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Reaumuria soongorica-plant model to understand drought adaptive mechanisms of xerophyte and their potentials in improving stress tolerance in plants

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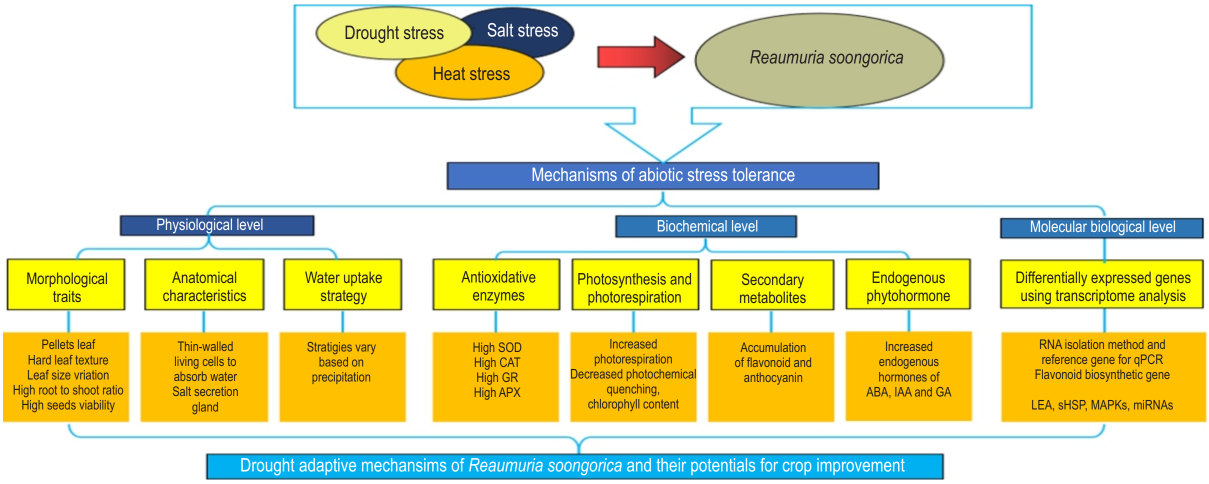
Abstract

Reaumuria soongorica plays critical role in withstanding wind-induced soil erosion and combating desertification due to its unique drought adaptive networks involved in physiological, morphological, biochemical, and molecular biological levels. This review was conceived to summarize the most updated information on drought adaptive mechanisms of *R. soongorica* to formulate valuable strategies for non-xerophytes crop species to be drought tolerant. Research indicates that *R. soongorica* can be drought resistant via posing a high root to shoot ratio, having salt secreting gland, subsidized stomata, hard leaf texture, pallet leaf shape, high seeds viability, actively working antioxidative enzymes, secondary metabolites, phytohormones, and differentially expressed drought resistant genes. These characteristics interlink at morpho-physiological, biochemical, metobolic, molecular, and genetic level in *R. soongorica* to adapt the extreme abitotic stress conditions in desert regions as a plant model in xerophyte.

The potentials of using the genetic elements in *R. soongorica* to produce drought tolerant crop species for yield production on growing on marginal lands could be vital for maintaining future food security. However, functional gene cloning and their transformation in crop species should be conducted as pre-requisite.

Key words: Abiotic stress, Crop improvement, Drought adaptive mechanisms, *Reaumuria soongorica*, Xerophytes,



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Introduction

Land degradation and crop yield loss resulting from abiotic stresses pose a threat to sustainable agriculture and future food security (FAO, 2019). It also reported that the world population is going to be 9.7 billion by 2050, which would require 70% higher food production by that time and exert additional pressure on agricultural land (United Nations Department of Economic Social Affffairs, 2017). To meet the requirement of growing human population, in many parts of the world salt-contaminated water is being used for irrigating crops (Minhas *et al.,* 2019) and expanding agricultural area in drylands and deserts (Finlayson *et al.,* 2011). Therefore, improving crop yields and preventing yield losses on marginal land under stressed conditions is vital to meet the world's future food security. Halophytes, with their intrinsic salt tolerance characteristics are known to have great potential in rehabilitating salt-contaminated soils to support plant growth in saline soils by employing various strategies. The recent identification and characterization of salt tolerant-related genes encoding signaling components from halophytes have paved the way for developing transgenic crops with improved salt tolerance (Rahman *et al.,* 2021).

Ammopiptanthus mongolicus, a xerophyte plant that belongs to family Leguminosae, adapts to extremely arid, hot, and cold environments, making it an excellent woody plant to study the molecular mechanisms underlying abiotic stress tolerance. Three dehydrin genes, *AmDHN132, AmDHN154,* and *AmDHN200* were cloned from abiotic stress in *A. mongolicus* seedlings. Cytomembrane-located *AmDHN200*, nucleus-located *AmDHN154*, and cytoplasm and nucleus-located *AmDHN132* were characterized by constitutive over-expression of their genes in *Arabidopsis thaliana*. Over-expression of *AmDHN132, AmDHN154*, and *AmDHN200* in transgenic Arabidopsis has improved salt, osmotic, and cold tolerances. These results indicate that *AmDHNs* contribute to the abiotic stress tolerance of *A. mongolicus* and that *AmDHN* genes function differently in response to abiotic stresses (Cui *et al.,* 2020). The resurrection plant *Reaumuria soongorica* plays critical role in controlling wind-induced soil erosion and combating desertification in its territory. It also serves as a forage species to sheep and camel in the steep desert areas. *R. soongorica* has great potential of revealing unique genetic bases over naturally stress-tolerant plants.

The populations of *R. soongorica* show typical zonal distribution at an altitude of of 500 to 2,000 m above sea level in arid Central Asia, Southern Europe, and North Africa which is considered to be a constructive keystone species in desert ecosystems (Zhang *et al.,* 2018; Ma *et al.,* 2007a). *R. soongorica* can survive under temperature ranging from -35.2 to 42.5°C with only 7 to 100 mm annual precipitation as well as tolerance of salt concentrations as high as 13.81 g kg^{-1} with soil pH as high as 8.27 (Wang *et al.,* 2011). *R. soongorica* displays extensive adaptability in a broad range of moisture, temperature, and soil condition which occurs in typical desert, steppe desert, desert steppe, and typical steppe (Yang *et al.,* 2015). Under these abiotic stress conditions, *R. soongorica* is evolved with stress-resistance mechanisms. Resurrection plants and xerophytes have been studied under various degrees of drought stress and desiccation, a large number of genes, proteins and metabolites that respond to severe drought stress or desiccation are identified to reveal their drought resistance mechanisms. It is vital to find the plants having capability to tolerate the maximum effect of drought stress by producing higher biomass with some economic importance in agriculture using drought resistant genetic bases of xerophyte. The forthcoming challenge for using xerophyte is the identification of novel genes with high biomass yield characteristics and the subsequent development of transgenic plants with superior drought tolerant features would be crucial for such type of research. This review focuses on the special adaptive features of Xerophyte plant, *R. soongorica*, under drought condition and the possible ways to utilize this plant to improve drought tolerance in crop species. However, many resurrection derived desiccation inducible genes have been identified, there still remains a gap from gene to field to improved crop drought tolerance and yield stability. In future, experimental approaches and transformation of merit genes to confirm their drought resistance and improve crop tolerance will be vital (Fig 3).

Physiological level

Morphological traits: Drought is one of the detrimental environmental stresses that affect morphological growth in plants. Fan *et al.* (2020) used 30 wild populations of *R. soongarica* and 16 populations grown in a common garden as material to reveal the influence of genetic and ecological factors on leaf morphology. The study revealed that leaf length, width, and leaf length to width ratio (L/W) of the northern lineage were significantly larger than other genetic lineages based on principal component analysis. With increasing latitude, leaf length, width, and L/W in the wild populations increased significantly. Leaf length and L/W were negatively correlated with altitude, and first increased and then decreased with increasing mean annual temperature and mean annual precipitation. Stepwise regression analyses further indicated that variation in leaf length variation was mainly affected by latitude. These indicate that *R. soongarica* preferentially changes leaf length to adjust leaf size to cope with environmental change (Fan *et al.,* 2020). Low salt stress condition (200 mM) signifcantly promoted the vegetative growth in total leaf area, total fresh weight, and root shoot ratio of *R. soongorica* seedlings (Yan *et al.,* 2022).

Root as initial part of plant acts as the most crucial organ for absorbing water and nutrient, root-derived chemical signals such as abscisic acid to influence stomatal responses to drought stress is affected by soil drought and its morphological and physiological characteristics are closely correlated with plant drought resistance (Yang *et al.,* 2011). Plant root meets transpirational demand via maintaining a reasonable leaf water status, changing root physiological or morphological responses to environmental stress are important adaptation strategies among plants that live in extreme environments (Joan and Hacke, 2013). The effect of drought stress on biomass allocation manifests itself more on roots than shoots, which have a greater increase in total root biomass and levels of lateral root so as to have a better chance of regrowth after drought. Studies on *R. soongorica* seedling growth under drought stress have found that roots are the only source to acquire water and nutrition from soil, therefore, increasing root size and biomass via proliferation under drought stress condition acts as an adaptive response to drought stress (Shan *et al.,* 2015).

Many organisms have evolved to respond to abiotic stresses and select between competitive and facilitative strategies to improve fitness (Godoy *et al.,* 2021). Shrub allometry was affected by variation in biomass partitioning, where the allometric relationships were strongly related to basal shrub diameter for almost all shrub components as one of the strategies for its sustainability in arid ecosystems (Ma *et al.,* 2020). Biomass accumulation, allocation patterns, and allometric relationships for above- and below-ground components of the desert shrub *R. soongorica* were studied across five age classes (0-10, 11-20, 21-30, 31-40, and > 40 years) in Alxa desert steppe, North-western China. The results revealed that biomass accumulation has an obvious gradient across the five age classes, branch, and coarse root biomass were the main biomass pool as mature shrub. *R. soongorica* shrub partitioned a greater proportion of total biomass to roots with age in order to adapt to extreme arid conditions. The morphological responses of *R. soongorica* to changes in rainfall quantity (30% reduction and 30% increase in rainfall quantity) and interval (50% longer drought interval between rainfall events) were tested. It was found that reduced rainfall decreased the above-ground and total biomass, while additional precipitation generally advanced *R. soongorica* growth and biomass accumulation. An increased interval between rainfall events resulted in an increase in root biomass in the middle of the growing season, followed by a decrease towards the end.

The response to the combination of increased rainfall quantity and interval was similar to the response to increased interval alone. These findings suggest that the effects of changes in rainfall patterns exert a greater influence than increased rainfall quantity and induced rainfall variability may have significant effects on the structure and functioning of desert ecosystems (Zhang *et al.,* 2018; Fig 1). Seed germination and early seedling growth are crucial for plant establishment. Two neutral (NaCl and Na_2SO_4) and two alkali ($NaHCO_3$ and Na_2CO_3) salts were used to investigate their effect on germination and recovery in *R. soongorica*. It was found that salinity, buffering capacity, and pH affected embryo growth, and salinity concentration had the most pronounced effect on germination. Seed viability under highly saline conditions appear to be a more sensitive indicator for the adaptation to saline environments than seed germination (Wang *et al.,* 2017).

Anatomical traits: Plant anatomy plays an important role in combating abiotic stresses. Leaf surfaces are covered by a waxy cuticle which is, in general, hydrophobic and the leaf cuticle functions as the main barrier for limiting ion transport and loss or leaching of water from the leaf interior as well as controlling foliar uptake with the environment (Kerstiens 1996; Koch *et al.,* 2009). Desert plants are widely distributed in the arid region of North-west China. Their long history of living in arid or saline habitats has frequently resulted in unique morphological or anatomical characteristics on their leaves or stems, such as leaves that are generally degraded; some leaves have trichomes or verruca or papillae; some have salt glands, some have lenticels, and some have epidermal hydathodes on the leaves or specialized pores on the leaf surface. These specialized features of the leaf surface of desert plants facilitate the absorption of more water from the atmosphere, as reported by a few previous studies (Wang *et al.*, 2016). Most studies on *R. soongorica* have focused mainly on the morphology and anatomy (Liu *et al.,* 2007) where *R. soongorica* developed leaves with pellets forms, and hard textures (Wang *et al.,* 2011). Scanning electronic microscopic analysis have shown that *R. soongorica* is able to absorb unsaturated atmospheric water via a leaf water absorbing scale which is formed by four to seven thin-walled living cells and functions as leaf stomata under 75%-95% relative humidity (Wang *et al.,* 2016). It has been also found that excess of chloride, sulfate, and potassium are involved in the process of gauging the scale (Wang *et al.,* 2016). Liu *et al.* (2018) found that sunk stomata reduce water loss and secrete extra salt (Fig. 1).

Water using strategies: Wang *et al.* (2011) reported that *R. soongorica* can absorb atmospheric moisture to survive in Ejinaqi Region where water table is at a depth of 2-3 m and deep groundwater is 10-15 m deep, while its root distribution is usually 1-2 m. Three years of field observations conducted at three sites along an aridity gradient from middle to lower reaches of the Heihe River Basin, North-western China using stable oxygen composition ($\delta^{18}O$) from plant xylem water showed that *R. soongorica* relies on groundwater rather than precipitation-derived water (Zhang *et al.,* 2017). Difference in water source uptake between the coexisting species was more apparent in more arid locations. Comparison of water use strategies of *R. soongorica* and *Nitraria sphaerocarpa* using stable isotope analysis showed that *R. soongorica* maintained consistent groundwater using strategy (Zhang *et al.,* 2017). Lately, we found similar result that *R. soongorica* could absorb soil moisture depending on the depth of plant roots using stable isotope ($\delta^{18}O$ and δ^2H) analysis (Liu *et al.,* 2022).

Another research showed that the flexible water uptake pattern of *C. korshinskii* and its faster response to precipitation pulse, compared with *R. soongorica* might help it to make full use of water and nutrients and adapt to dry environment. However, *R. soongorica* progressively switched to suck up deeper soil water and increased the water use proportion from 0.5% to 84.4% as the seasons changed, indicating a greater degree of ecological plasticity and enhanced adaptability to arid environments (Zhang *et al.,* 2020). Weighing lysimeters was used to quantify the actual evapotranspiration (ET) variation of sparsely distributed xerophytic shrubs community to reflect desert ecosystem. Jin *et al.* (2018) found that variation in soil moisture within 0-40 cm depth plays a vital role in regulating evporation (E) and ET. The

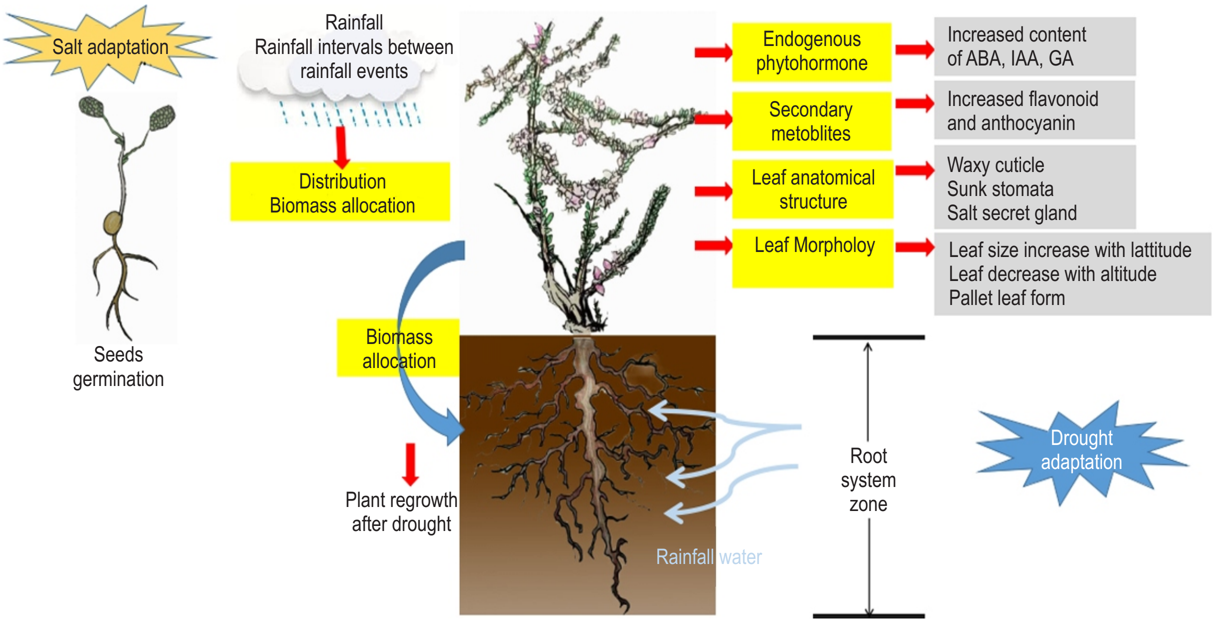

Fig. 1: Physiological and biochemical changes in *Reaumuria soongorica* under salt stress conditions during seeds germination and mature plants under drought stress conditions.

new shoot length, as one of important parameters of xerophytic shrub, was significantly exponentially related to the cumulative ET. From the long- and short-term perspective, event-based precipitation and wind speed are dominant driving factors behind changes in E and ET, respectively. Relative humidity is the main influencing factor for E and ET after a large rainfall event within eight days (Jin *et al.,* 2018). Field investigations on vegetation patterns of *R. soongorica* and heterogeneity in soil properties were conducted during 2014 and 2015. The authors used a conceptual model, which integrated water availability and plant facilitation and competition effects. They found that *R. soongorica* changed from a flexible water use strategy in high precipitation regions to a consistent water use strategy in low precipitation areas (Li *et al.,* 2019). They also found that patch height, size and plant-to-patch distance were smaller in high precipitation habitats than in low precipitation sites. Climate, soil and vegetation explained 82.5% variance in patch structure (Li *et al.,* 2019).

Biochemical level

Antioxidative enzyme activities: Due to drought, salt or other biotic or abiotic stresses, reactive oxygen species (ROS), including singlet oxygen ($^{1}O^{2}$), superoxide ($O^{2}\bullet-$), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH•) as well as reactive nitrogen species (RNS) can be generated which in turn affect the redox regulatory state of cell and induces oxidative stress in plants from peroxidation of unsaturated fatty acids in membranes, denaturation of proteins, carbohydrates, and nucleic acids (Laxa *et al.,* 2019). Plants prevent these free radicles by stimulating the antioxidant system. For instance, low molecular mass antioxidants including ascorbic acid (AsA), glutathione (GSH), and tocopherols, enzymes including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), and glutathione S-transferase (GST). In plant tissues, many phenolic compounds including avonoids, tannins and lignin precursors, carotenoids, alkaloids, flavanones, anthocyanins are potential antioxidants and may work as ROS-scavenging compounds (Blokhina *et al.,* 2003; Parvin *et al.,* 2019). The protective roles of SOD, POD, CAT, APX, and GR against oxidative damage and their activities in different phases of drought stress of 100 days and rewatering after 16, 72, and 100 days in *R. soongorica* leaves were evaluated by Bai *et al.* (2009). Their results showed that the concentration of H_2O_2, MDA and SOD activities increased significantly with progressing of drought stress. POD and CAT activities increased markedly in the early phase of drought and decreased significantly with further drought stress continuation while POD activity was unable to recover after rewatering. Ascorbate, GR, and APX activities declined in the initial stages of drought process, elevated significantly with further increasing water deficit progression and recovered after rewatering.

Further, the results indicate that SOD removing superoxide anion is highly effective during the whole drought stress, CAT scavenges H_2O_2 in the early phase of drought and enzymes of ascorbate-glutathione cycle scavenge H_2O_2 in further increasing drought stress, and POD does not contribute to protect against oxidative damage caused by H_2O_2 under drought stress

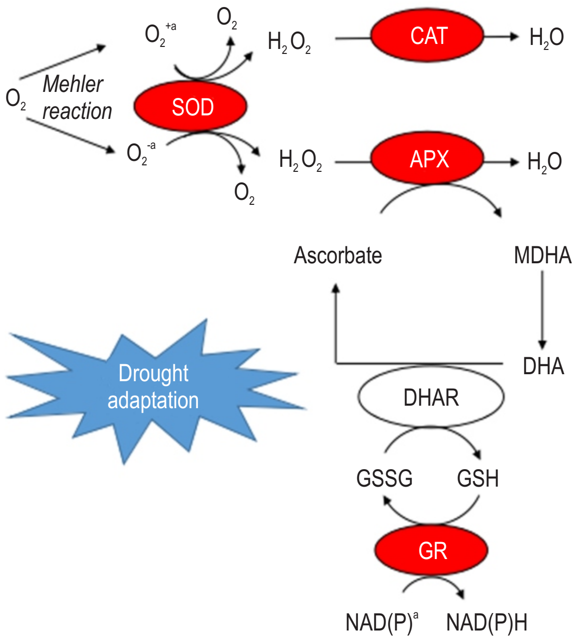

Fig. 2: Antioxidant system of *Reaumuria soongorica* under drought stress conditions where the antioxidents in red ovals showed increased content.

(Fig. 2). Under short-term (3 days) mild salt stress (200 mM NaCl), the salt injury index and membrane lipid peroxidation levels in leaves of *R. soongorica* seedlings are low. However, SOD activity, content of osmotic regulation substances and the net photosynthetic rate were high which shows that *R. soongorica* seedlings eliminated harmful superoxide anion free radicals and reduced oxidative damage by controlling the content of osmotic regulators and antioxidant enzyme activities (Yan *et al.,* 2022).

Photosynthesis and photorespiration: Photosynthesis is one of the most important water stress sensitive processes in all non-desiccant tolerant green plants. Effect of UV-B radiation on the photosynthetic properties and antioxidant enzyme activities in *R. soongorica* have been conducted (Ma *et al.,* 2005; Bai *et al.,* 2009; Liu *et al.,* 2007). Down-regulation of genes associated with photosynthesis and other chloroplast-localized proteins demonstrated deleterious effects of UV-B radiation on *R. soongorica* plants (Liu *et al.,* 2015). Photosynthesis in plants is impaired due to reduced carbon assimilation under drought stress via stomatal closure (Medrano *et al.,* 2002) and increased excessive photon energy which decrease photochemical efficiency, destruction of photosynthetic apparatus, impaired ATP synthesis, carboxylation enzyme activities (Farooq *et al.,* 2009), and photorespiration which is a wasteful process imposing a strong carbon drain on plants (Wingler *et al.,* 2000). However, excess photon energy consumed by photorespiration in C3 plants and thermal energy dissipation of absorbed photons is associated with the formation of zeaxanthin (Roland *et al.,* 2006) which might be an important photoprotective mechanism to protect the photosynthetic apparatus against photodamage (Osmond and Björkman, 1972). Experiment conducted by Bai *et al.* (2008) demonstrated that photorespiration in *R. soongorica* consumed excess electrons and protected photosynthetic apparatus under moderate drought stress, whereas it accelerated H_2O_2 accumulation markedly and induced leaf abscission under severe drought stress. In consistent with this research, Xu *et al.* (2008) found that with the increase in drought stress, the net photosynthetic rate, maximum photochemical efficiency of PSII, quantum efficiency of non-cyclic electron

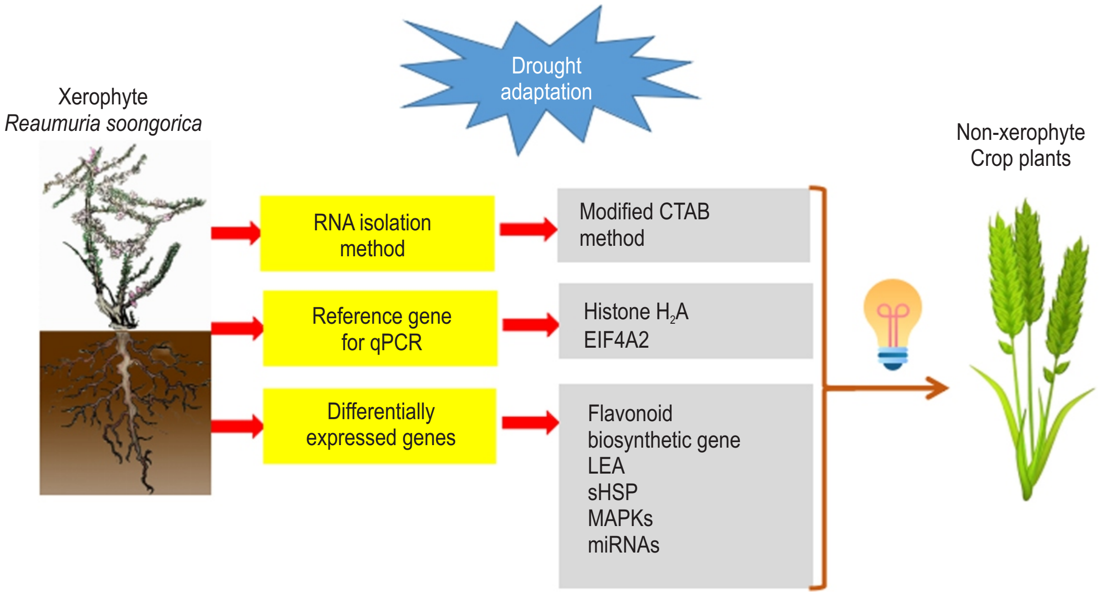

Fig. 3: RNA isolation method, reference genes for qPCR, and differentiallly expressed genes in *Reaumuria soongorica* under drought stress conditions and their possible implications in non-xerophyte crop plants. EIF4A2=Eukaryotic initiation factor 4A-2.

transport of PSII, and chlorophyll content decreased while non-photochemical quenching of fluorescence and carotenoid content increased in stems of *R. soongorica*. Re-hydration of *R. soongorica* showed new leaves from stems and restored chloroplast function and control level of chlorophyll which suggested that *R. soongorica* plants are able to sustain drought stress through leaf abscission and keep part of chlorophyll content in stems for photosynthesis (Xu *et al.,* 2010). Recently, Yan *et al.* (2022) reported that application of 400 and 500 mM NaCl decrease in net photosynthetic rate (Pn), transpiration rate (Tr), and water use efficiency (WUE) in *R. soongorica* seedlings.

Nutrient allocation: Nutrient allocation is a strategy for plants to invest carbon (C) and other nutrients strategically to plant structure, defense, and growth maintenance to be abiotic stress tolerant. He *et al.* (2015) investigated nutrient allocation and stoichiometric traits in *R. soongorica* in relation to the geographical, climatic, and soil conditions. The results showed that stem and root accumulated higher carbon and less nitrogen concentrations than leaf due to low soil moisture caused limited availability. Due to limited nutrient uptake, leaf C assimilation in *R. soongorica* is used for increasing root proliferation, root length, root density, and rooting depth (Shan *et al.,* 2012). Phosphorus concentration and N/P did not differ among plant organs (He *et al.,* 2015). This nutrient stoichiometry of *R. soongorica* is useful for understanding the plant-environment relationships and nutrient cycling in desert ecosystems (He *et al.,* 2015). However, stable isotope method investigating the source of water being used by the plant showed that leaf δ^{13} C was significantly correlated with the soil water content and the total dissolved soil solids was negatively correlated with the soil pH, soil organic matter, total phosphorus and effective phosphorus which indicates that the limiting factor of *R. soongorica* in desert ecosystem is stomatal conductance rather than nutrient content (Ma *et al.,* 2007b).

Secondary metabolites: Induction of secondary metabolites is another approach that plants adapt to extreme environment. Flavonoid plays an important role in plant growth, development, reproduction, and stress responses (Winkel-Shirley, 2001; 2002). Flavanone 3-hydroxylase gene (F3H) is a key enzyme in the flavonoid biosynthetic pathway, catalyzing the 3-hydroxylation of (2S)-flavanones, such as naringenin to dihydroflavonols (Ueyama *et al.,* 2002). UV-B and drought stress induced an increased expression of flavanone 3-hydroxylase gene (F3H), enzyme activities, and accumulation of flavonoid and anthocyanin content involved in the flavonoid biosynthetic pathway. Increased anthocyanin accumulation leads to enhanced antioxidant abilities of *R. soongorica* for its survival under UV-B and drought stress conditions (Liu *et al.,* 2013). Treatment of 200 mM of NaCl for 3 days significantly increased endogenous hormone content (ABA, ZR) in *R. soongorica* seedlings. Treatment of 400 and 500 mM NaCl solutions caused decrease in IAA content (Yan *et al.,* 2022).

Molecular biological level

Molecular biological techniques: *R. soongorica* is well equipped with genes encoding morphological, physiological, or biochemical traits at transcriptional level. During development and under stressful conditions, modifications of genome are achieved by changes in gene expression and chromosome changes. Changes in gene expression include methylation of DNA, gene amplification or deletion, and activation of transposable elements (Mesnage *et al.,* 2016). *R. soongorica* is a diploid with chromosome number of 22 (2n = 2x = 22) based on chromosome counting in which size ranges from 3.38 to 5.51 µm with predicted genome size of 778 Mb (Wang *et al.,* 2011). Wang *et al.* (2011) suggests that the extreme drought and salt resistance of *R. soongorica* is attributed to small diploid. Although diploid *R. soongorica* is considered as a good desert model plant for studying adverse environments resistance because of its small genome size with strong resistance, ploidy level tends to change in order for the plants to be adaptive to abiotic stressed environment. Genetic diversity of *R. soongorica* was investigated using molecular marker, such as inter-simple sequence repeats (ISSR), simple sequence repeats (SSR), and enzymes. Ten novel polymorphic microsatellite loci primer sets, covers five to 14 alleles per locus, were developed in 90 individuals from six populations of *R. soongorica* to investigate its genetic diversity and population genetic structure using the combined biotin capture technique (Chen *et al.,* 2011). Due to different gradient of precipitation, the flowering phenology of *R. soongorica* based on mediating the pollination, seed diffusion, differential gene flow, and reproductive isolation is the driver of genetic differentiation which revealed using genetic structure in Mongolia Plateau (Yang *et al.,* 2015). RNA isolation is a prerequisite for studying the upstream and downstream molecular procedures of stress tolerance in *R. soongorica*. However, the RNA of *R. soongorica* contains high levels of secondary metabolites which lead to difficult RNA isolation. A modified CTAB method was developed in which polyvinyl pyrrolidone was added for grinding to effectively inhibit the phenolics oxidation, DNase I was used to remove contaminating DNA, and NaAc along with ethanol was used for precipitation to enhance RNA yield and shorten the precipitation time (Wang *et al.,* 2011).

Differentially expressed genes based on transcriptome analysis: A systematic study was conducted to analyze and validate ten candidate reference genes for its stability as reference genes during quantitative reverse chain reaction procedure under drought, salt, dark, and heat stress within four *R. soongorica* accessions, HG010, HG020, XGG030, and XGG040, from two different habitats using three algorithms (geNorm, NormFinder, and BestKeeper). The authors found histone H2A (H2A) and eukaryotic initiation factor 4A-2 (EIF4A2) were the most stable reference genes, cyclophilin (CYCL) was moderate, and ACT, UBQ, and TUA were inappropriate for *R. soongorica* (Yan *et al.,* 2014; Fig 3). 77,647 unigenes were generated from a tertiary relic species *R. soongorica* using the Illumina HiSeq™ 2000 platform and more than half of unigenes have been annotated. At least 123 candidate genes related to drought adaptation were identified by the KEGG annotation and local BLAST. Population genetic study on these candidate genes can be useful to better understand the adaptive evolutionary mechanism of *R.*

soongorica. Expression and function analysis of un-annotated unigenes may also be employed to unravel specific drought adaptation mechanism in *R. soongorica* (Shi *et al.,* 2013; Yan *et al.,* 2013). Transcriptome analysis showed PEG-induced differentially expressed genes from *R. soongorica* included a number of regulatory proteins and functional proteins. Regulatory proteins, such as transcription factors and protein kinase were identified as involved in signal transduction. Functional proteins, including flavonoid biosynthetic proteins (Zhu *et al.,* 2018), late embryogenesis abundant (LEA) proteins, small heat shock proteins (sHSP), and aquaporin and proline transporter were identified as protective response to drought stress. Flavonoids, LEA proteins and sHSP also function as reactive oxygen species scavenger or molecular chaperone. Aquaporin and proline transporters regulate distribution of water and proline throughout the whole plant. Thus, the tolerance of *R. soongorica* may be gained through effective signal transduction and enhanced protection of functional proteins to reestablish cellular homeostasis (Liu *et al.,* 2014; Fig 3).

R. soongorica is one of the typical desert plants that present excellent tolerance to adverse environments. Induction of genes for signal transduction and protective proteins may be a strategy for regulating phototropism, stomatal opening, and chloroplast relocation in response to UV-B radiation in *R. soongorica* (Liu *et al.,* 2015; Fig 3). Specific gene functions as antioxidative enzyme involved in abiotic stress tolerance in *R. soongorica* have been explored. The function of mitogen-activated protein kinases (MAPKs) was investigated using forward and reverse genetic methods which indicates that MAPK is involved in the regulation of antioxidant defense system in the response to stress signaling under stress in *R. soongorica*. The novel MAPK cDNA (RsMPK2) was isolated from *R. soongorica* that encodes 374 amino acid protein and contains all 11 of the conserved MAPK subdomains and the TEY phosphorylation motif under stress. Dehydration, salinity, abscisic acid or hydrogen peroxide induced rapid accumulation of *RsMPK2* transcripts expression in vegetative (root, stem, leaf, and callus) and reproductive (flower) organs. Inhibition of expression of *RsMPK2* using inhibitor U0126 showed decrease of antioxidative enzyme activity under stresses (Liu *et al.,* 2010).

miRNAs and targeted mRNAs involved in seed germination during salt stress were identified by using nine small-RNA libraries and transcriptome analysis employed from *R. soongorica* seeds treated with various concentrations of NaCl. The authors identified 88 conserved miRNAs representing 25 defined families and discovered 13 novel miRNAs from nine libraries. Transcriptome data identified 13 differentially expressed miRNAs and 23 corresponding target mRNAs based on different concentration of salt stress. When compared between 43 mM NaCl and non-salt-stress conditions, one differentially expressed miRNA and one corresponding target mRNA was uncovered, respectively (Zhang *et al.,* 2020; Fig 3).

As a salt-secreting plant, *R. soongorica* undergoes a series of changes in its growth and diferentially expressed proteins in its leaves while under controlled salt stress conditions. Proteomic analysis revealed that energy-and metabolism-related proteins (P5CR, CSY4) and ribosomal proteins (RPL2-A, RPL12A, RPS6B) are up-regulated under low salt stress. Under high salinity (500 mM) treatment, the growth of *R. soongorica* seedlings is significantly inhibited based on deregulating the abundance of proteins associated with photosynthesis (RCA, PSAF, PSAN, PSB27-1) and ribosomal proteins (RPS10, RPS2D, RPS9, RPL7AA) while energy and metabolism (VHA-A, VHA-E1, AHA4, CSY4, PCK1), defense and anti-stress related proteins (P5CR, FC2, SYP71, SYP131), ribosomal proteins (RPL2-A, RPL12A), and peptide chain-releasing factor (AT2G47020) are up-regulated (Yan *et al.,* 2022).

Ecological responses of *R. soongorica*: Understanding the relationships among species is central to ecological research. In order to investigate significant increase in the concentration of carbon dioxide and changes in precipitation patterns, Chong *et al.* (2019) studied the impacts of CO_2 concentration and precipitation on root morphology, endogenous phytohormone, and soluble sugars content to predict the responses of *R. soongorica* in desert ecosystems to the global climate change. The study reported that higher CO_2 levels caused a significant increase in root length, mean root diameter, root biomass, total root surface area and total root volume regardless of alterations in precipitation, whereas the root-shoot ratio increased only with increased precipitation. Elevated concentrations of CO_2 and decreased precipitation significantly increased the contents of fructose, sucrose, glucose and other soluble sugars in the *R. soongorica* root system. Meanwhile, the two environmental factors showed significantly synergistic effects on *R. soongorica* root morphology. With elevated concentrations of CO_2, *R. soongorica* roots showed increased levels of endogenous hormones, including abscisic acid, indole-3-acetic acid and gibberellin. Significant correlation was found between root morphology and the levels of soluble sugars and endogenous hormone, as well as between the levels of soluble sugars and endogenous hormones (Chong *et al.,* 2019). These findings indicate that future changes in climate conditions such as CO_2 levels and precipitation will synergistically induce the root system of *R. soongorica* to undergo morphological and physiological alterations (Chong *et al.,* 2019).

Recently, Zhang *et al.* (2020) conducted a study to assess the effect of rainfall on belowground interactions and root morphology of *Reaumuria soongorica* and *Salsola passerina* from three communities with similar landforms and soil environments. They found a symbiotic relationship between these two shrub species via deep rooting and under low rainfall availability. Combined with the output results of climate change models, they speculated that the distribution area of these two species will expand to the west, which has important implications on how the interactions of other desert species may change in response to climate variability. Due to efficient salt secretion ability of *R. soongarica* leaf, the rhizosphere soil conductivity under its canopy is higher than other two species (*S. glareosa* and *A.*

polyrhizum) which leads to formation of a “saline island” and promote competitiveness of *R. soongarica* to inhibit interspecies competition of *S. glareosa* and *A. polyrhizum* and establish dominant communities in saline regions of desert grassland (Wang *et al.,* 2022).

Conclusions and perspective: In summary, studies of *R. soongorica* on the morphology and anatomy, seed germination, and foliar stable carbon isotope ratios illustrated that drought tolerance of *R. soongorica* is based on increasing the water use efficiency, photosynthesis, lowering leaf water potential, expanding the specialized stomata, excreting salt by leaf salt glands, accumulating abundant osmotic substances such as sucrose, malate and proline, raising the antioxidative enzyme activities, and drought regulated genes. In future, research can be conducted to illustrate the mechanism of heat and high radiation tolerance in *R. soongorica*. Research also can be conducted on the root structures and its shape, functional gene cloning, the mechanisms of salt gland regulating salt secretion, and transformation of the noval and key genetically stress tolerant elements to the non-xerophyte to be drought tolerant to fill the gap between gene to field. In addition, can *R. soongorica* absorb atmospheric water through its leaves to supplement its water requirements is the question to be answered.

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Add-on Information

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