Growth and yield responses of sunflower to drainage in waterlogged saline soil are caused by changes in plant-water relations and ion concentrations in leaves

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Research Article

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Abstract

Purpose While proper drainage systems could improve crop growth and yield by mitigating waterlogging and salinity stresses, field evidence of the responses in plant-water relations and ion concentrations in leaves is scarce. We investigated the changes in solute potential in soil (Y_s), plant-water relations and ion concentrations in leaves of sunflower caused by drainage in waterlogged saline soil, and their impacts on growth and yield.

Methods Over two growing seasons, we tested four drainage treatments: undrained, surface drains (SD; 0.1 m deep, 1.8 m apart), subsoil drains (SSD; 0.5 m deep, 4.5 m apart) and SSD+SD. All plots were inundated (2–3 cm depth; EC_w 1.5–2.5 dS m^{-1}) for 24 h at vegetative emergence and at 8-leaf stage before opening drains.

Results Relative to the most drained treatment (SSD+SD), the undrained treatment caused higher waterlogging at 0–30 cm depth, and decreased Y_s of soil at 7.5 cm to 52–374 kPa, leaf K^+ by 5–20%, stomatal conductance by 5–37% and leaf greenness by 12–25%, but increased leaf Na^+ by 25–70%, Na^+/K^+ ratio by 38–100% and leaf water potential by 90–250 kPa throughout the cropping season; these changes were closely related with reduced growth and yield.

*Conclusion*s The improved yield from the combination of shallow surface and sub-surface drains was attributed to an alleviation of salinity-waterlogging stress early in the season and to increased soil water late in the season that increased Y_s and decreased Na^+/K^+ ratio in leaves.

Introduction

Waterlogged saline soils are a serious threat to agricultural productivity (Barrett-Lennard 2003; Falakboland et al. 2017). Globally, around 20% of irrigated areas are affected by secondary salinization, and one-third are facing waterlogging (Dagar and Minhas 2016). Coastal deltas, many of which are important food production regions, are at particular risk because their low elevation, flat terrain and shallow groundwater create both waterlogging and salinization of soils (van der Zee et al. 2017). Salinity and waterlogging affect morphological, physiological, and biochemical processes, seed germination, plant growth, and water and nutrient uptake (Falakboland et al. 2017; Paul et al. 2021c; Wu et al. 2015), resulting in low agricultural productivity, low-income returns and soil degradation (Hu and Schmidhalter 2004).

A major effect of salinity and/or waterlogging is the increased Na^+ concentration in shoots, with correspondingly lower K^+ and K^+/Na^+ ratio in the leaf, which are correlated with reduced photosynthetic rate, stomatal conductance (g_s) and shoot growth (Akram et al. 2008; Kirmizi and Bell 2012; Saqib et al. 2005). Several researchers have reported that waterlogging and/or salinity decrease leaf water potentials (Ψ_{leaf}), i.e., increased water stress (Akram et al. 2008; Katerji et al. 1996; Shaw 2015). By contrast, there is also evidence that Ψ_{leaf} in sunflower and tomato plants can be increased rather than decreased by waterlogging (Bradford and Hsiao 1982; Jackson et al. 1978), and in these cases was associated with decreased g_s (Jackson et al. 1978). Solute potential (Ψ_s) in the soil is also influenced by waterlogging and salinity, and the lower Ψ_s in the salt-affected soil adversely affected sunflower growth and yield (Paul et al. 2020). Part of the differences in responses among studies may be that for many crops, the combination of waterlogging and salinity stresses have more severe impacts on plant growth and yield than either salinity or waterlogging alone (Barrett-Lennard 2003; Barrett-Lennard and Shabala 2013; Falakboland et al. 2017).

The coastal zone of Bangladesh in the Ganges Delta covers more than 30% of the total cultivable lands of the country, and around 40% of this area is affected by various degrees of soil salinity (SRDI 2010). This zone is also subject to waterlogging during heavy monsoon (aman) season rainfall, river flooding and the shallow water-table (Mainuddin et al. 2021). The excess soil water after the aman rice harvest causes waterlogging, which delays the sowing of rabi (dry season) crops. However, later planted rabi crops may be exposed to drought, pre-monsoon rainfall and salt stresses at the end of rabi season, which increase the risk of crop failure (Paul et al. 2021a). Consequently, most smallholder farms leave the land fallow in this season. In addition, heavy dry season rainfall often occurs, particularly from December to February, and creates waterlogging, which is another barrier to the rabi crop cultivation in this region (Yu et al. 2019). Our study has focused on sunflower (Hysun-33) as a typical rabi crop in the study area because of its moderate salt-tolerant and drought-adapted features (Elsheikh et al. 2012). While sunflower is a high-value crop and is becoming a popular rabi crop in this region, it is sensitive to waterlogging like other rabi crops for this area (e.g., mung bean, lentil, sesame, maize, watermelon).

Generally, drainage is important for alleviating both waterlogging and salinity for optimal plant growth and yield. Either surface or subsurface drainage is practiced in many parts of the world to alleviate these constraints. Surface drains can be effective for improving aeration and reducing salinity in the upper root zone of the growing crop (Hou et al. 2016), while deep drains (> 1.75 m) are often recommended for mitigating salinity (Gupta 2002). Islam et al. (2021) found that the combination of shallow surface (10 cm depth) and subsurface drains (50 cm depth) alleviated waterlogging and salinity, and gave a 2-fold higher sunflower yield than the undrained treatment. While previous field-based studies have reported the effects of drains on waterlogging, salinity, plant morphology and yield, information has not been presented on impacts on plant water relations or ion concentrations in shoots (Ritzema et al. 2008; Sharma et al. 2000). Hence, while Islam et al. (2021) found that the combination of shallow surface and subsurface drains alleviated waterlogging and salinity and increased sunflower yield, the physiological mechanisms accounting for these responses were not determined. In contrast to previous studies under controlled (net house) conditions in coarse-textured soil, our studies were on the fine-textured soils typical of a large proportion of agricultural land in the Ganges delta.

In this study, therefore, we investigated the changes in Ψ_s in soil, plant-water relations and ion concentrations in leaves and their relation to sunflower growth and yield due to drainage in waterlogged saline soil. We examined two hypotheses to account for the range of drainage responses in sunflower.

Firstly, early in the season, waterlogging and salinity increase the salinity of soil solution (i.e., decreased Ψ_s of the soil), leading to increases in the Na^+/K^+ ratio in leaves and water deficits (i.e., decreased Ψ_{leaf}) and decrease g_s, all of which decrease growth and yield of sunflower. Secondly, in the 1st paper (Islam et al. 2021), we also hypothesized that yield damage would occur due to decreasing soil water content and increasing soil salinity late in the season. We found this not to be true, and in this present paper, we present further information to shed light on why this occurred. In addition, we also present the decrease in soil Ψ_s late in the season by the most drained treatment and its response to reduced plant growth and yield caused by physiological changes.

Materials And Methods

Experimental site and season

The field experiments were undertaken during two consecutive dry (rabi, November–May) seasons in 2018–19 and 2019–20 on a clay-textured soil under waterlogged saline conditions in a farmer's field at Dacope, Khulna, Bangladesh (22.6321° N and 89.5034° E). The experimental site is in the Ganges Tidal Floodplain (Islam et al. 2021), located in the south-western coastal region of Bangladesh. The climate is sub-tropical monsoonal with an average annual rainfall of 1,850 mm, a dry and cool winter (December–February) and a wet and hot summer (March–June) (Rahman et al. 2015). During the first cropping season in 2018–19, total rainfall, monthly average minimum and maximum temperature were 338 mm, 12.4–24.1°C and 26.9–34.6°C, respectively, while in 2019–20, total rainfall, monthly average minimum and maximum temperature were 54 mm, 13.9–20.6°C and 24.0–32.3°C, respectively Islam et al. (2021). The general characteristics of soil in the experimental field were described in Islam et al. (2021).

Experimental details and crop husbandry

Drain establishment procedure, field layout and crop husbandry have been described by Islam et al. (2021). Sunflower cv. Hysun-33 was used as a test crop as it is a promising high-value rabi crop (moderately salt-tolerant and drought-adapted) for the coastal zone. In the field experiment, undrained, open surface drains (SD; 0.1 m deep, 1.8 m apart), slotted-pipe subsoil drains (SSD; 0.5 m deep, 4.5 m apart) and SSD + SD treatments were present with three replicates. Replicates of the SSD and SSD + SD treatments were blocked together to avoid hydrological interference between treatments: the rationale for this has been discussed in Islam et al. (2021).

Each plot was 10 m × 6 m in size and polyethylene sheets were placed vertically around each plot to a depth of 0.6 m to prevent the lateral flow of water from one plot to another plot. A levee of 1 m wide was made between adjacent plots to minimize cross-flow of water. There were two waterlogging events in a season. The plots were inundated (2–3 cm above the soil surface) for 24 hours at both vegetative emergence (the VE stage of sunflower development, 14 days after sowing) and at the mid-vegetative stage when the crop had 8 leaves (V8 stage, Schneiter and Miller 1981). After 24 hours of inundation, drains were opened in the drainage treatments but not in the undrained treatment. The first inundation was supplied artificially using canal water (EC: 1.5–2.5 dS m^{-1}), while the second inundation occurred naturally because of heavy rainfall (151 mm on 27–28 February in the first season and 25 mm on 4 January in the second season, Islam et al. 2021) in both years.

Sunflower seeds were sown by dibbling on 18 January 2019 and 25 November 2019 with a row to row distance of 60 cm and a plant to plant distance of 30 cm. According to the recommendation of the Bangladesh Agricultural Research Institute (Islam et al. 2021), urea-triple super phosphate-muriate of potash-gypsum-zinc sulphate-boric acid were applied at 200-200-170-170-10-12 kg ha^{-1} in both seasons. Details of agronomic practices are given in Islam et al. (2021). The crops were harvested at physiological maturity on 29 April 2019 and 19 March 2020 in the first and second seasons, respectively.

Sampling and measurements techniques

Soil samples for EC, soil water content (SWC), waterlogging severity and soil solute potential (Ψ_s), together with stomatal conductance (g_s), leaf water potential (Ψ_{leaf}) and achene yield were collected from the edge and centre of each plot. In the subsoil drainage treatments (SSD and SSD + SD), the samples were collected from the edge of the drain pipe and midway between two pipes in the centre of the plot. In the SD and control treatments, soils were sampled near the edge and centre of the plot. In addition, three plants in each plot were randomly sampled and composited to one sample for measuring shoot dry weight (SDW) and leaf Na^+ and K^+ concentrations.

Solute potential

The three soil samples that were collected from each of the positions (centre and edge) at each depth (0–15, 15–30, 30–45, and 45–60 cm) were mixed thoroughly to make a composite sample for each depth. Soil samples were collected at 7 and 14 days after first inundation (DAFI), 10 and 17 days after second inundation (DASI), 30–50% flowering (FL) and harvest (HRV). The gravimetric method (oven-drying) was used for measuring soil water content (SWC). The $EC_{1:5}$ was measured by mixing 10 g of air-dried soil with 50 mL of distilled water. Solute potential (Ψ_s) of the soil solutions was calculated using the following equation (Paul et al. 2020).

$$\Psi_s = -22580 \times EC_{1:5}/W$$

Where Ψ_s is the solute potential (kPa), $EC_{1:5}$ is the electrical conductivity (dS/m) of an extract from soil to water ratio of 1:5, and W is the soil water content (%, w/w).

Waterlogging (SEW_{30})

The sum of excess water in the 0–30 cm layer (SEW_{30}), referred to as waterlogging, was measured daily throughout the season according to the method of Sieben (1964) and Cox (1988). Details of this have been presented in Islam et al. (2021).

Stomatal conductance and leaf water potential

Stomatal conductance (g_s) and leaf water potential (Ψ_{leaf}) were measured with a leaf porometer (SC-1 Leaf Porometer, Decagon Devices, USA) and a Pressure Chamber Instrument (Model-1000, PMS Instrument Company, USA), respectively. In the first season (2019), we measured g_s at 3 DASI, 10 DASI and 17 DASI, and Ψ_{leaf} at 3 DASI and FL. In the second season (2019–20), Ψ_{leaf} was measured at 3 DASI, 10 DASI, 17 DASI and FL. Three plants were selected randomly from each position (the edge and centre in a plot), and one fully expanded youngest leaf from each plant was measured for g_s and Ψ_{leaf}. Measurements were taken between noon and 2 pm.

Shoot dry weight and relative growth rate of shoot

Four shoots were collected randomly from each plot before first inundation, 7 DAFI, 14 DAFI, 10 DASI, 17 DASI and FL, and were dried in an oven at 70°C for 72 h and weighed. The relative growth rate (RGR) for the single shoot was calculated following Hunt (1982).

$$RGR = \frac{\ln\left(W_2\right) - \ln\left(W_1\right)}{t_2 - t_1}$$

where W_1 and W_2 are shoot dry weights at times t_1 and t_2.

Leaf Na^+ and K^+ concentrations and the Na^+/K^+ ratio

Three plants were randomly selected in each plot and all leaves at 7 DAFI, the 2–3 youngest fully expanded and the oldest live leaf blades at 10 DASI and flowering from each plant were detached from the petiole. Leaves were then rinsed in deionized water (EC ~ 0.0 µS cm^{-1}), blotted with tissue paper and dried in an oven at 70˚C for 72 h. About 0.2 g of ground leaves were digested by di-acid mixture (nitric and perchloric acid of 5:2 ratio), Na^+ and K^+ were measured with a flame photometer (Model: 410, Sherwood) (Yamakawa 1992). The concentration of ions was expressed in mmol kg^{-1} and the ratio of Na^+ and K^+ was calculated.

Statistical analysis

STAR software (version 2.0.1) was used to do the analysis of variance (ANOVA). The regression analyses for different factors were done using Jamovi software (version 1.1.9.0) and the graphs were prepared using Microsoft Office 365. One-way ANOVA was used to test the significance of the effects of the drains on SDW, RGR, Na^+ and K^+ concentration in leaf, ratio of Na^+ and K^+. The effects of drains and position within the plot on g_s, Ψ_{leaf} and leaf chlorophyll content (LCC) were measured using two-way ANOVA. The significance of the effects of the drain on Ψ_s of soil was determined using three-way (treatment, position and soil depth) factorial ANOVA models that also considered the effects of soil depth as a repeated measure. The comparison of means was made using the least significant difference (LSD) at $P = 0.05$. Single-factor regression analysis was done to investigate the relationship between achene yield or SDW and Ψ_s of soil or g_s or Ψ_{leaf} or LCC or Na^+ or K^+ or Na^+/K^+ in leaves at different times. The correlations of Na^+ or K^+ or Na^+/K^+ in leaves with Ψ_s or $EC_{1:5}$ or SEW_{30} at different times during the cropping season were also tested using single factor regression analysis. We also tested relationships among different factors (Ψ_s, $EC_{1:5}$, g_s, LCC, Ψ_{leaf} and SEW_{30}) during the crop growing season.

Results

In our previous study (Islam et al. 2021) drainage treatments showed up to 50% increase in achene yield in sunflower relative to the undrained treatment under waterlogged saline conditions in 2018–19 and 2019–20. In this paper, we were seeking physiological causes for these effects. Here, there was a consistency between years in response to drainage treatments in waterlogged saline soil for all parameters measured (ion concentrations in leaves, leaf water potential, shoot growth rate and soil solute potential), but values in the first (2018–19) and second year (2019–20) differed slightly due to variations in rainfall, temperature, soil salinity, and dates of planting, waterlogging and harvesting.

Concentrations of Na^+ and K^+ in leaves and their ratio (Na^+/K^+)

In both years, Na^+ concentration and Na^+/K^+ ratio in all leaves at 7 DAFI and in the older leaves at 10 DASI and FL were decreased by drainage treatments compared with the undrained treatment, while the K^+ concentration was increased (Fig. 1). At 7 DAFI, the lowest leaf Na^+ concentration was found in the most drained (SSD + SD) treatment (838 mmol kg^{-1} in 2018–19 and 485 mmol kg^{-1} in 2019–20), whereas the highest was with undrained treatment (1374 mmol kg^{-1} in 2018–19 and 825 mmol kg^{-1} in 2019–20). The SD and SSD treatments had Na^+ concentrations between the SSD + SD treatment and the undrained treatment. Similar trends were observed at 10 DASI and FL (Fig. 1). By contrast, leaf K^+ concentrations at 7 DAFI, 10 DASI and FL were 894–972 mmol kg^{-1} in 2018–19 and 980–1023 mmol kg^{-1} in 2019–20 with most drained treatment and 764–926 mmol kg^{-1} in 2018–19 and 788–938 mmol kg^{-1} in 2019–20 with the undrained treatment (Fig. 1). In both years, the most drained treatment had the lowest Na^+/K^+ ratio at 7 DAFI (all leaves), 10 DASI (older leaves) and FL (older leaves), which was 9–37, 19–32 and 32–52% lower than the SSD, SD and undrained treatments, respectively (Fig. 1). However, younger leaves did not show significant changes in leaf ion concentration or the Na^+/K^+ ratio (Supplementary Material, Fig. S1).

Leaf Na^+ concentration and Na^+/K^+ ratio during the season were significantly and negatively associated with achene yield, while leaf K^+ positively correlated with the achene yield (Figs. 2 and 3; yield data reported in Islam et al. 2021). Leaf Na^+ concentration at different times explained 46–81% and 40–81% of the yield variation in 2018–19 (Fig. 2) and 2019–20 (Fig. 3), respectively. The achene yield variation explained by K^+ concentration ranged from 53 to 70% in 2018–19 and 50 to 75% in 2019–20. The Na^+/K^+ ratio explained 50–79% of the yield variation in 2018–19 and 64–86% in 2019–20. The younger leaves showed weak relationships between the ion parameters and achene yield compared with older leaves.

In both years, increased SEW_{30} and soil $EC_{1:5}$ at 0–15 cm, and decreased Ψ_s at 0–15 cm were significantly correlated with increased Na^+, decreased K^+ and increased Na^+/K^+ in leaves at different times during the crop growing season (Table 1). However, younger leaves showed either no relationship or weak relationships, particularly at flowering. The SEW_{30} explained 60–76, 52–54 and 56–73% of the variation in 2018–19 and 47–84, 43–79 and 34–89% of the variation in 2019–20 in leaf Na^+, K^+ and Na^+/K^+ respectively. The strongest correlations with Na^+ (r^2 = 0.76), K^+ (r^2 = 0.63) and Na^+/K^+ (r^2 = 0.73) were observed in the older leaves at 10 DASI in 2018–19. In 2019–20, leaf Na^+ (r^2 = 0.84) and Na^+/K^+ (r^2 = 0.89) showed similar response but leaf K^+ (r^2 = 0.79) showed strongest correlation at 7 DAFI. In the case of soil $EC_{1:5}$, the r^2 values for Na^+, K^+ and Na^+/K^+ were 0.49–0.72, 0.39–0.84 and 0.54–0.74, respectively in 2018–19 and 0.46–0.86, 0.43–0.78 and 0.72–0.90 in 2019–20. The strongest correlations with Na^+ (r^2 = 0.72 in 2018–19 and 0.86 in 2019–20) and Na^+/K^+ (r^2 = 0.74 in 2018–19 and 0.90 in 2019–20) were observed in the older leaves at FL in both years. The strongest correlation with K^+ (r^2 = 0.84) were observed in the young leaves at 10 DASI in 2018–19, but in 2019–20 the correlation was strongest (r^2 = 0.78) in the older leaves at 10 DASI.

The soil Ψ_s also showed significant linear relationship with leaf Na^+ (r^2 values of 0.58–0.75 in 2018–19 and 0.44–0.85 in 2019–20), K^+ (r^2 values of 0.46–0.77 and 0.47–0.70 in 2018–19 and 2019–20, respectively) and Na^+/K^+ (r^2 values of 0.42–0.78 in 2018–19 and 0.37–0.92 in 2019–20) in both years although no correlation was found at 7 DAFI in 2018–19 (Table 1). The strongest correlation with leaf Na^+ and Na^+/K^+ occurred in the older leaves at FL in both years. However, the strongest correlation with leaf K^+ differed between years. In 2018–19, it was highest in the young leaves at 10 DASI, while in 2019–20, it was highest in the older leaves at 10 DASI.

Table 1. Significance of effects of SEW_{30}, soil $EC_{1:5}$ at 0–15 cm and Ψ_s at 0–15 cm on Na^+, K^+ and Na^+/K^+ in leaves at different times during the growing season in 2018–19 and 2019–20.

	Significance level with r^2 values and direction of the slope (in brackets)					
	2018–19			2019–20		
	SEW_{30} (cm days)	$EC_{1:5}$ ($dS\ m^{-1}$)	Y_s (kPa)	SEW_{30} (cm days)	$EC_{1:5}$ ($dS\ m^{-1}$)	Y_s (kPa)
At 7 DAFI						
Na^+ (AL)	(+) 0.74***	(+) 0.57**	NS	(+) 0.81***	(+) 0.72***	(-) 0.63**
K^+ (AL)	(-) 0.52**	(-) 0.41*	NS	(-) 0.79**	(-) 0.59**	(+) 0.47*
Na^+/K^+ (AL)	(+) 0.73***	(+) 0.60**	NS	(+) 0.88***	(+) 0.73***	(-) 0.61**
At 10 DASI						
Na^+ (YL)	NS	(+) 0.49*	(-) 0.58***	(+) 0.47*	(+) 0.46*	(-) 0.44*
K^+ (YL)	(-) 0.54**	(-) 0.84***	(+) 0.77***	(-) 0.43*	(-) 0.72***	(+) 0.57**
Na^+/K^+ (YL)	NS	(+) 0.54**	(-) 0.62**	(+) 0.61**	(+) 0.73***	(-) 0.65**
Na^+ (OL)	(+) 0.76***	(+) 0.62**	NS	(+) 0.84***	(+) 0.60**	(-) 0.48*
K^+ (OL)	(-) 0.63***	(-) 0.74***	(+) 0.53**	(-) 0.71***	(-) 0.78***	(+) 0.70***
Na^+/K^+ (OL)	(+) 0.73***	(+) 0.69***	(-) 0.42*	(+) 0.89***	(+) 0.72***	(-) 0.60**
At FL						
Na^+ (YL)	NS	NS	NS	NS	NS	NS
K^+ (YL)	NS	(-) 0.49*	(+) 0.46*	NS	(-) 0.43*	(+) 0.48*
Na^+/K^+ (YL)	NS	NS	NS	(+) 0.34*	NS	(-) 0.37*
Na^+ (OL)	(+) 0.60**	(+) 0.72***	(-) 0.75***	(+) 0.70***	(+) 0.86***	(-) 0.85***
K^+ (OL)	NS	(-) 0.39*	(+) 0.42*	NS	(-) 0.57**	(+) 0.60**
Na^+/K^+ (OL)	(+) 0.56**	(+) 0.74***	(-) 0.78***	(+) 0.68***	(+) 0.90***	(-) 0.92***

Abbreviations: DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, AL = all leaves, YL = younger leaves, OL = older leaves, Y_s = solute potential, * = P<0.05, ** = P<0.01, *** = P<0.001, NS = non-significant. For all relationships n = 12.

Stomatal conductance, leaf water potential and leaf chlorophyll content

There was a significant difference (P<0.001) in stomatal conductance (g_s) among the treatments at 3 DASI but no difference at 10 and 17 DASI (Table 2). The combined drain treatment (SSD+SD) showed the highest g_s (633 mmol m^{-2} s^{-1}), while the lowest g_s was with the undrained treatment (401 mmol m^{-2} s^{-1}) at 3 DASI, compared with the g_s of 552 mmol m^{-2} s^{-1} for SSD and 562 mmol m^{-2} s^{-1} for SD treatments. Drainage treatments also influenced the leaf water potential (Y_{leaf}) at different times in both years (Table 3). In 2018-19, the lowest Y_{leaf} was with the SSD+SD treatment (-1.29 to -1.40 MPa) during the season, while the highest Y_{leaf} was with the undrained treatment (-1.18 to -1.25 MPa). There was no difference between SD and SSD treatments. Similar trend was observed in 2019–20, showing the lowest Y_{leaf} of -1.27 to -1.58 MPa with the most drained treatment and the highest Y_{leaf} of -1.16 to -1.33 MPa with the undrained treatment) throughout the cropping season.

Measurements of leaf chlorophyll content (LCC) are reported in the Supplementary Materials (Table S1) with the units of chlorophyll content index (CCI). In 2018–19, the most drained treatment had the highest LCC (12.0–17.2 CCI) throughout the season, whereas the undrained treatment had the lowest LCC (9.0–14.8 CCI) (Supplementary Material, Table S1). The variation in LCC between SD and SSD was not significant, although the values were higher than the undrained treatment but lower than the SSD+SD treatment. In 2019–20, the response of LCC to drainage treatments was similar to the previous year. The ranges of LCC during the crop growing season in SSD+SD, SSD, SD and undrained treatments were 13.7–23.1, 12.1–21.0, 12.2–21.4 and 11.3–19.2 CCI, respectively.

The achene yield was significantly associated with g_s (positive correlation; one year of data only), Y_{leaf} (negative correlation) and LCC (positive correlation) in both years (Supplementary Material, Table S2). The g_s, Y_{leaf} and LCC accounted for 17–68, 45–67 and 47–69% of the variation in achene yield, respectively. In most cases, the greatest variation was observed at 3 DASI at P<0.001. In addition, soil Y_s, $EC_{1:5}$ at 0–15 cm soil depth and SEW_{30} all showed significant relationships with g_s, LCC and Y_{leaf} at different times during the cropping season (Supplementary Material, Table S3). The Y_s in soil was positively correlated with g_s (r^2 = 0.45 at 17 DASI) and LCC (r^2 values of 0.33–0.67), and negatively correlated with Y_{leaf} (r^2 values of 0.44–0.63). The strongest correlations with g_s, LCC and Y_{leaf} were at 17 DASI, FL and FL, respectively. In contrast, the soil $EC_{1:5}$ gave a negative correlation with g_s (r^2 = 0.34 at 17 DASI) and LCC (r^2 values of 0.59– 0.74), and a positive correlation with Y_{leaf} (r^2 values of 0.42–0.63). The strongest relationships with g_s, LCC and Y_{leaf} were at 17 DASI, FL and FL, respectively. The SEW_{30} also showed negative correlation with g_s (r^2 values of 0.19–0.80) and LCC (r^2 values of 0.57–0.90), and a positive correlation with Y_{leaf} (r^2 values of 0.25–0.68). The highest r^2 values were observed at 3 DASI. The results also showed that plant height (Supplementary Material, Fig. S2) and leaf area (Supplementary Material, Fig. S3) were negatively correlated with Y_{leaf} at 3 DASI and at FL in both years. Plant height and leaf area explained 58–64% and 56–72% of the variation in Y_{leaf}, respectively.

Table 2. Effects of drains on stomatal conductance at different times in 2018–19.

Treatment	Stomatal conductance (mmol m^{-2} s^{-1})		
	3 DASI	10 DASI	17 DASI
SSD+SD	633 a	944	955
SSD	552 b	946	952
SD	562 b	937	947
Undrained	401 c	900	898
P-value	<0.001	NS	NS

Means with the same letter are not significantly different at 5% level of significance. Abbreviations: SSD = subsoil drain, SD = surface drain, DASI = days after second inundation.

Table 3. Effects of drains on leaf water potential at different times in 2018–19 and 2019–20.

Treatment	Leaf water potential (MPa)							
	2018–19				2019–20			
	3 DASI	10 DASI	17 DASI	FL	3 DASI	10 DASI	17 DASI	FL
SSD+SD	-1.29 c	-	-	-1.27 b	-1.29 b	-1.35 b	-1.58 c	-1.27 b
SSD	-1.22 ab	-	-	-1.19 ab	-1.22 a	-1.27 a	-1.44 b	-1.19 ab
SD	-1.24 b	-	-	-1.22 b	-1.25 ab	-1.29 ab	-1.47 b	-1.22 b
Undrained	-1.18 a	-	-	-1.16 a	-1.20 a	-1.25 a	-1.33 a	-1.16 a
P-value	<0.01	-	-	<0.001	<0.01	<0.05	<0.001	<0.001

Means with the same letter are not significantly different at 5% level of significance. Abbreviations: SSD = subsoil drain, SD = surface drain, DASI = days after second inundation, FL = flowering.

Solute potential

The drainage treatments and soil depths significantly influenced solute potential (Y_s) in the soil at different times during the crop growing season in 2018–19 (Fig. 4) and 2019–20 (Fig. 5). In both years, the treatments and soil depths showed interaction effects throughout the sunflower growing period, but no interaction was found between treatments and position in the plot, or between depth and position. In general, the lowest Y_s was measured in the undrained treatment (-148 to -614 kPa in 2018–19 and -75 to -555 kPa in 2019–20), while in most cases, the highest Y_s was with the SSD+SD treatment (-79 to -482 kPa in 2018–19 and -51 to -300 kPa in 2019–20) throughout the cropping season. Late in the sunflower growing season (FL–HRV), the Y_s in the undrained treatment was either lower or similar to the most draining treatment (SSD+SD). The Y_s was lowest at the upper soil (average depth 7.5 cm) and increased sharply at average depth 22.5 cm. The values from average depths of 22.5 to 52.5 cm remained almost stable or slightly increased in SD and undrained treatments, while the SSD and SSD+SD treatments showed decreasing trends. Finally, at the deeper soil (average depth 52.5 cm), there was a little variation of Y_s among the treatments.

At average depth 7.5 cm, the higher Y_s was with SSD+SD treatment (-87 to -482 kPa) and the lower values with the undrained treatment (-177 to -614 kPa) throughout the season in both years. The SSD and SD treatments had a similar Y_s in the topsoil (average depth 7.5 cm), but at average depth 22.5 cm, the SSD treatment had higher Y_s than the SD treatment. Increasing Y_s at average depth 7.5 cm during the cropping season was significantly correlated with increasing sunflower yield with r^2 values of 0.29–0.92 in 2018–19 and 0.51–0.77 in 2019–20 (Fig. 6). In both years, the strongest relationship was observed at FL.

Relative growth rate and dry weight of shoot

The dry weight data used to calculate the relative growth rate (RGR) of the shoots are reported in Supplementary Materials (Table S4). In 2018–19, the RGR of the shoot during the period of T1 (before inundation, BI, to 7 DAFI), T2 (7 DAFI to 14 DAFI) and T3 (10 DASI to 17 DASI) were highest in the most drained treatment (0.07–0.17 g g^{-1} d^{-1}) (Fig. 7). In contrast, the lowest RGR occurred in the undrained treatment (0.03–0.11 g g^{-1} d^{-1}) during T1 and T2, but the values were higher than both SD and SSD treatments at T3. There was no variation among the treatments at T4. Similarly, in 2019–20, the undrained treatment had the lowest RGR during T1–T3 (0.06–0.11 g g^{-1} d^{-1}), and at T4, the values were similar to other treatments (Fig. 7). In contrast, the highest RGR was in the SSD+SD treatments, although the values were not different from SD and SSD treatments at T1, T3 and T4.

In both years, the shoot dry weight at different times during the study period showed strong negative correlations with SEW_{30} (r^2 values of 0.85–0.95 in 2018–19, and 0.82–0.94 in 2019–20) and soil $EC_{1:5}$ (r^2 values of 0.66–0.93 in 2018–19, and 0.69–0.84 in 2019–20) (Supplementary Material, Figs. S4 and S5). In contrast, there were positive linear relationships with Y_s in soil, which explained 41–90 and 52–86% of the variation in shoot dry weight in 2018–19 and 2019–20, respectively (Supplementary Material, Fig. S6). In addition, the higher shoot dry weights at different times throughout the season were significantly correlated with higher leaf K^+ (r^2 values between 0.46 and 0.73 in 2018–19, and 0.47 and 0.80 in 2019–20) and lower leaf Na^+ (r^2 values between 0.78 and 0.80 in 2018–19, and 0.47 and 0.82 in 2019–20) and Na^+/K^+ ratio (r^2 values ranged 0.34–0.78 in 2018–19, and 0.65–0.90 in 2019–20) (Supplementary Material, Figs. S7 and S8). The LCC also showed positive and linear relationships with shoot dry weight, which accounted for 75–89 and 62–80% of the variation in 2018–19 and 2019–20, respectively (Supplementary Material, Fig. S9).

Discussion

Although sunflower is a moderately salt-tolerant crop, this study shows that the plant is adversely affected by elevated concentrations of Na^+ in leaves. Previous studies have focused on the interaction between waterlogging and salinity and focusing the fact that waterlogging increases the concentration of Na^+ in leaves (Barrett-Lennard 2003; Barrett-Lennard and Shabala 2013). In our previous paper (Islam et al. 2021), we reported that a combination of shallow drains (SSD with 0.5 m depth and SD with 0.1 m depth) yielded 20–37, 16–45 and 92–95% higher achene weight than SSD, SD and undrained treatments, respectively. Here we investigated the possible mechanisms behind these growth and yield responses in sunflower to drainage treatments under waterlogged saline conditions. We found that the yield responses were correlated with higher Y_s, leaf K^+ and g_s, and lower leaf Na^+, leaf Na^+/K^+ ratio and Y_{leaf}. This discussion focuses on two hypotheses. In accord with our first hypothesis, we found that the undrained treatment decreased the Y_s of the soil relative to the drained treatments, and this decreased Y_s was correlated with an increased Na^+/K^+ ratio in leaves and Y_{leaf}, decreased g_s and achene yield. Contrary to the second hypothesis, we found that SSD+SD treatments actually increased SWC and reduced soil $EC_{1:5}$ late in the season, resulting in increased Y_s and reduced Y_{leaf} and Na^+ concentration in leaves. The discussion below focuses further on these two families of effects.

Waterlogging and salinity early in the growing season reduce soil solute potential, leading to decreases in plant growth and yield

This section of the discussion focuses on two possible sequences of physiological changes (causes and effects) that could have occurred early in the growing season. We have termed these the ‘adverse ion relations’ and ‘stomatal closure’ sequences (Fig. 8).

Adverse ion relations

In saline soils that waterlog, drainage has the potential to overcome adverse ion relations in plants (i.e., increased Na^+, decreased K^+, increased Na^+/K^+) in two ways: by decreasing soil salinity (i.e., increasing Y_s) (c.f. Munns 2002) and by improving soil aeration thereby overcoming adverse waterlogging-salinity interactions (c.f. Barrett-Lennard 2003; Barrett-Lennard and Shabala 2013). In overview, our data suggest that there are beneficial effects of drainage on ion relations which may occur through both mechanisms.

The Y_s of the soil is proportional to the salt concentration in the soil and is inversely related to the soil water content of the soil (Rengasamy 2006). Since Y_s incorporates both soil salt and water content, it has the potential to explain better salt effects on plant growth and yield than either SWC or soil EC alone (Ben-Gal et al. 2009; Paul et al. 2020). In our previous paper (Islam et al. 2021), the shallow combined drain treatment decreased SEW_{30} and soil $EC_{1:5}$ at 0–60 cm depth by 60–63 and 35–52%, respectively, early in the season (7 DAFI to 17 DASI) relative to the undrained treatment. This study showed that during the period of 7 DAFI to 17 DASI, the Y_s was decreased more in the undrained treatment by (about 40–90 kPa) relative to the most drained treatment throughout the season, which coincided with increased Na^+ concentrations (25–70%) and decreased K^+ concentrations (9–20%) in leaves, resulting in a higher Na^+/K^+ ratio. These changes were all strongly correlated with the reduced growth and yield of sunflower (Fig. 8). The second possible cause of the beneficial effect of drainage derives from the analysis of Barrett-Lennard and Shabala (2013). There is now a substantial body of published evidence that suggests that when root-zones become waterlogged (i.e., hypoxic), plants lose their ability to maintain their regulation of Na^+ exclusion and K^+ uptake, which can also increase the concentrations of Na^+ and decrease K^+ in the leaf tissues, leading to reduced plant growth and yield (Barrett-Lennard and Shabala 2013).

For both of these scenarios, Na^+ is taken up from the soil by roots and transported to the leaf through the xylem in response to transpiration (Yu and Assmann 2016). Excessive Na^+ accumulation in the cytosol due to hypoxia and salinity, enhances leakage of K^+ from root cells, Na^+ blocking of the K^+-specific transporters in the root cells and the increased Na^+/K^+ ratio in leaves (Zhu 2003) can result in osmotic damage and disorder enzyme activation and protein synthesis (Tester and Davenport 2003), which might be plausible reasons for reduced crop growth and yield.

In our study, Na^+ and Na^+/K^+ ratios in sunflower leaves in the undrained treatment (soil $EC_{1:5}$ at 0–15 cm depth: 0.25–0.58 dS m^{-1}; SEW_{30}: 235–240 cm days) early in the season (7 DAFI–10 DASI) were 25–70 and 47–108% higher, respectively, relative to the most drained treatment (soil $EC_{1:5}$ at 0–15 cm: 0.11–0.38 dS m^{-1}; SEW_{30}: 89–95 cm days). We are aware of one other study which has reported the effects of hypoxia and salinity on the concentration of Na^+ in 50-day old sunflower (cv. Grey stripe) grown in nutrient solution (Kriedemann and Sands 1984). In this work, the combination of salinity (50 mM NaCl) and hypoxia (bubbling with N_2 gas) from days 24 to 50 increased Na^+ concentration in leaves 35-fold relative to aerated non-saline conditions; by contrast, salinity alone increased Na^+ concentration by 4.5-fold. In addition, hypoxia from the plant age of 20 days to 30 days along with 4 days (21–24 days of the plant) salinization (150 mM NaCl) increased the Na^+/K^+ ratio in leaves 6.8-fold relative to aerated non-saline conditions.

In our study, we also found that Na^+ and Na^+/K^+ ratios in older leaves at 10 DASI under waterlogged saline conditions were around 350–400 and 450–500% higher than in younger leaves, respectively. This is supported by an earlier study (de Azevedo Neto et al. 2020) which reported that Na^+ and Na^+/K^+ ratios were about 70 and 585% higher, respectively, in older leaves of sunflower (cv. AG967) relative to younger leaves during the vegetative stage (at 35 days after germination) under saline conditions (100 mM NaCl for 20 days). Salts are continuously deposited in leaves through the transpiration stream, and salt accumulation in leaves therefore gradually increases with time. Relative to the import in the transpiration stream, there is little re-translocation of salt from older leaves. The presence of salt in leaves, already absorbed, therefore continues despite the salt around the root being removed (Munns 2002), so salt concentrations remain higher in older than in younger leaves. As Na^+ may block the K^+-specific transporters, the leaf Na^+ and Na^+/K^+ ratios increase and K^+ concentration decreases under saline conditions. Overall, all the studies reported significant differences in Na^+ and K^+ in sunflower leaves between waterlogged and/or saline treatment and drained and/or least-saline treatment. The results are consistent with the view that the implementation of drainage systems can mitigate soil salinity and waterlogging, decreasing the leaf Na^+ and Na^+/K^+ ratio and improving plant growth and yield (Hou et al. 2016; Islam et al. 2021; Ritzema et al. 2008).

Stomatal closure

The g_s of leaves control CO_2 uptake and transpiration, which affect photosynthesis, and water and nutrient uptake (Farooq et al. 2009). Increased salt concentration (i.e., decreased Y_s of the soil) and waterlogging stresses enhance the efflux of K^+ from stomatal guard cells, leading to the loss of cell turgor, which induces stomatal closure that reduces CO_2 assimilation and photosynthetic rate, resulting in reduced carbohydrate production and less water and nutrient uptake (Lambers and Bassham 2021). These conditions can also lead to the accumulation of toxic metabolites, combined with an increase in free radicles/reactive oxygen species (ROS), decreased evaporative cooling, a decrease in LCC, leading to cell death (Zhang et al. 2017; Zheng et al. 2009), all of which might be causes of reduced plant growth and yield.

In the present study, we found decreases in g_s associated with the undrained treatment early in the season. These lower g_s linked to increased SEW_{30} and soil $EC_{1:5}$, and decreased Y_s (Supplementary Material, Table S3) were correlated with reduced achene yield. In our work, the undrained treatment had a decreased g_s (37%) at 3 DASI, although there was no difference in g_s between drained and undrained treatments at the later times of measurement (Table 2), suggesting that the plants recovered after waterlogging. The Y_{leaf} of sunflower was 0.11–0.25 MPa higher (less negative) in the undrained treatment relative to the most drained treatment (Table 3). Waterlogging is known to decrease the stomatal conductance in a range of dicots including: sunflower (Kriedemann and Sands 1984), tomato (Jackson et al. 1978; Bradford and Hsiao 1982) and a range of tree species (Pereira and Kozlowski 1977; Sena Gomes and Kozlowski 1980). Evidence from some of these studies (Jackson et al. 1978; Bradford and Hsiao 1982; Pereira and Kozlowski 1977) shows that these decreases in conductance were not associated with decreases in Y_{leaf}, suggesting that the plants communicate the presence of waterlogging to the leaves by means of a chemical/hormonal signal, believed to be abscisic acid (Pan et al. 2020). Our observation of a recovery in g_s by 10 days after waterlogging in sunflower in the field, is consistent with the results from a previous study with *Fraxinus pennsylvanica* that stomata closed due to waterlogging began to reopen after 15 days; in this study, the recovery in g_s was associated with the formation of new adventitious roots (Sena Gomes and Kozlowski 1980).

The most drained treatment reduces soil solute potential late in the season, leading to decreases in plant growth and yield

Generally, at the end (March–April) of the dry rabi season, soil salinity increases and SWC decreases in the study area (Rahman et al. 2015; Salehin et al. 2018). Based on previous studies, we hypothesized (incorrectly) that the presence of deep drains (i.e., excess drainage) might dry the soil early in the growing season, decreasing the availability of water late in the growing season and having an adverse effect on crop growth. The hypothesis may have been wrong because of light rainfall late in the growing season (flowering to harvest) and the presence of deep soil cracks in contact with the slotted pipe drains that actually delivered water to the subsoil. Another possibility is that the most drained plots had greater leaf area index (LAI), which could have protected the soil surface from direct sunlight and decreased soil evaporation, which could have maintained better crop growth and yield.

At the end of the season, the drained treatments had increased growth and yield, and yet the Y_{leaf} were more negative with drainage, suggesting that the adverse effect on growth were not caused by adverse water relations. However, late in the season (flowering), we also found that the most drained treatment had lower leaf Na^+ and Na^+/K^+ ratios than the undrained treatment. This indicates that shallow combined drains decreased leaf Na^+ and Na^+/K^+ ratios late in the dry season. This was due to higher soil water content and lower $EC_{1:5}$ (i.e., higher Y_s) in the combined drain treatment relative to the undrained treatment (Islam et al. 2021). It was also observed that in the younger leaves, Na^+ concentration and Na^+/K^+ ratios decreased at the flowering stage relative to the earlier (10 DASI) stage (vegetative) of the sunflower. Measurements of SEW_{30} showed that there was no waterlogging at the end of the growing season (Islam et al. 2021). The increase in Na^+ concentration and Na^+/K^+ ratios in leaves of undrained sunflower late in the season could not, therefore, have been caused by the waterlogging-salinity interactions discussed in the previous section.

How could the drains actually increase SWC? Our observations suggest that the drains appear to be ‘watering’ the plants. The soils of the Ganges Delta are generally ‘shrink-swell’ clays (Moslehuddin et al. 1999) that form deep cracks as the soil dries out (c.f. Paul et al. 2021b). It is likely that when rain falls on the soil surface late in the growing season, a large proportion of this water rapidly runs down these cracks. Interception of the cracks by the slotted pipe drains provides a route for this water to then be rapidly redistributed laterally through a whole plot, where it can then recharge the soil profile to depths greater than 50 cm. At these depths in the bulk of the soil, there is less evaporation, so the water is conserved for later crop growth. By contrast, in undrained soils, there may still be some movement of rainwater to the bottom of cracks, but the water remains in the immediate locality of that crack where it is susceptible to more rapid evaporation, which is exacerbated by the lower soil shading due to lower LAI (Islam et al. 2021; Villalobos and Fereres 1990). We conclude that drained soils experience better rather than worse water relations at the end of the growing season.

It should be noted that our explanation for these effects requires the combination of cracks plus drains to harvest late season rainfall. In situations where there was no late season rainfall, the combination of cracks plus drains may be even worse for crop yields than in the undrained soils. The key question is whether plants late in the season used predominantly rainwater associated with subsurface drains or groundwater or both. The sources of water being used by plants could be investigated by measuring the stable isotope composition of water (δD and $\delta^{18}O$) if the isotopic signatures vary between the groundwater and rainwater. For example, based on different isotopic signatures in groundwater and rainwater, Mensforth et al. (1994) and Thorburn and Walker (1993) concluded that groundwater was the dominant source of water for trees, despite its salinity, but the proportion of groundwater used by trees declined after rainfall.

Conclusion

In a salt-affected, waterlogged coastal zone clay soil in the Ganges Delta, shallow drains improved sunflower growth and yield by increasing the Y_s of soil, leaf K^+ and g_s, and decreasing leaf Na^+ and Na^+/K^+ ratio. However, the Y_{leaf} increased in the undrained treatment. Indeed, decreased Y_{leaf} was significantly correlated with increased LA and plant height. Early in the season, the most drained treatment (SSD+SD) reduced the waterlogging and soil salinity impacts on the plant-water relations and ion concentrations in leaves of sunflower more efficiently than other treatments. In the late-season, shallow combined drains increased Y_s of soil by increasing water availability and reducing soil salinity, resulting in better plant-water and ion relations.

Declarations

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Figures

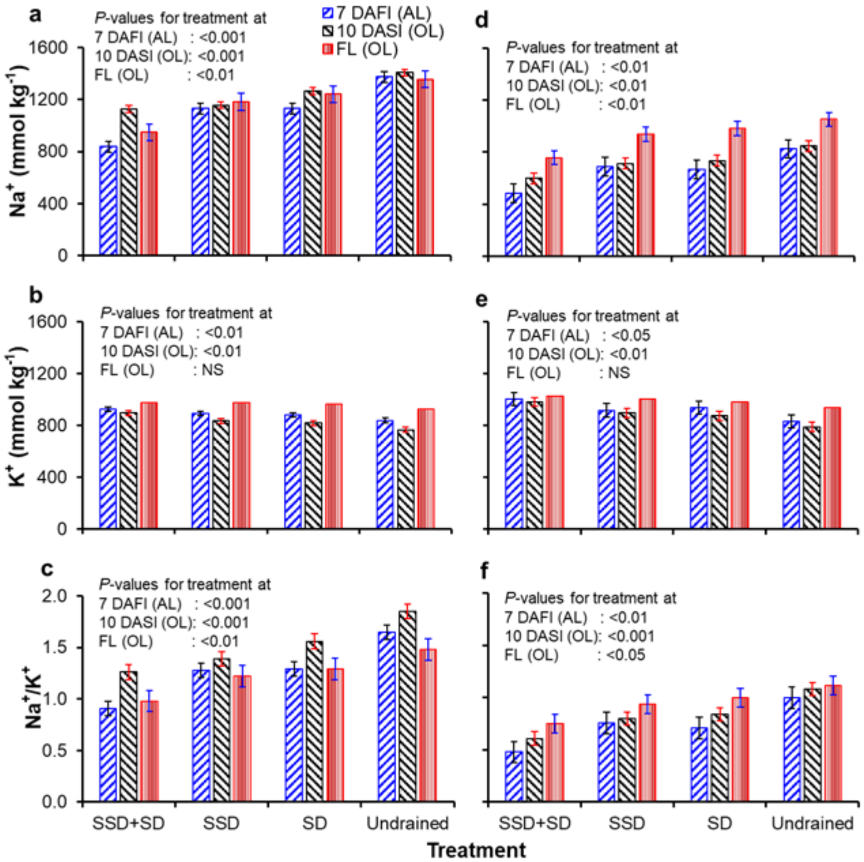

Figure 1

Effect of drains on the concentration of Na and K ions in leaves and its ratio (Na^+/K^+) in 2018–19 (a–c) and 2019–20 (d–f). Abbreviations: SSD = subsoil drain, SD = surface drain, DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, AL = all leaves, OL = older leaves. Vertical bars at the top of columns indicate the LSD at 5% level of significance.

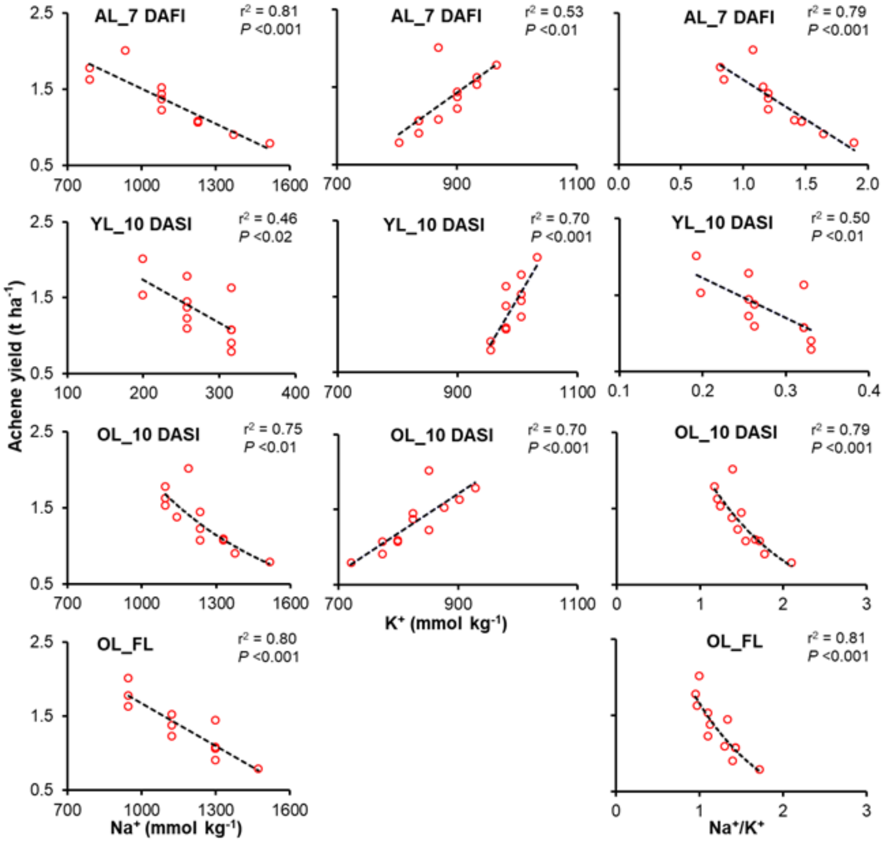

Figure 2

Correlation between achene yield and Na^+ or K^+ or Na^+/K^+ in leaves at different times in 2018–19. Abbreviations: DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, AL = all leaves, YL = younger leaves, OL = older leaves.

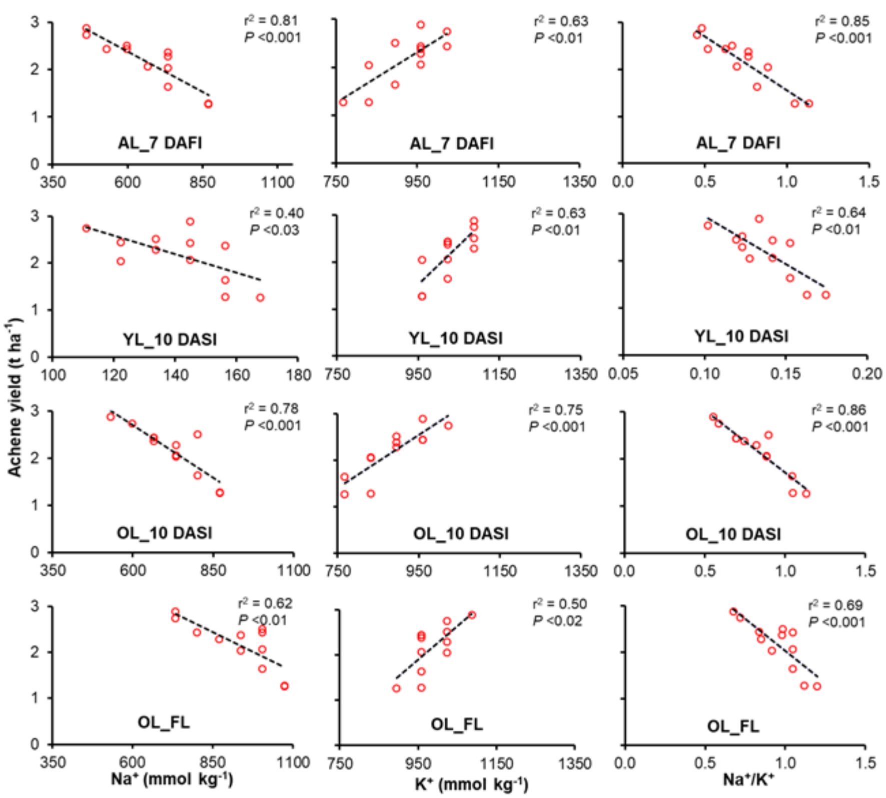

Figure 3

Correlation between achene yield and Na^+ or K^+ or Na^+/K^+ in leaves at different times in 2019–20. Abbreviations: DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, AL = all leaves, YL = younger leaves, OL = older leaves.

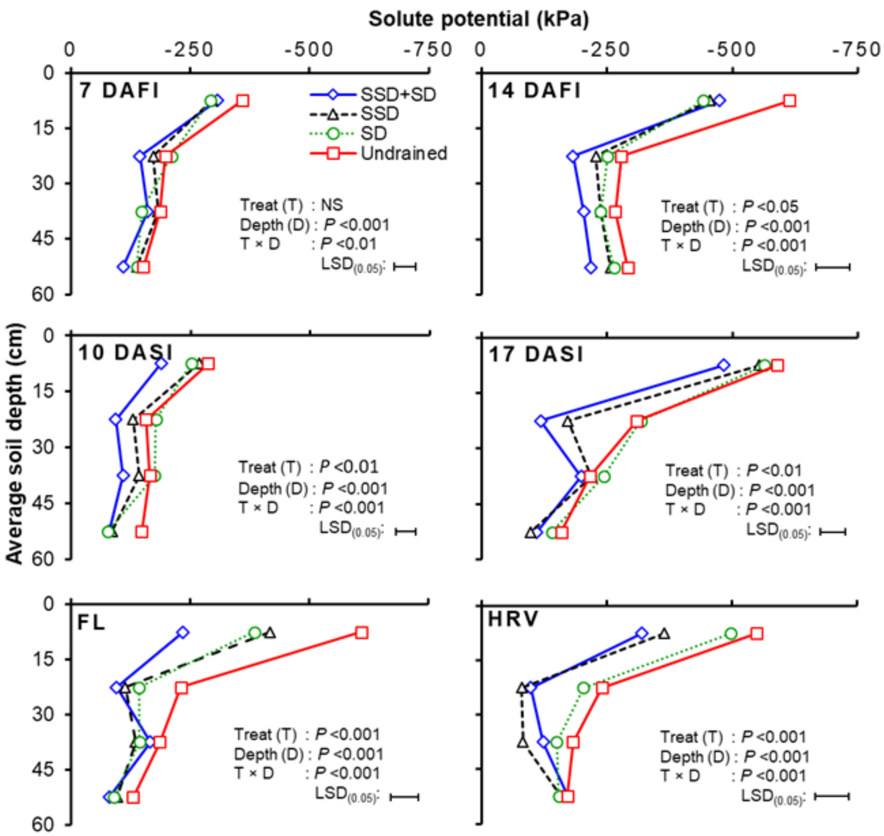

Figure 4

Effect of different drains on solute potential at different soil depths at different times during the crop growing season in Dacope, Bangladesh, in 2018–19. Abbreviations: SSD = subsoil drain, SD = surface drain, DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, HRV = harvest.

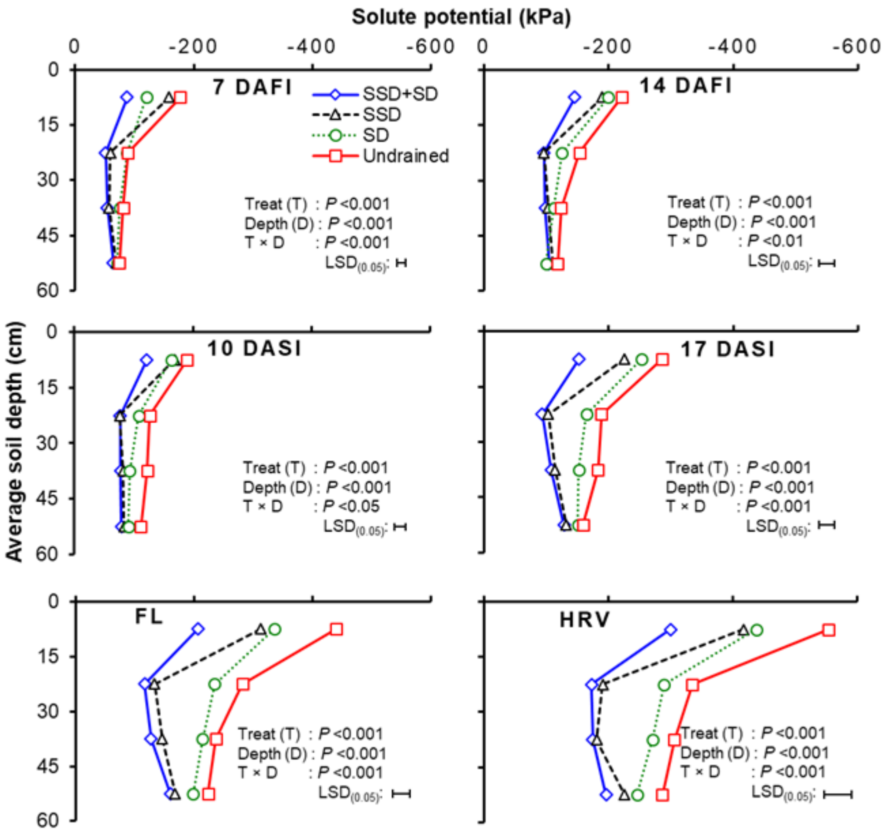

Figure 5

Effect of different drains on solute potential at different soil depths at different times during the crop growing season in Dacope, Bangladesh, in 2019–20. Abbreviations: SSD = subsoil drain, SD = surface drain, DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, HRV = harvest.

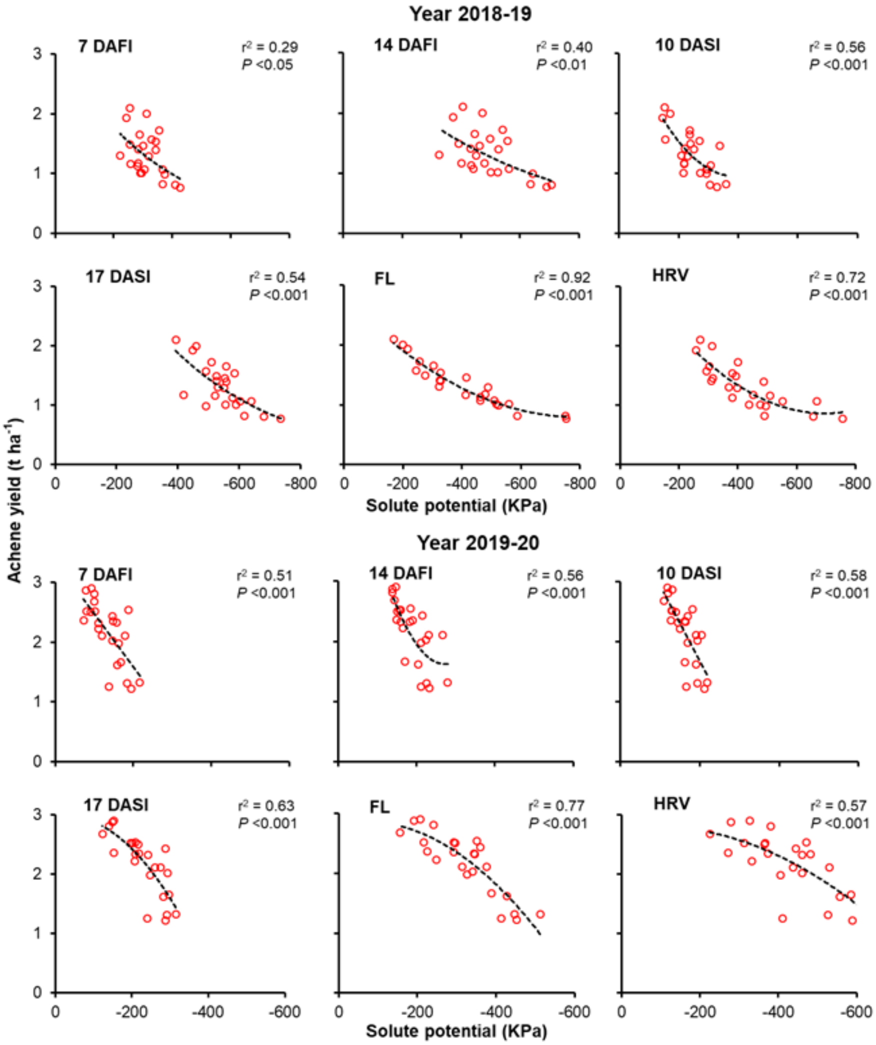

Figure 6

Relationship between sunflower yield and solute potential at 0–15 cm soil depth at different times during the crop growing period in Dacope, Bangladesh, in 2018–19 and 2019–20. Abbreviations: DAFI = days after first inundation, DASI = days after second inundation, FL = flowering, HRV = harvest.

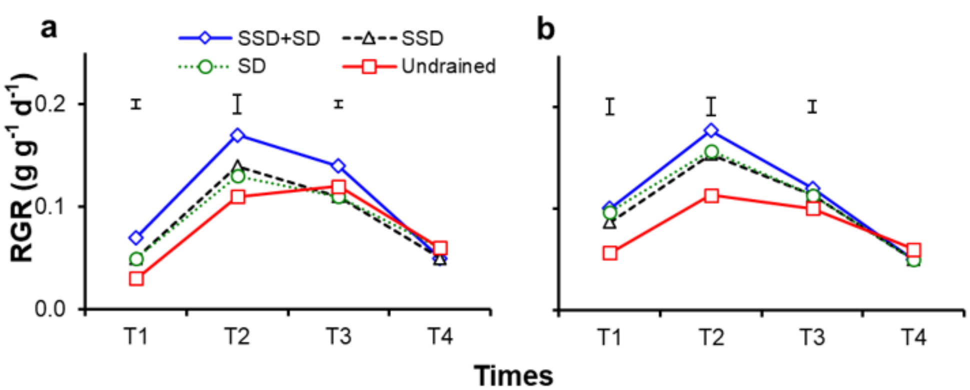

Figure 7

Effect of drains on the RGR of the shoot during the cropping season in 2018–19 (a) and 2019–20 (b). Abbreviations: RGR = relative growth rate, T1 = before inundation to 7 days after first inundation (DAFI), T2 = 7 DAFI to 14 DAFI, T3 = 10 days after second inundation (DASI) to 17 DASI and T4 = 17 DASI to flowering.

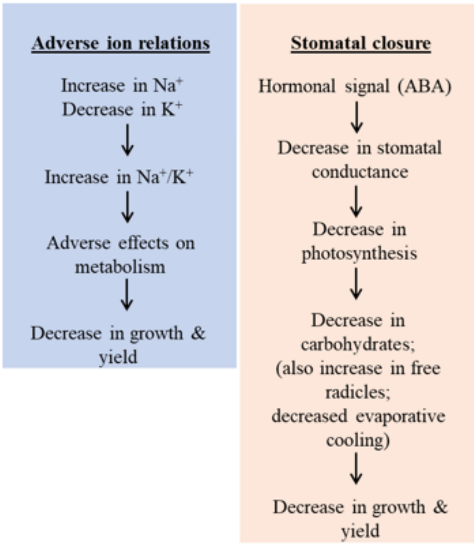

Figure 8

Schema of possible mechanisms of growth and yield reduction under waterlogged saline conditions early in the season. Abbreviations: ABA = abscisic acid

Supplementary Files

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