while intercellular CO_2 concentration also partially recovered. A more plausible interpretation is that Si helped re-establish the balance between root water uptake and transpirational demand, rather than simply reducing water loss.

Based on the available evidence, Si appears to support photosynthetic performance through at least three pathways: protection of photosynthetic pigments and membrane structures, improvement of stomatal function and leaf water status, and alleviation of non-stomatal limitations associated with Na^+ toxicity and ROS accumulation. Singh et al. (2022) likewise observed recovery of photosynthetic pigments, gas exchange, and photochemical efficiency following Si treatment. However, in pepper, data on parameters such as Fv/Fm, electron transport rate, and photosystem I activity remain much more limited than gas-exchange measurements. Therefore, direct evidence that Si protects the photosystems themselves is still insufficient and requires further investigation.

4.3 Water relations and osmotic adjustment

Foliar Si experiments in sweet pepper have shown that salinity stress decreases relative water content, whereas Si treatment can partially restore it. Altuntas et al. (2018) reported a similar trend using leaf water potential as an indicator of plant water status. Across four salinity-genotype combinations, the improvement ranged from 9.2% to 26.8%, with a median of approximately 14%. The recovery of water status occurred broadly in parallel with increases in net photosynthetic rate, suggesting that water relations may represent an important link between root responses and the restoration of leaf photosynthesis in pepper.

The interpretation of proline and soluble sugar accumulation requires caution. Their concentrations often increase under salinity stress, but this increase may reflect either enhanced osmotic adjustment or greater stress injury. In sweet pepper, salinity markedly increased proline and soluble sugar contents, whereas some of these osmolytes declined after Si alleviated the stress. Badem and Söylemez (2022) also observed a tendency toward lower proline concentrations following Si application. Therefore, the assumption that "higher proline always indicates greater salt tolerance" is not appropriate when evaluating the effects of Si.

A more reliable assessment is to consider relative water content, leaf water potential, proline, soluble sugars, and stomatal parameters together. Si may promote the osmotic adjustment required to maintain cellular water relations, while at the same time reducing the overall severity of stress so that some stress-associated metabolites no longer need to remain at very high concentrations. Similar bidirectional changes were reported by Zhang et al. (2017). Thus, inconsistencies in proline responses among studies do not necessarily indicate contradictory effects of Si.

5 Effects of Exogenous Silicon on Antioxidant Defense and Cellular Protection

5.1 Regulation of antioxidant enzyme activities

Following the onset of salinity stress, superoxide dismutase (SOD) generally converts O_2^- to H_2O_2, which is subsequently scavenged by catalase (CAT). Data from nanosilicon experiments in pepper illustrate this response clearly. Under 100 mM NaCl, application of 1 mM nSi increased SOD activity from 182.47 to 300.46, corresponding to an increase of approximately 64.7%, while under 150 mM NaCl the increase was about 55.7%. The corresponding increases in CAT activity were approximately 70.2% and 65.6%, respectively (Kusvuran et al., 2024). By contrast, the increases in both enzymes were much smaller under 50 mM NaCl. These results suggest that Si-induced antioxidant responses may depend, at least in part, on stress intensity.

Ascorbate peroxidase (APX), peroxidase (POD), and glutathione peroxidase (GPX) further contribute to H_2O_2 detoxification, particularly in the chloroplast and cytosol. In 'Bugwang' pepper, Si application increased GPX, CAT, and APX activities relative to the salt-only treatment. In the nanosilicon study, 1 mM nSi increased APX activity by approximately 91% and 60% under 100 and 150 mM NaCl, respectively, while glutathione reductase (GR) increased by about 49% and 43% (Manivannan et al., 2016). Mycorrhiza-Si experiments have also shown that the responses of CAT, APX, and related enzymes vary among genotypes. Sensitive genotypes do not necessarily exhibit lower enzyme activities; in some cases, the opposite occurs because they experience stronger oxidative stress (Altuntas et al., 2025).