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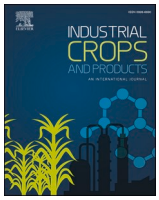

Guayule as an alternative crop for natural rubber production grown in B- and Se-laden soil in Central California

Gary S. Bañuelos [a], Dante F. Placido [b,c], Hui Zhu [d], Tiziana Centofanti [e,*], Maria C. Zambrano [f], Claire Heinitz [a], Todd A. Lone [g], Colleen M. McMahan [b,c]

[a] United States Department of Agriculture/Agricultural Research Service, San Joaquin Valley Agricultural Science Center, 9611 South Riverbend Avenue, Parlier, CA 93648–9757 USA
[b] Western Regional Research Laboratory, 800 Buchanan St., Albany, CA 94710, USA
[c] United States Department of Agriculture/Agricultural Research Service, 800 Buchanan St., Albany, CA 94710, USA
[d] Key Laboratory of Wetland Ecology, Environment, Northeast Institute of Geography, and Agroecology, Chinese Academy of Sciences, Changchun 130102, PR China
[e] Central European University, Department. of Environmental Sciences and Policy, Quellenstrasse 51, 1100 Vienna, Austria
[f] Center for Irrigation Technology, California State University Fresno, Fresno, CA 93740, USA
[g] California State University Fresno, Agriculture Business, Fresno, CA 93740 USA

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ABSTRACT

The potential of growing guayule (*Parthenium argentatum* A. Gray) as an alternative crop for saline, boron- and selenium-laden soils in the Westside of central California was evaluated in both greenhouse and drainage sediment field experiments. In the greenhouse experiment, salt and boron (B) tolerance and selenium (Se) accumulation were evaluated in guayule accessions AZ-1 thru AZ-6 grown in saline soil and irrigated with simulated saline drainage water. The guayule accessions AZ1, AZ5, and AZ6 tolerated salinity and B levels better than the others. Consequently, AZ1, AZ5, and AZ6 were then planted in field sediment plots with slight salinity and moderate B levels. In both greenhouse and field studies, concentrations of Se, B, and Na in the leaves were as high as 0.6–8 mg/kg dry weight (DW), 2000 mg/kg DW, and 17,500 mg/kg DW, respectively, in both experiments. In both experiments, concentrations of rubber and resin ranged from 4 to 14 w/w% in the stems, and applied salinity increased rubber and resin production in some accessions. This two-phase study provides additional evidence for guayule accessions (AZ1–6) as a promising rubber-producing crop that tolerates saline irrigation water in poor quality soils. In addition, guayule may be useful in the gentle phytoremediation of Se in poor quality soils or in soils irrigated with Se-laden drainage water.

1. Introduction

Guayule (*Parthenium argentatum* A. Gray), a native plant in the southwestern United States and northern Mexico, is under development as a source of natural rubber (Ray et al., 2010). Natural rubber is a Critical Agricultural Material required for transportation, medicine, and defense, and alternatives such as guayule are needed to assure supply security of this material. Rasutis et al. (2015) report average rubber yield of 300–2000 kg ha^{-1} year^{-1} in field production; i.e., the natural rubber content varies depending on accession, area of cultivation, soil type/quality, harvest time, and amounts of irrigation water applied (Rasutis et al., 2015). Besides its promising natural rubber production, guayule is also a source of terpene resins and biomass for biofuel production. (Sabaini et al., 2018; Cheng et al., 2020). Due to guayule's drought tolerance (Nelson et al., 2019), it has been considered as an alternative crop for arid and semiarid areas of the southwestern United States, north central Mexico, and other regions of the world with similar arid climates (Campos et al., 2019; Piluzza et al., 2020).

In Central California, one of the most productive agricultural regions of the world, continued irrigated agricultural production will become increasingly dependent upon expanding and identifying new sources of water. Persistent drought conditions and increased urbanization have greatly reduced the amount of good quality water available for irrigated agriculture. Consequently, other sources of water must be sought and utilized, which includes poor quality drainage and groundwater. In this regard, researchers have demonstrated that drainage water produced in

* Corresponding author.
E-mail address: centofantit@ceu.edu (T. Centofanti).

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the Westside of Central California can be used successfully to grow selected crops without long-term hazardous consequences to the crops and/or soils (Bañuelos and Lin, 2010; Centofanti and Bañuelos, 2015; Centofanti et al., 2017). One practical strategy to re-use drainage water produced in Central California is to irrigate salt and B tolerant crops and trees, an approach known as the Integrated-on Farm Drainage Management (IFDM) System (Schoups et al., 2005; Lin, 2011; Ayars and Soppe, 2014). In this practice, different crops are systematically irrigated with drainage water of different qualities. The quality of available water will, however, determine the selection of the crop. In the Westside of Central California, the accumulation of natural-occurring salts, Se and B in the ground and drainage waters must also be considered (Presser and Schwarzbach, 2008). In this regard, drainage water produced in the San Joaquin Valley (SJV) of California can contain unusually high levels of B (6–10 mg/L), and salinity (5–8 dS m^{-1}), as well as high levels of Se (100–200 μg L^{-1}) (Presser and Schwarzbach, 2008).

Using poor quality water can, however, have consequences on soil quality. For example, when B is applied to the soil with irrigation water, it is strongly adsorbed by the soil. Consequently, three times more water is needed to manage B via leaching than the amount of water needed to manage salinity by leaching (Grattan et al., 2014). In addition to the long-term accumulation of potential inorganic contaminants, e.g., B, the accumulation of Na in the soil adversely impacts soil structure and reduces water availability for plant uptake. Selenium is another natural occurring trace-element of particular concern in drainage water reuse strategies due to its potential harmful effects on the biological environment. Therefore, ideal crops irrigated with drainage water should not only be salt and B tolerant but also have the ability to tolerate and/or accumulate Se. Plant accumulation of Se is a form of phytomanagement of Se (Bañuelos and Dhillon, 2011). Thus, viable alternative crops should be salt and B tolerant, accumulate Se, and most importantly, produce products of economic value. This topic has very recently been explored under greenhouse conditions in six guayule accessions (Placido et al., 2021). They found that salt and B tolerance, and Se accumulation varied by accession, with N566 as the most tolerant line.

Guayule AZ-named accessions (Ray et al., 1999) have proven to provide the most robust germplasm sources for commercial breeders, likely owing to their interspecific hybrid tetraploid genetics (Ilut et al., 2015, 2017). The objective of the present study was to evaluate salt, B, and Se tolerance of AZ-guayule accessions under greenhouse and field conditions. Tolerance and accumulation of soil and water contaminants in plant tissues was quantified, as well as growth, rubber, and resin production. Results will be applicable to current production accessions and will assist selection of breeding germplasm for areas with poor quality soil and/or irrigation waters.

2. Materials and methods

2.1. Experiment 1-greenhouse

Seeds of guayule (*Parthenium argentatum* A. Gray), accessions: AZ1(PI 599674, AZ2 (PI 599675), AZ3 (PI 599676), AZ4 (PI 599677), AZ5 (PI 599678), and AZ6 (PI 599679), were obtained from National Arid Land Plant Genetic Resource Unit (NALPGRU) in Parlier, CA, USA. The seeds were harvested in 2013 from 10-year-old guayule shrubs at NALPGRU in Parlier, CA, which were previously identified to possess important traits related to greater biomass and rubber production (Ray et al., 2010). The greenhouse experiment was carried out under the following conditions at SJV Agricultural Research Center in Parlier, CA; day/night temperatures 28/20 ℃, supplemental light to create 16 h photoperiod (average daily 200–400 mmol photons m^{-2} s^{-1}) and a 40–50% relative humidity of ambient air. The seeds were pre-germinated in plastic flats filled with potting soil for 18 days. They were watered daily twice a day with low saline water (electrical conductivity (EC) < 0.5 dS/m). Four seedlings per pot were transplanted on 6 June 2016 into 4 L pots containing 2.5 kg typical saline soil from the Westside of Central California, which consisted of an Oxalis silty clay loam (fine montmorillonitic, thermic Pachic Haploxeral with a well-developed salinity profile). Plants were later thinned to 2 seedlings/pot. Soil electrical conductivity (EC) was 10.2 dS/m, pH of 8.02, and contained water extractable B, Se and sodium (Na) concentrations of 10.5 mg/L, 0.2 mg/L, and 1469 mg/L, respectively. The irrigation treatments with salinity, B and Se are shown in Table 1. Their respective levels represented typical poor quality drainage waters present in the Westside of central California. Five replications (one 4 L pot per replication) per treatment were used in a complete randomized block design. Saline solutions were prepared with $CaCl_2$, NaCl, and Na_2SO_4 salts, which are the typical dominating salts in Westside soils of central California (Bañuelos et al., 2009; Centofanti et al., 2017). Boron solutions were prepared with H_3BO_3 and deionized water to make both 10 and 20 mg B /L solutions, respectively, and Se was prepared as 0.100 mg Se/ L with Na_2O_4Se. All chemical reagents used in this study were purchased from Fisher Scientific, Pittsburgh, PA. For the first 4 weeks, all pots were watered twice a day with 60 mL low salinity water (EC < 0.5 dS/m) to allow for plant acclimation (Sanchez et al., 2014). Irrigation treatments (shown in Table 1) were initiated on July 10, 2016, when plants were ~ 4 weeks old. Saline and B-laden water was applied into a perforated receptacle placed in the center of each pot. This mode of irrigation allowed for a more uniform distribution of water added to the potted soils and minimized splashing onto leaves. Leaching of applied salts was minimized by irrigating twice daily. Differences in water applied (Table 1) were to be expected with treatments containing 10 dS m^{-1} because saline soil retains more moisture than non-saline soils. Consequently, saline soils in T2, T4 and T5 remained wetter for a longer period. Plants were monitored weekly for insect infestation and for the appearance of any toxicity and/or deficiency symptoms.

Table 1
Description of irrigation treatments including levels of salinity, selenium, and boron and total water applied as simulated drainage water to guayule accessions in greenhouse experiment.

Treatment	Salinity (dS m^{-1})	Selenium (mg L^{-1})	Boron (mg L^{-1})	Applied irrigation water (L)
T1 (control)	< 1	0.1	< 0.2	4.3
T2	10	0.1	< 0.7	3.6
T3	< 1	0.1	10	4.3
T4	10	0.1	10	3.5
T5	10	0.1	20	3.5
T6	< 1	0.1	20	4.3

2.2. Harvest-greenhouse

All plants were harvested between 41 and 56 days after initiation of irrigation treatment. Harvest date within this time range was determined by the severity of B and/or salt toxicity symptoms exhibited by plants (Figs. 1–6S in Supplementary material). Shoots were cut 1 cm above soil surface, weighed, and whole plants were then washed in deionized water. From each plant, ≈ 0.5 g fresh weight (FW) leaf, comprised of upper (young) and lower (old) leaves, stem, and root tissue, respectively, was combined from each replicate for ion analyses (described below). The remaining stems were placed in Ziploc bag over wet ice and shipped overnight to USDA-ARS Albany CA for rubber and resin analyses (described below). After plant sampling, circa 150 g fresh soil were collected from each replicate for each treatment respectively, oven dried at 55 °C for at least five days for analysis of soluble elements and total Se (described below). All dried leaves, stems, root sub-samples and soil samples were ground in a stainless-steel Wiley mill equipped with a 0.83 mm screen before being acid digested for mineral analysis (described below). Dry weights were recorded for all plants.

Table 2
Description of the soil characteristics at post-harvest in the control and drainage sediment plots.

Soil parameter	Control soil (0–30 cm)	Control soil (30–60 cm)	Sediment (0–30 cm)	Sediment (30–60 cm)
pH	7.96 ± 0.17	7.87 ± 0.20	7.68 ± 0.03	7.69 ± 0.06
EC (dS/m)	0.31 ± 0.03	0.22 ± 0.07	2.66 ± 0.27	3.31 ± 0.73
Boron (mg/L)	0.05 ± 0.02	0.04 ± 0.01	2.00 ± 0.26	3.04 ± 1.45
Chloride (mg/L)	19 ± 7	23 ± 11	285 ± 47	414 ± 69
Soluble Se (μg/L)	1.04 ± 0.26	1.06 ± 0.43	93.7 ± 32.2	170 ± 54
Total Se (mg/kg)	0.39 ± 0.02	0.39 ± 0.02	2.64 ± 0.85	3.72 ± 1.79
Sodium (mg/L)	39.13 ± 3.78	26.99 ± 10.39	120 ± 40	323 ± 97

2.3. Experiment 2 - Field sediment plot

The 0.5 ha experimental field site used in this study was located at the USDA Research Facility in Parlier, CA. The field site consisted both of non-saline soil (control; <0.3 dS/m) and slightly saline soil-drainage sediment [EC of 2–4 dS/m (salinity level defined by Vargas et al., 2018)]. Mineral soil chemical characteristics, B and Se concentrations in soil at harvest are shown in Table 2. The drainage sediment with naturally elevated Se and B concentrations was initially collected from the top 25-cm layer of residual sediment in the San Luis Drain, near Mendota of CA, and spread to a depth of 40 cm at the current the field site at the USDA Research Facility in Parlier, CA in 1999. The control soil consisted of Hanford sandy loam (coarse-loamy, mixed, super active, nonacid, thermic Typic Xerothents) with a 60 % sand, 30 % silt, and 10 % clay. The drainage sediment had a texture of a silt loam with a 19 % sand, 55 % silt, and 26 % clay, a bulk density of 0.98 g/cm^3, and an organic matter (OM) content of 2.6 %. At the field site, beds were created (33 m long and 1 m wide) on the drainage sediment and control soil plots. Standard agronomic management practices were applied on the test plots throughout each growing season. A surface-drip irrigation system was installed consisting of one in-line turbulent flow emitter per bed with an emitter spacing of 0.45 m and a flow rate of 4 L/h. All guayule field plots were drip-irrigated with good quality water (electrical conductivity<0.8 dS/m) based on the rate of evapotranspiration (ET) losses recorded at the CIMIS weather station located 2 km away at the University of California Kearney Research Station in Parlier, CA. Plot treatments consisted of 1) control (non-saline sandy loam soil) and 2) drainage sediment (slight saline). After 5 months of initial plant establishment under greenhouse growing conditions, three AZ accessions (AZ-1, AZ-5, AZ-6) were transplanted as a group of 4 plants from each accession into four saline sediment beds and on two non-saline control beds with a 0.7 m field spacing within each bed on July 3, 2017. Each accession (comprised of 4 plants) was randomly replicated at least 9 times on the four drainage sediment beds, and 6 times on the two control soil beds. After 18 months of growth in the sediment, plants ($n = 3$) from each accession were pollard-harvested, i.e., parts of the plants were cut-off from the base of the primary stems, and fresh weight recorded (leaves and stems). Subsamples of defoliated stem tissues (~ 7 mm diameter) were collected, placed into Ziploc bags, and transported to Albany, CA for natural rubber and resin concentration. Randomly selected older and younger leaf tissues and stems were subsampled for Se and ion analyses (both procedures described below).

2.4. Analyses

2.4.1. Water soluble mineral elements, Se, chloride, electrical conductivity, and pH in soil

Water soluble elements, including Se, concentrations (expressed as mg L^{-1}), chloride, salinity [electrical conductivity (EC); dS/m] and pH were determined in a 1:1 soil-water extract. Selenium was analyzed using an inductively coupled plasma spectrometer (ICP-MS); Agilent 7500X (Santa Clara, CA) and other soluble ions (i.e., Na, B) were measured using Varian Vista Pro inductively coupled plasma optimal emission spectrometer ICP-OES (Palo Alto, CA) after preparing the samples, as described by (Bañuelos et al., 2009). Soil EC was measured at room temperature using an Orion Model 150 Conductivity Meter (Thermo Scientific, Waltham, USA), chloride analysis was performed at room temperature with a Mettler Toledo Titrator (Mettler Toledo, Columbus, OH, USA), and pH was determined at room temperature using an Orion 420 A pH meter (Thermo Scientific, Waltham, USA).

2.4.2. Total acid digestible Se in plant tissues and in soil

Soil and plant tissue subsamples were wet-acid digested with HNO_3-H_2O_2-HCl, as described by Bañuelos and Akohoue (1994). NIST coal fly ash (SRM 1633; Se content of 10.3 ± 0.6 mg/kg, with a recovery of 93 %) and NIST wheat flour (SRM 1567; Se content of 1.1 ± 0.2 mg/kg, with a recovery of 94 %) were used as an external quality control standards for total Se in soil and plant material, respectively. Total Se and other elements were determined by ICP-MS and ICP-OES (described above), respectively, and expressed in mg kg^{-1} DW.

2.4.3. Rubber and resin quantification

In the field drainage sediment plot, pencil-sized guayule stem subsamples were initially collected from harvested plants on December 03, 2019. The tissues were wrapped in aluminum foil, stored on ice, and transported to USDA-ARS Albany, CA, where they were wrapped in Kimwipes and lyophilized for 48 h in FreeZone 4.5 L Console Freeze Dry System (LabConCo, USA). After drying, tissues were frozen in liquid nitrogen, ground to a fine power (30 Hz, 1 min) using a mixer mill MM 400 (Retsch, Haan, Germany), and stored at − 80 °C until analyzed. Approximately 300 mg of ground tissue was placed into an 11 mL ASE extraction cell (Dionex, Sunnyvale, CA) with Ottawa sand as dispersant (Fisher Scientific, USA). A three-solvent sequential extraction method was applied. Resin was extracted with acetone at room temperature, followed by a methanol extraction at room temperature, then rubber extracted with cyclohexane at 100 °C. Solvent containing analytes were evaporated using a TurboVap LV (Biotage, Charlotte, NC) evaporator at 50 °C with 15 psi N_2. Rubber and resin dry weights were determined gravimetrically (weight/weight%). For molecular weight, stems from the field harvest were defoliated, branches cut into medium-sized stems, and bark tissue removed by peeling. Latex rubber particles were extracted according to previously published methods (Cornish and Backhaus, 1990). Gel permeation chromatography (GPC) was used to determine the natural rubber molecular weight from latex particles using a previously described method (Placido et al., 2019). Weight-average molecular weight was calculated by Astra Software (Wyatt Technologies, Santa Barbara CA).

2.4.4. Gene expression analysis (RT-qPCR)

Leaf, stembark, and root tissues were collected and snap-frozen in liquid nitrogen for total RNA extraction. RNA was extracted from ~100 mg tissues using the TRIzol method (Ambion, Pittsburg, PA, United States), cleaned with RNeasy MiniElute kit (Qiagen Inc., Valencia, CA, United States) and DNase1 treated (Qiagen Inc., Valencia, CA, United States). RNA concentration was quantified with NanoDrop ND1000 (ThermoScientific, Wilmington, DE, United States). The iScript cDNA synthesis kit (Bio-Rad, Hercules, CA, United States) was used to synthesize complementary DNA (cDNA) for real-time qPCR. Four mL of 5× iScript reaction mix, 1 mL of iScript reverse transcriptase, 1 mg of total RNA and nuclease-free water were used in a 20 mL reaction volume. The reaction mix was incubated in Eppendorf thermal cycler (Hauppauge, NY) with the following set-up: 5 min at 25 °C for priming, 20 min at 46 °C for reverse transcription, 1 min at 95 °C for enzyme inactivation. For qPCR, 100 nM of forward and reverse primers, 7.5 mL of iQ SYBR Green Supermix Bio-Rad, Hercules, CA, United States), 2 mL

Table 3
Dry weight (g) of biomass of guayule plants grown in saline soils and irrigated with different water irrigation treatments under greenhouse conditions. Values represent average ± SD.

Accession	Treatment						ANOVA		
	T1	T2	T3	T4	T5	T6	*A*	*T*	*AxT*
g									
AZ1	3.5 ± 0.4a	2.2 ± 0.6b	3.0 ± 0.4a	2.2 ± 0.3b	2.5 ± 0.8b	2.3 ± 0.4b	***	***	***
AZ2	3.1 ± 0.4a	1.5 ± 0.6b	2.5 ± 0.8a	1.4 ± 0.8b	1.3 ± 0.9b	2.2 ± 0.5ab			
AZ3	2.0 ± 0.8a	1.1 ± 0.5a	2.1 ± 0.6a	1.3 ± 0.6a	1.1 ± 0.5a	1.8 ± 0.2a			
AZ4	3.5 ± 0.5a	2.7 ± 0.2a	3.4 ± 0.7a	3.2 ± 0.3a	2.5 ± 1.0b	2.2 ± 0.8b			
AZ5	4.4 ± 0.2a	3.2 ± 0.4b	4.1 ± 0.6a	3.5 ± 0.6b	3.9 ± 0.4a	2.7 ± 0.9b			
AZ6	4.4 ± 0.5a	2.0 ± 1.0b	3.9 ± 0.7a	1.8 ± 0.9b	0.9 ± 0.4c	3.1 ± 1.1d			

Values represent average and SD ($n = 5$). Two-way analysis of variance to evaluate 'accession' (*A*), 'treatment' (*T*) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5 %, 1%, and 0.1 % probability levels, respectively. Means followed by same letters in the same row indicate no significant difference among accession. See Table 1 for description of water irrigation treatments.

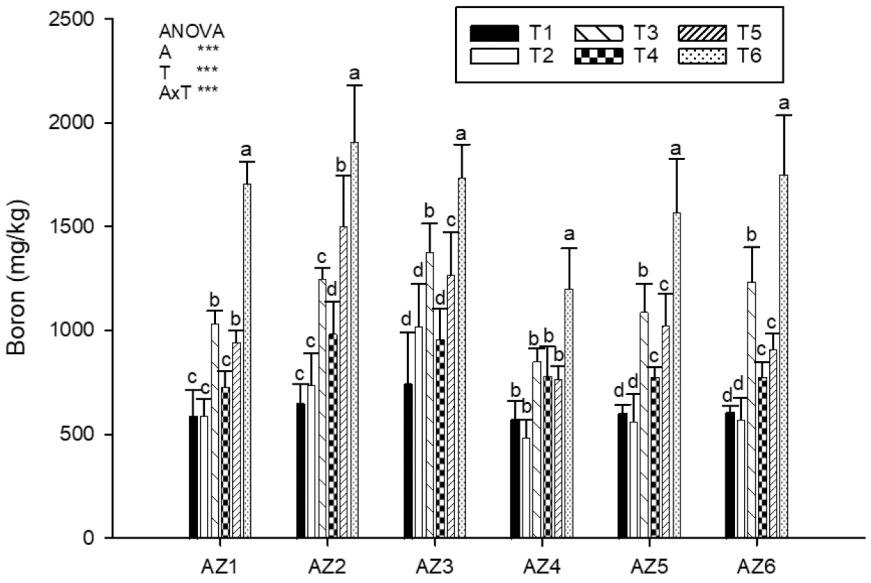


Fig. 1. Concentration (mg kg^{-1} DW) of B in leaves of six different accessions of guayule grown in saline soils and irrigated with different water treatments under greenhouse conditions. Values represent average and SD ($n = 5$). Two-way analysis of variance to evaluate 'accession' (*A*), 'treatment' (*T*) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5 %, 1 %, and 0.1 % probability levels, respectively. Different letters indicate that values for each treatment in each accession differed significantly ($P \leq 0.05$). See Table 1 for description of water treatments.

of diluted cDNA (1:20) and nuclease free water were used in a 15 mL reaction volume. The 7500 Fast Real-Time PCR system (Applied Biosystem, Foster City, CA, United States) was used with the following thermal cycle: 95 °C pre-incubation for 3 min; amplification for 40 cycles at 95 °C for 15 s and 60 °C for 30 s; the dissociation stage for 95 °C for 15 s, 60 °C for 1 min, and 95 °C for 15 s. Each qPCR run was performed with three independent tissue samples, each sample having two technical replicates. The 18S gene was used as an internal control. The relative expression values were calculated using the $2^{-\Delta\Delta C}$T method (Livak and Schmittgen, 2001). Expression of AOS gene was normalized to the expression of the endogenous reference 18 S gene and then to the expression of the WT plant.

2.4.5. Statistical analysis

Variance (ANOVA) analyses have been conducted to determine statistical differences between accession (*A*) and treatment (*T*) and the interactions of the two (AxT) as the main factors influencing the biomass and biochemical parameters evaluated. Statistically significant differences were assumed for $P \leq 0.05$ and statistical data analysis was performed using Gretl (Gnu Regression, Econometrics and Time-series Library, (Baiocchi and Distaso, 2003)). Data were plotted graphically using SIGMA PLOT version 14.5.

3. Results

3.1. Plant biomass and mineral element concentrations

3.1.1. Experiment 1 - Greenhouse

Plant dry biomass yields were between 1.1 and 4.4 g DW per plant for all accessions, irrespective of treatment (Table 3). There was a significant effect of treatment and accession and their interaction on biomass production. With the presence of salt in the treatment (e.g., T2, T4, and T5), biomass production was lower in AZ2, AZ3, and AZ6, than other accessions. In T1 (control) and T3 (10 mg B/L), biomass production was higher than other treatments, irrespective of accession. In T1 (control) and T3 (10 mg B/L), biomass production was higher than other treatments, irrespective of accession.

On average, AZ1, AZ5, and AZ6 visually showed less toxicity symptoms in treatments containing salinity (T2, T4 and T5) (Figs. 1–6S in supplementary material). The strongest visual symptoms, i.e., leaf necrosis, yellowing of the leaves and necrotic leaf edges (symptom of B toxicity), were mostly found for plants in T4 and T5 (treatments with a combination of salts and B, in most of the accessions).

In the greenhouse study, the concentration of B in leaves increased up to 5-fold, and there was a significant effect of treatment and accession and their interaction (Fig. 1). Boron concentrations were significantly

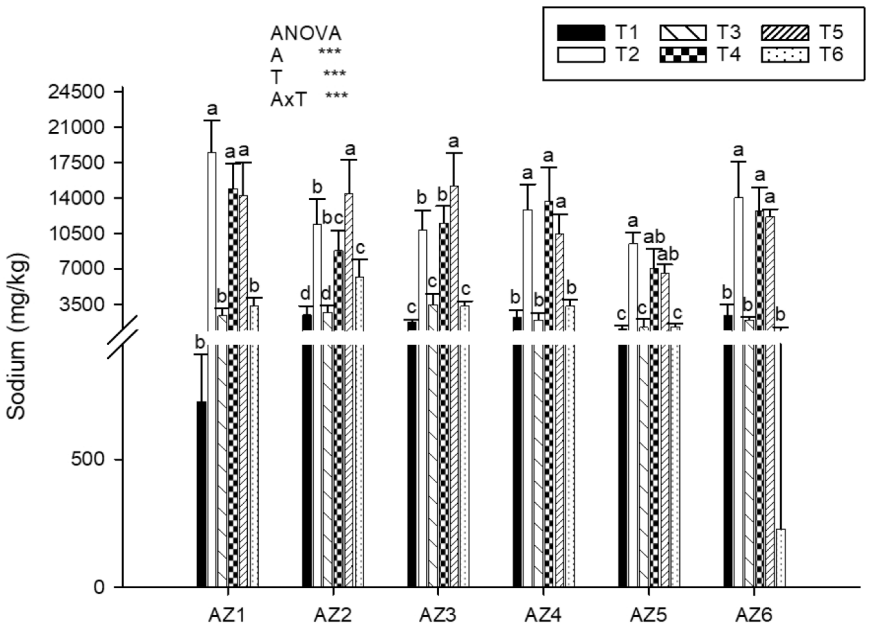


Fig. 2. Concentration (mg kg^{-1} DW) of Na in leaves of six different accessions of guayule grown in saline soils and irrigated with different water treatments under greenhouse conditions. Values represent average and SD ($n = 5$). Two-way analysis of variance to evaluate 'accession' (A), 'treatment' (T) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5 %, 1 %, and 0.1 % probability levels, respectively. Different letters indicate that values for each treatment in each accession differed significantly ($P \leq 0.05$). See Table 1 for description of water treatments.

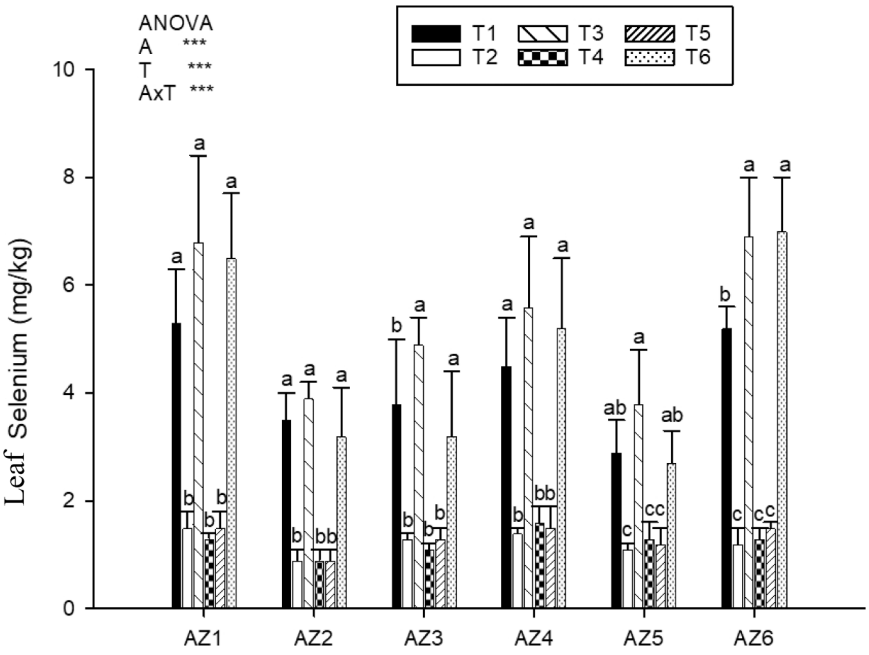


Fig. 3. Concentration (mg kg^{-1} DW) of Se in leaves of six different accessions of guayule grown in saline soils and irrigated with different water treatments under greenhouse conditions. Values represent average and SD ($n = 5$). Two-way analysis of variance to evaluate 'accession' (A), 'treatment' (T) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5%, 1%, and 0.1% probability levels, respectively. Different letters indicate that values for each treatment in each accession differed significantly ($P \leq 0.05$). See Table 1 for description of water treatments.

higher in plants in all accessions in T6, when only 20 mg B/L was part of the irrigation treatment.[1] Within the treatments, the combination of B and salts (e.g., T4 and T5) and slightly lower rate of irrigation, caused a reduction of B accumulation in leaves of all accessions compared with treatments with B and no salt (e.g., T3 and T6). Signs of B toxicity (necrotic leaf edges) and a slightly stunted growth were more pronounced in accessions AZ2, AZ3, and AZ4 from treatments T5 and T6. The concentration of B in composited roots and stems ranged from 40 to 180 mg/kg and 50–120 mg/kg, respectively, for all accessions in this study (Figs. 7S and 8S). Clearly most B accumulation in guayule took place in transpiring leaf tissue when mobile ion was present in soil and/or irrigation water. Generally, fewer differences among accessions were observed in response to treatments in stem tissues; but T6 treated plants (with 20 mg B/L and no salt) had the highest B concentrations in stems.

For root tissue, boron was most concentrated in roots of AZ2 and AZ3 in T5 and T6 (Fig. 8S).

Sodium was most concentrated in leaf (Fig. 2) than in stem (Fig. 9S) and root (Fig. 10S) tissues and was significantly higher in treatments with the addition of salts (e.g., T2, T4, and T5; Fig. 2). There was a significant effect of treatment and accession and their interaction on Na concentrations in leaves. In addition, we observed stronger symptoms of yellowing of leaves and mild stunted growth in AZ2, AZ3, and AZ5 under the highest salinity treatments (T2, T4, and T5).

Selenium concentrations in leaves of guayule grown in the greenhouse experiment (Fig. 3). ranged from 2 to 7 mg/kg. There was a significant effect of treatment and accession and their interaction on Se concentration in leaves. Selenium concentration was significantly

[1] Slightly more water was applied in T6

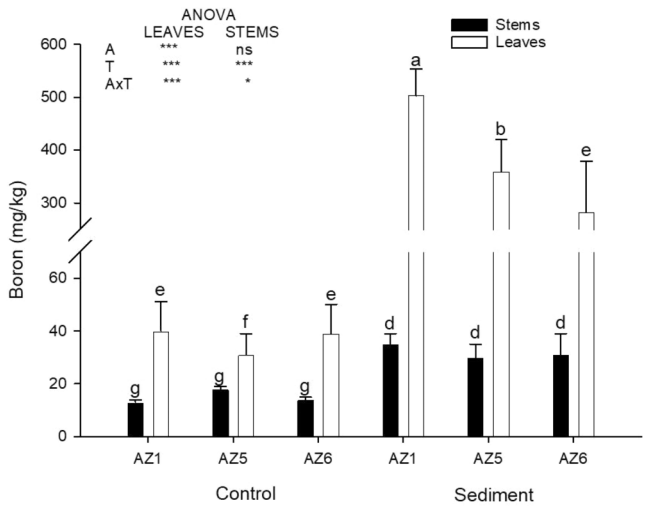


Fig. 4. Boron concentration (mg/kg) in stems and leaves of guayule accessions field-grown in sediment and control plots. Values represent average and SD (n = 4). Two-way analysis of variance was used to evaluate 'accession' (*A*), 'treatment' (*T*) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5 %, 1 %, and 0.1 % probability levels, respectively. Different letters indicate that values for each treatment in each accession differed significantly ($P \leq 0.05$) (See Table 2 for soil description of treatments).

higher in T1 (control), (absorption of natural-occurring soil Se), and in T3 and T6, when there were no salts in the irrigation treatment. AZ1 and AZ6 had the highest leaf Se concentrations when grown without added salt in irrigation water (T1, T3, and T6). Stem (Fig. 11S) and root (Fig. 12S) Se concentrations were generally lower (0.5–3 mg/kg,), in T2, T4, T5 when salts were part of the irrigation water treatment.

3.1.2. Experiment 2- Field sediment plot

Based on the results of the greenhouse experiment 1, accessions AZ1, AZ5 and AZ6 were selected to grow under field conditions on slightly saline (< 3.5 dS/m) sediment plots and control non-saline soil (<0.3 dS/m) and irrigated with non-saline water. Irrespective of accession, guayule grown on the sediment plot did not show any symptoms of toxicity. under these conditions. Although the plants were irrigated with non-saline water, in contrast to irrigation with saline and B-rich water in the greenhouse experiment, significant differences were observed for B and Se concentrations in leaves and stems amongst accessions grown in control and sediment plots (Figs. 4 and 5). The concentration of B in leaf and stem for plants grown in the sediment plot were dramatically higher (5 times) than for plants grown in the control plot, indicating absorption directly from the soil. AZ1 showed a significantly higher concentration of B in leaves compared with AZ5 and AZ6 in the sediment plot (Fig. 4).

Similar to B, Se concentrations were significantly higher in the leaves and stems of plants grown in the sediment plot compared with plants grown in the control plot (Fig. 5). Differences in Se concentrations were significant in leaves amongst accessions grown in sediment plot with significantly higher Se concentrations in leaves of AZ6 compared with AZ5 and AZ1. There were significant differences in leaf Se concentrations and no significant differences amongst accessions grown in the control and sediment plots. Notably, there were no significant effects of accession and treatment (sediment vs control) on concentration of Na in leaves and stems (see Fig. 13S in supplementary material). Guayule did not accumulate Na to a level of concern when grown in either non-saline or low saline sediment plots.

3.2. Resins and rubber production

3.2.1. Greenhouse experiment

In greenhouse experiments, the natural rubber (NR) concentration (Fig. 6a and b in guayule stem tissue were surprisingly higher (7 +% DW for controls) than typically reported in other greenhouse experiments (Veatch-Blohm et al., 2006; Placido et al., 2019, 2022; Dong et al., 2017). The rubber content was significantly higher than controls when the soil was irrigated with 10 dS/m salt (T2, T4, and T5) in most accessions (except for AZ5) ((Fig. 6a and b), up to 11 % DW NR for AZ1 (T2). In treatments T3 and T6 (containing 10 and 20 mg B/L, respectively and no salt), the rubber concentration was generally significantly lower or similar to control (T1).

In the greenhouse study, the resin content (9–13 % DW for controls)

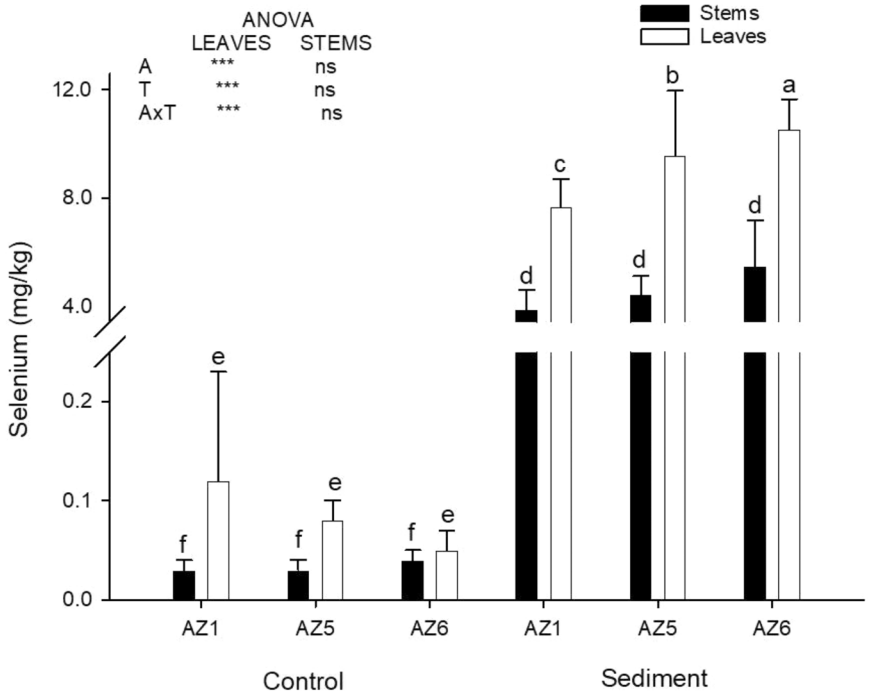
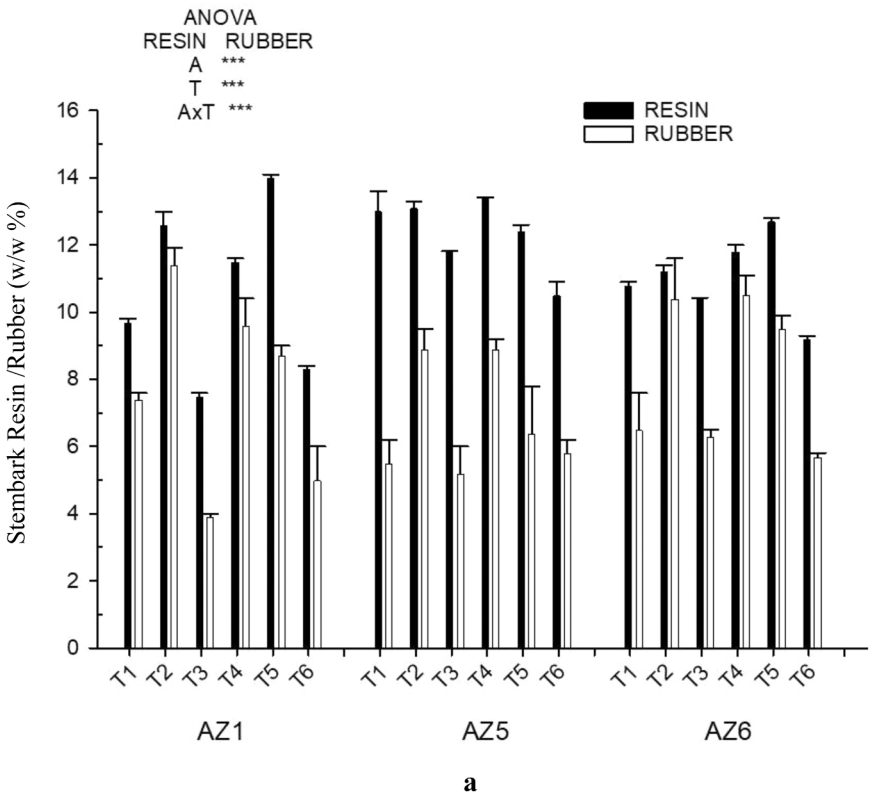
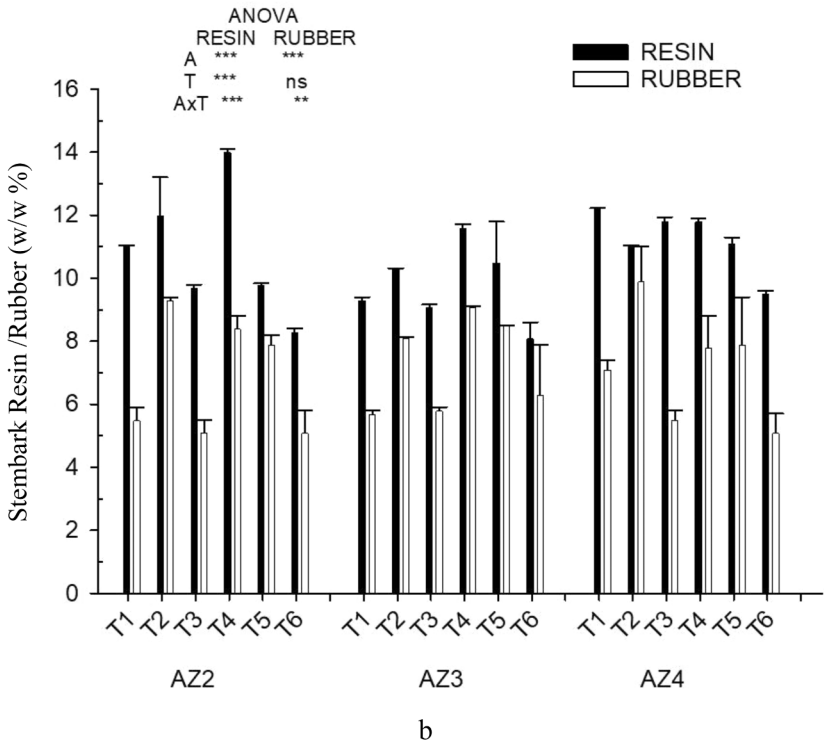


Fig. 5. Selenium concentration (mg/kg) in stems and leaves of guayule accessions grown in sediment and control plots. Values represent average and SD ($n = 4$). Two-way analysis of variance was used to evaluate 'accession' (*A*), 'treatment' (*T*) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5 %, 1 %, and 0.1 % probability levels, respectively. Different letters indicate that values for each treatment in each accession differed significantly ($P \leq 0.05$). (See Table 2 for soil description of treatments).



a



b

Fig. 6. a. Concentration of natural rubber and resin in stem tissues of guayule (AZ1, AZ5, AZ6) grown in saline soils and irrigated with different water treatments under greenhouse conditions. Values represent average and SD ($n = 4$). Two-way analysis of variance to evaluate 'accession' (A), 'treatment' (T) and interaction ($A \times T$) effects was performed (ns, *, **, and *** indicate non-significance or significance at 5%, 1%, and 0.1% probability levels, respectively). See Table 1 for description of irrigation treatments. b. Concentration of natural rubber and resin in stem tissues of guayule (AZ2, AZ3, AZ4) grown in saline soils and irrigated with different water treatments under greenhouse conditions. Values represent average and SD ($n = 4$). Two-way analysis of variance was used to evaluate 'accession' (A), 'treatment' (T) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5%, 1%, and 0.1% probability levels, respectively. See Table 1 for description of irrigation treatments.

was also higher than typically reported in greenhouse experiments and was similar to or significantly higher than the control (T1) in all treatments containing 10 dS/m salt (T2, T4, T5). The highest resin concentration (~14 %) was found for AZ1 in the most severe condition (T5, i.e., 10 dS/m salt, 20 mg/L B). In the absence of salt (T3 and T6; treatments with 10 and 20 mg/L B, respectively), the concentration of resin was significantly lower than the control in all three accessions (Fig. 6a and b). Interestingly, we found negative correlations between B concentration in leaves and resin content in stems in AZ5 ($r^2 = 0.86$) and in AZ3 ($r^2 = 0.74$); and between leaf B concentration and stem rubber concentration in AZ4 ($r^2 = 0.69$).

3.2.2. *Field sediment plot*

For AZ1, AZ5, and AZ6 grown in control plots, stem tissue rubber and

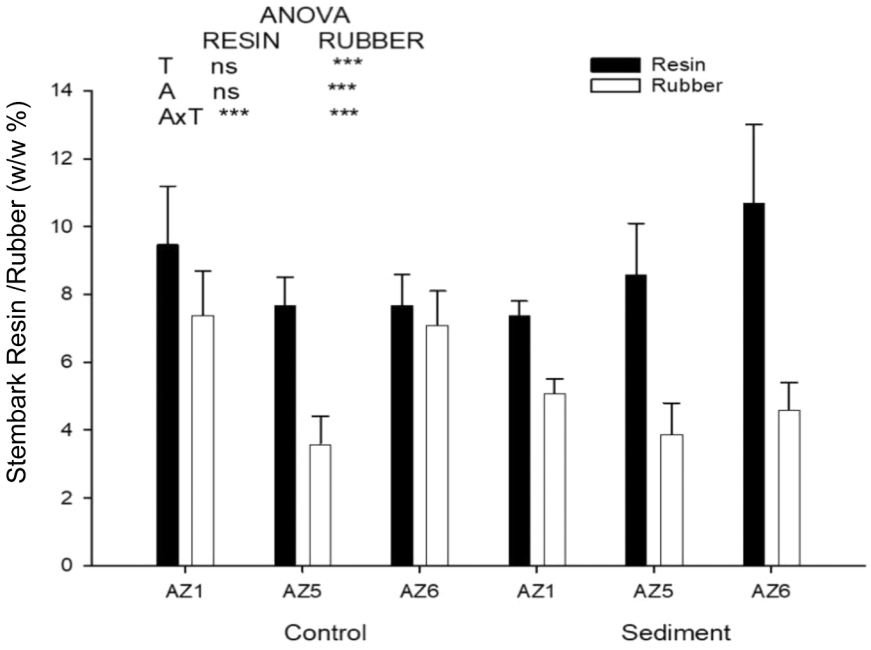


Fig. 7. Concentration of natural rubber and resin in stembark of field-grown guayule in control and sediment plots. The plants were harvested in 2019 after 18 months of growth in both plots. Values represent average and SD ($n = 4$). Two-way analysis of variance to evaluate 'accession' (A), 'treatment' (T) and interaction ($A \times T$) effects was performed. ns, *, **, and *** indicate non-significance or significance at 5%, 1%, and 0.1% probability levels, respectively. (See Table 2 for soil description of treatments).

resin concentrations (4–8 w/w% rubber and 8–10 w/w% resin), were similar to those reported elsewhere for field-grown plants (Placido et al., 2020) (Fig. 7). AZ5 had quite similar rubber concentrations in stems of plants grown in both control and sediment plots (Fig. 7), whereas AZ1 and AZ6 showed a significant decrease (~23 % lower for AZ1 and 52 % lower for AZ6) in rubber production when grown in the field sediment plot. Overall, resin concentrations in stems were mixed with respect to treatments, and not significantly different amongst the accessions grown in control or in sediment field plot (Fig. 7).

3.2.3. *Results of gene expression analysis (RT-qPCR)*

We investigated the expression level of 3 genes known to play a role in salt tolerance in plants: 1) *HKT1-like* high affinity potassium transporter, 2) *NHX1* sodium-hydrogen antiporter (NHX), important antiporter genes which help plants to exclude Na+ and Cl ions through membranes or deposits in the vacuole to maintain the cell osmotic level, and 3) Salt Overly Sensitive (SOS) stress signaling pathway, which is essential in regulating Na+ efflux at cellular level, and in long distance transport of Na+ from root to shoot (Gupta and Huang, 2014). We chose field-grown AZ-5 plants; leaf, stem, and root tissues were flash frozen. RNA extraction was performed, and the expression level of the target genes was quantified. From the qPCR result, the NHX1 gene was downregulated under salt stress in all tissues, the SOS1 was downregulated in stem and leaf. Most interesting, an *HKT1-like* gene was highly expressed in the stem but lowly expressed in the leaf and root tissues (Fig. 8A-C).

4. Discussion

4.1. *Plant growth and mineral elements concentration*

In this study, we have demonstrated the ability of vigorous AZ guayule accessions to tolerate soil and water salinity, B and Se under greenhouse conditions in which plants were irrigated with simulated drainage water containing salinity, and B, and grown on saline, B- and Se-laden soil. By the end of the experiment, the plants were quite small (Table 3), long thin stems with a few leaves. Nevertheless, differences were noted, and accessions AZ1, AZ5, and AZ6 showed the highest biomass production and exhibited the lowest symptoms of toxicity. They were able to tolerate Na, B, and Se naturally present in the soil and the additional salt ions Cl and B applied via irrigation water treatments-hence, they were selected for further evaluation in field sediment study. In the greenhouse study, concentrations of Na in the leaves (>1 % DW) were highest with saline irrigation treatments containing 10 dS/m (T2, T4 and T5), which is a high salinity level for non-halophytic plants. Our results clearly show that the AZ guayule accessions can tolerate high tissue Na concentrations. Placido et al. (2021) and Lorenzi (2020) reported similar leaf Na concentrations in other guayule accessions either grown hydroponically or treated with NaCl in the irrigation waters, respectively. In all cases, both research groups reported that guayule tolerated the saline conditions. In our study, chloride was also accumulated up to 27,000 mg/kg^{-1} DW in leaves up to 10,000 mg/kg^{-1} DW in stems and up to16,000 mg/kg^{-1} DW in roots. These high Cl concentrations in leaf indicate that guayule is likewise tolerant to high levels of Cl applied via irrigation with simulated drainage waters. Such Cl levels are toxic to most sensitive plant species, but levels as high as 30, 000 mg/kg^{-1} DW are tolerated by barley, spinach, and sugar beet (Marschner, 1995).

Similar to other accessions evaluated by Placido et al. (2021), we showed that AZ accessions of guayule can be safely grown on saline soil with elevated B levels under greenhouse conditions and irrigated with waters high in salinity (10 dS/m) and B (20 mg B/L). Indeed, germination studies with guayule AZ accessions have shown that B applied with irrigation water positively influenced germination and growth of AZ1, AZ2, and AZ4 (Zhu and Bañuelos, 2016). In regard to B, we observed that B concentration in leaves was negatively affected by salinity in two different ways. Firstly, there are reported antagonistic relationships between salinity and B accumulation in plants (Yermiyahu et al., 2008; Díaz and Grattan, 2009; Placido et al., 2021). Secondly, the inclusion of salinity in treatments (T2, T4, and T5) soils retained moisture longer and slightly less irrigation water was needed.

Similarly, we observed inhibition of Se uptake with the same saline treatments (e.g., T2, T4, and T5) in the greenhouse study. Others have reported that salinity in the soil or in the irrigation water can reduce the uptake of soluble Se (Bañuelos et al., 2005; Jiang et al., 2017; Placido et al., 2021). In this study, Se concentrations in leaves (>2 mg/kg) of guayule were high enough to consider guayule as a moderately Se-enriched plant (Broadley et al., 2006; Bañuelos et al., 2009) when grown under high B and salinity levels in the soil and irrigated with saline and B rich waters. Because the plant is an industrial non-edible

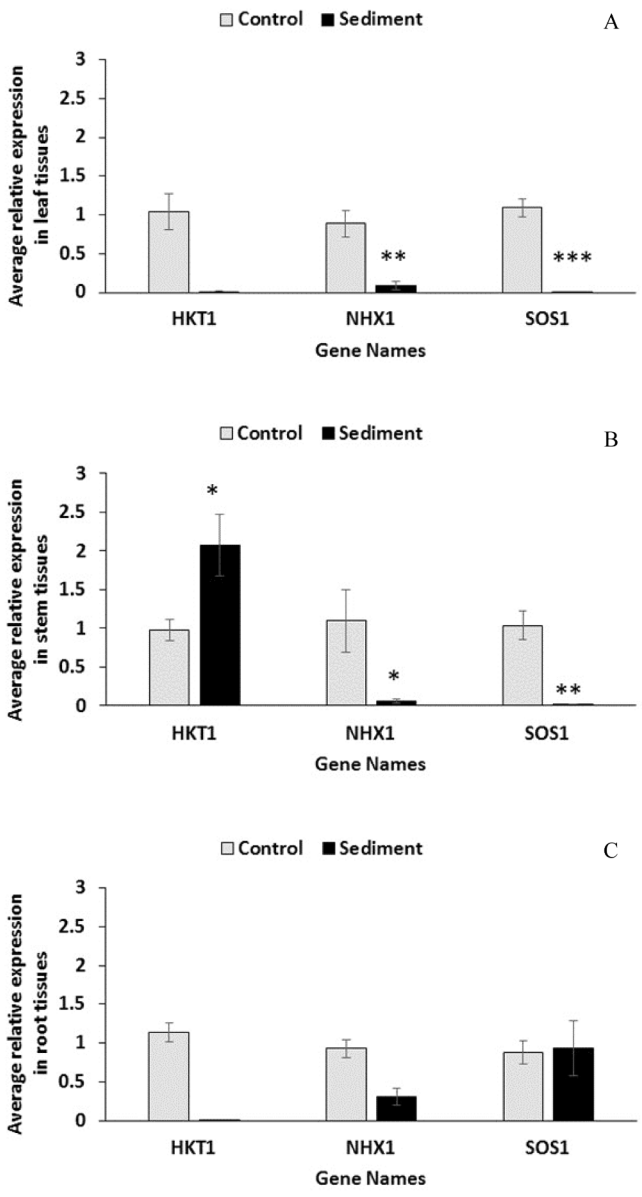


Fig. 8. (A-C). Average relative expression of *HKT1*, *NHX1*, and *SOS1*. AZ5 plants grown under non-saline and saline environments at USDA/ARS San Joaquin Valley Agricultural Sciences Cent in Parlier, CA. HKT1 = high affinity K^+ transporter; NHX1 = Na^+/H^+ antiporter; SOS1 = Salt Overly Sensitive 1; The error bars represent the standard deviation of three biological AZ5 guayule plants; $n = 3$ plants per treatment. Date of harvest: 12–11–2018.

crop, its ability to accumulate Se may be useful for the gentle bioremediation of Se (removal of Se) present in soil or added to soil with poor quality water (Placido et. al, 2021). Combining production of natural rubber with the ability to gently remediate Se-laden soils is a sustainable and resource efficient approach to the utilization of guayule in degraded and drought-stricken areas (Centofanti and Bañuelos, 2015; Attia-Ismail, 2018).

4.2. Resin and rubber production

Our greenhouse experiment design provided an independent assessment of rubber and resin production when AZ accessions were grown in poor quality soil and irrigated with poor quality water. Overall, the presence of salts, B, and Se in the soil and irrigation water did not strongly affect the production of rubber in greenhouse-grown guayule plants, which is in agreement with previous reports (Placido et al., 2021). But surprisingly, the small greenhouse plants produced remarkably high levels of natural rubber and resin. Abiotic stress is known to increase rubber content in guayule (Bonner, 1943), and the plants clearly showed signs of stress and ion accumulation in tissues, from the chemical environment. Most ions, tend to accumulate in leaves, as observed in our study, e.g., B, Na and Cl, while rubber production in guayule is concentrated in stem and root tissue. The greenhouse study therefore identified guayule accessions AZ1, AZ5, and AZ6 as tolerant to soil and irrigation water salinity, while producing high levels of natural rubber and resin. Surprisingly, rubber and resin content generally increased (for AZ1 and AZ6) as salt and B level increased in irrigation water (T1, T4, T5), but B alone (T3, T6) had little or no effect on rubber production. High levels of natural rubber (11 %) and resin (14 %) resulted when plants were grown under the double stress of poor quality soil and irrigation water under greenhouse conditions. High salinity (~10 dS/m) led to higher rubber concentration in all three accessions (AZ1, AZ5, AZ6) grown under greenhouse conditions. However, biomass was reduced under both saline and B treatments (T2 thru T6). Consistent with this greenhouse study, Placido et al. (2021) found higher rubber content and reduced biomass for other guayule accessions grown under similar (poor quality) irrigation water conditions. However, field studies have shown mixed results, including increased rubber concentrations under saline (3–7.2 dS/m) conditions in 2-year-old field plants (Miyamoto et al., 1985) and conversely decreased rubber content in guayule plants grown under higher salinity conditions (9–12 dS/m) (Hoffman et al., 1988). Yet, in these studies and others (Retzer and Mogen, 1946), rubber yield (per acre) was lower due to the decrease in shrub biomass.

The sediment plot challenged the plants with moderate salinity (2.6–3.3 dS/m), as well as elevated levels of Se and B in the sediment soil. Nevertheless, rubber and resin concentrations were comparable to previous reports for guayule grown in good quality soil (Luo and Abdel-Haleem, 2019). Notably, the quality of rubber (molecular weight) was not affected when guayule was field grown under these challenging conditions. The natural rubber content for AZ1 and AZ6 was lower for plants grown in the sediment plot compared with control; but AZ5 accession merits further study under marginal agricultural soils. Overall, our results showed that the natural and applied levels of salt, B, and Se in soil and irrigation water, respectively can be tolerated by guayule, mostly without negative impacts on the resin and rubber content.

Plants have evolved adaptive mechanisms to regulate the accumulation of salt through osmoprotection, salt exclusion, and tissue tolerance (Munns and Tester, 2008; Gupta and Huang, 2014). Measuring differences in guayule genetic response to salinity may lead to a better understanding of how guayule has adapted to saline/calciferous soils. The expression analysis suggests that *HKT1* system plays an important role in regulating sodium accumulation in stem tissues, and salinity stress tolerance in guayule. While these results are just a glimpse of the molecular machinery involved, they document different responses for different tissues in guayule. Additional studies will be needed to unravel the full mechanistic understanding.

5. Conclusions

As an industrial crop, guayule has potential to be used in marginal soils to produce natural rubber resins, and biomass. The ability of guayule to tolerate salinity, B, Na, Cl and Se salts naturally present in soil and irrigation water appears to vary by accession; here we identify AZ5 as particularly suited to breeders and growers seeking alternative crops in the Westside of the SJV in Central California. Our results suggest that guayule can be potentially grown as an alternative crop on semi-arid lands, or parts of the Southwestern U.S., with poor quality waters (high salinity and B) that are unsuitable for typical agronomic crops, mostly without negative impacts on the resin and rubber content. In addition, because of the plant's ability to take up moderate concentrations of Se, the production of natural rubber can be combined with

guayule's apparent ability to gentle remediate Se rich soils like those present in the Western SJV in Central California or soils irrigated with Se with saline waters containing Se and B.

Note

Mention of trade names or commercial in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S Department of Agriculture USDA is an equal opportunity provider and employer.

CRediT authorship contribution statement

Gary Bañuelos: Conceptualization, Methodology, Reviewing and Editing. **Dante Placido**: Conceptualization, Methodology, data analysis. **Hui Zhu**: Methodology. **Tiziana Centofanti**: Writing- Original draft preparation, methodology, data analysis, reviewing. **Colleen M. McMahan**: Conceptualization, Methodology, Reviewing and Editing. **Hui Zhu**: Methodology. **Claire Heinitz**: Methodology. **Maria Zambrano**: assisting with Data curation, **Todd Lone**: Reviewing and Editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gary Banuelos reports financial support was provided by California State University Agricultural Research Institute (Grant number ARI 17-02-007).

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.indcrop.2022.115799.

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