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Relative differences in salinity tolerance and genetic expression of salt-tolerant and sensitive varieties of commercially important Solanaceae crops

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Abstract

Members of the Solanaceae family, such as tomatoes (*Solanum lycopersicum*), eggplants (*Solanum melongena* L.), and peppers (*Capsicum chinense* L.), are moderately sensitive to salinity, which could limit their production, especially under future water limitations and decreasing irrigation water quality. Heirloom cultivars provide valuable genetic resources for enhancing salinity resilience, yet their potential for intrinsic tolerance in Solanaceae crops remains unexplored. In this study, we built on earlier research by comparing relatively salt-sensitive and salt-tolerant cultivars of tomato, eggplant, and pepper under multiple salinity treatments using both chloride- and sulfate-dominant irrigation waters. For each cultivar, we measured yield, biomass, ion concentrations, and gene expression profiles to gain insights into the mechanisms underlying salinity tolerance. The results indicate that these Solanaceae varieties may have higher salinity tolerance than reported in the literature (e.g., Food and Agriculture Organization Irrigation and Drainage Paper 61), with a notable increase in the yield reduction threshold for the sulfate treatments and potentially lower slope as assessed with the Maas–Hoffman model. Gene expression results revealed that salt-tolerant cultivars in eggplant, tomato, and pepper (e.g., ‘Long Purple’, ‘Red

Abbreviations: AKT1, *Arabidopsis K⁺ Transporter 1*; ALMT9, *Aluminum-Activated Malate Transporter 9*; ANOVA, analysis of variance; CCC, *Cation-Chloride Co-transporter 1*; EC, electrical conductivity; FAO, Food and Agriculture Organization; NHX1, *Na⁺/H⁺ Exchanger 1*; NHX2, *Na⁺/H⁺ Exchanger 2*; qRT-PCR, quantitative reverse transcription–polymerase chain reaction; SLAH3, *Slow Anion Channel–Associated Homologue 3*; SOS, *Salt Overly Sensitive*.

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Pear', and 'Ancho') showed consistently more effective regulation of key Na^+ - and Cl^- -transport genes than their salt-sensitive counterparts (e.g., 'Black Beauty', 'Jaune Flamme', and 'Corbaci'). This included enhanced ion extrusion at the root surface, improved vacuolar sequestration of ions within cells, and tighter control over root-to-shoot ion movement. Together, these traits promoted tissue-level tolerance by maintaining ionic homeostasis and preventing excessive ion accumulation. These results suggest that heirloom varieties are a potential genetic source for future plant breeding efforts to improve salinity tolerance in the "solanaceous" species studied.

Plain Language Summary

Vegetables such as tomatoes, eggplants, and peppers are important human food sources. These crops have historically been viewed as moderately sensitive to soil and water salinity, which could limit their production where they are grown. Heirloom varieties are an important source for breeding improved varieties that are more salt-tolerant. In this study, we evaluate two cultivars for salinity tolerance in tomatoes, eggplants, and peppers. Yield, root and shoot biomass, root and shoot ion concentrations, and root and shoot gene expressions were analyzed. These vegetables may have higher salinity tolerance than reported in literature. Gene expression was consistent with assessed variety salinity tolerance, with salt-tolerant varieties better expressing genes that limited sodium and chloride concentrations in plant tissues. These results suggest that heirloom varieties are a genetic source for future plant breeding efforts to improve Solanaceae vegetable salinity tolerance.

1 | INTRODUCTION

Agricultural irrigation constitutes the largest anthropogenic use of fresh water (Döll & Siebert, 2002). This irrigation has led to substantial groundwater depletion (Jain et al., 2021; P.-W. Liu, Famiglietti, et al., 2022; Scanlon et al., 2023), increased reliance on variable surface-water supplies (Anderson et al., 2012), and increased need to use or reuse lower quality irrigation waters that have higher salinities (Ashu & Lee, 2021; Hristov et al., 2021). Furthermore, climate change is expected to increase soil salinity in both irrigation-dependent regions (Corwin, 2021) and dryland agricultural regions (Hassani et al., 2021).

One important group of crops is the Solanaceae family: tomatoes (*Solanum lycopersicum*), eggplants (*Solanum melongena* L.), and peppers (*Capsicum chinense* L.). While smaller in production area and volume compared to cereal crops, vegetables of the Solanaceae family are mostly grown for direct human consumption. For example, tomatoes are the second most commonly consumed vegetable in the United States (Reimers & Keast, 2016). However, these vegetables are most frequently grown in subtropical and semiarid regions

(Cammarano et al., 2022; Chapman, 2020; Crosby, 2008; Cuartero & Fernández-Muñoz, 1998) that currently have the greatest irrigation ("blue water") water stress (Rosa et al., 2020) and are expected to have increased stress in the future (X. Liu, Liu, et al., 2022; Schewe et al., 2014). These regions have the greatest pressure for agriculture to use or reuse lower quality irrigation waters with higher salinity (Marangon et al., 2020; Mizyed, 2013; Petousi et al., 2015); thus, there is a need for improved salinity tolerance for these vegetables for lower quality degraded waters to be effectively used as alternative sources of irrigation.

Concerning salinity tolerance for these vegetables, eggplant is considered to be moderately sensitive to salinity (Heuer et al., 1986; Ünlükara et al., 2010) as assessed with the commonly used Maas–Hoffman model (Maas & Hoffman, 1977). Pepper plants are also moderately sensitive (De Pascale et al., 2003), while tomatoes are moderate tolerant to salinity (Pérez-Alfocea et al., 1996). A "moderately sensitive" plant expresses negative effects on growth and yield at moderate levels of salinity, while a "moderately tolerant" plant can withstand somewhat higher salinity levels before showing significant stress, meaning the moderately tolerant plant can handle more salt than the moderately sensitive one before showing significant salt damage (Katerji et al., 2000). However, substantial

variations in salinity tolerance have been reported in all three vegetables: both in the salinity threshold (where yield reductions begin to occur) and the rate of decreasing yield with increasing electrical conductivity (EC). Caro et al. (1991) found that the slope of the salinity–yield relationship varied by more than a factor of three and the salinity threshold for the saturated extract EC (EC_e) varied from ~ 1.5 to more than 5 dS m^{-1} among 11 regular-sized and cherry tomato cultivars. Cantore et al. (2008) found that the EC_e threshold ranged from 1.5 to 3 dS m^{-1} and the slope from 10% to 20% per dS m^{-1} among three tomato cultivars. With eggplant, Sanwal et al. (2022) found that a variety with a non-salinity tolerant rootstock had a relative yield reduction of 80% when irrigated with water of electrical conductivity (EC_{iw}) of 9 dS m^{-1} , while the tolerant rootstocks had yield reductions of 56% and 50% at the same treatment. Ünlükara et al. (2010) reported a low EC_e threshold of less than 1.5 dS m^{-1} and a slope of 4.4% per dS m^{-1} . However, Semiz and Suarez (2019) found a much larger slope of 12% per dS m^{-1} with eggplant with grafted rootstock. Finally, with peppers, Sá et al. (2019) found similar thresholds (1.2 dS m^{-1}) among pepper varieties but highly varying slopes ranging from $\sim 5\%$ to 25% per dS m^{-1} . Orosco-Alcalá et al. (2021) found that grafting rootstocks increased bell pepper yield and resulted in higher EC_e thresholds of around 4 dS m^{-1} and slopes of 10% – 25% per dS m^{-1} .

Genetic variation within vegetable species provides the basis for selective breeding to improve salinity tolerance (Ashraf & Wu, 1994). However, many major crops have relatively limited and restricted genetic variation (Turan et al., 2012), due to the focus on breeding traits in hybrid plants that have widespread commercial acceptance (Fita et al., 2015). Genetic engineering has the potential to increase crop salinity tolerance (Bressan et al., 2008; Wani et al., 2020), but in the past 30 years genetic engineering has not produced salt-tolerant crops that are commercially in use today and is less common for vegetable crops, likely due to consumer resistance to genetically engineered crops (Lusk et al., 2015; Spendrup et al., 2021). However, crops that are selected and bred for salt tolerance or other desired traits will have wide acceptance among consumers. An example is the Sea Rice 86 or SR86, a new cultivar that was domesticated from a wild strain of rice found in saline-alkaline soils near Zhanjiang, China (Qin et al., 2020). This is only possible by exploring wild genotypes that were not widely used in breeding programs like the ones used in large-scale agriculture. Heirloom vegetables fit this definition.

Heirloom vegetables are older (>50 years), open-pollinated varieties that are frequently maintained by gardeners and other small commercial entities (Jordan, 2007; Preston et al., 2012). Interest in heirloom vegetables has increased due to their perceived improved taste and nutritional quality compared to commercial hybrids (Constantino et al., 2022; Dwivedi et al., 2019; Rodriguez-Burruezo et al., 2005). However, heirlooms

Core Ideas

- Heirloom vegetable cultivars provide an important genetic repository to breed stress-tolerant cultivars.
- We conducted a field salinity-tolerance experiment with two cultivars each of eggplant, tomato, and pepper.
- Significant yield differences between cultivars occurred for eggplant but not for the other vegetables.
- Chloride-based treatments were more damaging than sulfate-based treatments.
- Salt-tolerant cultivars exhibited stable or adaptive expression of ion-transport genes, enhancing salt tolerance.

also provide a large potential gene pool to explore how vegetables of the Solanaceae family respond and express genes concerning salinity stress (Boyacı et al., 2020; Gramazio et al., 2019; Kulus, 2022; Oladosu et al., 2021; Rathinasabapathi, 2020) and to provide the potential for new hybrids that have greater salinity tolerance.

Building on our initial survey by Suarez et al. (2021)—which screened eight eggplant, seven tomato, and eight pepper cultivars at a single chloride-dominated salinity level ($EC_{iw} = 4 \text{ dS m}^{-1}$) and recorded yield responses—we now focus on the most salt-tolerant and most salt-sensitive cultivar from each crop for a deeper mechanistic analysis. Specifically, this study (i) applies a broader salinity gradient (0.65 – 6 dS m^{-1}) under both sulfate- and chloride-dominant irrigation, (ii) quantifies root- and shoot-specific ion accumulation, and (iii) profiles expression of key sodium- and chloride-transport genes in both organs. Integrating these molecular and physiological data with yield and biomass metrics allows us to pinpoint the ionic and genetic bases of salinity tolerance that were only hinted at in the earlier survey.

2 | MATERIALS AND METHODS

2.1 | Experimental design and irrigation

Our experimental protocol largely mirrored a previous salinity tolerance experiment in Solanaceae (Suarez et al., 2021) and is briefly discussed here. We used two heirloom cultivars each of eggplant (*S. melongena* L.—‘Black Beauty’ and ‘Long Purple’), tomato (*S. lycopersicum*—‘Jaune-Flamme’ and ‘Red Pear’), and pepper (*C. chinense* L.—‘Corbaci’ and ‘Ancho’ or ‘Poblano’), which were grown from May (transplanting to field) to October 2019. Black Beauty, Jaune Flamme, and Corbaci represent the relatively salt-sensitive varieties for each

TABLE 1 Annotations for control and treatment indicating the dominant anion, the electrical conductivity of the irrigation water (EC_{iw}), and the ion concentration of the irrigation water. The target ionic composition of the irrigation waters was achieved by dissolving the following salts (in appropriate proportions): Na_2SO_4 , $NaCl$, $CaCl_2$, $MgCl_2$, KCl , K_2SO_4 , and $MgSO_4$.

Treatment	Dominant anion	EC_{iw} (dS m^{-1})	Ion concentration (mmol L^{-1})						
			Cl^{-}	SO_4^{2-}	NO_3^{-}	PO_4^{3-}	Na^{+}	K^{+}	Ca^{2+}
T0S0 (control)		0.65	2.87	2.27	0.39	0	1.88	0.99	3.9
T1S1	Cl^{-}	3.0	23.79	1.4	0.39	0	21	0.99	4.83
T1S2	Cl^{-}	4.5	37.79	1.4	0.39	0	35	0.99	4.93
T1S3	Cl^{-}	6.0	50.79	1.4	0.39	0	48	0.99	4.83
T2S1	SO_4^{2-}	3.0	2.98	26.37	0.39	0	25	0.99	4.99
T2S2	SO_4^{2-}	4.5	2.98	42.37	0.39	0	41	0.99	4.99
T2S3	SO_4^{2-}	6.0	2.98	59.37	0.39	0	58	0.99	4.99

vegetable while Long Purple, Red Pear, and Ancho represent the relatively salt-tolerant varieties (Suarez et al., 2021).

Our trial included 168 plants of each species (504 total plants) with control irrigation, three salinity levels of irrigation water or EC_{iw} (3.0, 4.5, and 6.0 dS m^{-1}), and two irrigation water ionic compositions (sulfate and chloride dominant) in a full factorial design (Table 1), thus resulting in 24 plants per treatment for each species. These EC_{iw} targets bracket the moderate-to-high salinity range typically encountered in semiarid vegetable production (~ 2 – 6 dS m^{-1}) and align with the yield-response thresholds identified in our earlier Solanaceae screening. Individual plants were planted in 21 rows of 24 plants each. Control irrigation water was Riverside, CA, municipal water ($EC_{iw} = 0.65$ dS m^{-1}) with approximately equal compositions between chloride and sulfate anions (Ferreira et al., 2022). The treatments were classified as: control with balanced anion composition and low salinity of $EC_{iw} = 0.65$ dS m^{-1} (T0S0), chloride-dominant as T1 and sulfate-dominant as T2, and salinity treatments of 3.0 (S1), 4.5 (S2), and 6.0 (S3) dS m^{-1} .

Irrigation and fertilization followed the same strategy as in Suarez et al. (2021), with daily irrigation adjusted according to the local state meteorological network (California Irrigation Management Information System). In mid-June 2019, 12 g of Osmocote Plus slow-release fertilizer was added. Irrigation supply tanks and waters were adjusted biweekly to maintain a consistent irrigation water composition throughout the growing season.

2.2 | Plant measurements and statistical analyses

Weekly harvests of ripe fruits were carried out between late June and late September 2019, which we then used to calculate the average fruit weight per plant. Leaf samples of 9–30 leaves were collected in late September 2019 after the final harvest. Total shoot and root biomass were collected at

the same time. Shoots and washed roots were oven-dried in forced air at 70°C for 72 h, then weighed to determine dry biomass. Both leaves and roots were processed in the same manner as Suarez et al. (2021), with a final elemental analysis conducted using Inductively Coupled Plasma Optical Emission spectroscopy (Perkin Elmer Optima 3300 DV ICP OES). Chloride concentrations were determined by amperometric chloride titration. Statistical significance was assessed using analysis of variance (ANOVA). Salinity treatments were evaluated using a single-factor ANOVA with replication, while cultivar-specific differences were assessed using a two-factor ANOVA with replication.

2.3 | Genetic analyses

Samples of leaf and root tissues were collected from salt-tolerant and salt-sensitive cultivars of eggplant, tomato, and pepper (2 cultivars $\times$ 3 crops $\times$ 2 tissue types $\times$ 3 replicates $\times$ 7 water composition and salinity treatments), 48 h after initiating salinity exposure. The young tissue samples were immediately frozen using liquid nitrogen, and RNA was extracted using TRIzol reagent (Invitrogen). To remove any DNA contamination, DNase I treatment was applied to the isolated RNA following the manufacturer's guidelines (Thermo Scientific). Quantitative reverse transcription–polymerase chain reaction (qRT-PCR) was conducted using the iTaq Universal SYBR Green One-Step Kit on the Bio-Rad CFX96 system (Bio-Rad Laboratories). Each qRT-PCR reaction was performed in a 10 μ L mixture containing 100 ng of total RNA, 0.125 μ L iScript Reverse Transcriptase, 0.75 μ M of each primer, and 5 μ L of 2x SYBR Green Reaction mix. The thermal cycling conditions included an initial incubation at 50°C for 10 min, followed by 95°C for 1 min, and then 40 cycles of denaturation at 95°C for 10 s, annealing at 57°C for 30 s, and extension at 68°C for 30 s. To ensure consistency across different plates, four samples were used as inter-plate controls. Reference genes

utilized included Cyclophilin (AF126551), 18S ribosomal RNA (X67238), and glyceraldehyde-3-phosphate dehydrogenase (U17005) for eggplant; Actin (TC194780), protein phosphatase 2A catalytic subunit (AY325817), and ribosomal protein L2 (X64562) for tomato; and Actin (GQ339766), glyceraldehyde-3-phosphate dehydrogenase (AJ246009), and EF1 α (AY496125) for pepper. Gene expression was measured by comparing the cycle threshold values of target genes with those of the reference genes, identifying differentially expressed genes. The specificity of the amplification was confirmed via melt curve analysis, which involved ramping the temperature to 95°C for 10 s, then reducing it to 65°C for 5 s, followed by incremental increases of 0.5°C per cycle until reaching 95°C.

3 | RESULTS AND DISCUSSION

3.1 | Yield and relative yield

For eggplant, Black Beauty showed a greater range (1007–1981 g) than Long Purple (1286–1832 g) (Figure 1a). Within each anion treatment, Black Beauty had lower yields for T1S3 compared to the other chloride treatments. For the sulfate treatments, T2S2 and T2S3 were lower than T2S1. In general, yield followed the expected pattern of progressive decreases with increasing salinity, apart from the lowest sulfate salinity treatment (T2S1) that had higher yields for both cultivars than the non-saline control. However, no statistical significance was found with the ANOVA tests. With relative yields, the salt-sensitive cultivar, Black Beauty showed the greatest decline (40%) for some of the higher salinities (T1S3, T2S2, and T2S3) (Figure 1b). For tomato, the absolute yield ranged from 2269–3578 g across treatments (Figure 1c). Like eggplant, tomato exhibited a higher relative yield under the T2S1 compared to T0S0 (Figure 1d). Notably Red Pear had relative yield higher than 100%, albeit not significantly higher. However, no distinct pattern emerged concerning either the salinity treatment or the cultivar. There were no statistically significant differences observed with any EC level, dominant anion, or cultivar.

For pepper, the actual yields ranged from 530–1162 g across treatments (Figure 1e). Most treatments (T1S1, T1S2, T2S2, and T2S3) had similar relative yields and actual yields (Figure 1e,f). As observed for other vegetables, T2S1 had significantly higher yields than other salinity treatments, but the peak relative yield was below the one achieved with the control salinity (T0S0) of 100%. Conversely, T1S3 had significantly lower yield and relative yield, with the T1S3 treatment for the salt-tolerant cultivar (Ancho) showing the lowest relative yield.

Based on our results, chloride-based treatments were more detrimental to plants compared to the sulfate-based

treatments. For example, both pepper cultivars exhibited significantly lower relative yields in T1S1 and T1S3 compared to T2S1 and T2S3, respectively (Figure 1f). A similar pattern was observed in eggplant and tomato, with lower relative yields in T1S1 compared to T2S1, though these differences were not statistically significant (Figure 1b,d). A comparable chloride-induced yield penalty has also been documented in almond, underscoring the broader relevance of this trend (Sandhu et al., 2020). In complex field experiments, a lack of statistical significance can result from underlying genetic variability, environmental noise, or limited sample size. However, these nonsignificant trends may still point to biologically meaningful patterns, especially when they are consistent with previous findings or physiological expectations.

3.2 | Leaf and root ion concentrations

Leaf and root ion concentrations varied significantly among the three Solanaceae vegetables (Figures 2–4).

3.2.1 | Eggplant

For eggplant, leaf sodium (Na) concentrations ranged from under 10–187 mmol kg⁻¹ dry biomass; this was generally lower than root Na concentrations (149–487 mmol kg⁻¹ dry biomass) by at least a factor of 4 (Figure 2a,b). The eggplant cultivars showed significant differences in leaf Na at the S2 and S3 treatments, whereas there were no cultivar-specific differences in root Na.

Concerning chloride (Cl) in eggplant, both varieties unsurprisingly showed different uptake responses to Cl versus sulfate-dominated irrigation water (Figure 2c,d). Both leaf and roots showed increasing uptake of Cl at higher salinities dominated by Cl, with the highest salinity (S3) showing cultivar differences with Black Beauty having higher leaf and lower root Cl than Long Purple. For the Black Beauty cultivar, leaf Cl concentrations continued to rise with increasing salinity in Cl-based treatments, whereas in Long Purple, they plateaued at T1S2 (Figure 3c). Conversely, root Cl concentrations increased with salinity in Cl-based treatments for Long Purple but plateaued at T1S2 for Black Beauty (Figure 3d). This indicates that the salt tolerant cultivar Long Purple retained Cl in the roots to protect shoots from Cl toxicity, while Black Beauty had no such control and the Cl from the roots were readily transferred to the shoots. Chloride uptake showed smaller differences between leaves and roots compared to Na, with Cl-based treatments generally resulting in leaf uptake that was 100%–200% higher than in roots (Figure 2a–d).

Regarding potassium (K) in eggplant, the concentration in leaves (601–932 mmol kg⁻¹ dry biomass) was generally

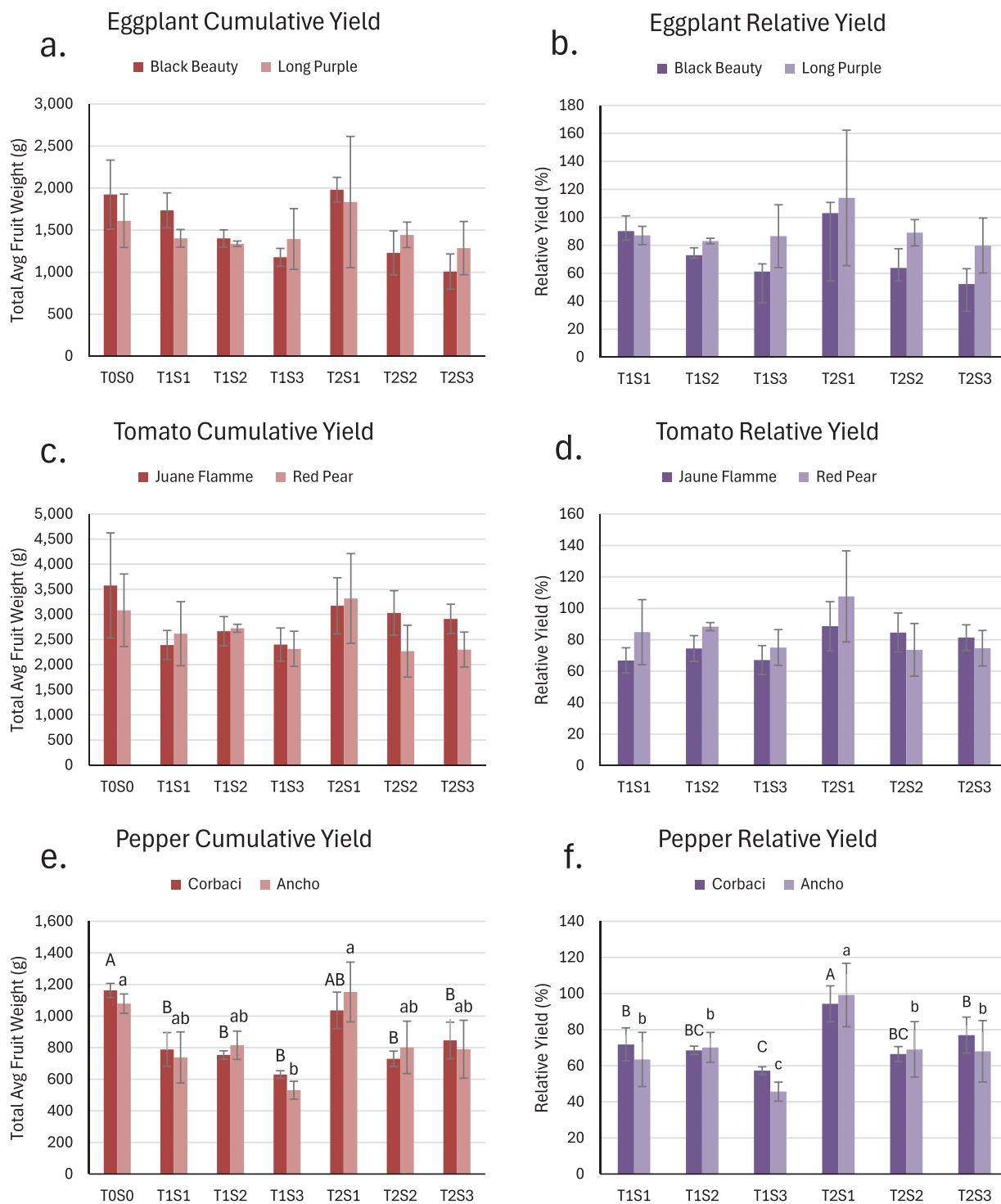


FIGURE 1 Yield and relative yield for each of the three Solanaceae vegetables. Capital letters denote statistically significant ($p < 0.05$) differences among treatments for the salt-sensitive variety. Lowercase letters denote significant differences among treatments for salt-tolerant variety. Asterisks denote significant differences between varieties for each treatment. Error bars indicate standard error of individual plant observations.

at least three times higher than in roots (160–240 mmol kg^{-1} dry biomass) (Figure 2e,f). Cultivar-specific differences were apparent in leaf K for all S2 and S3 treatments, while fewer differences in root K were observed between cultivars, primarily in T1S1, T1S2, and T2S2 (Figure 2c,d).

3.2.2 | Tomato

As for tomato plants, both leaves and roots had increasing and frequently significant differences in ion uptake with higher salinity, but the rate of increase was relatively muted

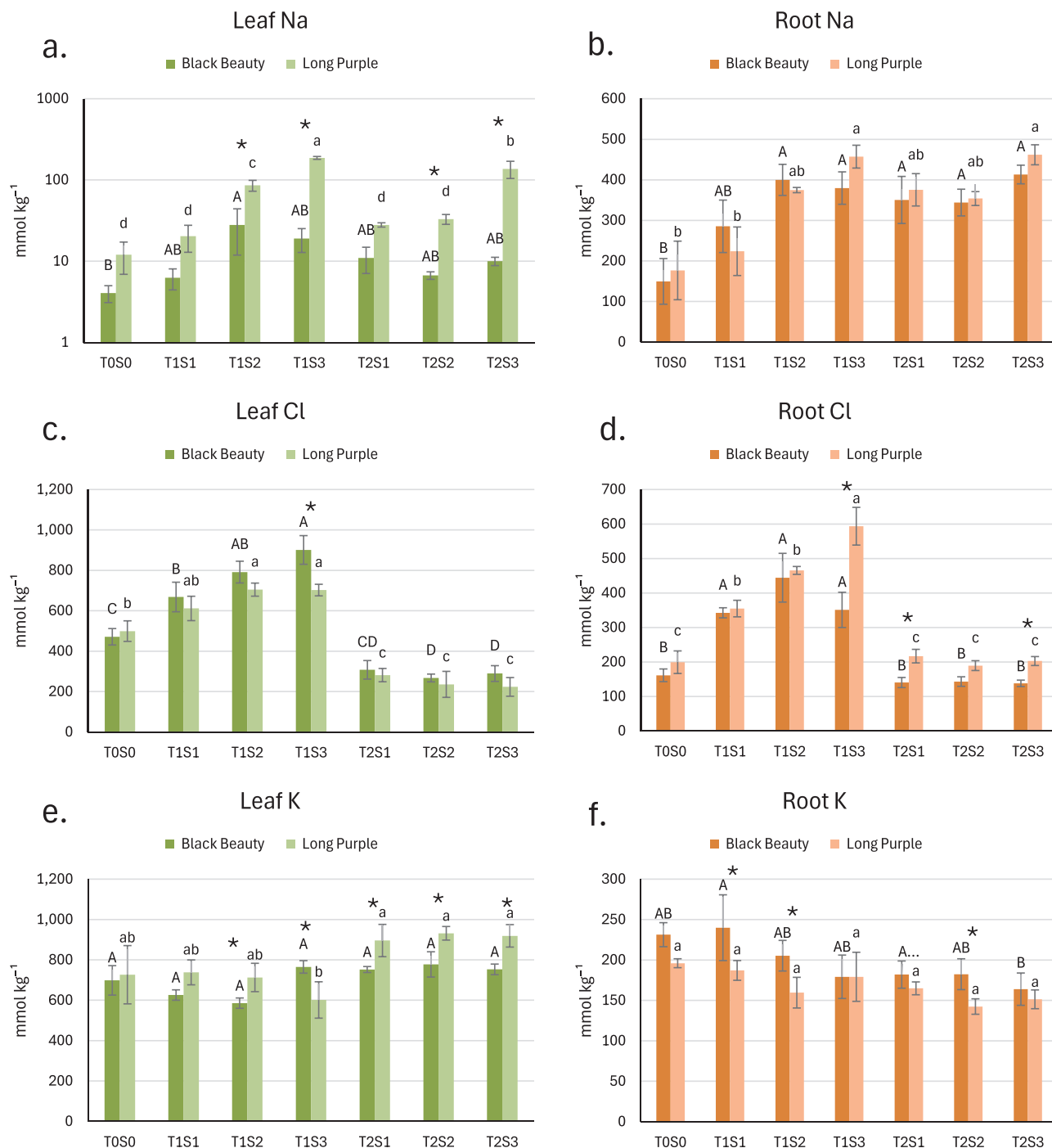


FIGURE 2 Leaf and root sodium, chloride, and potassium concentrations (mmol kg^{-1} dry biomass) for eggplant. Capital letters denote statistically significant ($p < 0.05$) differences among treatments for the salt-sensitive variety. Lowercase letters denote significant differences among treatments for salt-tolerant variety. Asterisks denote significant differences between varieties for each treatment. Error bars indicate standard error of individual plant observations.

for the sulfate treatments, especially with root-Na uptake (Figure 3a,b). There were no cultivar-specific differences across all treatments for leaf or root sodium uptake. Leaf and root Na uptake showed less variation than in eggplant but with stronger, significant, differences compared to the control treatment (Figure 3a,b).

With chloride, there were, unsurprisingly, strong and significant differences between the Cl and the sulfate-dominated treatments (Figure 3c,d). The sulfate salinity treatments did not differ from the control. Root Cl showed increasing concentrations across the Cl treatments, whereas leaf Cl had maximum uptake with T1S2.

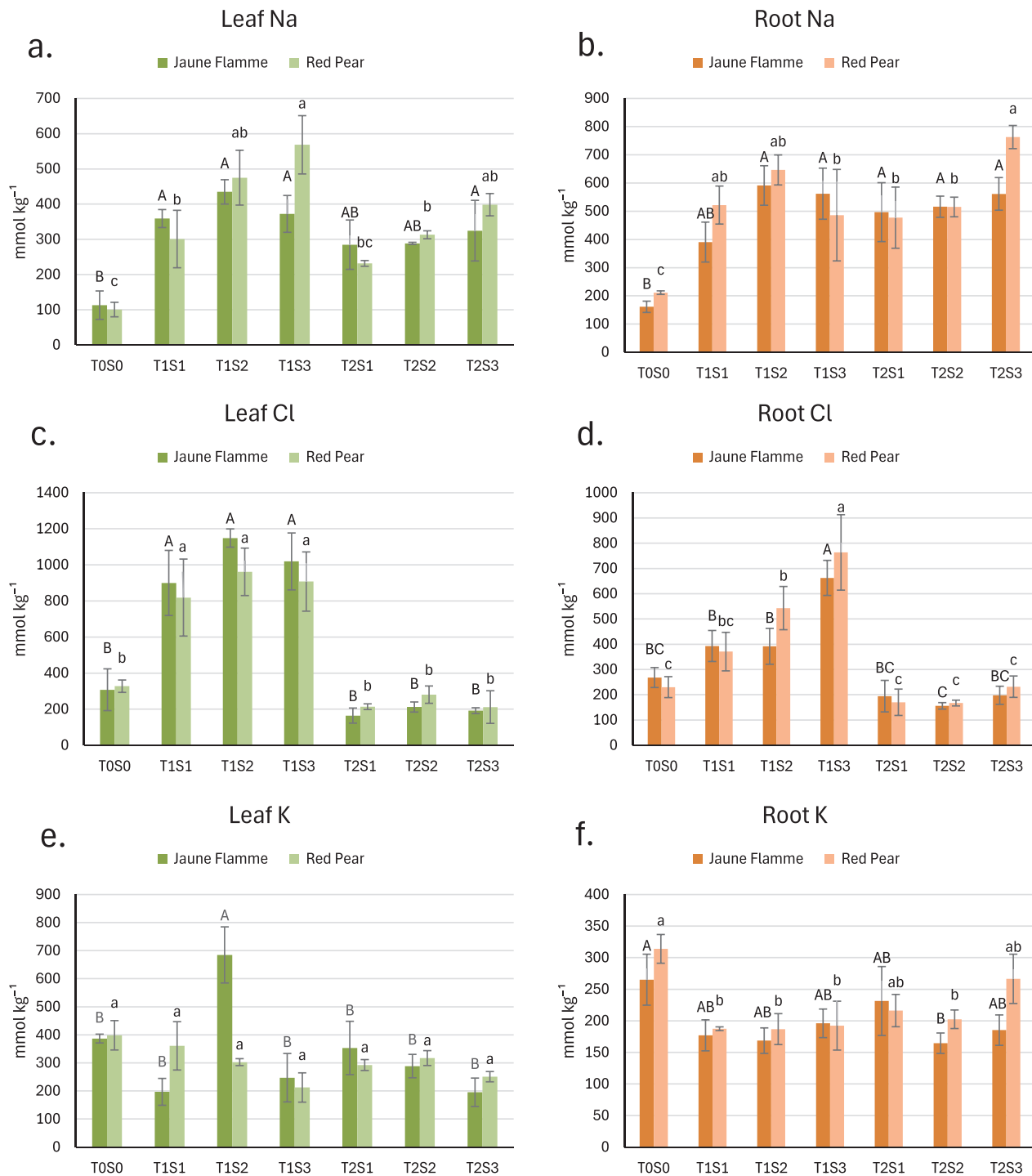


FIGURE 3 Leaf and root sodium, chloride, and potassium concentrations (mmol kg⁻¹ dry biomass) for tomato. Capital letters denote statistically significant ($p < 0.05$) differences among treatments for the salt-sensitive variety. Lowercase letters denote significant differences among treatments for salt-tolerant variety. Asterisks denote significant differences between varieties for each treatment. Error bars indicate standard error of individual plant observations.

With K, there were fewer clear trends, including between cultivars. The highest leaf Cl treatment (T1S2) had the highest leaf K with Jaune Flamme while root K levels were significantly higher in the control versus all other treatments (Figure 3e,f).

3.2.3 | Pepper

For pepper, the strongest differences were between leaf and root Na concentrations, with differences between root and leaf concentrations of over an order of magnitude (Figure 4a,b).

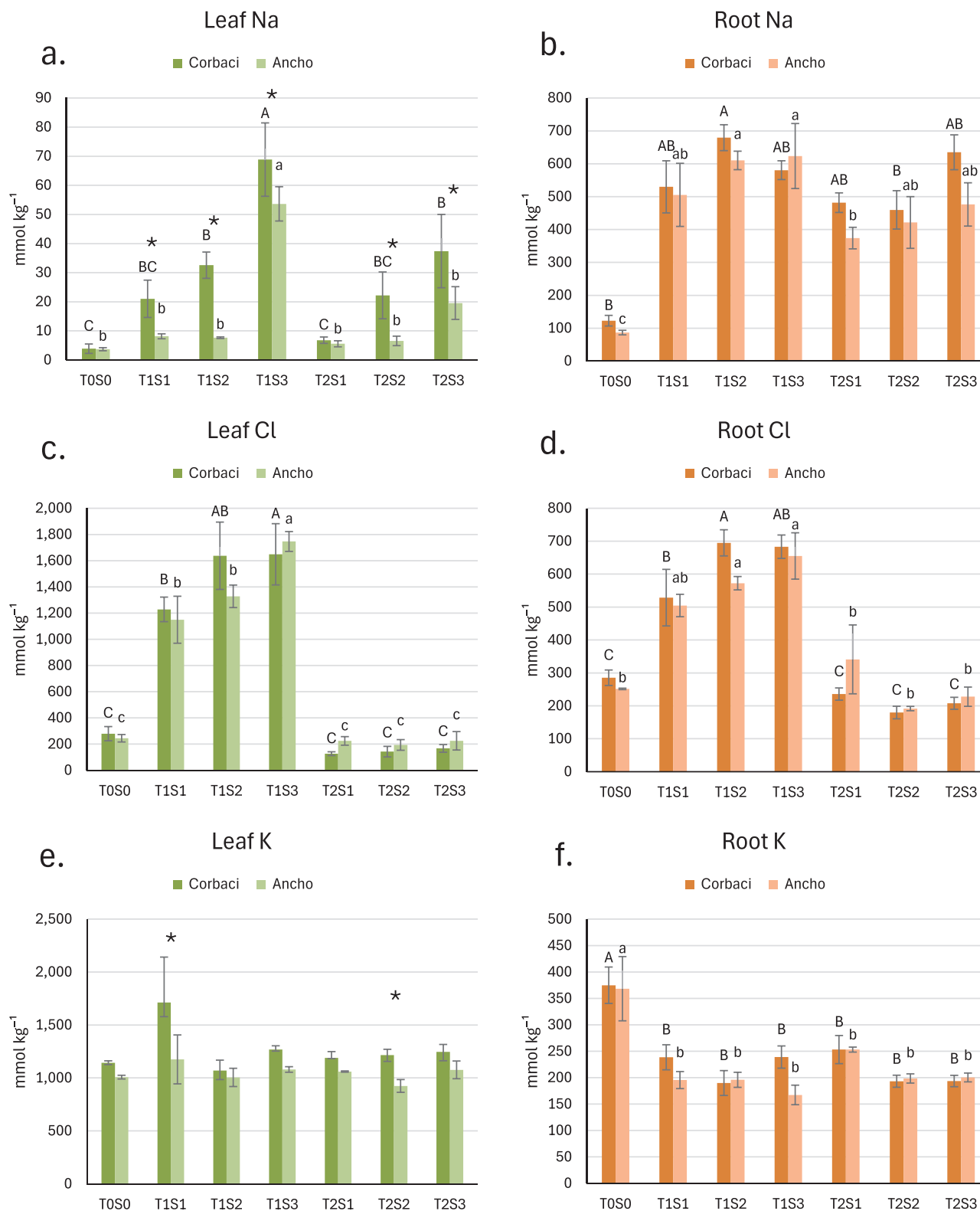


FIGURE 4 Leaf and root sodium, chloride, and potassium concentrations (mmol kg⁻¹ dry biomass) for pepper. Capital letters denote statistically significant ($p < 0.05$) differences among treatments for the salt-sensitive variety. Lowercase letters denote significant differences among treatments for salt-tolerant variety. Asterisks denote significant differences between varieties for each treatment. Error bars indicate standard error of individual plant observations.

Leaf-Na levels varied greatly among treatments with cultivar-level differences for five of the six treatments.

There were expected differences between the Cl and sulfate anion treatments regarding Cl levels. While both leaf and root Cl concentrations increased with higher salinity in Cl-based treatments, they remained consistent across sulfate-based treatments (Figure 4c,d). For Ancho, both leaf and root chloride concentrations steadily increased with rising salinity in Cl-based treatments, while for Corbaci, they plateaued at T1S2 (Figure 4c,d). Notably, there were no significant differences between cultivars with respect to chloride tissue concentrations for either leaves or roots (Figure 4c,d).

For K, Corbaci exhibited significantly higher leaf K than Ancho under both T1S1 (low chloride-based salinity) and T2S2 (moderate sulfate salinity), while no such differences between cultivars were observed in the other treatments (Figure 4e). Both cultivars showed a significant reduction in root K under all salinity treatments compared to the control (T0S0) (Figure 4f). Ancho's more stable leaf K and similar root K decline under stress may reflect tighter regulation of K distribution, potentially contributing to its greater salinity tolerance.

3.2.4 | Comparative Na, Cl, and K profiles in eggplant, tomato, and pepper

Eggplants and peppers accumulated significantly less Na in their leaves compared to tomatoes (Figures 2a, 3a, and 4a), probably due to more effective exclusion at the root level or enhanced sequestration in root tissues, preventing excessive Na^+ transport to the shoots. In eggplant, this strategy aligns well with tissue-level tolerance mechanisms, allowing it to maintain growth and productivity despite reduced leaf Na accumulation. In contrast, tomato may tolerate higher leaf Na by relying on robust intracellular compartmentalization and other tissue-level tolerance traits, enabling it to achieve salinity tolerance levels comparable to eggplant. Peppers, although limiting leaf Na^+ accumulation, appear to lack sufficient tissue-level tolerance or compensatory mechanisms, resulting in lower overall salinity tolerance despite reduced Na^+ in the leaves.

Pepper plants accumulate more Cl^- in their leaves than eggplant and tomato (Figures 2c, 3c, and 4c), indicating that they are less effective in controlling Cl^- transport and compartmentalization under salinity stress. This may result from weaker regulation of Cl^- uptake at the roots or less efficient vacuolar sequestration mechanisms, leading to greater ion buildup in leaf tissue. Although peppers limit Na^+ accumulation, their inability to similarly control Cl^- influx and distribution compromises their overall salinity tolerance.

3.3 | Biomass

Eggplant shoot and root biomasses were significantly larger for the Black Beauty versus Long Purple across all treatments (Figure 5a,b), which is unsurprising considering that Black Beauty is a larger statured eggplant. However, no significant treatment differences were observed for either shoot or root biomass. Shoot biomass decreased slightly for salinity treatments versus the control, whereas the highest root biomasses were observed with T2S1 and T1S3 (Figure 5a,b).

For tomatoes, T1S1, T1S3, and T2S1 all had significant cultivar differences for both root and shoot biomass that were not present in the control, with Red Pear having higher biomass than Jaune Flamme (Figure 5c,d). However, there were no consistent biomass patterns with either increasing salinity or anion treatment.

Finally, for pepper, there were significant differences for treatments for both shoot and root biomass, with T1S2, T1S3, and T2S3 having significantly lower biomasses for both shoot and root biomasses (Figure 5e,f). With shoot biomass, the sulfate treatments all showed significant cultivar differences, with Ancho having higher biomasses than Corbaci.

3.4 | Comparison of relative yield to previous studies in Solanaceae

We focus our comparison to previous studies in Solanaceae on relative yield, given the intrinsic differences in variety size and yield and the focus of previous work on relative yield. The Food and Agriculture Organization Irrigation and Drainage Paper 61 (FAO-61) (Tanji & Kielen, 2002) classifies peppers (Bernstein, 1954), eggplant (Heuer et al., 1986), and tomatoes (Bierhuizen & Ploegman, 1967; Hayward & Long, 1943; Lyon, 1941; Shalhevet & Yaron, 1973) as moderately salt sensitive based on relative fruit yield. More recent studies cited in the introduction also demonstrated similar moderate sensitivity with relative yield. Our work demonstrated notable differences in the Maas–Hoffman model (Maas & Hoffman, 1977) parameters between chloride- and sulfate-dominated treatments. For salinity thresholds in sulfate treatments, plants irrigated with the lowest salinity ($\text{EC}_w = 3 \text{ dS m}^{-1}$) did not have relative yields different than 100% for any of the varieties of any of the three vegetable species, suggesting an EC_w threshold greater than 3 dS m^{-1} , which is higher than the FAO thresholds of 2.5, 1.1, and 1.5 dS m^{-1} for tomatoes, eggplant, and peppers, respectively. For the chloride treatments, every mean value was below 100%, but some of the error bars exceeded 100% for eggplant and tomato.

Given the relatively low number of salinity treatments and the uncertainty over the exact threshold for yield loss from salinity, we calculated the Maas–Hoffman slope (% relative

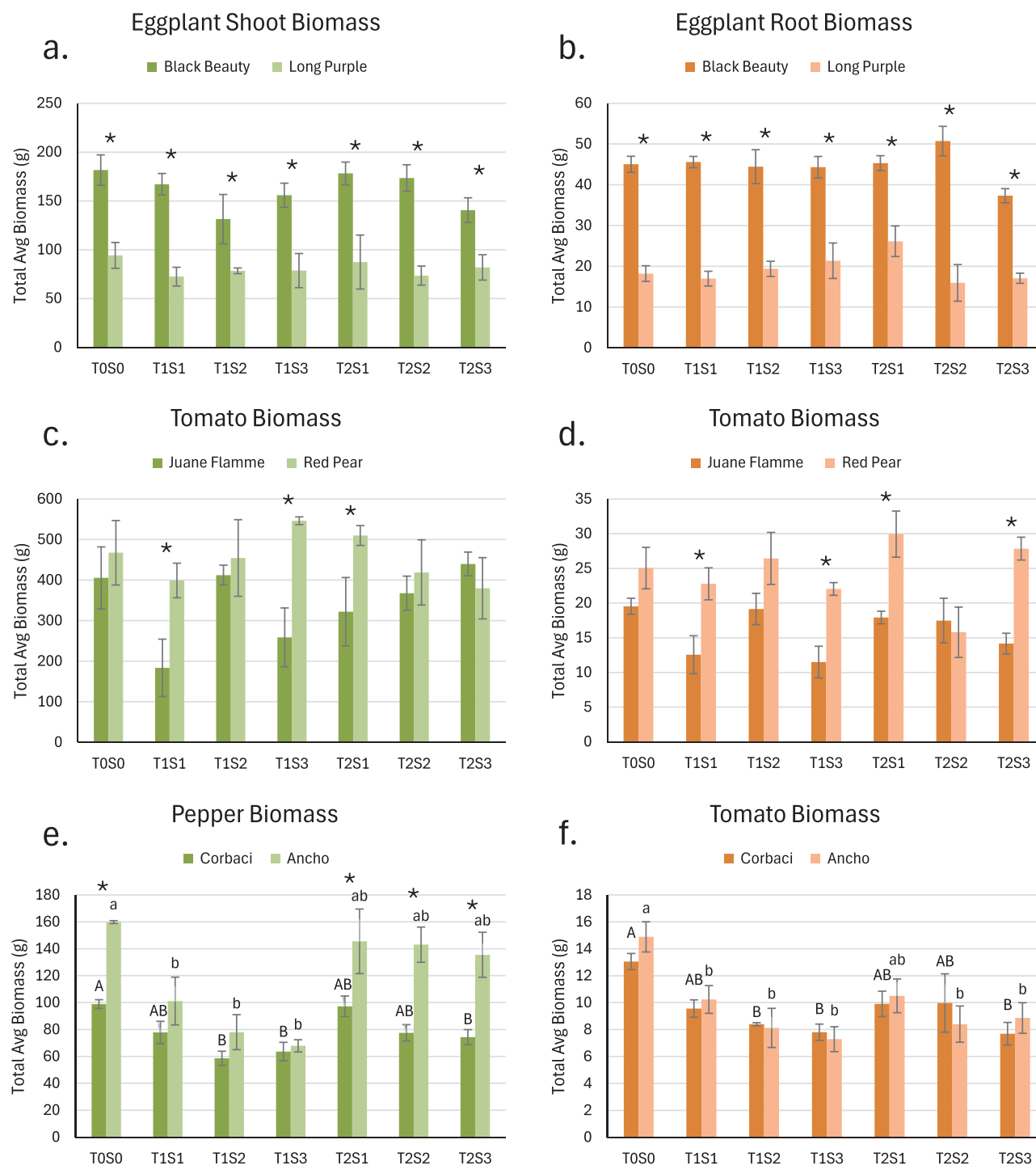


FIGURE 5 Shoot and root biomass for the three Solanaceae vegetables. Capital letters denote statistically significant ($p < 0.05$) differences among treatments for the salt-sensitive variety. Lowercase letters denote significant differences among treatments for salt-tolerant variety. Asterisks denote significant differences between varieties for each treatment. Error bars indicate standard error of individual plant observations.

yield loss per dS m^{-1}) using the difference between the 3 and 6 dS m^{-1} treatments as well as the 4.5 and 6 dS m^{-1} . When using the second approach, the slopes were considerably lower than those reported in FAO-61 (Tanji & Kielen, 2002). With the first approach, the slopes only approached literature values for the treatments where relative yield exceeded

100% for the S1 (3.0 dS m^{-1}) level. These differences in both slope and salinity threshold suggest that the heirloom cultivars may have greater salinity tolerances than reported previously. However, we limit further analysis, given the small sample sizes, limited number of salinity treatments, and large uncertainties for some treatments.

3.5 | Relative gene expression

This section presents a comparative analysis of the relative gene expression patterns of genes involved in sodium (Na^+) and chloride (Cl^-) transport in three Solanaceae species: eggplant, tomato, and pepper. Na transport genes include *Arabidopsis K⁺ Transporter 1 (AKT1)*, *Vacuolar H⁺-pyrophosphatase 1 (AVP1)*, *Na⁺/H⁺ Exchanger 1 (NHX1)*, *Na⁺/H⁺ Exchanger 2 (NHX2)*, *Salt Overly Sensitive 1 (SOS1)*, *Salt Overly Sensitive 2 (SOS2)*, *Salt Overly Sensitive 3 (SOS3)*, and Cl transport genes include *Aluminum-Activated Malate Transporter 9 (ALMT9)*, *Cation-Chloride Co-transporter 1 (CCC)*, *Chloride Channel Protein CLC-c (CLCc)*, *Chloride Channel Protein CLC-g (CLCg)*, and *Slow Anion Channel-Associated Homologue 3 (SLAH3)*. Among Na⁺ transport genes *AKT1* regulates K⁺ uptake and K⁺/Na⁺ balance; *AVP1* provides the proton gradient needed for vacuolar Na⁺ sequestration via *NHX1* and *NHX2*, which exchange Na⁺ for H⁺ across the tonoplast; and the SOS pathway genes, *SOS1*, *SOS2*, and *SOS3*, function together to extrude Na⁺ from cells and coordinate Na⁺ detoxification (Munns & Tester, 2008). Among Cl⁻ transport genes, *ALMT9*, *CLCc*, and *CLCg* encode vacuolar chloride channels that aid in Cl⁻ sequestration; *CCC* facilitates cotransport of Cl⁻ with cations; and *SLAH3* is involved in Cl⁻ efflux from root cells to regulate root-to-shoot Cl⁻ transport (Li et al., 2017). Collectively, these genes help maintain ion balance and reduce toxic ion accumulation under saline conditions. By examining both salt-sensitive and salt-tolerant genotypes under varying salinity treatments, we aim to elucidate the mechanisms underlying salinity tolerance in these species. Genes were selected based on their well-established roles in Na⁺ and Cl⁻ transport, ion homeostasis, and salinity tolerance, supported by prior studies in Solanaceae and other crop species.

3.5.1 | Na⁺ transport in leaves

Eggplant

In eggplant, the salt-tolerant genotype Long Purple exhibited significant downregulation of all seven Na⁺ transport genes *AKT1*, *AVP1*, *NHX1*, *NHX2*, *SOS1*, *SOS2*, and *SOS3* across all salinity treatments compared to the control (T0S0) (Table 2). This is consistent with leaf Na accumulation results where Long Purple accumulated statistically greater amounts of Na in leaves under S2 and S3 for chloride- and sulfate-based treatments (Figure 2). In contrast, the salt-sensitive genotype Black Beauty did not display a consistent pattern of gene regulation, indicating a less effective response to salinity stress. The downregulation observed in Long Purple likely reflects a reduced reliance on active Na⁺ transport mechanisms in the leaves. Instead, Long Purple may tolerate higher internal Na⁺ levels through enhanced tissue-level tolerance, such as

vacuolar sequestration at earlier time points, greater antioxidant capacity, or better osmotic adjustment—mechanisms that were not directly captured in this study. Notably, no significant differences were observed between chloride-based (T1) and sulfate-based (T2) treatments in either genotype, suggesting that the type of salinity had a similar impact on Na⁺ transport to leaves. This data are consistent with shoot biomass accumulation in these cultivars in response to salinity.

Tomato

In tomato, contrasting gene expression patterns were observed between the salt-sensitive Jaune Flamme and the salt-tolerant Red Pear. In Jaune Flamme, *AKT1* was consistently downregulated across all treatments, indicating impaired K⁺ uptake and ion homeostasis under salinity stress (Table 2). Conversely, Red Pear exhibited selective upregulation of *AKT1* in specific treatments (T1S1, T2S2, and T2S3), suggesting a more adaptive response to maintain ion balance under salinity stress.

Both genotypes showed significant downregulation of *AVP1* under higher salinity levels (T1S3, T2S2, and T2S3) (Table 2). Since *AVP1* is involved in vacuolar Na⁺ sequestration (Gaxiola et al., 2001), its downregulation may indicate limitations in the capacity to sequester Na⁺ into vacuoles under severe stress. Interestingly, *HKT1* was upregulated in Red Pear under the highest sulfate-based salinity (T2S3) but downregulated in Jaune Flamme, highlighting its role in enhancing salt tolerance in Red Pear by reducing Na⁺ uptake in the tolerant genotype.

Genes involved in vacuolar Na⁺ compartmentalization, *NHX1* and *NHX2*, exhibited contrasting patterns (Table 2). In Jaune Flamme, *NHX1* was downregulated while *NHX2* was upregulated under T2S2, possibly indicating a compensatory mechanism under sulfate stress. In Red Pear, these genes remained relatively stable, suggesting a consistent ability to manage Na⁺ under salinity stress, which is expected for a salt-tolerant cultivar. Additionally, *NHX2* and the SOS pathway genes (*SOS1*, *SOS2*, and *SOS3*) were significantly upregulated in Jaune Flamme under T2S2 but not in Red Pear (Table 2), implying that Jaune Flamme attempted to activate stress responses under moderate sulfate salinity, albeit less effectively than Red Pear.

Pepper

In pepper, the salt-tolerant Ancho showed downregulation of key ion transport genes (*AVP1*, *NHX2*, and *SOS1*) under sulfate-based salinity treatments compared to chloride-based treatments (Table 2). This pattern suggests that under sulfate-based salinity, Ancho may experience lower Na⁺ stress, reducing the need to activate genes involved in Na⁺ sequestration and extrusion. In contrast, under chloride-based salinity, higher expression of these genes may be required to mitigate greater Na⁺ accumulation and maintain ionic homeostasis.

TABLE 2 Relative normalized gene expression for sodium-transport controlling genes in leaves.

Gene	Cultivar	Relative normalized expression of Na ⁺ genes in leaves						
		T0S0	T1S1	T1S2	T1S3	T2S1	T2S2	T2S3
<i>AKT1</i> (Inward-rectifying K ⁺ channel AKT1)	Black Beauty	1.28	1.68	1.39	1.50	1.25	0.91	1.03
	Long Purple	2.36	1.54	1.21	1.07	0.86	1.20	1.29
	Jaune Flamme	0.43	0.27	0.21	0.21	0.12	0.34	0.16
	Red Pear	0.15	0.31	0.18	0.18	0.11	0.25	0.22
<i>AVP1</i> (Vacuolar H ⁺ -pyrophosphatase)	Black Beauty	0.98	1.45	1.13	1.37	0.88	0.63	0.93
	Long Purple	2.23	1.29	1.06	1.47	1.03	1.36	1.34
	Jaune Flamme	0.90	1.26	0.30	0.60	1.07	0.62	0.73
	Red Pear	0.93	0.84	1.54	0.49	1.03	0.52	0.73
	Corbaci	1.20	1.50	1.10	1.35	0.96	0.90	1.09
	Ancho	1.54	1.47	1.71	1.05	0.64	1.22	0.77
<i>NHX1</i> (Vacuolar Na ⁺ /H ⁺ antiporter 1)	Black Beauty	1.01	1.42	1.03	1.51	1.21	1.02	1.20
	Long Purple	2.07	1.55	1.36	1.14	1.01	1.21	1.19
	Jaune Flamme	1.16	1.64	2.07	2.02	1.31	2.15	0.73
	Red Pear	1.46	1.30	1.15	1.06	1.16	0.75	1.20
	Corbaci	1.80	1.17	1.12	1.12	1.00	1.02	1.11
	Ancho	1.24	1.25	0.85	2.04	1.57	1.21	1.34
<i>NHX2</i> (Vacuolar Na ⁺ /H ⁺ antiporter 2)	Black Beauty	0.47	0.62	0.50	0.68	0.67	0.46	0.59
	Long Purple	0.92	0.66	0.66	0.52	0.55	0.58	0.60
	Jaune Flamme	0.50	0.63	0.39	0.42	0.29	1.51	0.29
	Red Pear	0.37	0.55	0.38	0.42	0.43	0.33	0.26
	Corbaci	0.59	0.59	0.41	0.61	0.58	0.55	0.73
	Ancho	0.73	0.68	0.76	0.56	0.37	0.53	0.40
<i>SOS1</i> (Plasma-membrane Na ⁺ /H ⁺ antiporter)	Black Beauty	0.90	1.37	0.93	1.39	1.00	0.90	1.30
	Long Purple	2.43	1.50	1.37	1.31	1.13	1.21	1.34
	Jaune Flamme	0.71	0.63	0.16	0.46	0.58	1.30	0.26
	Red Pear	0.55	0.62	0.49	0.62	0.47	0.31	0.26
	Corbaci	0.67	0.66	0.58	0.82	0.61	0.48	0.84
	Ancho	1.11	0.97	1.21	0.85	0.57	0.73	0.56
<i>SOS2</i> (Serine/threonine protein kinase)	Black Beauty	0.51	0.70	0.56	0.74	0.60	0.47	0.62
	Long Purple	0.96	0.72	0.62	0.60	0.56	0.60	0.69
	Jaune Flamme	1.66	1.20	0.41	1.28	0.52	2.43	0.67
	Red Pear	1.14	1.39	0.99	0.22	1.16	0.58	0.80
	Corbaci	1.62	1.50	1.21	1.51	1.34	1.13	1.37
	Ancho	1.46	1.39	1.61	1.18	1.27	1.64	1.07
<i>SOS3</i> (Calcineurin B-like Ca ²⁺ sensor)	Black Beauty	0.07	0.07	0.06	0.08	0.06	0.04	0.05
	Long Purple	0.16	0.07	0.06	0.07	0.06	0.07	0.07
	Jaune Flamme	0.07	0.01	0.02	0.03	0.01	0.10	0.02
	Red Pear	0.01	0.02	0.01	0.01	0.01	0.02	0.01
	Corbaci	0.16	0.10	0.08	0.12	0.09	0.10	0.13
	Ancho	0.07	0.07	0.09	0.07	0.06	0.09	0.06

Note: Color map comes from Microsoft Excel's conditional formatting function using blue (low)–white (middle)–red (high) colormap applied within each gene.

TABLE 3 Relative normalized gene expression for chloride-transport controlling genes in leaves.

Gene	Cultivar	Relative normalized expression of Cl ⁻ genes in leaves						
		T0S0	T1S1	T1S2	T1S3	T2S1	T2S2	T2S3
<i>ALMT9</i> (Vacuolar anion/Cl ⁻ channel)	Black Beauty	1.05	1.49	1.24	1.83	1.10	0.95	1.23
	Long Purple	2.14	1.35	1.09	1.47	1.13	1.20	1.13
	Jaune Flamme	2.33	2.60	0.55	1.18	1.31	2.79	0.31
	Red Pear	1.02	1.43	0.67	1.49	0.73	0.87	0.15
	Corbaci	0.89	0.87	0.64	0.98	0.65	0.66	1.05
	Ancho	1.49	1.25	1.62	0.84	0.52	1.12	0.66
<i>CCC</i> (Cation-Chloride Co-transporter 1)	Jaune Flamme	0.83	1.12	0.32	0.41	0.50	0.39	0.21
	Red Pear	0.53	1.17	0.27	0.94	0.57	0.43	0.26
	Corbaci	1.26	1.39	1.12	1.45	1.14	1.07	1.58
	Ancho	1.48	1.59	1.70	1.06	0.74	1.22	0.75
<i>CLCc</i> (Chloride Channel Protein CLC-c)	Black Beauty	0.83	1.17	0.72	1.56	1.26	0.92	1.13
	Long Purple	1.64	1.04	1.03	1.01	1.20	0.87	1.09
	Jaune Flamme	1.76	1.68	0.54	1.12	1.42	5.27	0.64
	Red Pear	1.48	0.83	0.33	1.76	0.92	0.86	1.00
	Corbaci	1.42	1.50	1.13	1.62	1.14	1.02	1.82
	Ancho	1.96	1.60	2.25	1.46	0.87	1.48	0.95
<i>CLCg</i> (Chloride Channel Protein CLC-g)	Jaune Flamme	2.05	2.00	0.90	1.28	0.89	5.60	0.69
	Red Pear	1.47	1.66	0.81	1.76	0.99	1.04	0.87
	Corbaci	1.24	1.50	0.98	1.30	1.05	1.19	1.21
	Ancho	1.21	1.33	1.70	1.11	0.69	1.59	0.86
<i>SLAH3</i> (Slow Anion Channel–Associated Homologue 3)	Black Beauty	0.93	1.31	1.08	1.46	1.01	0.78	1.03
	Long Purple	1.69	0.98	0.75	1.30	0.86	0.81	1.10
	Corbaci	1.14	1.00	0.58	1.32	0.69	0.75	1.05
	Ancho	1.10	0.87	1.29	0.77	0.39	0.76	0.44

Note: Color map comes from Microsoft Excel's conditional formatting function using blue (low)–white (middle)–red (high) colormap applied within each gene.

In contrast, the salt-sensitive Corbaci did not exhibit such differential expression between treatments. Moreover, in Corbaci, *NHX1* and *SOS3* were consistently downregulated across all salinity treatments, indicating a diminished capacity to manage ion homeostasis. Ancho, however, maintained stable expression of these genes, suggesting more effective management of salinity stress.

3.5.2 | Cl⁻ transport in leaves

Eggplant

In eggplant, chloride transport genes also exhibited genotype-specific expression patterns. The salt-tolerant Long Purple significantly downregulated *ALMT9*, *CLCc*, and *SLAH3* across all salinity treatments compared to control (Table 3). This downregulation likely contributes to limiting Cl⁻ accumulation in leaves, thereby enhancing salt tolerance. In contrast, Black Beauty upregulated these genes under the highest chloride-based salinity treatment (T1S3), potentially leading to excessive Cl⁻ accumulation and contributing to its salt sensitivity.

Tomato

In tomato, both genotypes downregulated *ALMT9* under the highest salinity level (S3), which may be a protective response to prevent Cl⁻ overaccumulation in leaves (Table 3).

Additionally, *CCC*, *CLCc*, and *CLCg* showed contrasting expression patterns. In Red Pear, these genes were upregulated under the highest chloride salinity (T1S3), which may enhance Cl⁻ compartmentalization or retrieval from the xylem, reducing Cl⁻ delivery to the leaves and contributing to salt tolerance. In Jaune Flamme, these genes were downregulated under the same conditions, possibly leading to inadequate Cl⁻ management.

Pepper

In pepper, the salt-tolerant Ancho showed significant downregulation of *ALMT9* under high salinity levels (T1S3 and T2S3) (Table 3). This downregulation likely limits Cl⁻ translocation to shoots, preventing toxicity (Baetz et al., 2016). The salt-sensitive Corbaci did not downregulate these genes, which may result in higher Cl⁻ accumulation in leaves. Furthermore, *CCC*, *CLCc*, and *CLCg* were downregulated in

Ancho under sulfate-based salinity but not in Corbaci, indicating genotype-specific responses to sulfate stress and better Cl^- management in the tolerant genotype.

3.5.3 | Na^+ transport in roots

Eggplant

In the roots of eggplant, the expression of Na^+ transport genes also differed notably between genotypes (Table 4). The salt-tolerant Long Purple upregulated *AKT1* in most salinity treatments, enhancing its capacity for K^+ uptake and maintaining ion homeostasis under stress. In contrast, Black Beauty did not show significant *AKT1* upregulation, potentially compromising its ability to maintain ion balance.

Additionally, Long Purple upregulated *AVP1* under sulfate-based salinity (T2S1 and T2S2) (Table 4), supporting vacuolar Na^+ sequestration and reducing cytosolic Na^+ toxicity. Black Beauty, however, downregulated *AVP1* under high chloride salinity (T1S3), potentially impairing its stress response mechanisms.

Stress-related genes *NHX1*, *NHX2*, *SOS1*, *SOS2*, and *SOS3* were upregulated at moderate salinity levels (S1 and S2) in Long Purple but not in Black Beauty (Table 4). This indicates that Long Purple effectively activates Na^+ extrusion and compartmentalization mechanisms under moderate stress. However, at the highest salinity level (S3), these genes were downregulated in Long Purple, suggesting that extreme salinity may overwhelm its stress response capacity.

Tomato

In tomato roots, the salt-tolerant Red Pear upregulated *AKT1* under the highest salinity (S3), enhancing ion homeostasis (Table 4). Jaune Flamme did not exhibit such upregulation, possibly leading to disrupted ion balance under stress. *AVP1* was downregulated in Jaune Flamme under T2S3 but upregulated in Red Pear (Table 4), suggesting better vacuolar Na^+ sequestration in the tolerant genotype. Interestingly, Jaune Flamme upregulated *AVP1* under T1S3, indicating different responses to chloride and sulfate salinity. This divergence may reflect genotype-specific sensitivity to different anions, where Jaune Flamme activates *AVP1* in response to higher Na^+ influx under chloride stress, but fails to mount a similar response under sulfate stress, potentially contributing to its overall lower tolerance.

NHX1 and *NHX2* were significantly upregulated in Red Pear under T2S3 but not in Jaune Flamme (Table 4), indicating more effective Na^+ compartmentalization in the tolerant genotype. The *SOS* pathway genes were downregulated in Jaune Flamme under T2S3 but upregulated in Red Pear, further emphasizing the more effective Na^+ extrusion mechanisms in Red Pear.

Pepper

In pepper roots, the salt-tolerant Ancho upregulated *AVP1* under both high chloride (T1S3) and moderate sulfate salinity (T2S2), enhancing vacuolar Na^+ sequestration and reducing cytosolic Na^+ levels (Table 4). Corbaci did not show such upregulation, possibly compromising its ability to sequester Na^+ effectively. *NHX1* was significantly upregulated in Ancho across several treatments but not in Corbaci, indicating more effective Na^+ compartmentalization in the tolerant genotype.

3.5.4 | Cl^- transport in roots

Eggplant

In eggplant roots, chloride transport genes showed genotype-specific expression patterns (Table 5). The salt-tolerant Long Purple upregulated *ALMT9* across multiple treatments (T1S2, T1S3, T2S1, and T2S2), suggesting active regulation of Cl^- transport to avoid toxicity. *CLCc* was also upregulated in Long Purple under high chloride salinity (T1S2 and T1S3), potentially enhancing Cl^- sequestration into vacuoles. In contrast, Black Beauty showed limited upregulation of *ALMT9* and even downregulated it under high chloride salinity (T1S3), indicating a less adaptive response. The significant upregulation of *SLAH3* in Long Purple but not in Black Beauty (Table 5) further highlights the more effective Cl^- management in the tolerant genotype.

Tomato

In tomato, both genotypes displayed upregulation of *ALMT9* under S3 compared to S0 on both chloride- and sulfate-based treatments (Table 5), indicating its general role in salinity response.

CCC, *CLCc*, and *CLCg* showed contrasting patterns between genotypes (Table 5). In Red Pear, these genes were upregulated under high sulfate salinity (T2S3), suggesting enhanced Cl^- compartmentalization in roots, reducing Cl^- translocation to shoots. Jaune Flamme downregulated these genes under the same conditions, potentially leading to inadequate Cl^- management. Under high chloride salinity (T1S3), Jaune Flamme upregulated these genes, possibly as an attempt to mitigate Cl^- stress, but this response may not be sufficient to prevent toxicity.

Pepper

In pepper, the salt-tolerant Ancho upregulated *ALMT9* in all salinity treatments, suggesting active Cl^- management to prevent toxicity (Table 5). Corbaci showed upregulation of *ALMT9* only under the lowest salinity (T1S1), indicating a less robust response. *CCC*, *CLCc*, and *CLCg* were significantly upregulated in Ancho under moderate to high chloride salinity

TABLE 4 Relative normalized gene expression for sodium-transport controlling genes in roots.

Gene		Relative normalized expression of Na ⁺ genes in roots						
		T0S0	T1S1	T1S2	T1S3	T2S1	T2S2	T2S3
<i>AKT1</i> (Inward-rectifying K ⁺ channel AKT1)	Black Beauty	9.93	10.99	10.99	5.11	29.22	4.67	4.36
	Long Purple	3.42	4.15	38.17	13.22	104.95	31.62	6.84
	Jaune Flamme	2.52	0.00	1.03	2.23	1.71	0.07	0.00
	Red Pear	1.34	2.77	1.92	2.20	1.21	1.17	3.44
<i>AVP1</i> (Vacuolar H ⁺ -pyrophosphatase)	Black Beauty	1.98	1.89	2.07	0.70	4.58	1.21	1.73
	Long Purple	5.06	2.88	8.22	6.77	67.88	11.04	3.19
	Jaune Flamme	2.63	3.44	1.29	13.94	3.62	1.21	0.43
	Red Pear	1.95	1.10	0.35	1.25	4.17	7.58	3.32
	Corbaci	1.56	5.19	2.12	2.31	2.02	1.66	2.66
	Ancho	2.45	4.16	5.56	10.70	4.10	4.79	9.46
<i>NHX1</i> (Vacuolar Na ⁺ /H ⁺ antiporter 1)	Black Beauty	1.85	3.50	1.91	0.56	1.79	1.72	1.79
	Long Purple	0.87	1.74	7.11	0.40	11.04	11.61	1.34
	Jaune Flamme	0.55	1.21	1.07	1.87	0.23	0.16	0.63
	Red Pear	0.40	0.69	0.26	0.60	0.48	0.75	2.42
	Corbaci	2.51	1.16	2.94	1.74	2.30	2.51	2.43
	Ancho	0.27	1.37	3.42	0.10	3.12	4.00	3.02
<i>NHX2</i> (Vacuolar Na ⁺ /H ⁺ antiporter 2)	Black Beauty	4.45	5.60	3.65	2.87	2.92	3.62	2.38
	Long Purple	6.77	3.57	14.83	4.62	5.67	24.34	3.15
	Jaune Flamme	3.26	1.60	2.10	6.28	3.44	0.13	0.99
	Red Pear	1.19	2.26	3.48	1.79	2.06	1.36	3.18
	Corbaci	5.62	13.49	9.03	7.67	11.78	8.98	9.66
	Ancho	14.68	8.41	17.22	22.39	11.84	14.78	10.74
<i>SOS1</i> (Plasma-membrane Na ⁺ /H ⁺ antiporter)	Black Beauty	2.94	3.37	3.66	2.41	3.09	3.79	2.62
	Long Purple	4.72	2.25	10.65	0.99	13.37	1.26	3.93
	Jaune Flamme	3.26	0.99	3.26	4.67	3.36	0.30	0.34
	Red Pear	0.75	1.75	0.92	1.90	2.03	0.43	2.21
	Corbaci	9.14	19.17	11.76	10.87	13.55	9.15	12.67
	Ancho	11.73	19.86	30.64	10.36	11.80	27.82	14.23
<i>SOS2</i> (Serine/threonine protein kinase)	Black Beauty	5.15	8.46	5.89	1.28	7.10	5.34	3.15
	Long Purple	6.77	4.96	29.26	9.56	28.61	2.39	4.38
	Jaune Flamme	2.11	0.43	1.27	3.45	3.23	0.32	1.60
	Red Pear	1.00	1.43	0.47	1.04	1.50	0.77	1.21
	Corbaci	4.30	6.57	4.29	3.36	4.94	4.86	5.56
	Ancho	10.30	8.81	12.75	4.08	5.59	10.71	4.58
<i>SOS3</i> (Calcineurin B-like Ca ²⁺ sensor)	Black Beauty	4.94	6.85	9.48	2.50	12.62	7.06	4.68
	Long Purple	6.77	5.74	30.53	13.91	93.01	2.26	5.24
	Jaune Flamme	3.26	0.28	1.30	2.91	2.00	0.07	0.08
	Red Pear	0.32	1.47	0.87	0.90	1.05	1.48	1.08
	Corbaci	8.67	23.21	13.81	9.38	10.42	11.66	13.09
	Ancho	14.68	17.94	14.84	9.75	9.20	35.30	7.21

Note: Color map comes from Microsoft Excel's conditional formatting function using blue (low)–white (middle)–red (high) colormap applied within each gene.

(T1S2 and T1S3) but not in Corbaci, further indicating better Cl[−] regulation in Ancho.

Interestingly, *SLAH3*, which is involved in moving Cl[−] from roots to shoots, was significantly upregulated in Ancho

under salinity stress (Table 5). While this could potentially increase Cl[−] accumulation in shoots, Ancho may employ other mechanisms, such as enhanced vacuolar sequestration or reduced Cl[−] uptake, to prevent excessive Cl[−]

TABLE 5 Relative normalized gene expression for chloride-transport controlling genes in roots.

Gene	Cultivar	Relative normalized expression of Cl ⁻ genes in roots						
		T0S0	T1S1	T1S2	T1S3	T2S1	T2S2	T2S3
<i>ALMT9</i> (vacuolar anion/Cl ⁻ channel)	Black Beauty	1.33	1.66	1.55	0.45	10.35	0.60	1.17
	Long Purple	2.62	0.81	8.11	4.47	8.23	23.80	2.01
	Jaune Flamme	0.59	3.77	2.73	11.89	1.31	3.08	4.97
	Red Pear	0.26	0.60	0.69	0.64	3.27	0.60	3.99
	Corbaci	4.62	19.19	5.05	5.85	6.68	7.31	5.25
	Ancho	3.45	17.71	30.64	45.97	10.75	18.52	19.73
<i>CLC</i> (Chloride Channel Protein)	Jaune Flamme	0.82	6.00	5.42	12.24	1.40	1.39	3.06
	Red Pear	7.35	0.42	1.14	0.23	1.54	2.65	2.25
	Corbaci	7.12	17.45	7.97	9.69	9.24	9.58	10.51
	Ancho	8.58	18.44	30.64	44.45	10.78	15.76	19.59
<i>CLCc</i> (Chloride Channel Protein CLC-c)	Black Beauty	1.15	1.59	1.08	0.70	1.80	1.10	0.90
	Long Purple	2.32	1.40	9.37	8.41	26.57	2.71	1.21
	Jaune Flamme	1.30	2.07	1.44	5.56	1.23	0.59	0.35
	Red Pear	2.27	1.73	1.32	1.99	2.28	1.05	6.53
	Corbaci	9.49	25.31	8.46	10.58	13.50	10.01	11.04
	Ancho	6.02	16.36	24.14	55.45	8.35	14.43	19.53
<i>CLCg</i> (Chloride Channel Protein CLC-g)	Jaune Flamme	2.07	3.78	1.62	9.76	2.41	0.66	1.69
	Red Pear	5.73	0.94	1.92	0.78	1.54	1.31	3.80
	Corbaci	8.46	21.65	8.15	8.73	7.03	9.25	8.95
	Ancho	5.58	15.34	26.97	44.65	6.05	13.74	9.75
<i>SLAH3</i> (Slow Anion Channel–Associated Homologue 3)	Black Beauty	3.51	6.86	10.34	3.68	4.63	7.26	2.72
	Long Purple	4.59	3.63	45.74	19.42	36.73	29.60	6.43
	Corbaci	6.90	28.00	4.26	10.64	13.88	11.45	7.69
	Ancho	3.80	20.67	30.64	74.47	22.39	15.65	24.66

Note: Color map comes from Microsoft Excel's conditional formatting function using blue (low)–white (middle)–red (high) colormap applied within each gene.

accumulation in leaves. This is supported by ion concentration data, which showed that Ancho did not accumulate more Cl⁻ in leaves compared to Corbaci (Figure 4e), despite higher *SLAH3* expression (Table 5). Corbaci showed significant *SLAH3* upregulation only under mild salinity (T1S1), indicating a less responsive Cl⁻ transport system under higher stress levels. Nevertheless, the specific role of *SLAH3* in this context remains unclear, and its contribution to salinity tolerance requires further investigation.

3.5.5 | Comparative analysis and inter-tissue associations

Across the three Solanaceae species, salt-tolerant genotypes (Long Purple, Red Pear, and Ancho) exhibited gene expression patterns more consistent with adaptive responses to salinity stress, including modulation of known Na⁺ and Cl⁻ transport-related genes. In contrast, salt-sensitive genotypes (Black Beauty, Jaune Flamme, and Corbaci) more frequently showed inconsistent or limited transcriptional responses.

While these observations suggest genotype-specific regulation of ion homeostasis under stress, we emphasize that these patterns are correlative and do not establish direct functional causality. Associations between roots and leaves within the same species highlight coordinated stress responses. For example, in Long Purple, the downregulation of Cl⁻ transport genes in leaves (Table 3) coupled with upregulation in roots (Table 5) suggests a strategy to limit Cl⁻ accumulation in shoots by enhancing root sequestration or compartmentalization. Similarly, Red Pear maintains stable or adaptive expression of Na⁺ and Cl⁻ transport genes in both roots and leaves, contributing to its overall salt tolerance.

In Ancho, the upregulation of Cl⁻ transport genes in roots and their downregulation in leaves suggests a compartmentalized approach to managing Cl⁻ distribution, which may help prevent toxic shoot accumulation. Ion concentration data support this interpretation, as Ancho did not accumulate more Cl⁻ in leaves compared to the sensitive Corbaci. In contrast, Corbaci lacked such apparent coordination, with gene expression patterns and ion profiles indicating less effective Cl⁻ exclusion from shoot tissues.

Although these findings are based on gene expression and ion content data without direct functional assays, they underscore the value of exploring transcriptional regulation as a component of salinity tolerance. Future research should aim to validate these patterns through ion flux measurements, mutant analysis, and studies of transporter protein activity to confirm their mechanistic roles in conferring stress resilience.

4 | CONCLUSION

In this study, we evaluated two cultivars of three major Solanaceae vegetables (tomatoes, eggplants, and peppers) for their yield, physiological, and genetic responses to multiple salinity treatments, including differing dominant anions. We found relatively higher salinity thresholds for fruit-yield reduction, especially for sulfate-dominated treatments. Root versus shoot ion-accumulation differences between cultivars were most pronounced for eggplant. Gene expression followed anticipated patterns, with salt-tolerant cultivars more frequently expressing genes that would limit Na and Cl concentrations in tissues, mainly shoots. Although these data come from a single year of a field trial with relatively limited levels of salinity, they match our previous results for salinity tolerance from a field experiment involving 23 cultivars of heirloom tomatoes, eggplants, and peppers. Thus, the data are promising for guiding future research and breeding directions. To ensure these insights are broadly applicable, however, they should be validated across a wider genetic background encompassing additional heirloom lines, commercial hybrids, and wild relatives. Future work with more salinity levels and cultivars is therefore needed to establish salinity tolerance in tomatoes, eggplants, and peppers and to determine whether the robust tolerance traits found in heirloom lines can be introgressed into high-yielding but salt-sensitive commercial cultivars.

AUTHOR CONTRIBUTIONS

Ray G. Anderson: Formal analysis; methodology; project administration; supervision; writing—original draft; writing—review and editing. **Emile F. Tannous:** Formal analysis; visualization; writing—review and editing. **Yunyun Sun:** Data curation; formal analysis; investigation; methodology; writing—review and editing. **Donald L. Suarez:** Conceptualization; methodology; project administration; supervision; writing—review and editing. **Jorge F. S. Ferreira:** Conceptualization; methodology; project administration; writing—review and editing. **Devinder Sandhu:** Conceptualization; data curation; formal analysis; project administration; resources; supervision; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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