes in RWC and succulence were observed in plants (Fig. 3). Little to no changes in plant succulence under saline conditions indicates water conserving strategy that helps in maintaining growth (Shoukat *et al*., 2018). Shoot growth promotion under saline conditions indicates that *S. imbricata* is an obligate halophyte which requires salt for promoting optimal growth (Khan *et al*., 2000a).

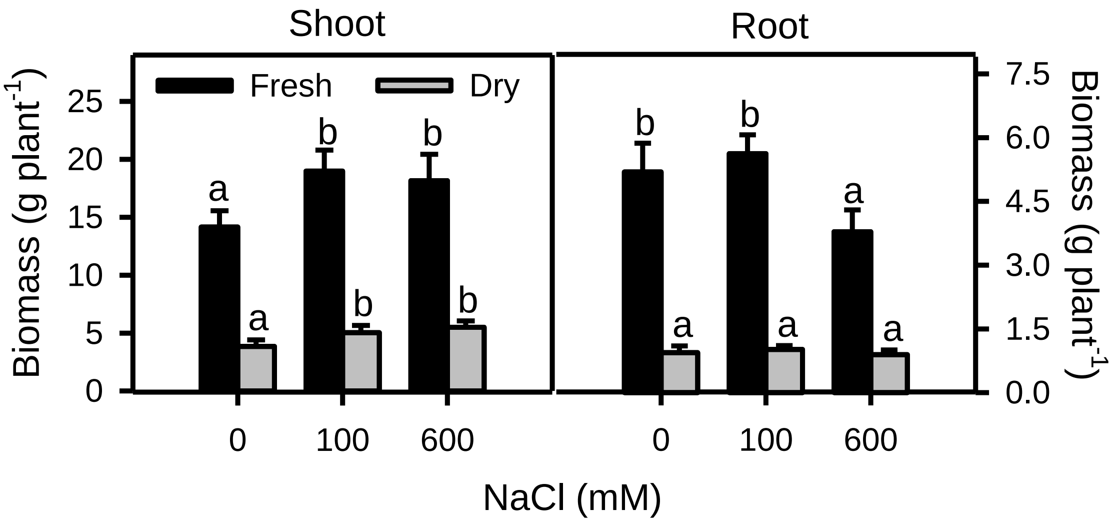

Fig. 1. Effect of salinity on shoot and root biomass of *Salsola imbricata*. Bars are means (±S.E.; n=3) while different alphabets indicate significant variations between salinity levels.

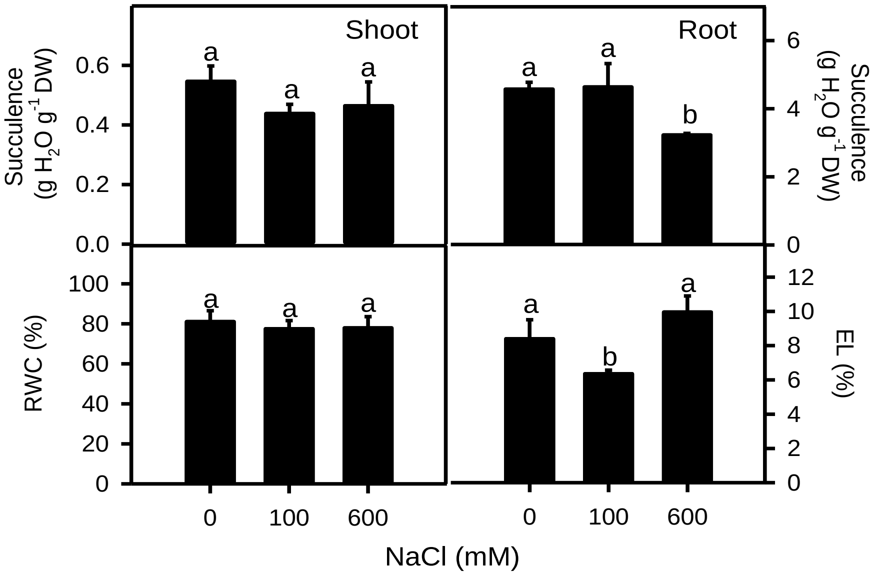

Fig. 2. Effect of salinity on tissue succulence, relative water content (RWC) and electrolyte leakage (EL) of *Salsola imbricata.* Bars are means (±S.E.; n=3) while different alphabets indicate significant variations between salinity levels.

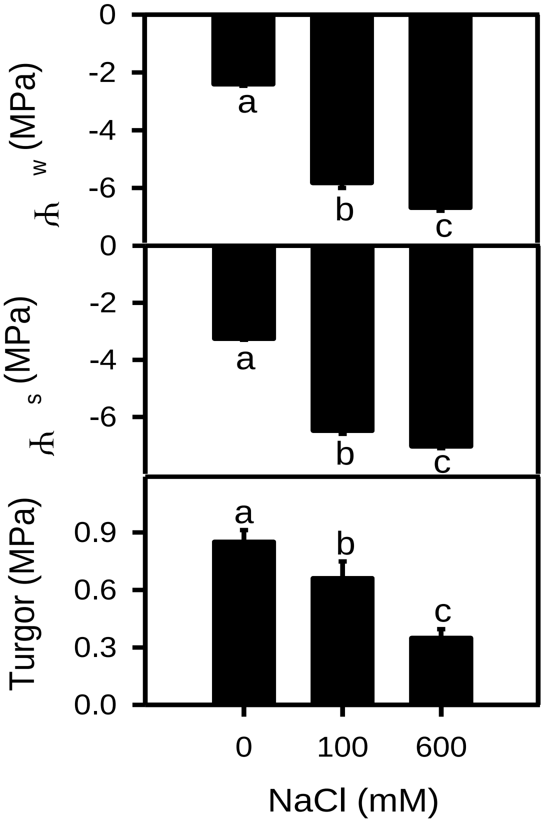

Fig. 3. Effect of salinity on leaf water (ψ_w), osmotic (ψ_s) and turgor potentials of *Salsola imbricata* leaves. Bars are means (±S.E.; n=3) while different alphabets indicate significant variations between salinity levels.

Electrolyte leakage (% EL) is one of the most important stress markers in plants growing in harsh environments (Hasegawa, 2013). Increased EL under saline conditions shows early signs of stress which may influence membrane permeability and biochemical reactions (Flowers *et al*., 2015). A transient decrease in electrolyte leakage (% EL) was found in 100 mM (the optimal salinity) while in 600 mM NaCl it was slightly increased though not significantly different than non-saline control (Fig. 2). Somewhat higher EL at 600 mM NaCl hints towards the initiation of stress though shoot growth remained unaffected. Total leaf chlorophyll remained unchanged under salinity treatments, but carotenoids (CAR) increased with increasing salinity (Fig. 4). This result was corroborated by unchanged leaf light absorbance. Decrease in transmittance was complemented by increase in transmittance with progressive increases in salinity (Fig. 5). Higher leaf reflectance could indicate a possible role of leaf surface structures such as leaf trichomes in *S. imbricata* (Nazzish *et al*., 2020) to avoid harmful radiation under stressful conditions (Tarchoune *et al*., 2015).

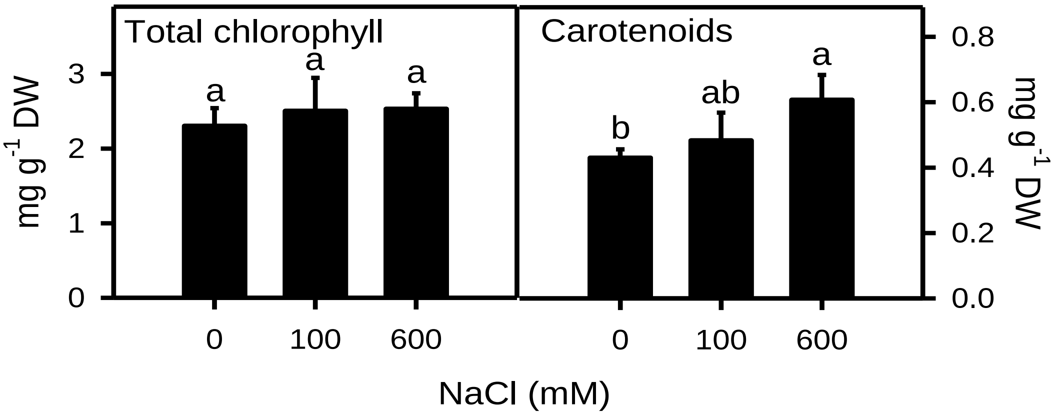

Fig. 4. Effect of salinity on total chlorophyll and carotenoid content of *Salsola imbricata*. Bars are means (±S.E.; n=3) while different alphabets indicate significant variations between salinity levels.

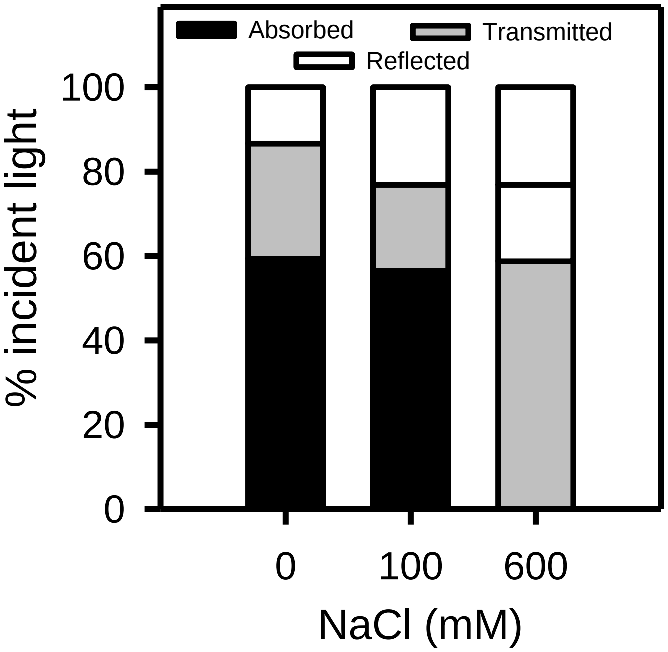

Fig. 5. Effect of salinity on the mean percentage of absorbed, transmitted and reflected light incident on leaves of *Salsola imbricata.*

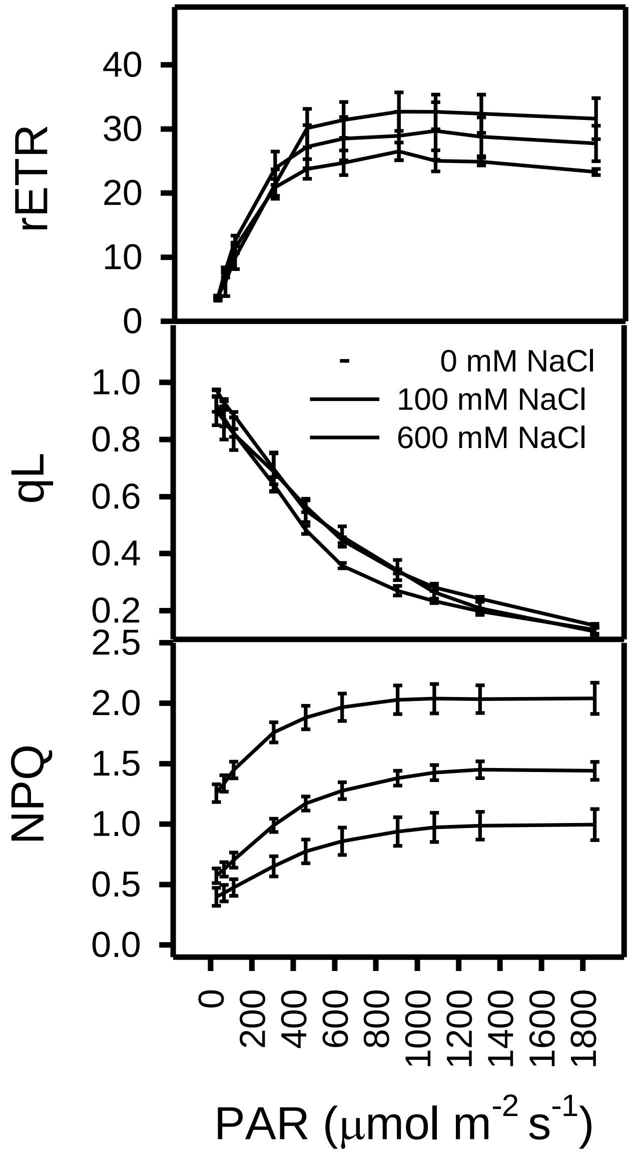

Fig. 6. Effect of salinity on leaf relative electron transport rate (rETR), photochemical quenching (qL) and non-photochemical quenching (NPQ) in *Salsola imbricata* leaves. Symbols are means (±S.E.; n=3).

Relative electron transport rate (rETR) could be used as an indicator of photosynthetic rate in C_4 plants due to the absence of photorespiration as evaluated in many plant taxa (Huang *et al*., 2021; Wong *et al*., 2014). In *S. imbricata* rETR in 100 mM NaCl treatment was slightly lower than non-saline control and lowest at 600 mM NaCl (Fig. 6). Increased non-photochemical quenching (NPQ) suggested higher susceptibility of PSII reaction center under salt stress conditions (Lu *et al*., 2002). There was an increase in non-photochemical quenching (NPQ) at 100 mM and 600 mM NaCl (Fig. 6) which indicates salt stimulated heat dissipation (Bilger and Bjorkman, 1994). Salt stimulated NPQ through the xanthophyll cycle protects PSII integrity by releasing excess light energy absorbed by photosynthetic tissues when rETR is low (Moinuddin *et al*., 2017). No significant changes were observed in photochemical quenching (qL) (Fig. 6) which indicates that effect photochemical quantum yield of PSII remained unaffected in any NaCl treatment. Increased electrolyte leakage (%EL) in 600 mM NaCl treatment could indicate early signs of salt stress. Reduction in photosynthesis (indicated by lower rETR) in the 600 mM NaCl but not in growth of *S. imbricata* compared to the non-saline control could possibly be explained by increased shoot growth under saline conditions (Leisner *et al*., 2010).

In brief, both hypotheses tested in this experiment were partially true as plants maintained leaf succulence and relative water content by lowering water and osmotic potentials for improved water balance under saline conditions. The present data suggests that *S. imbricata* is a highly salt tolerant plant that tolerate more than 600 mM NaCl treatment. Kubásek *et al*. (2013) reported the limited ability of C_4 species to acclimate to variable light environments. Pre-culture growth in moderate light (400 µmol m^{-2} s^{-1}) followed by growth under high light and salinity treatments could have effects on the results of growth and metabolic functions. Hence, future salinity experiments with continuous growth under moderate and high light conditions would confirm its limits of salt tolerance and underlying mechanisms to deal with variable light and salinity conditions.

ACKNOWLEDGEMENTS

The corresponding author would like to thank the Higher Education Commission, Islamabad and the University of Karachi for providing financial assistance.

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(*Accepted for publication June 2021*)