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ORIGINAL PAPER

Root K^+ and H^+ Transport Dynamics in Salt-Stressed Silicon-Pretreated Barley Seedlings

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Abstract
Cytosolic K^+ retention is a key determinant of salinity tolerance, and H^+ transport can support K^+ homeostasis under salt stress. Silicon (Si) often improves plant performance under salinity, but its short-term mechanisms remain debated. We tested whether Si pretreatment reduces early NaCl-induced K^+ efflux in barley roots via modulation of H^+ transport. Net K^+ and H^+ fluxes were measured in vivo and in real-time in the mature root zone (at 10–20 mm from the tip) of barley (*Hordeum vulgare* var. Esperanza) using microelectrode ion flux estimation (MIFE) technique. Seedlings were treated with 0, 1, or 2 mM Si supplied as Na_2SiO_3 from germination and exposed to 80, 160, or 320 mM NaCl. Flux responses were analyzed during the first 30 min, emphasizing the 15–20 min post-treatment window. Longer-term effects were assessed by K^+ leakage (2 h) and Na^+ accumulation (24 h) assays. NaCl induced a rapid, dose-dependent K^+ efflux peaking within 15–20 min. Si pretreatment reduced NaCl-induced K^+ loss in a concentration-dependent manner and was consistently associated with stimulation of H^+ efflux in the mature root zone. Si rapidly modulates root ion transport under salinity by enhancing H^+ efflux, which likely supports membrane potential, limits NaCl-induced depolarization, and/or facilitates Na^+ management, thereby improving early cytosolic K^+ retention.

Keywords Electrophysiology · Ionic fluxes · Hydroponic · Salinity

1 Introduction

Under salinity, plants deploy tolerance mechanisms that depend strongly on ion homeostasis and stress signaling (Rasouli et al. 2024; Wu et al. 2024). Potassium (K^+) is central to osmotic adjustment, enzyme activation and ionic signaling, and its intracellular level reflects the balance between uptake, redistribution and loss through plasma membrane and tonoplast transport systems (Malakar and Chattopadhyay 2021; Shabala 2017; Shabala and Pottosin 2014). Salt stress commonly impairs K^+ nutrition by promoting K^+ loss and/or limiting uptake in the presence of excess Na^+ (Adem et al. 2014; Luo et al. 2023). Depletion of cytosolic K^+ can amplify stress through reactive oxygen species (ROS) production and activation of K^+ efflux pathways, potentially contributing to downstream cellular dysfunction and programmed cell death (Wu et al. 2018).

Silicon (Si) is widely regarded as beneficial under salinity, yet its mechanistic contribution over short time scales remains unresolved (Coskun et al. 2019; Dhiman et al. 2021). Si influx is mediated by the transporter Lsi1 (Chiba et al. 2009) and the intracellular Si has been associated with enhanced H^+-ATPase activity and improved K^+ status under stress (Liang 1999; Shen et al. 2022; Soleimannejad et al. 2019), raising the possibility that Si-driven stimulation of proton pumping supports membrane potential and K^+ retention. However, whether Si directly influences K^+ transport through stimulation of H^+ transport, or acts through indirect/secondary effects, remains debated (Liang et al. 2006;

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Pavlovic et al. 2021; Yan et al. 2021). Previous work in barley roots has identified key transport components controlling K^+/Na^+ homeostasis and highlighted H^+-ATPase as a major determinant of membrane potential and K^+ retention under salinity (Chen et al. 2007a; Rubio et al. 2020; Zepeda-Jazo et al. 2008). Although silicon-induced improvements in K^+/Na^+ homeostasis and H^+-ATPase activity under salinity have been widely reported, most studies rely on ion content analysis or indirect enzymatic assays at later time points. Real-time, simultaneous measurements of K^+ and H^+ fluxes during the early minutes of salt exposure remain scarce. In particular, it remains unclear whether enhanced proton efflux coincides dynamically with reduced NaCl-induced K^+ loss during the initial minutes of salt exposure.

Here, we hypothesize that Si pretreatment reduces early NaCl-induced K^+ efflux in the mature root zone of barley by enhancing H^+ efflux, improving short-term K^+ retention under salinity. Using electrophysiological and ion-content assays, we characterized the temporal coupling dynamics of K^+ and H^+ fluxes following NaCl exposure and evaluated whether Si also limits net Na^+ accumulation under salt stress.

2 Materials and Methods

2.1 Plant Material, Growth Conditions, and Treatment

Seeds of *Hordeum vulgare* var. Esperanza were surface-sterilized with commercial bleach (10% v/v) for 10 min and rinsed at least five times with sterile distilled water. Seeds were germinated in basic salt medium (BSM: 0.5 mM KCl, 0.1 mM $CaCl_2$; pH 5.7 adjusted with HCl) supplemented with 0, 1, or 2 mM Si (Na_2SiO_3).

2.2 Ion Flux Measurements

Net H^+ and K^+ fluxes were measured in the mature root zone using the non-invasive microelectrode ion flux estimation (MIFE, UTas Innovation Ltd, Hobart, Australia) technique (Newman 2001; Shabala et al. 2013). Three-day-old seedlings were mounted in a Perspex chamber containing fresh BSM. Where applicable, NaOH was added to control solutions to match the Na^+ contribution from Na_2SiO_3 and pH adjustment. After 60 min acclimation, steady baseline fluxes were recorded for 5–10 min, then NaCl was added to final concentrations of 80, 160, or 320 mM and measurements continued for 30 min. Steady-state flux was calculated as the mean flux between 25 and 30 min after NaCl addition. To identify the effect of Si on H^+ flux, 1 mM sodium orthovanadate (OV, H^+-ATPase inhibitor) was added to BSM during the acclimation time and measurements were performed as previously described.

2.3 K^+ Leakage Experiments

Four-day-old seedlings grown hydroponically (25 °C, darkness) in BSM containing 0, 1, or 2 mM Si were transferred (three seedlings per treatment) to 10 mL NaCl (80, 160, or 320 mM) for 2 h. Fresh root biomass and K^+ in the bathing solution were quantified by flame photometry (Jenway PFP7) (Chen et al. 2005).

2.4 Ion Depletion

To assess net Na^+ accumulation, roots of three seedlings were incubated in 10 mL BSM containing 0, 1, or 2 mM Si plus 80, 160, or 320 mM NaCl for 24 h. Fresh root biomass and Na^+ and K^+ in the solution were measured by flame photometry (Chen et al. 2005).

2.5 Statistical Analysis

The experiments were conducted using a completely randomized design. Data were processed using a one-way analysis of variance (ANOVA), followed by a comparison of means using Tukey´s honest difference (HSD) test, with a significance level of $p < 0.05$. All statistical analyses were performed using InfoStat software version 2020.

3 Results

3.1 Effect of NaCl on K^+ Transport

NaCl triggered an immediate net K^+ efflux from the mature root zone of barley seedlings, increasing with external salinity (Fig. 1). The magnitude of the response scaled with stress severity, with a pronounced transient component during the first minutes after treatment (Fig. 1).

4 Effect of Si on K^+ and H^+ Dynamics

The role of silicon in K^+ and H^+ transport during the early response to salt stress was evaluated. Measurements of K^+ and H^+ fluxes were conducted in barley seedlings pretreated since germination with 1 and 2 mM Si in response to NaCl exposure. Silicon pretreatment significantly reduced K^+ loss during the early (real-time) response to 80 mM NaCl (Fig. 2A) and stimulated H^+ efflux (Fig. 2B).

Si supply may influence, at least during the initial minutes of exposure to 80 mM NaCl, to retain K^+ through

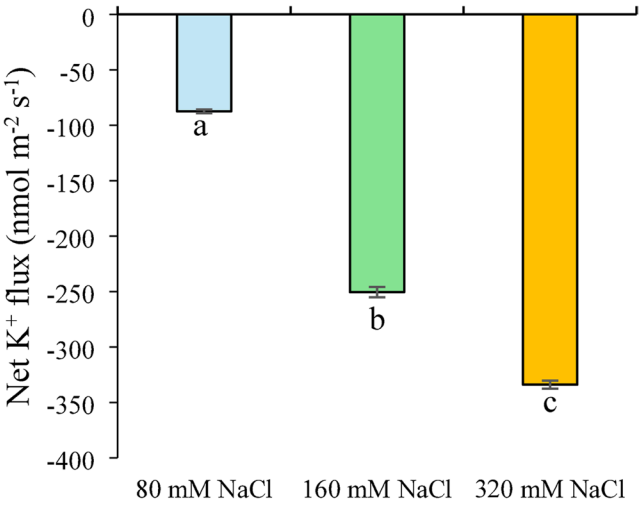


Fig. 1 K^+ fluxes in response to NaCl (without Si in BSM solution). The bars indicate the means between minute 25−30 ± SE. Different letters denote significant differences among treatments ($p<0.05$; n=4−6). The sign convention is that negative values indicate efflux

the modulation of H^+ transport. This effect persists under steady-state conditions (25–30 min), as well as under relatively high NaCl concentrations (160 and 320 mM) (Fig. 3).

To test whether the Si-induced stimulation of H^+ efflux was associated with proton pump activity, barley seedlings pretreated with 2 mM Si were exposed to 1 mM sodium orthovanadate for 1 h before flux measurements under salt stress of 80, 160, and 320 mM NaCl ($n=3$–5). Orthovanadate reduced the Si-stimulated H^+ efflux by 82, 74 and 66% respectively (data not shown, available upon reasonable request).

More prolonged NaCl exposure (2 h) also stimulated K^+ loss in a dose-dependent manner, whereas pretreatment with Na_2SiO_3 improved K^+ retention (Fig. 4).

4.1 Effect of Si on Na^+ Uptake Under Salt Stress

Ion depletion assays (Fig. 5) showed that Na^+ uptake increased after 24 h with rising external NaCl, while 1–2 mM Na_2SiO_3 reduced root Na^+ accumulation only under 160 and 320 mM NaCl.

5 Discussion

The magnitude of steady-state K^+ efflux observed in barley cv. Esperanza suggests a relatively tolerant electrophysiological response to salinity when compared with previously reported barley responses, although growth- and yield-based assays are still required for agronomic classification. This interpretation agrees with previous studies showing that salt-induced K^+ loss is a key component of the early root response and a highly predictive trait of salt tolerance in barley (Chen et al. 2005, 2007a, b). Importantly, Chen et al. (2005) provided evidence that NaCl-induced K^+ efflux cannot be attributed solely to osmotic pressure, indicating that ionic stress plays a central role in this response. Within this context, our results suggest that Si pretreatment contributes to the regulation of K^+ transport under salinity by reducing NaCl-induced K^+ efflux in the mature root zone. Thus, the main point emerging from these data is that Si-mediated K^+ retention represents an early electrophysiological trait associated with improved ionic stability under salt stress. This raises the question of whether the reduction in K^+ loss induced by Silicon (Si), is associated with a broader regulation of Na^+ accumulation and K^+/Na^+ balance.

Si pretreatment also influenced Na^+ accumulation and K^+/Na^+ homeostasis in salt-stressed barley roots. In barley cv. Esperanza, the 24 h Na^+ depletion data indicate that Si reduced net Na^+ accumulation over time, although the occurrence of this effect in the initial minutes following NaCl exposure, and its possible connection to enhanced Na^+ exclusion mediated by the SOS1 (Na^+/H^+) antiporter, remain uncertain. This response is consistent with a large body of evidence showing that Si supply under salinity can reduce Na^+ accumulation and improve the K^+/Na^+ ratio, thereby contributing to salt tolerance in cereals and other crops (Calero-Hurtado et al. 2024; Dhiman et al. 2021; Ellouzi et al. 2023; Khan et al. 2019; Liang et al. 2005, 2006; Peña-Calzada et al. 2023a, b; Shen et al. 2022; Ullah et al. 2025). However, this response is not universal. In rice, for example, sodium silicate did not alter Na^+ transport between contrasting varieties, and subsequent studies suggest that the effect of Si on Na^+ transport depends strongly on species, cultivar, organ, and the specific transport process evaluated (Flam-Shepherd et al. 2018; Yan et al. 2020). In several cases, Si appears to affect Na^+ partitioning between roots and shoots or apoplastic bypass flow rather than directly modifying unidirectional Na^+ fluxes across root cell membranes (Flam-Shepherd et al. 2018; Gong et al. 2006; Yeo et al. 1999). Within this framework, our results show that Si significantly reduced net Na^+ uptake in roots over 24 h under salt stress, indicating restricted Na^+ entry in barley cv. Esperanza under our conditions. This lower Na^+ influx likely mitigated membrane depolarization, thereby reducing K^+ efflux and cytosolic K^+ loss. Consistent with this, Si improved K^+ homeostasis by decreasing NaCl-induced K^+ efflux and enhancing H^+ efflux in the mature root zone, which may further contribute to membrane stabilization and K^+ retention.

The coordinated changes in K^+ and H^+ fluxes further suggest that Si may improve K^+ retention through mechanisms related to membrane potential maintenance and plasma membrane H^+ transport. Our real-time MIFE measurements

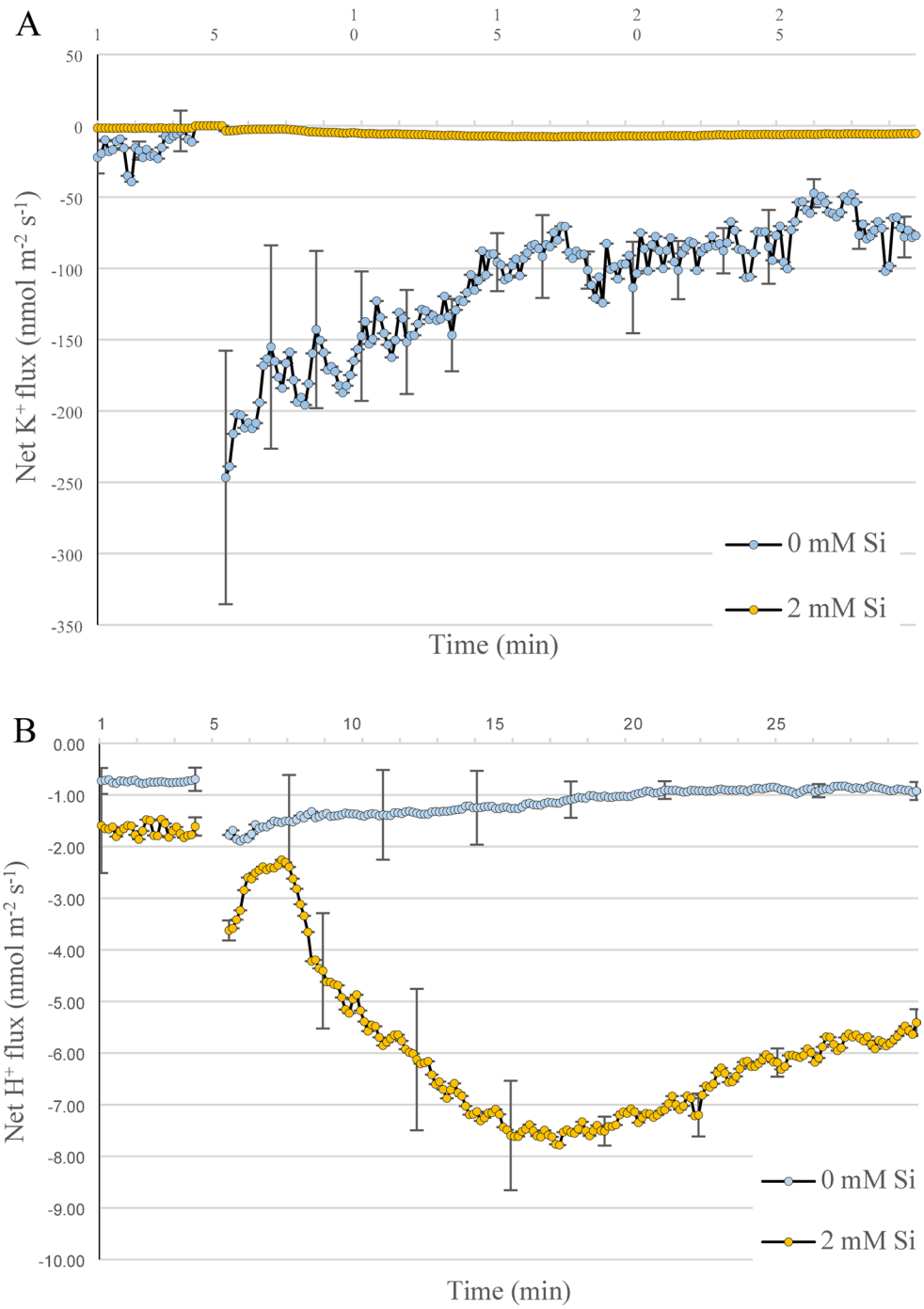


Fig. 2 Transient net K^+ (**A**) and H^+ (**B**) fluxes measured in the mature root zone of *Hordeum vulgare* var. Esperanza plants pretreated with 0 or 2 mM Na_2SiO_3 in response to acute 80 mM NaCl treatment at minute 5. Mean ± SE (n = 4–6). The sign convention is that negative values indicate efflux

showed that Si effects were detected within minutes after NaCl exposure, persisted at 2 h as reduced K^+ leakage, and were accompanied by lower net Na^+ accumulation after 24 h. The stimulation of H^+ efflux coincided with the inhibition of K^+ efflux, producing comparable response kinetics under NaCl and Si treatments. In addition, the partial inhibition caused by sodium orthovanadate suggests that the enhanced H^+ efflux observed in Si-pretreated seedlings was mainly associated with plasma membrane H^+-ATPase activity rather than passive H^+ movement through the cell wall (Table S1), although other components may also contribute to the observed H^+ loss. This interpretation is consistent with reports of Si-enhanced H^+-ATPase activity under salinity (Liang 1999; Liang et al. 1996, , 2006) and with evidence of altered K^+ transporter expression under low-K^+ conditions in barley (Beier et al. 2022). Nevertheless, because membrane potential and H^+-ATPase activity were not directly measured, the proposed coupling between Si, H^+ transport, and K^+ retention should be considered as a working model (Fig. 6). Si-induced antioxidant effects may

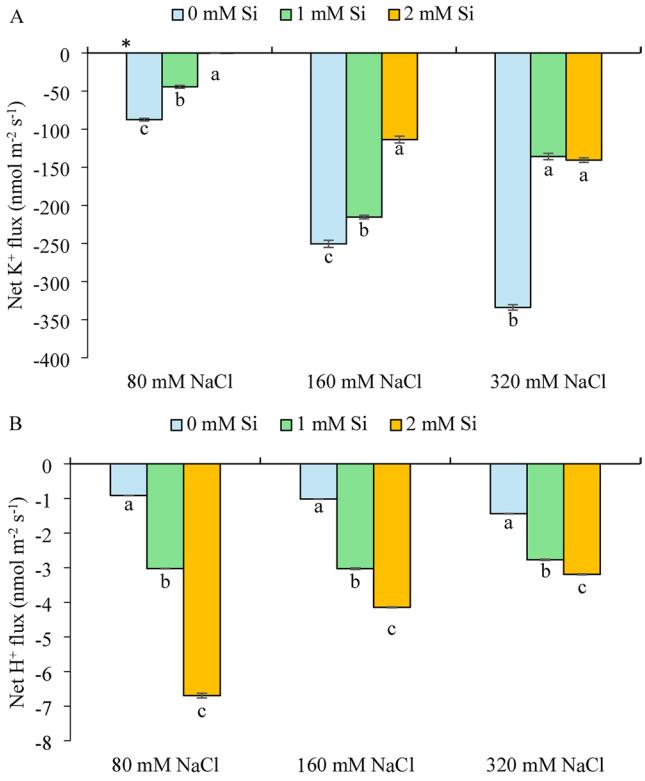


Fig. 3 Steady-state K^+ (**A**) and H^+ (**B**) fluxes measured in the mature root zone of *Hordeum vulgare* var. Esperanza plants pretreated with 0, 1 or 2 mM Na_2SiO_3 in response to acute 80, 160 and 320 mM NaCl treatments. The bars indicate the means between minute 25–30 ± SE. Different letters denote significant differences among treatments ($p<0.05$; $n=4$–6). The sign convention is that negative values indicate efflux. *Data for 0 mM Si in A, were obtained in the same experimental series as shown in Fig. 1

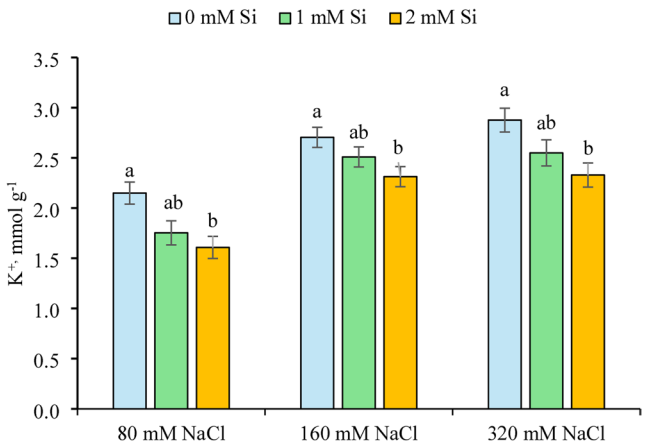


Fig. 4 K^+ leakage in response to 2 h of NaCl exposure in the presence of Si. The bars indicate the means ± SE. Different letters denote significant differences among treatments ($p<0.05$; $n=5$–7)

also contribute to this response, since Si can enhance antioxidant capacity and reduce oxidative damage under salinity, including in barley and other species (Calero-Hurtado et al. 2024; Ellouzi et al. 2023; Ullah et al. 2025). Because ROS

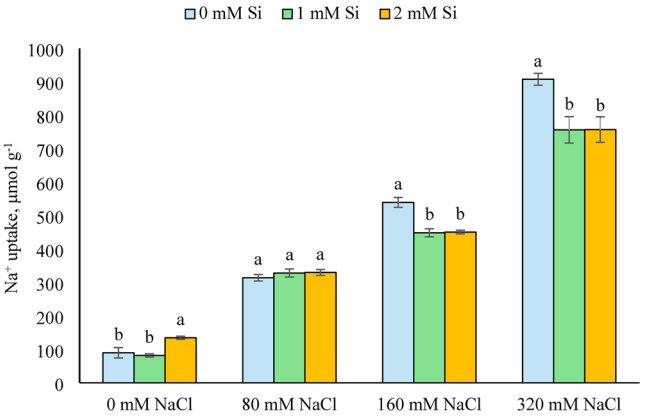


Fig. 5 Net Na^+ uptake from the bathing solution induced by 0, 80, 160, and 320 mM NaCl for 24 h in plants grown for 4 days in BSM with 0, 1 and 2 mM Si (Na_2SiO_3). The bars indicate the means ± SE. Different letters denote significant differences among treatments ($p<0.05$; $n=3$–4)

can activate GORK-type depolarization-sensitive K^+ channels and promote K^+ efflux, the final effect of Si on K^+ retention may depend on the balance between ROS dynamics, antioxidant defenses, H^+-ATPase activity, and membrane depolarization control (Demidchik 2014, 2018; Shabala and Pottosin 2014; Wang et al. 2018). Overall, our findings support a simplified plasma membrane model in which Si reduced NaCl-induced K^+ efflux and increased H^+ efflux in a manner dependent on Si dose and stress intensity, while also decreasing net Na^+ input after 24 h (under stronger salt stress, 160 and 320 mM), suggesting improved K^+/Na^+ balance via restricted Na^+ entry; however, direct measurements of membrane potential, H^+-ATPase activity, and early Na^+ fluxes are needed to confirm the proposed mechanism.

6 Conclusion

This study supports the hypothesis that silicon pretreatment improves salinity tolerance in barley by promoting early ionic homeostasis, particularly through enhanced K^+ retention in roots. Our findings demonstrate that this response occurs rapidly after salt exposure and is associated with increased H^+ efflux in the mature root zone, suggesting that silicon may contribute to the maintenance of membrane potential and the reduction of depolarization-driven K^+ loss. Together with the observed reduction in Na^+ accumulation, these responses indicate that silicon helps improve K^+/Na^+ homeostasis during the initial stages of salt stress. The novelty of this study lies in identifying early root K^+ retention, linked to H^+ transport dynamics mediated by H^+-ATPase, as a relevant physiological marker of silicon-mediated salinity tolerance in barley. Beyond its mechanistic contribution, this finding has practical implications for crop management,

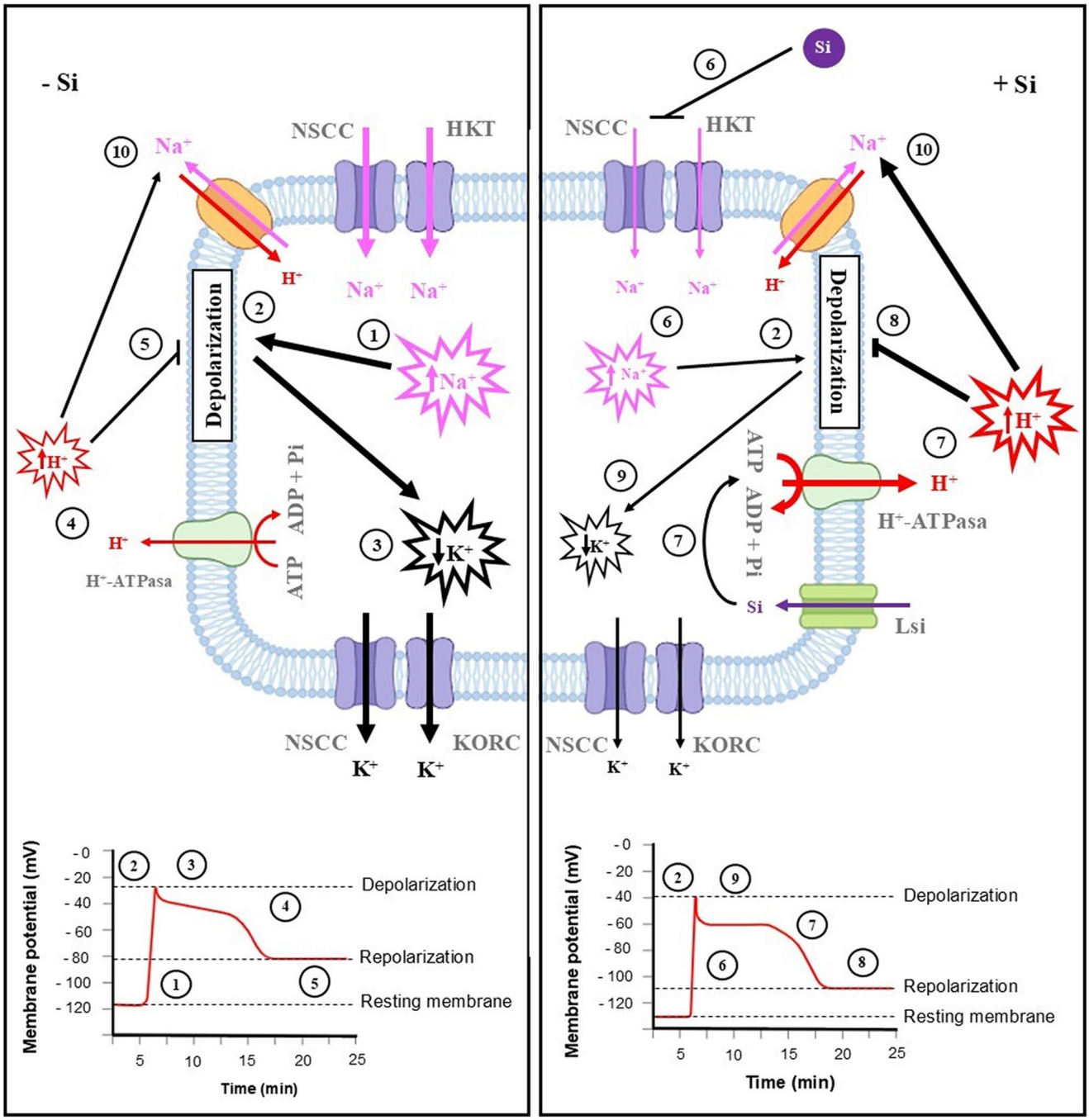


Fig. 6 Proposed working model of how plasma membrane transporters control cytosolic K^+/Na^+ in barley root epidermal cells under salt stress in the presence of Si. The thickness of the lines and the size of the letters represent the magnitude of the effects. (1) NaCl promotes Na^+ influx and membrane depolarization (2). (3) Triggering K^+ efflux through K^+-permeable pathways. (4) Enhanced H^+ pumping counteracts depolarization and supports K^+ retention (5). (6) Si reduces Na^+ entry and stimulates H^+ efflux (7), thereby limiting K^+ loss (8,9). The H^+ gradient may also facilitate Na^+ extrusion via Na^+/H^+ exchange (10)

as silicon supplementation could be considered as an early-stage strategy to improve plant performance in saline environments. In a broader context, these results contribute to the development of sustainable approaches for managing salinity stress in cereal crops and provide a physiological basis for future breeding, screening, and agronomic programs aimed at improving crop resilience under increasing soil salinization.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42729-026-03372-9.

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Data Availability The materials used in this study will be made available to researchers upon reasonable request.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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