Othman YA *et al.* (2024)
Notulae Botanicae Horti Agrobotanici Cluj-Napoca
Volume 52, Issue 4, Article number 14102
DOI:10.15835/nbha52414102
Research Article

Comparative analysis of lily responses to elevated salinity in irrigation water: Effects on physiology, anatomy, and postharvest flower quality

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Abstract

Saline water irrigation presents a significant challenge in agriculture, especially in regions with water scarcity and soil salinity. Lilies are economically significant ornamental plants renowned for their aesthetic value and commercial importance. This study aims to evaluate the effects of saline water irrigation on lily anatomy, physiology, and postharvest flower quality. Three NaCl salinity levels with varying electrical conductivities (EC) (control 0.65, 3, and 6 dS m^{-1}) were applied to three hybrid lilies (*Lilium* × *elegans*): fragrant Orienpet ('Maytime', white), non-fragrant Longiflorum-Asiatic ('Pavia', yellow), and 'Fangio' (pink). Overall, moderate salinity (3 dS m^{-1}) significantly altered lily anatomy and physiology, resulting in reduced postharvest quality, particularly evident in leaf greenness, flower size, quantity, and vase life. Exposure of plants to higher salinity levels (6 dS m^{-1}) resulted in significant reductions in leaf area (40%), plant height (21%), stem diameter (15%), chlorophyll content (29%), and photosynthesis (Pn) (20%) compared to the control. Analysis revealed thinner epidermal cell and parenchyma tissues, along with decreased ground tissue thickness, contributing to reduced stem diameter. Reduced photosynthesis in salt-stressed lilies was attributed to significant declines in stomatal conductance (gs) (72-80%) and abaxial stomatal index (69%). High salinity levels also led to decreased flower diameter, size, number of flowers per stem, and vase life. However, irrigation with saline water at 6 dS m^{-1} enhanced certain color attributes, including petal redness (a*) in 'Fangio' and yellow hue (b*) in both 'Fangio' and 'Pavia' hybrids, along with increased colorfulness/saturation levels (C*) across all cultivars. In conclusion, this study offers valuable insights into identifying anatomical stress indicators that elucidate physiological responses. These findings could contribute significantly to the development of effective stress mitigation strategies for lily cultivation, particularly in water-scarce and saline environments.

Keywords: colour coordinates; hybrid lilies; NaCl; photosynthesis; vase life

Introduction

Salinity poses a significant threat to the growth and productivity of horticultural crops including cut flower industry (Feizi *et al.*, 2021; Othman *et al.*, 2022). Salt stress affect nearly every aspect of the growth and development of cut flower plants. Salt stress condition induces osmotic stress, oxidative stress, ion toxicity,

Received: 04 Sep 2024. Received in revised form: 20 Oct 2024. Accepted: 14 Nov 2024. Published online: 18 Nov 2024.
From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

nutritional imbalance, disturbance in Na^+/K^+ homeostasis and reduces gas exchange components including [photosynthesis (Pn), stomatal conductance (gs) and transpiration (E)] (Ayad *et al*., 2019; Feizi *et al*., 2021). Canonical discriminant analysis of 26 lily hybrids irrigated with saline water (8 dS m^{-1}) showed that the middle leaf width, leaf chlorophyll a fluorescence, and flower components (number of flowers, first flower diameter, petal width) were correlated with salt stress (Kang *et al*., 2021). Elevated salinity (5 and 10 dS m^{-1}) in irrigation water reduced hydrangea (*Hydrangea macrophylla*) height, leaf area, leaf greenness [Soil Plant Analysis Development (SPAD) readings], chlorophyll fluorescence (Fv/Fm); maximal photochemical efficiency of photosynthetic apparatus (performance index), and leaf N, P, K^+, Fe^{+3} (Sun *et al*., 2022). *Zinnia elegans* cultivars ('Short Stuff' and 'Profusion') irrigated with saline water for 120-day growing period using a drip irrigation system showed that all flowering characteristics (number, diameter) decreased as the level of salinity increased (1.6, 3.1, 6.3, 9.4 dS m^{-1}) (El-Nashar and Hassan, 2020). In addition, both cultivars did not flower at salinity levels of 6.3 and 9.4 dS m^{-1} (El-Nashar and Hassan, 2020). Irrigation with saline water (4.5 dS m^{-1}) significantly reduced gerbera (*Gerbera jamesonii*) chlorophyll content index, Pn, gs, E, flower yield and quality, specifically vase life (Othman *et al*., 2022). The number of flowers in saffron (*Crocus sativus*) decreased by 20%, 34% and 31% when subjected to increased salinity ranging from 5 to 15 dS m^{-1} compared to the control (Feizi *et al*., 2021). Carnation (*Dianthus caryophyllus*) plants flower weight and quality decreased significantly at NaCl concentrations of 3 and 6 dS m^{-1} while flowering was retarded in plants treated with NaCl ranging from 12 to 24 dS m^{-1} (Kwon *et al*., 2019).

The response to salinity varies not only among various floriculture crops but also among different organs within a plant (Küçükahmetler, 2022). Depending on osmotic adjustment, certain physiological modifications take place in gas exchange parameters (Pn, gs, E), chlorophyll content, and the growth of roots and leaves (Küçükahmetler, 2022; Othman *et al*., 2022). Consequently, yield and flower quality reduction especially color, vase life, flower diameter may become apparent (Küçükahmetler, 2022; Othman *et al*., 2022). Although salinity (12 to 24 dS m^{-1}) reduced the duration and extent of sap flow, gas exchange (Pn, gs, E) in carnation at flowering stage, ABA content increased with increasing NaCl salinity, 3.0 to 24 dS m^{-1} (Kwon *et al*., 2019). Flowers of *Carthamus tinctorius* grown in soil containing 5 or 10 g L^{-1} NaCl had higher total phenols, flavonoids, antioxidant activity, condensed tannins and carotenoid contents than 0.0 L^{-1} NaCl treatment (Salem *et al*., 2014). A consistent rise in antioxidant compounds at salt stress highlighting the swift response of defense mechanisms, both enzymatic and non-enzymatic, to combat stress (Guzman and Marques, 2023). Salt-stressed leaves of carnations specifically at 24 dS m^{-1} NaCl had lower leaf cell size, stomatal density, stomata size and larger intercellular spaces, and thicker epicuticular wax layer compared to 0 and 3 dS m^{-1} (Kwon *et al*., 2019). The stem anatomical analysis of *Salicornia freitagii* revealed several key adaptations to salt stress. Notably, a reduction in both xylem thickness and vessel diameter was observed, suggesting a potential mechanism to minimize water loss. The leaf stomatal index, defined as the ratio of stomata to the total of stomata and epidermal cells, also significantly decreased under high salinity, likely as an adaptation to reduce transpiration. Interestingly, despite these reductions, the diameter of the pith in the stem increased with higher salt levels, possibly indicating an anatomical adjustment to maintain structural integrity or storage capacity under stress (Akcin *et al*., 2017). Further investigation into the molecular mechanisms underlying plant adaptations to salt stress has included studies on Tiger Lily (*Lilium lancifolium*), where the expression of the *LiMAPK* gene was analyzed under saline conditions. After 12 and 24 hours of salt stress exposure, *LiMAPK* expression levels in Tiger Lily remained relatively stable, yet consistently doubled compared to the control (Su *et al*., 2018). This persistent upregulation of *LiMAPK* suggests its involvement in the plant's salt tolerance mechanisms, potentially playing a crucial role in the adaptive responses of Tiger Lily to salt stress (Su *et al*., 2018).

The global cut flower industry is expanding, and in 2022, Royal Flora Holland, the largest marketplace for the floriculture industry, disclosed a revenue of 5.17 billion euros (RFH, 2023). In addition to rose and tulip, Lilium has risen to become one of the top five cut flowers sold by Royal Flora Holland, contributing to a total value of around $150 million (RFH, 2023). The economic value of cut flower production relies significantly on pre-harvest factors such as the consistent shape, size, and colour of flowers, as well as the length and diameter of stems, along with post-harvest longevity (Al-Ajlouni *et al*., 2023). Achieving a balance between cut flower yield and quality, particularly for lilies, poses a challenge in the floriculture industry, especially in dryland regions. Production in such areas lacks a fully controlled environment and is further complicated by the use of low-quality water, often saline in nature. While irrigation with saline water is inevitable in these dry regions (where freshwater resources are limited), it presents unique challenges for cut flower industry. High salt content in irrigation water can negatively impact soil structure and fertility, hinder nutrient absorption by cult flowers root, and ultimately compromise the overall health and productivity of these flowering crops (Othman *et al*., 2022). While the impact of saline water on plant growth and productivity is widely recognized (Ayad *et al*., 2019; Kang *et al*., 2021), specific effects of salt stress (NaCl) on leaf and stem anatomy, gas exchange, and flower quality—including vase life and color coordinates—are not yet fully understood. Previous studies have primarily focused on general growth responses, leaving significant gaps in our knowledge regarding how salt stress affects the physiological and anatomical traits of fragrant-Orienpet and non-fragrant Longiflorum-Asiatic lily hybrids. Exploring lily's anatomical responses to salinity could reveal adaptation mechanisms and the effectiveness of mitigation strategies such as enhanced irrigation and nutrient management, significantly benefiting lily cultivation in saline environments. Therefore, the objective of this study was to assess the effects of elevated salt stress in irrigation water on the morphology, physiology, anatomy, and flower quality of lily hybrids.

Materials and Methods

Site setup and plant material

The study was conducted in a glasshouse at the School of Agriculture, University of Jordan, Jordan, between July 2021 and May 2022. Three hybrid lilies [(*Lilium* × *elegans*); fragrant Orienpet ('Maytime', white), non-fragrant Longiflorum-Asiatic, L.A. ('Pavia', yellow), and 'Fangio', pink] were assessed. The non-fragrant Longiflorum-Asiatic (L.A.) referring to a hybridization between the Longiflorum and Asiatic groups of lilies while the Orienpet fragrant lily are the result of crossing between Oriental lilies with Trumpet type (Bany Hani *et al*., 2022). Two lily bulbs (1-year-old, diameter 5-6 cm) were transplanted into a 10 L plastic pot filled with growing medium (1:1:1 peatmoss: sand: clay by volume). Growing media pH was about 6.5 and electrical conductivity was 0.3 dS m^{-1}. The pots were placed on a bench (6 m × 3 m) within the greenhouse facility. Fertigation was applied once a month starting 6 weeks after the planting date using commercial fertilizer ($20N-20P_2O_5-20K_2O$) at rate of 220 mg L^{-1} N, 65 mg L^{-1} P and 200 mg L^{-1} K during vegetative stage and ($20N-20P_2O_5-30K_2O$ plus potassium chloride) at rate of 100 mg L^{-1} N, 44 mg L^{-1} P and 300 K mg L^{-1} K from early flowering to harvesting. During the experimental period, mean minimum and maximum temperatures were 16 and 23 °C, respectively, with relative humidity ranging from 50 to 70%. Day-time light intensity ranged from 250 to 650 µmol s^{-1} m^{-2}.

Experimental treatments

One week after transplanting, lily bulbs were fertigated with three distinct NaCl salinity levels, with electrical conductivity (EC) set at 0.65, 3, and 6 dS m^{-1}, respectively. For the control treatment, irrigation water with an EC value of 0.65 dS m^{-1} was used, while NaCl was added to achieve the desired salinity levels for the other two treatments. The volumetric water content at field capacity was determined by saturating the soil mixture and allowing it to drain until no further drainage occurred, typically at a soil water potential of around -33 kPa. Based on these measurements, the irrigation schedule and volume for pots were established to maintain moisture content above 70% of field capacity, achieved by manually applying 300 ml of irrigation water along with the desired NaCl level once or twice a week to each pot.

Plant growth parameters at flowering

Plant height, stem diameter, and leaf area were determined at flowering stage. Leaf area was determined using leaf area meter (LI-3100; ADC BioScientific, Hoddesdon, UK). Three representative leaves were chosen from the upper, middle, lower sections of each flowering stem for leaf area measurements across the salinity levels and cultivars, then measurements were subsequently averaged to obtain a single value for each replicate.

Leaf gas exchange and chlorophyll content

Leaf gas exchange components (*Pn*, *E*, and *gs*) were measured at flowering stage using a portable photosynthesis system (LI-6400XT; LI-COR, Lincoln, NE) and following the system calibration inputs of Leskovar and Othman (2021). The portable photosynthesis system CO_2 reference was set at rate of 400 µmol, the total area of the chamber head was 6 cm^2 (2×3 cm), the flow rate was set at rate of 500 µmol s^{-1} and light intensity was set to track ambient photosynthetically active radiation. Leaf gas exchange was conducted between 11:00 am and 1:00 pm from two fully-mature and sun-exposed lily leaves located at the top and the middle part of the flowering stem. Similarly, chlorophyll content was determined on the same leaves using a chlorophyll concentration meter (MC-100; Apogee Instruments, UT, USA).

Flower quality and vase life

Lily stems across cultivars and over the salinity treatments were harvested when one of the flowering buds began to open but was not fully opened. Flower quality components including the number of days to flowering (from transplanting to harvest), flower diameter, petal color coordinates, the number of flowers per stem and vase life were determined. Petal color coordinates (L*, C*, a* and b*) were determined on two flowers per stem using a colorimeter (CR-400, Konica Minolta, Ramsey, NJ, USA) and following the procedure of Alsmairat *et al.* (2018). Vase life was determined by recutting the stems (2-3 cm from the base) under water to remove the emboli (small bubbles of air in the xylem) and placing them directly in a commercial preservative solution (Spring Pro-Florist, Spring from Holland B.V., Sassenheim, Nederland) con-taining 2 % sugar + bactericide and fungicide, pH 3.5–4.2. The vase life of a lily flower was specified as the duration in days from the harvesting of stems and their placement in the holding solution until the first lily flower per stem either fell off or wilted (Al-Ajlouni *et al*., 2023).

Leaf and stem anatomy of 'Fangio' cultivar via light microscopy

Cross sections of leaves and stems were observed under a light microscope. Leaf and stem samples were selected randomly (three replicates per treatment) from 'Fangio' cultivar for anatomy. Leaf and stem samples (about 10 mm^2) were fixed with formalin–acetic acid and prepared for anatomy analysis according to (Yao *et al*., 2023). Leaf and stem anatomy component were viewed with a light microscope (B-Scope Trino E-plan, Euromax Microscopes Holland, Arnhem, The Netherlands) and photographed using 12-pixel camera (CMEX 12, Euromax Microscopes Holland, Arnhem, The Netherlands). Leaf and stem anatomy variables were analyzed using image analysis software (Image Focus Plus, Euromax Microscopes Holland, Arnhem, The Netherlands). The stomatal index of a leaf is defined as the ratio of the number of stomatal cells to the total number of stomata and epidermal cells in the leaf expressed as a percentage (Stomatal index = (number of stomata) / (number of stomata + number of epidermal cells) × 100%) (Zhu *et al.*, 2021).

Statistical analysis

The experiment was carried out utilizing a randomized complete block design, which incorporated two factors: three salinity levels and three different cultivars of lilies. Each treatment combination was replicated four times to ensure robust data collection and analysis. Statistical analysis was conducted using SAS software (Version 9.4 for Windows; SAS Institute, Cary, NC). To evaluate the effects of salinity and cultivar on various parameters, we employed analysis of variance (ANOVA) followed by the least significant difference test ($P < 0.05$) to identify significant differences between treatments and their interactions.

Results

Morphology, physiology and flower quality

Table 1 presents the ANOVA and mean separation (LSD) for morpho-physiological variables of lily cultivars as affected by different salt levels (0.65, 3 and 6 dS m^{-1}). Irrigation with saline water of EC 3 and 6 dS m^{-1} reduced all morphological parameters (leaf area) and physiological variables (chlorophyll content, *Pn*, *gs*, and *E*) variables. Compared to non-stressed lily, the 6 dS m^{-1} treatment reduced the leaf area by 45%, chlorophyll content by 15% and *Pn* by 10%, *gs* by 75% and *E* by 66%. In term of cultivars, Orienpet hybrid (‘Maytime’) had higher leaf area, plant height, stem diameter and chlorophyll content than both L.A. cultivars (‘Pavia’ and ‘Fangio’). However, gas exchange (*Pn*, *gs* and *E*) within the same salinity level was similar across the three cultivars

Table 1. Leaf area, plant height, stem diameter, chlorophyll content (Chlo.), photosynthesis (*Pn*), stomatal conductance (*gs*), and transpiration (*E*) of three hybrid lilies [fragrant Orienpet (‘Maytime’, white) and non-fragrant Longiflorum-Asiatic (‘Pavia’, yellow), ‘Fangio’, pink] grown under different salinity levels

Salinity level (dS m^{-1})	Cultivar (C)	Leaf area (cm^2)	Plant height (cm)	Stem diameter (mm)	Chlo. (mg kg^{-1} dwt.)	*Pn* (µmol m^{-2} s^{-1})	*gs* (mol m^{-2} s^{-1})	*E* (mmol m^{-2} s^{-1})
‘Fangio’	**0.65**	22.7 d	114 d	7.37 c	371 bc	20.8 a	0.11 b	2.28 b
	3.0	18.5 e	102 e	7.01 c	330 cde	17.9 cd	0.07 c	1.47 c
	6.0	15.5 ef	84.4 f	6.37 d	287ef	16.3 d	0.03 d	0.74 d
‘Maytime’	**0.65**	48.3 a	165 a	8.88 a	499 a	19.9 ab	0.13 ab	2.13 b
	3.0	36.1 b	148 b	8.51 ab	407 b	17.7 cd	0.06 cd	1.17 cd
	6.0	27.8 c	132 c	8.20 b	338 cd	16.5 cd	0.04 d	0.92 d
‘Pavia’	**0.65**	25.5 cd	78.8 fg	7.18 c	367 bc	20.3 ab	0.15 a	3.17 a
	3.0	22.6 d	74.1 g	6.34 d	293 def	18.4 bc	0.05 cd	1.12 cd
	6.0	14.1 f	62.5 h	5.59 e	246 f	16.0 d	0.03 d	0.77 d
ANOVA	**S**	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	C	<0.0001	<0.0001	<0.0001	<0.0001	0.86	0.791	0.152
	S × C	<0.0001	0.003	0.15	0.292	0.871	0.041	0.002

Means in columns followed by different letters are significantly different at $p \leq 0.05$

Irrigation with saline water significantly affect flower yield and quality components (Table 2). Both saline water levels 30 and 60 mM NaCl reduced flower number per stem, flower diameter, vase life while increasing the petal color coordinates C* and b* across cultivars. Both L.A. cultivars (‘Fangio’, and ‘Pavia’) had higher flower number per stem and vase life than ‘Maytime’. Conversely, Orienpet lily ‘Maytime’ had larger flower diameter (16.3 cm) and required a longer period to flower (115 day) compared to L.A. hybrids ‘Fangio’ (75 day) and ‘Pavia’ (96 day). However, salt stress did not affect the earliness of flowering across cultivars (Table 2). In term of color coordinate, the white-petals Orienpet lily ‘Maytime’ had higher L*, than the yellow ‘Pavia’ and pink 'Fangio' cultivars. Meanwhile, 'Pavia' had the highest C* and b* color coordinates while 'Fangio' had the highest a* color coordinate.

Table 2. Flower number per stem, flower diameter, number of days to flowering, vase life and petal color coordinates (L*, C*, a* and b*) of three hybrid lilies [fragrant Orienpet ('Maytime', white) and non-fragrant Longiflorum-Asiatic ('Pavia', yellow), 'Fangio', pink] grown under different salinity levels

Cultivars (C)	Salinity level (S) (dS m^{-1})	Flowers No. $stem^{-1}$	Flower diameter *(cm)*	Days to flowering	Vase life *(days)*	Petal color coordinates			
						L*	C*	a*	b*
'Fangio'	**0.65**	5.14 ab	16.3 b	73.4 c	15.2 a	37.6 d	36.3 d	33.5 b	9.17 e
	3	5.25 a	14.4 de	76.9 c	12.5 b	38.8 d	38.5 cd	35.2 b	13.7 d
	6	5.00 ab	13.6 ef	76.0 c	12.4 b	41.3 c	40.1 c	38.6 a	13.8 d
'Maytime'	**0.65**	3.40 c	17.8 a	115.7 a	11.5 b	84.9 a	3.83 f	-0.80 c	3.35 f
	3	2.33 d	16.1 bc	116 a	9.43 c	85.2 a	4.40 e	-0.89 c	4.02 f
	6	1.40 e	14.3 e	112 a	7.67 d	85.2 a	4.80 e	-0.94 c	4.80 f
'Pavia'	**0.65**	4.38 b	15.3 cd	93.1 b	12.4 b	76.4 b	75.3 b	-5.56 d	72.7 c
	3	2.75 cd	12.7 fg	98.0 b	10.3 c	77.3 b	80.9 a	-6.88 d	79.9 b
	6	2.38 d	12.6 g	98.2 b	9.75 c	77.1 b	79.9 a	-7.07 d	87.8 a
ANOVA	**S**	<0.001	<0.001	0.133	<0.001	<0.05	<0.001	<0.01	<0.001
	C	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	S × C	0.01	0.13	0.543	0.296	0.163	<0.05	<0.001	<0.001

Means in columns followed by different letters are significantly different at p ≤ 0.05.

Leaf and stem anatomy

Figure 1 and Table 3 show the impact of varying salinity levels on the leaf anatomy of *Lilium* cv. 'Fangio'. Compared to control plants, the application of saline water at both EC values (3 and 6 dS m^{-1}) resulted in reduced leaf thickness, upper and lower epidermal cells thickness, xylem vessels and phloem tubes area as well as stomatal index percentage. Additionally, the stomatal index of lily leaves irrigated with saline water at 3 dS m^{-1} was significantly higher, nearly doubling that of those irrigated with 6 dS m^{-1}. However, no significant difference was noticed between the 3 and 6 dS m^{-1} treatments in leaf and epidermis thickness as well as xylem vessels and phloem tubes area (Table 3).

Table 3. Leaf anatomy components, leaf thickness, upper and lower epidermis cell thickness, xylem conduits and phloem area, stomatal index of leaf minor veins of Longiflorum-Asiatic hybrid lily cultivar 'Fangio' grown under different salinity levels

Salinity level (dS m^{-1})	Leaf thickness (μm)	Upper epidermis thickness (μm)	Lower epidermis thickness (μm)	Xylem vessel area (μm^2)	Phloem tubes area (μm^2)	Stomatal index (%)
0.65	760 a*	44.4 a	34.3 a	13410 a	4820 a	16.0 a
3.0	601 b	36.0 b	29.2 b	10860 b	3950 b	10.0 b
6.0	502 b	33.8 b	25.5 b	9920 b	3420 b	5.00 c
P-value	0.004	0.01	0.007	0.002	0.003	0.001

Means in columns followed by different letters are significantly different at p ≤ 0.05

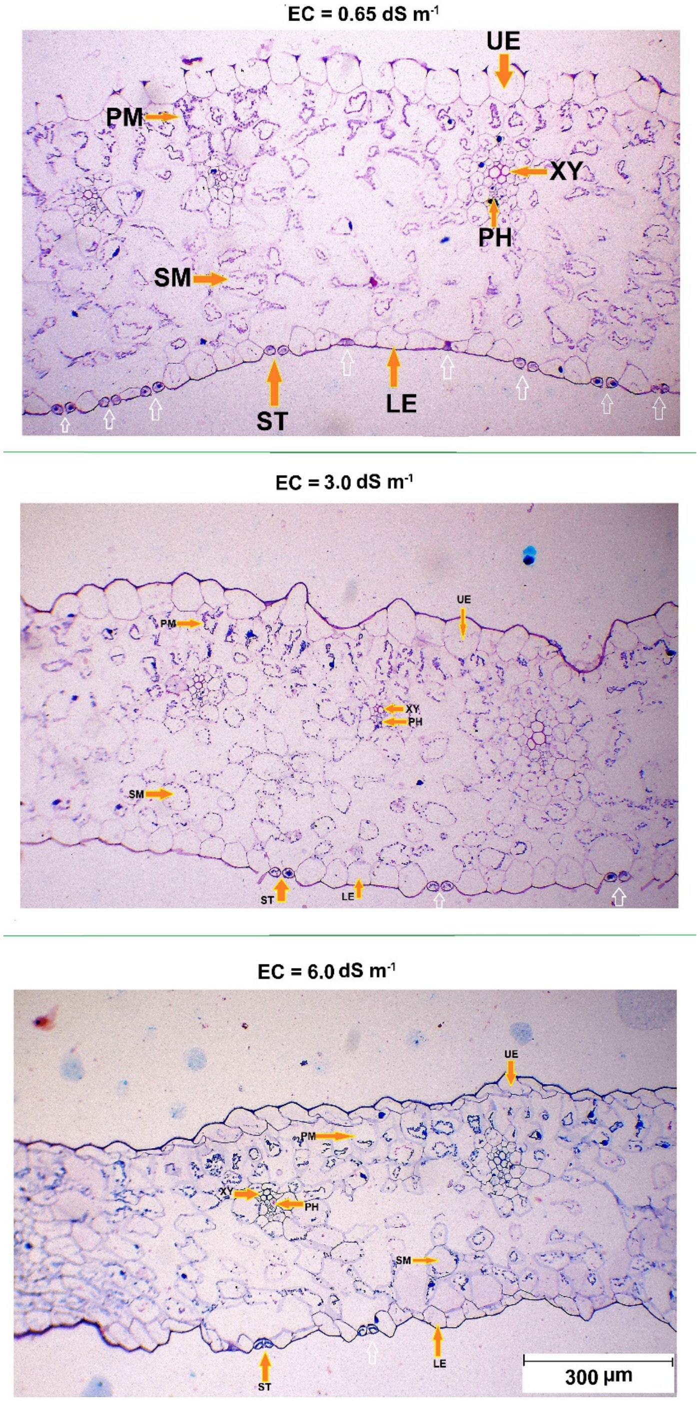

Figure 1. Leaf cross section of Longiflorum-Asiatic hybrid lily cultivar ‘Fangio’ grown under different water salinity levels (EC of 0.65, 3.0 and 6.0 dS m^{-1})

UE, upper epidermis; LE, lower epidermis; XY, xylem vessels; PH, phloem tubes; PC, palisade cells; SC, spongy cells; ST, stomata. Magnification 100 × (all images have a scale of 300 µm).

Similarly, there were consistent trends in the effects of irrigation water salinity on stem anatomy, with high salinity level (6 dS m^{-1}) significantly reducing epidermal cell thickness, parenchyma and ground tissues thickness as well as the longitudinal cell length of ground tissues when compared to control (Table 4, Figures 2 and 3). Compared to highly stressed lilies (6 dS m^{-1}), none-stressed control lily plants (0.65 dS m^{-1}) exhibited increased epidermal cell thickness by 24%, parenchyma tissues thickness by 49%, ground tissues thickness by 26% (Table 4, Figure 2) and ground tissues longitudinal cell length by 36% (Table 4, Figure 3). However, the total vascular bundle number per mm^2 was similar across the three salinity levels.

Table 4. Stem anatomy components, epidermal cells, parenchyma tissues, ground tissues thickness and the vascular bundles number of Longiflorum-Asiatic hybrid lily cultivar 'Fangio' grown under different salinity levels

Salinity level (dS m^{-1})	Epidermal cell thickness (µm)	Parenchyma tissues thickness (mm)	Ground tissues thickness (mm)	Ground tissues longitudinal cell length (mm)	Number of vascular bundles (per mm^2)
0.65	51.3 a*	121 a	201 a	916 a	8.14 a
3.0	45.1 b	110 a	181 a	875 a	7.92 a
6.0	41.4 b	81.4 b	160 b	675 b	8.26 a
P-value	0.003	<0.0001	0.004	0.001	0.63

Means in columns followed by different letters are significantly different at $p \leq 0.05$.

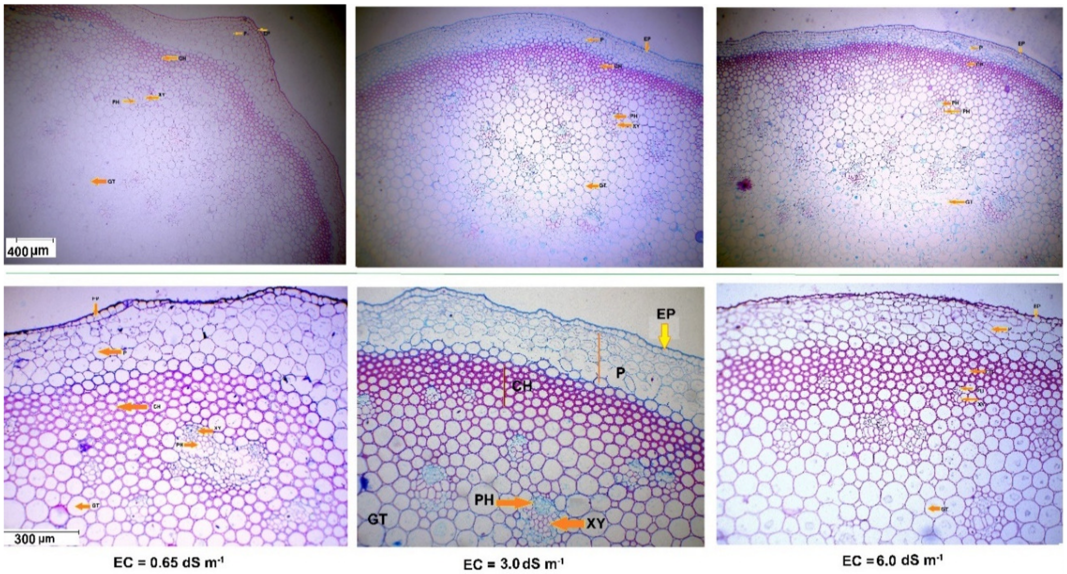

Figure 2. Stem cross section of Longiflorum-Asiatic hybrid lily cultivar 'Fangio' grown under three different water salinity levels (EC of 0.65, 3.0 and 6.0 dS m^{-1})

EP, epidermal cells, XY, xylem; PH, phloem; GT, ground tissues, P, parenchyma; CH, collenchyma. Magnification, upper row 40X, lower row 100 ×.

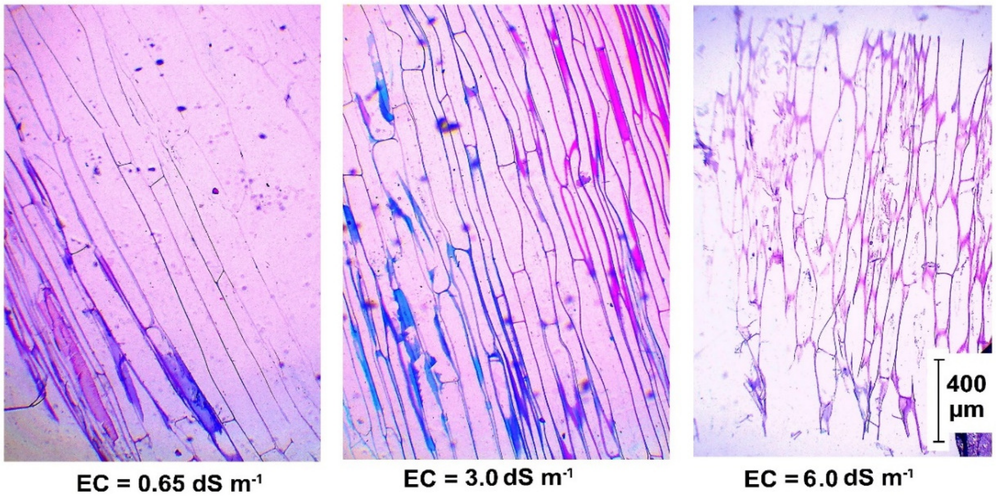

Figure 3. Longitudinal stem section (ground tissues cells) of Longiflorum-Asiatic hybrid lily cultivar 'Fangio' grown under three different water salinity levels (EC of 0.65, 3.0 and 6.0 dS m^{-1})
Magnification 40×.

Discussion

Effects of salt stress on chlorophyll, gas exchange, and growth in lilies

This study confirms that salt stress (EC of 3 to 6 dS m^{-1}) significantly reduces chlorophyll content, gas exchange, and growth in lily cultivars, as shown in Table 1. The observed reductions leaf area and greenness, both critical postharvest visual traits, are likely due to physiological changes caused by salt stress (Ayad *et al*., 2019; Kang *et al*., 2021; Othman *et al*., 2022). Photosynthesis is a vital process for the growth and development of lily plants and is significantly influenced by biotic stress such as salinity (Ayad *et al*., 2019). Furthermore, the importance of leaf chlorophyll cannot be over-stated, as these pigments play a critical role in providing the necessary energy for the photosynthesis process by absorbing light (Wen *et al*., 2018). Salt stress reduces photochemical efficiency (Fv/Fm), photochemical (qP) and non-photochemical (qN) quenching coefficients in photosynthesis system (Jamil *et al*., 2007).

In this study, a 6 dS m^{-1} salinity level reduced the stomatal index by 69%, leading to a 75% reduction in stomatal conductance (*gs*) and a 10% decrease in photosynthesis rate (*Pn*). Similar patterns of salinity-induced reductions in growth parameters, such as stem diameter, plant height, leaf area, and chlorophyll content, have been observed in other species. For instance, Kiremit and Arslan (2016) reported that increasing salinity (up to 7 dS m^{-1}) reduced leek (*Allium porrum* L.) growth, leaf area, and water-use efficiency. In lilies, Bai et al. (2021) found that salinity levels above 3.5 dS m^{-1} significantly reduced shoot fresh weight, chlorophyll content, and photosynthesis rate, with further reductions in gas exchange (*gs, E*) and peroxidase enzyme activity at 7 dS m^{-1}. At even higher salinity (14 dS m^{-1}), chlorophyll fluorescence and other physiological parameters showed dramatic declines. Similar reductions in gas exchange parameters (*Pn, gs, E*) and relative water content were seen in daffodils under saline irrigation (10 dS m^{-1}), with 50–75% reductions compared to non-saline conditions (Veatch-Blohm *et al*., 2019). Overall, irrigation with saline water resulted in significant reduction in chlorophyll content and gas exchange performance and consequently reduced the size of lily plants.

Salinity also caused notable anatomical changes in lily plants. Irrigation with saline water (6 dS m^{-1}) resulted in a significant reduction in stem diameter for 'Fangio' (14%), 'Pavia' (22%), and 'Maytime' (8%) when compared to control. This reduction in stem diameter can be attributed to a significant decrease in epidermal cell thickness (19.3%), parenchyma tissues thickness (32.7%), and ground tissues thickness (20.3%). Regarding plant height, the higher salinity stress (6 dS m^{-1}) led to a reduction in stem length by 22% for 'Fangio', 21% for 'Pavia', and 20% for 'Maytime'. This reduction could be attributed to the shorter cell length in salt-stressed lilies. In fact, the stem anatomy of 'Fangio' lily revealed that the longitudinal cell length of ground tissues in the 6 dS m^{-1} treatment was 26.3% shorter than that of the non-stressed (0.65 dS m^{-1}) lily (Figure 3, Table 4).

The morphology and physiological function of stomata provide key insights into plant responses to salinity. Stomata regulate gas exchange, balancing carbon dioxide uptake for photosynthesis with water vapor loss (Royer, 2001; Zhu et al., 2021). Stomatal density and size are indicators of a plant's ability to adapt to environmental stress, and these traits help assess the anatomical limitations on gas exchange (Sack and Buckley, 2016). The stomatal index, which reflects stomatal cell density per mm^2 of leaf surface, is a crucial parameter in assessing plant responses to abiotic stress (Zhu *et al.*, 2021). In this study, saline irrigation (6 dS m^{-1}) reduced leaf thickness by 34% and abaxial stomatal index by 69% compared to control plants (Figure 1, Table 3). Similar reductions in stomatal density have been observed in *Chenopodium quinoa* under salt stress, where adaxial stomatal area decreased by 14% and abaxial by 8% (Prado *et al.*, 2017). Overall, irrigating lilies with saline water (3-6 dS m^{-1}) resulted in significant anatomical modifications, including the reduction of leaf thickness as well as the abaxial stomatal density (stomatal index). These findings provide valuable insights into how lilies respond to salinity, with implications for improving their cultivation in saline environments.

Plants respond to salinity by triggering morphological, anatomical, osmotic, and hormonal adaptations to cope with elevated salt levels in their environment (Prado *et al.*, 2017). These mechanisms are essential for maintaining water balance, ion homeostasis, and growth under stress. For instance, exposing calla lilies (*Zantedeschia* K. Koch) to salt stress (5 dS m^{-1}) showed no apparent decline in visual quality despite a significant reduction in carbon assimilation rate by 50–80% compared to control plants (Veatch-Blohm *et al.*, 2012). This reduction in photosynthetic capacity was associated with notable decreases in stomatal conductance (*gs*), which ranged from 53% to 97% lower than the control, and was accompanied by an osmotic adjustment of 0.16–0.20 MPa. These findings underscore the critical role of osmotic adjustment and reduced gs in maintaining leaf turgor and water relations during stress periods. Increased ion accumulation is another key adaptive response. In calla lilies, leaves irrigated with saline water of 2.5 and 5 dS m^{-1} exhibited two to three times higher cation content (Na^+, Ca^{2+}, and Mg^{2+}) than those of the control plants, a reflection of the role of ion sequestration in osmotic adjustment (Veatch-Blohm *et al.*, 2012). This accumulation helps plants retain water by lowering leaf water potential, allowing for continued physiological processes under saline conditions.

In our study, we observed a substantial modification in stomatal density (stomatal index) under salt stress, with a reduction of 72%-80% in gs, further emphasizing the link between stomatal regulation and salt tolerance. The reduction in abaxial stomatal density likely serves as an anatomical adaptation to limit water loss through transpiration while maintaining gas exchange under lower *gs* conditions. This adaptation is consistent with the previous findings of Veatch-Blohm *et al.* (2012), where calla lilies also exhibited reduced *gs* under salt stress. Such a reduction in stomatal conductance minimizes water loss, helping plants to conserve water while coping with osmotic stress.

Effects of salt stress on lilies flower quality

Flower quality variables encompass a range of characteristics that determine the overall aesthetic appeal, commercial value, and vase life of cut flowers. Lily flower quality components such as color, diameter, size, number of flowers per stem, and vase life can potentially influence its commercial appearance and marketing (Burchi *et al.*, 2010; Othman *et al.*, 2022). Therefore, under-standing and optimizing these flower quality indices are essential for ensuring the success of the floral industry and enhancing the overall satisfaction of consumers (Othman *et al.*, 2022). In this study, irrigation with saline water (6 dS m^{-1}) reduced the number of flowers per stem by 36%, flower diameter by 18% and vase life by 24% on average across cultivars (Table 2). This reduction can be attributed partially to a signification decreased in the food supply, specifically *Pn*. Photosynthesis plays a crucial role in providing the energy necessary for flower development (Wen *et al.*, 2018).

Under salt stress, the microclimate becomes suboptimal for several processes including gas exchange (*Pn, gs, E*) and cell division and expansion (Zhang *et al.*, 2020). During this stress period, plants activate stress-response mechanisms that divert re-sources away from flower development. This active growth inhibition and the redirection of resources towards stress adaptation can limit flower size and yield (Zhang *et al.*, 2020).

In this study, exposure to high levels of salinity (6 dS m^{-1}) resulted in a significant reduction in the area of xylem vessels and phloem tubes in the leaves of cut-flower lilies. This reduction might reduce the food supply necessary for maintaining flower freshness. Consequently, the vase life of the tested lilies was reduced significantly (Table 2). Salinity stress has been observed to restrict the movement of water and nutrient through the plant by reducing both the number and size of vascular bundles, including xylem and phloem (Belda and Ho, 1992). Furthermore, salt stress has been shown to inhibit the development of xylem tissues, thereby compromising the efficient transport of food to the flowers, and ultimately reducing their longevity (Belda and Ho, 1992; Clark *et al.*, 2021). Additionally, an excess of salt ions, particularly Na^+ and Cl^-, can accumulate in plant tissues, disrupting cellular functions (El-Nashar and Hassan, 2020). This ion toxicity can lead to cellular damage and disrupt the normal physiological processes required for maintaining flower visual appearance. For instance, the visual quality, assessed on a scale from 0 to 5 (with 0 = dead and 5 = excellent), declined from 3 to 1 for Anemone coronaria and from 3 to 2 for *Ranunculus asiaticus* as irrigation water EC increased from 0.5 to 5.5 dS m^{-1} (Rauter *et al.*, 2021). Both *A. coronaria* and *R. asiaticus* exhibited a decrease in leaf greenness by 45-48%, *gs* by 70-79%, E by 23-75%, *Pn* by 15-92% as the irrigation solution's EC increased from 0.5 to 5.5 dS m^{-1} (Rauter *et al.*, 2021). Salt stress (3.1, 6.3, 9.4 dS m^{-1}) resulted in reduced leaf Ca^{2+} and increased Cl^- and Na^+ contents in *Zinnia elegans* plants leading to significant reduction in flower yield (El-Nashar and Hassan, 2020).

The colour coordinates are a fundamental aspect of the CIELAB color space, which has been widely used for the assessment of fruit and flower colour attributes (Khasawneh *et al.*, 2021; Manivannan *et al.*, 2021). This system defines colour using the coordinates L* (lightness), C* (saturation), a* (green/ red component), b* (yellow/blue component) (Khasawneh *et al.*, 2021; Lu *et al.*, 2021). In this system, L* values range from 0.0 (black, darker) to 100 (white, lighter), a* spans from -128 (green) to 127 (red), b* extends from -128 (blue) to 127 (yellow), with higher C* values (always > 0.0) indicating more saturated colours (Khasawneh *et al.*, 2021; Manivannan *et al.*, 2021). In this study, Orienpet white lily 'Maytime' had the highest L* value (85.1 for white vs. 38.6 for pink; 76.9 for yellow). Among the genotypes, the L.A. yellow cultivar 'Pavia' had the highest b* value (80.1 for yellow contrasting with 12.2 for pink and 4.05 for white) while the pink cultivar 'Fangio' had the highest a* value (35.8 for pink opposed to -6.5 for yellow and -0.88 for white). Partial least squares discriminant analysis showed that the attributes of white and red gerbera flowers were primarily affected by the L* value, a* value, C* values, and overall anthocyanin contents. In the yellow group, a positive correlation was observed with L* and b* values, alongside total anthocyanin contents (Zhou *et al.*, 2021). Concurrently, the pink group demonstrated a positive correlation with L* and H* values (Zhou *et al.*, 2021). Interestingly, higher salt level (60 mM NaCl) increased colourfulness/saturation levels C* compared to control across all cultivars, intensified redness a* in pink-lily ('Fangio') and enhanced yellowness b* in pink and yellow lilies ('Fangio' and 'Pavia') (Table 2). Furthermore, colour coordinates a* and C are positively correlated with carotenoid content, while flavonoids are positively correlated with antioxidant potential measured in terms of radical scavenging activity (Manivannan *et al.*, 2021). Flavonoids present a diverse spectrum of colours in plants, thereby affecting the quality and market value of cut flowers (Wang *et al.*, 2021). In *Chrysanthemum* spp., a* was positively ($r = 0.90$, $P < 0.01$) correlated with total anthocyanins, while b* was positively correlated with lutein ($r = 0.80$, $P < 0.01$) and total carotenoids ($r = 0.88$, $P < 0.01$) (Lu *et al.*, 2021). Irrigating marigold (*Tagetes patula*) with saline water (10-30 dS m^{-1} NaCl) has been found to enhance the synthesis of antioxidant enzymes, such as catalase and ascorbate peroxidase (Guzman and Marques, 2023). The consistent rise in antioxidant compounds in response to salinity stress highlights the immediate response of plant to com-bat stress (Guzman and Marques, 2023). In another study on marigold, plants exposed to short-term salinity (10 days) at a rate of 10 dS^{-1} NaCl, subsequent to 40 days of unstressed growth in a soilless system, exhibited elevated levels of flower polyphenols, antioxidant activities, total carotenoids, and nutrient concentrations, particularly in N, P, Na, and Zn (Chrysargyris *et al.*, 2018). Overall, salt stress significantly affects flower colour by increasing the petal colour coordinates, specifically C*, a* and b*.

Conclusions

This study highlights the detrimental effects of salt stress, particularly evident at EC levels of 3 and 6 dS m-^{1}, on the morphology, physiology, anatomy, and postharvest quality of Orienpet 'Maytime', Longiflorum-Asiatic 'Pavia', and 'Fangio' lilies. The findings demonstrate significant reductions in leaf size and greenness, which are crucial for visual quality, largely due to a decline in chlorophyll content and decreased photosynthetic assimilation rates. These physiological disruptions were further linked to a marked reduction in stomatal density, with the abaxial stomatal index decreasing by 69% at 6.0 dS m^{-1} NaCl and a corresponding 75% decrease in stomatal conductance. These anatomical and physiological impairments were accompanied by reductions in gas exchange parameters, ultimately contributing to reduced growth and vigour.

This study also highlights the adverse impact of salt stress on key postharvest quality traits vital to the commercial value of lilies, such as flower diameter, number of flowers per stem, and vase life. These reductions pose significant challenges to maintaining market standards and customer satisfaction. However, an unexpected yet valuable finding was the enhancement of certain petal colour attributes under salt stress. For instance, the increased red coloration (a*) in 'Fangio' and heightened yellow tones (b*) in both 'Fangio' and 'Pavia', alongside increased colour saturation (C*), suggest that salt stress may influence pigment biosynthesis, resulting in desirable aesthetic attributes in some cultivars. This discovery offers potential avenues for breeders seeking to enhance ornamental traits in lilies exposed to saline conditions.

In addition to physiological and postharvest impacts, this study highlights anatomical changes as a potential adaptive response to salinity. The reductions in leaf thickness, stomatal density, and cell dimensions observed in salt-stressed lilies indicate that anatomical modifications are an integral part of the plant's strategy to mitigate the effects of salinity. These findings suggest that further research into the anatomical responses of lilies to salt stress could offer new insights into the mechanisms behind their adaptation to saline environments.

Exploring strategies such as optimized irrigation techniques, soil amendments, and nutrient management could be crucial in mitigating the negative effects of salt stress. Future research should focus on integrating these approaches aimed at enhancing lily tolerance to salinity, ultimately improving cultivation practices in saline environments. This study provides a foundation for continued investigation into how lilies and other ornamental crops can thrive under challenging conditions, thus ensuring their commercial viability and aesthetic appeal in regions affected by soil salinity.

Authors' Contributions

Conceptualization, Y.O. and J.A.; methodology, Y.O. and T.A.; software, M. A.; validation, M. A. and T. A.; formal analysis, Y.O.; investigation, Y.O. and T.A.; resources, M.A. and J.A.; data curation, T.A.; writing—original draft preparation, Y.O.; writing—review and editing, J.A.; visualization, Y.O.; supervision, Y.O.; project administration, Y.O.; funding acquisition, Y.O. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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