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Research Article

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Maternal drip irrigation legacy programmes transgenerational saline–alkali tolerance in maize F_1 seed: yield advantage, rapid-initiation germination, and balanced root–shoot architecture under equal water quota

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Abstract: Soil salinization threatens global maize production, yet whether maternal irrigation during hybrid seed production transgenerationally programs saline–alkali tolerance in F_1 progeny remains unexplored. This study compared maternal drip irrigation (DI) and furrow irrigation (FI), both applied at an identical seasonal quota of 4800 m^3 hm^{-2}, during the production of two F_1 hybrids. Despite equal water supply, maternal DI significantly increased seed yield per unit area, with a 37.1 % advantage in cultivar A (14,073.50 versus 10,264.72 kg hm^{-2}) and an 11.0 % advantage in cultivar B (11,207.69 versus 10,095.36 kg hm^{-2}). DI also elevated thousand-seed weight (two-way ANOVA, $P = 0.011$) and seed pH in cultivar B ($P < 0.01$). Under saline–alkali stress, DI progeny exhibited superior germination speed—reaching 50 % cumulative germination approximately one day earlier and recording an approximately 8 % advantage in germination potential by day 4 in cultivar B under 180 mmol L^{-1} alkaline stress—while simultaneously maintaining markedly stronger root elongation that intensified with stress severity, expanding from approximately 26 % under control to approximately 73 % under severe alkalinity in cultivar A. Biomass allocation further favored DI: FI progeny displayed a compensatory root-foraging surge with root-to-shoot ratio (R/S) peaking at 4.0–4.5 under 60–120 mmol L^{-1} stress, indicating stress-induced carbon reallocation away from shoot development, whereas DI progeny maintained a balanced architecture (R/S approximately 0.5–1.5) that preserved shoot vigour while exploring deeper soil profiles. Pearson correlation matrices confirmed that DI sustained coordinated positive associations among seed size, baseline germination, and root length, whereas FI induced a zero-sum network state in which elevated R/S was strongly negatively correlated with shoot vigour (r = -0.78 in cultivar A). Notably, although FI progeny occasionally achieved marginally higher final germination percentages under specific severe stress conditions, this came at the cost of delayed emergence and substantially suppressed shoot growth, resulting in lower integrated seedling vigour. These findings establish maternal drip irrigation, under an equal water quota, as a

management-level lever that enhances both seed yield and transgenerational saline–alkali tolerance in maize F_1 seed, delivering a rapid-initiation, root-robust, and growth-balanced stress-coping phenotype that outperforms furrow irrigation.

Keywords： Transgenerational plasticity; Irrigation strategy; Maize seed production; Root elongation; Saline–alkali tolerance; Maternal effect

1.Introduction

Irrigation method represents a foundational management decision in agricultural production, profoundly influencing soil water distribution, salt–alkali dynamics, and ultimately maize productivity. Among the various irrigation techniques, drip irrigation and flood (furrow) irrigation constitute two widely adopted yet fundamentally contrasting strategies in arid and semi-arid regions. Drip irrigation delivers water precisely to the root zone through emitters, significantly enhancing water use efficiency; however, its localized wetting pattern often leads to salt and alkali accumulation at the periphery of the wetted bulb due to insufficient leaching, progressively elevating soil salinity and alkalinity in the root zone over time (Shokri et al. 2024). Conversely, flood irrigation applies water across the entire soil surface, generating greater leaching and displacement of soluble salts and alkaline ions to deeper soil profiles, yet its high water consumption and potential to raise groundwater tables can induce secondary salinization and alkalization through capillary rise (Shokri et al. 2024). These divergent hydrological consequences create distinct soil environments—differing not only in ionic composition but also in pH regimes—that differentially affect the physiological status of the maternal plant during reproductive development, thereby influencing seed formation and maturation.

Soil salinization and alkalinization, whether inherent or irrigation-induced, pose a severe and escalating threat to global agriculture. According to the latest Global Map of Salt-Affected Soils released by the Food and Agriculture Organization (FAO) in 2024, over 1 381 million hectares of land—approximately 10.7 % of the global land surface—are currently affected by excess salts, with roughly 10 % of irrigated croplands already impacted; projections indicate that by 2050, nearly 50 % of all arable land could be at risk (FAO 2024). In arid regions such as Xinjiang, China, saline–alkali soils are typically characterized by the coexistence of neutral salts (NaCl, Na_2SO_4) and alkaline salts (Na_2CO_3, $NaHCO_3$), resulting in complex stress scenarios where high pH exacerbates ion toxicity and nutrient precipitation (Kumar et al. 2024). Among staple maizes, maize (Zea mays L.) is particularly vulnerable to saline–alkali conditions, especially during seed germination and early seedling establishment—the most sensitive phases in the plant life cycle when physiological systems are not yet fully developed to counteract osmotic, ionic, and high-pH challenges (Wang et al. 2025; Ren et al. 2025). Salt stress primarily disrupts cellular osmotic potential and induces Na^+ toxicity, whereas alkaline stress imposes additional constraints: elevated pH damages root cell membrane integrity, precipitates essential mineral ions (Fe^{2+}, Ca^{2+}, Mg^{2+}, and phosphates) in the rhizosphere, and exacerbates K^+ efflux, leading to severe nutrient deficiencies and ionic imbalance that often exceed the damage caused by neutral salts alone. Consequently, parameters including germination number, germination rate, seedling vigour index,

root length, seed weight, and seed pH have been widely adopted as integrated indicators for evaluating saline–alkali tolerance in agronomic and breeding research (Ren et al. 2025).

The capacity of seeds to tolerate saline–alkali conditions is determined not solely by genetic constitution, but also by the environmental conditions experienced by the maternal plant during seed development. This phenomenon, broadly termed transgenerational plasticity or stress memory, posits that the maternal environment can be transmitted to the offspring, altering their phenotypic performance in subsequent generations (Brunel-Muguet et al. 2025). Evidence from diverse species demonstrates that maternal plants exposed to stressful environments produce offspring with altered germination behaviour, seedling vigour, and stress tolerance, indicating that parental conditions can significantly impact the development of offspring through epigenetic regulation or memory (Thenveettil et al. 2024). Far beyond traditional Mendelian inheritance, transgenerational epigenetic mechanisms—most notably DNA methylation, histone modifications, and small RNAs—can modulate hormonal balance and stress-responsive gene expression in offspring, influencing developmental trajectories and adaptation to saline–alkali environments (Abdulraheem et al. 2024; Dobránszki et al. 2025; Karalija et al. 2025). DNA methylation dynamics, orchestrated by methyltransferases and demethylases, control promoter accessibility at key loci regulating ion homeostasis and ABA signalling, while small RNA-mediated silencing establishes chromatin states that record stress episodes and prime faster reactivation upon recurrence (Siddique et al. 2024; Maimaiti et al. 2025). Maternal plants exposed to saline–alkali stress often alter the hormonal and ionic content of seeds, either through direct provisioning or epigenetic programming, thereby influencing dormancy, germination, and early growth responses to environmental conditions. Given that drip and flood irrigation create markedly different soil water–salt–alkali dynamics and maternal plant physiological states, it is plausible that the choice of irrigation method during seed production could induce transgenerational effects on the saline–alkali tolerance of harvested F_1 seeds. Nevertheless, whether maternal plants grown under drip vs. flood irrigation produce F_1 progeny with differential germination performance, seedling vigour, and root development under saline–alkali stress remains entirely unexplored. Elucidating these cross-generational effects is of considerable significance, as it could inform irrigation-based seed production protocols that enhance the inherent stress resilience of seed lots in saline–alkali environments. Therefore, the present study was designed to investigate the transgenerational effects of altered irrigation strategies—specifically drip vs. flood irrigation—on the saline–alkali tolerance of maize F_1 seeds. We aimed to: (i) evaluate the effects of maternal drip and flood irrigation treatments on F_1 seed physical characteristics (seed weight) and chemical properties (pH); (ii) assess germination performance of F_1 seeds under saline–alkali stress, including germination number, germination rate, and seedling vigour index; and (iii) characterize early seedling growth responses, with particular emphasis on root length as a key indicator of stress tolerance. By integrating these multi-dimensional parameters, this research seeks to provide novel insights into irrigation-method-mediated mechanisms governing cross-generational saline–alkali tolerance in maize, contributing to sustainable agriculture in salt-affected environments.

2 Materials and Methods

2.1 Experimental Design

F_1 hybrid seed production. The F_1 seeds used in this study were produced through a standard maize hybrid seed-production system at two locations in Ili, Xinjiang, China: Longyu 168 (female inbred line T418 × male inbred line M504, hereafter Cultivar A) at Regiment 64 (80°39′ E, 44°01′ N), and Leidan No. 1 (female P1023 × male SS1819, hereafter Cultivar B) at Regiment 69 (81°22′ E, 43°49′ N). To produce hybrid seeds, the tassels of all female parent plants were removed before pollen shed to prevent self-fertilization. Pollen from the adjacent male parent rows then fertilized the female silks. Only the ears borne on the female plants were harvested; these kernels are the F_1 hybrid seeds tested in the present study.

Irrigation treatments. Two treatments were applied during the entire growing season, both receiving the same total seasonal water quota of 4800 $m^3\ hm^{-2}$: (i) D4800 — subsurface drip irrigation (DI) beneath plastic mulch, with drip lines buried 15 cm below the soil surface and emitters spaced 30 cm apart (flow rate 2.3 L h^{-1}), delivering water directly to the root zone to create a localized wetted bulb; and (ii) M4800 — conventional furrow (surface) irrigation (FI), with water applied as surface flow between maize rows, flooding the furrows and wetting the entire soil profile. The field experiment followed a randomized complete block design with three replicates, yielding 12 plots in total (2 cultivars × 2 irrigation modes × 3 replicates). Each plot measured 15 m × 8 m, separated by 1 m buffer zones. Plants were arranged in wide–narrow rows (40 cm and 60 cm) with an intra-row spacing of 13.5 cm. Male and female parents were planted in a 1:6 row ratio (two male rows alternating with 12 female rows). Female parent density was 127 000 plants hm^{-2} and male parent density was 21 200 plants hm^{-2}. All other management practices—fertilization, pest control, and weed control—were identical between the two treatments.

Seed processing. At physiological maturity, ears from the female rows were hand-picked and threshed. The kernels were naturally air-dried to <14 % moisture, screened for plumpness and uniformity, and stored in paper bags in a ventilated dark room for three months to break dormancy. For each cultivar, seeds from the three field replicate plots under the same irrigation treatment were combined, thoroughly mixed, and stored as one seed lot. The field replicates ensured that the seed lot was representative of the treatment, but were not retained as separate statistical strata for the subsequent laboratory assay.

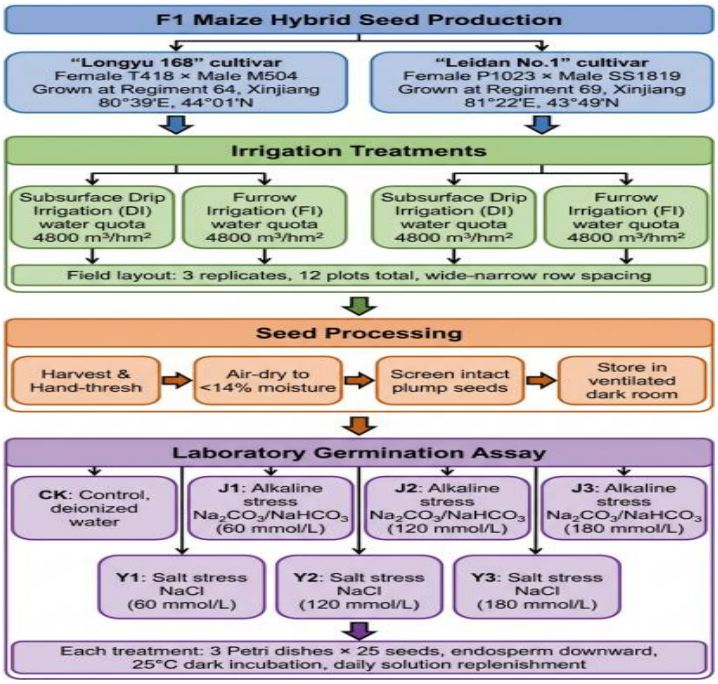


Fig. 1 Schematic overview of the experimental pipeline. The design was structured around three core treatment dimensions: (i) irrigation method (subsurface drip vs. furrow, equal quota of 4800 $m^3\ hm^{-2}$), (ii) stress chemistry (alkaline vs. salt), and (iii) stress intensity (0–180 mmol L^{-1}). (Top) Two maize hybrids were produced through a standard maize hybrid seed-production system: Longyu 168 (Cultivar A, female T418 × male M504) at Regiment 64 and Leidan No. 1 (Cultivar B, female P1023 × male SS1819) at Regiment 69, Ili, Xinjiang, China. (Middle) During the growing season, the two irrigation treatments—subsurface drip irrigation (D4800) and conventional furrow irrigation (M4800)—were applied at an identical seasonal water quota of 4800 $m^3\ hm^{-2}$. The field experiment comprised three replicates per cultivar × irrigation combination (12 plots total), with a wide–narrow row configuration and a 1:6 male-to-female row ratio. (Middle–lower) Ears from female rows were hand-harvested, threshed, air-dried to <14 % moisture, screened for plumpness, and stored for three months to break dormancy. (Bottom) The laboratory germination assay subjected the F_1 seeds to a control (CK, deionized water), three alkaline stress levels (J1–J3: Na_2CO_3/$NaHCO_3$, 5:1, 60–180 mmol L^{-1}), and three salt stress levels (Y1–Y3: NaCl, 60–180 mmol L^{-1}). Each treatment consisted of three Petri dishes × 25 seeds, incubated at 25 °C in darkness with daily solution replenishment. This design isolates the pure effect of water delivery mode on transgenerational saline–alkali tolerance under an equal water supply.

2.2 Data Survey

Measurements and Calculations. Normal germination was defined as radicle protrusion of at least 2 mm. Germination potential was recorded on the 4th day after treatment, and germination rate was determined on the 7th day. Upon completion of the incubation period, fresh shoot weight, fresh root weight, and root length were measured. The shoots and roots were subsequently

oven-dried at 105 °C for 72 h to determine their dry weights. Finally, germination potential, germination index, and vigour index were calculated according to standard formulae.

$GP = (G_4 / N) \times 100\ \%$

G_4 = number of normally germinated seeds on the 4th day

N = total number of tested seeds

Germination Rate = $(G_7 / N) \times 100\ \%$

G_7 = number of normally germinated seeds on the 7th day

N = total number of tested seeds

$GI = \Sigma\ (G_t / T_t)$

G_t = number of normally germinated seeds on day t

T_t = germination day (1, 2, 3, ..., n)

$VI = GI \times S$

GI = germination index

S = average seedling dry weight (g)

Stress tolerance index (STI) = $(GR_T / GR_CK) \times 100\ \%$

GR_T = germination rate of the treatment

GR_CK = germination rate of the control

Seed pH and electrical conductivity (EC) were determined according to standard International Seed Testing Association (ISTA) protocols. Briefly, 25 intact seeds were soaked in 50 mL deionised water (1:2, w/v) at 25 °C for 24 h. The pH of the leachate was measured with a calibrated glass-electrode pH meter, and EC was recorded with a conductivity cell and expressed as $\mu S\ cm^{-1}\ g^{-1}$ seed fresh weight.

2.3 Data Analysis

Data were analysed in two stages. Seed intrinsic traits (thousand-seed weight, pH, EC) were subjected to two-way ANOVA (cultivar × maternal irrigation) with the three field plots as replicates (n = 3). For germination and seedling variables, each Petri dish (25 seeds) served as the independent experimental unit, with three replicate dishes per treatment (n = 3). These variables were analysed by four-way ANOVA with cultivar, maternal irrigation, stress type, and concentration as fixed factors. Normality and homogeneity of variance were verified by Shapiro–Wilk and Levene's tests, respectively, and germination percentages were arcsine-square-root transformed prior to analysis. Where significant interactions were detected ($P < 0.05$), simple main effects were examined; pairwise comparisons among concentrations within

each irrigation regime were performed using the least significant difference (LSD) test with Bonferroni correction. DI vs. FI within each cultivar were compared by independent-samples t-test when the interaction was not significant. All analyses were conducted in SPSS 26.0, with significance set at $P < 0.05$. Figures were generated with Origin 2024.

3 Results

3.1 Maternal irrigation effects on F_1 seed physicochemical properties

Maternal irrigation method during hybrid seed production generated measurable transgenerational imprints on F_1 seed yield, size, weight, baseline germination and physicochemical traits. Two-way ANOVA revealed significant main effects of maternal irrigation on seed yield ($P < 0.001$), seed size ($P = 0.025$), thousand-seed weight ($P = 0.011$) and water-germination percentage ($P = 0.024$), while cultivar identity significantly influenced yield ($P = 0.023$) with a significant cultivar × irrigation interaction ($P = 0.040$). Seed yield per unit area was markedly enhanced by drip irrigation relative to furrow irrigation, though the magnitude of this advantage depended on cultivar: cultivar A showed a pronounced 37.1 % increase under DI (14 073.50 ± 844.26 vs. 10 264.72 ± 479.99 kg hm^{-2}), whereas cultivar B showed a more modest 11.0 % increase (11 207.69 ± 412.84 vs. 10 095.36 ± 501.47 kg hm^{-2}), indicating that cultivar A is more responsive to irrigation strategy in terms of maternal provisioning capacity while cultivar B maintains a more stable yield across water regimes. Individual seed size followed a similar directional trend, with DI-derived seeds significantly heavier than FI-derived seeds across both cultivars without significant interaction, averaging 190.31 ± 4.53 vs. 182.89 ± 1.19 mg in cultivar A and 198.03 ± 18.00 vs. 180.69 ± 5.34 mg in cultivar B (Fig. 2). Thousand-seed weight was consistently greater under maternal DI than under FI, with the pairwise difference reaching statistical significance in cultivar B but not in cultivar A, confirming that maternal DI improved both the overall quantity and the individual plumpness of F_1 seeds. Seed electrical conductivity and pH also varied with maternal irrigation treatment (Table 1), with maternal DI significantly elevating seed pH in cultivar B relative to FI ($P < 0.01$) but producing no significant difference in cultivar A. Electrical conductivity showed inconsistent directional trends between cultivars and did not differ significantly between irrigation regimes for either hybrid, suggesting that membrane-integrity readouts are more strongly modulated by genetic background than by the maternal water regime alone. Even under non-stress water-only conditions, maternal irrigation history left a detectable imprint on offspring germination capacity, as FI-derived seeds exhibited a statistically significant reduction in baseline germination percentage relative to DI-derived seeds, with the depression being more pronounced in cultivar B (0.91 ± 0.08 under FI vs. 0.95 ± 0.02 under DI) than in cultivar A. This subtle difference in intrinsic vigour suggests that the maternal FI environment may have compromised embryo membrane integrity or metabolic preparedness, an interpretation consistent with the directionally higher EC values observed in FI-derived seeds of cultivar A.

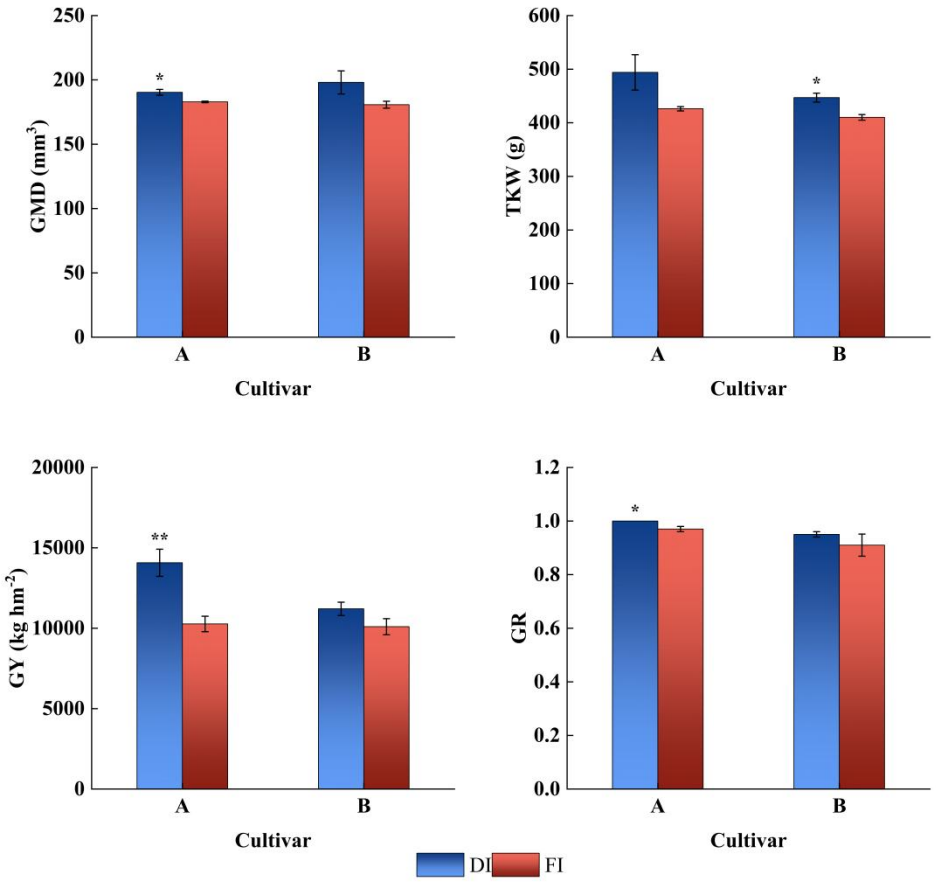


Fig. 2 Transgenerational effects of maternal drip irrigation (DI) versus furrow irrigation (FI) during hybrid seed production on F_1 seed yield, size, weight and baseline germination. Upper-left, individual seed size expressed as geometric mean diameter (GMD, mm^3); upper-right, thousand-seed weight (TKW, g); lower-left, seed yield per unit area expressed as grain yield (GY, kg hm^{-2}); lower-right, baseline water-germination percentage expressed as germination rate (GR). Blue bars denote DI-derived seeds; red bars denote FI-derived seeds. Values are mean ± SE (n = 3). Asterisks indicate significant differences between DI and FI within the same cultivar (*$P < 0.05$, **$P < 0.01$); ns, not significant.

Cultivar	Seed	EC(ms $cm^{-1}g^{-1}$)	pH
A	DI	198.90±28.53	6.65±0.08
	FI	235.40±16.93	6.61±0.10
B	DI	232.25±7.16	6.63±0.05**
	FI	212.00±26.12	6.55±0.05

Table 1 Effects of maternal irrigation method on seed electrical conductivity and pH of F_1 maize seeds.Values are mean ± SE (n = 3). Double asterisks indicate significant differences between DI and FI within the same cultivar (independent samples t-test, $P < 0.01$). EC, electrical conductivity.

3.2 Transgenerational effects of maternal irrigation on F_1 seed germination under saline-alkali stress

A four-way ANOVA revealed that stress concentration was the dominant driver of variation, exerting highly significant main effects on all traits except R/S ($P < 0.001$ or $P < 0.05$), while maternal seed source (Se; representing drip vs. furrow irrigation) and cultivar also contributed significantly to root dry weight, germination rate, and root length (Table 2). Significant interactions involving concentration (Se × Conc, C × Conc, S × Conc, and C × S × Conc; $P <$ 0.05–0.001) indicated that transgenerational effects were strongly stress-severity-dependent.

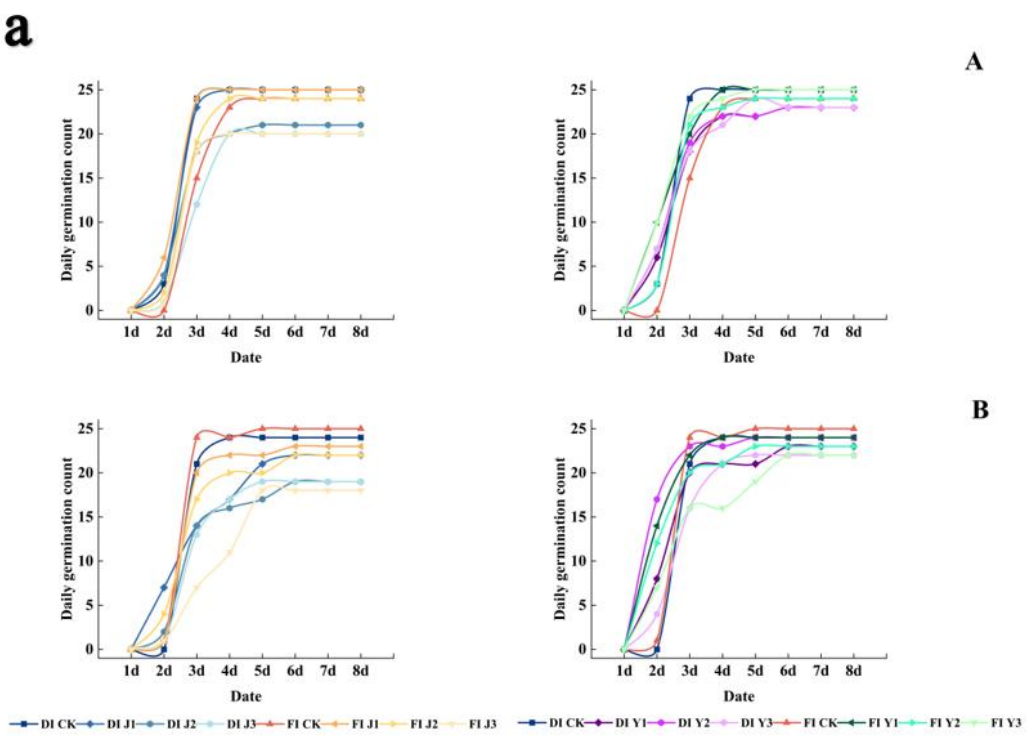
Daily germination records showed that maternal irrigation history altered the velocity and trajectory of radicle protrusion rather than simply shifting final counts. Under severe alkaline stress (180 mmol L^{-1}), cultivar B exhibited a pronounced temporal decoupling in Fig. 3a: DI-derived seeds reached 50 % cumulative germination approximately 1 day earlier than FI-derived seeds, and by day 4 the DI line recorded an approximately 8 % advantage in germination potential. Between days 4 and 7, however, the FI curve continued to rise while the DI curve plateaued, and by day 7 FI had achieved an approximately 15 % higher final germination rate and an approximately 13 % greater germination index (Fig. 3b). This pattern reveals a speed–completion trade-off: maternal DI programmed a rapid-initiation strategy, whereas maternal FI programmed a delayed-completion strategy with slower but more complete germination. The decoupling was amplified under NaCl stress: in cultivar B at 180 mmol L^{-1}, the FI advantage in germination index expanded to approximately 21 %, exceeding the approximately 13 % divergence observed under carbonate/bicarbonate alkalinity (Fig. 3b).

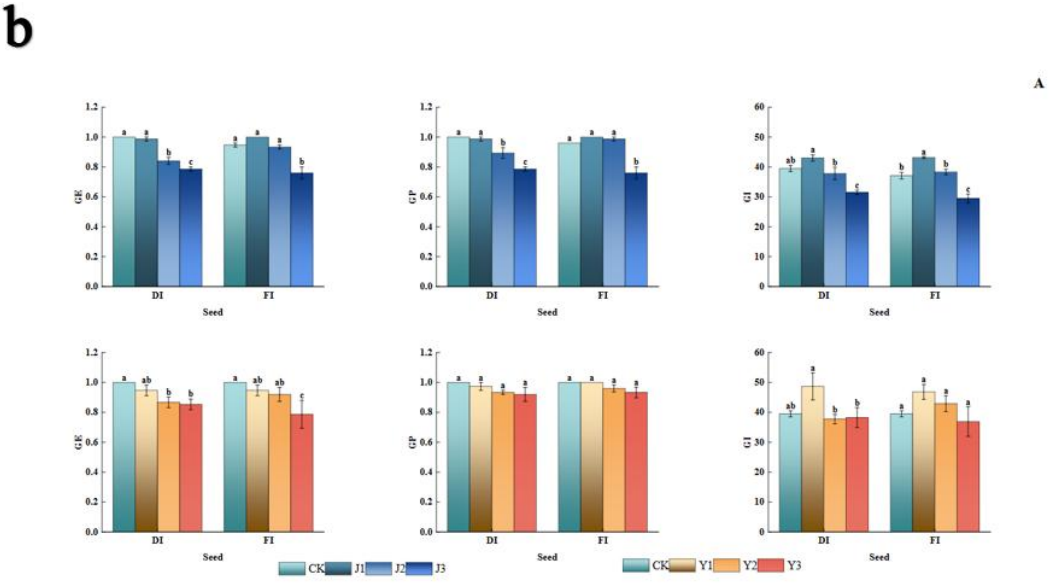
The direction of this trade-off was strictly cultivar-dependent. Under identical alkaline stress (180 mmol L^{-1}), DI-derived seeds of cultivar A outperformed FI-derived seeds in germination index by approximately 7 %—a direction completely reversed from that in cultivar B (Fig. 3b). Daily tracking in Fig. 3a showed that cultivar A DI seeds maintained a modest but consistent lead from day 3 onwards under alkalinity, whereas under salt stress the two curves for cultivar A remained nearly coincident until day 5 before diverging marginally in favour of DI.

Stress chemistry also modulated the absolute magnitude of suppression. Alkaline stress depressed daily germination more strongly than salt stress at equivalent concentrations; the final germination rate of DI-derived seeds in cultivar B under 180 mmol L^{-1} alkaline stress was approximately 26 % lower than under equivalent NaCl stress (Fig. 3b). Across both stress regimes, transgenerational divergence between DI and FI progeny became most pronounced at concentrations ≥120 mmol L^{-1}, while the daily germination curves largely overlapped under mild stress (60 mmol L^{-1}) and control conditions (Fig. 3a).

Source of variation	Shoot DW	Root DW	R/S	GR	GP	GI	RL
Cultivar (C)	ns	***	ns	*	*	ns	ns
Seed (Se)	ns	**	ns	*	*	ns	*
Stress type (S)	ns	ns	ns	ns	ns	ns	ns
Concentration (Conc)	***	***	ns	***	***	*	***
C×Se	ns	ns	ns	ns	ns	ns	ns
C×S	ns	ns	ns	ns	ns	ns	ns
C×Conc	ns	**	ns	ns	ns	ns	ns
Se×S	ns	ns	ns	ns	ns	ns	ns
Se×Conc	ns	*	ns	*	*	ns	ns
S×Conc	***	ns	ns	ns	ns	ns	ns
C×Se×S	ns	ns	ns	ns	ns	ns	ns
C×Se×Conc	ns	ns	ns	ns	ns	ns	ns
C×S×Conc	*	ns	ns	ns	ns	ns	ns
Se×S×Conc	ns	ns	ns	ns	ns	ns	ns
C×I×S×Conc	ns	ns	ns	ns	ns	ns	ns

Table 2 Four-way ANOVA summary of the effects of cultivar (C), Seed (Se), stress type (S), and concentration (Conc) on germination and seedling traits of F_1 maize progeny under saline–alkali stress. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant. Shoot DW, shoot dry weight; Root DW, root dry weight; R/S, root-to-shoot ratio; GR, germination rate; GP, germination potential; GI, germination index; RL, root length. GE and GP were arcsine-square-root transformed prior to analysis. Type III sum of squares was used. Total n = 96 observations (two cultivars × two irrigation regimes × two stress types × four concentrations × three replicates). Degrees of freedom: C, Se, S = 1; Conc = 3; two-way interactions = 1 to 3; three-way interactions = 1 to 3; four-way interaction = 3; Residual = 64.


a
A
B
Daily germination count
Date
1d 2d 3d 4d 5d 6d 7d 8d
DI CK DI J1 DI J2 DI J3 FI CK FI J1 FI J2 FI J3
DI CK DI Y1 DI Y2 DI Y3 FI CK FI Y1 FI Y2 FI Y3


b
A
GE
GP
GI
GR
Seed
DI
FI
CK J1 J2 J3
CK Y1 Y2 Y3

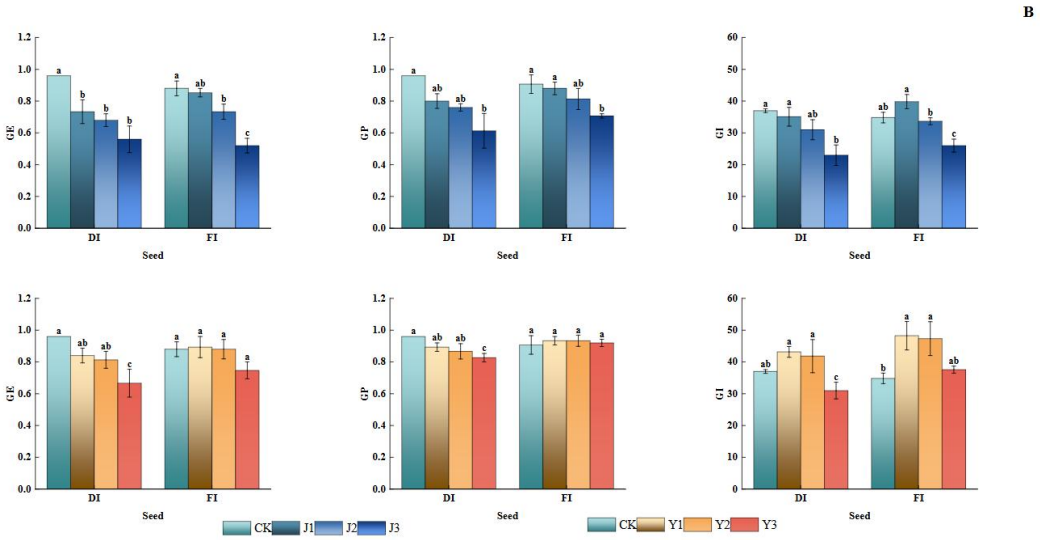


Fig. 3 Divergent germination dynamics and performance of F_1 maize seeds shaped by maternal irrigation history under saline–alkali stress. (a) Daily cumulative germination number from day 1 to day 7. Upper panels, cultivar A (Longyu 168); lower panels, cultivar B (Leidan No. 1). Left half, alkaline stress (Na_2CO_3/$NaHCO_3$, 5:1 molar ratio; J1, 60 mmol L^{-1}; J2, 120 mmol L^{-1}; J3, 180 mmol L^{-1}); right half, salt stress (NaCl; Y1, 60 mmol L^{-1}; Y2, 120 mmol L^{-1}; Y3, 180 mmol L^{-1}). Blue lines with circles, maternal drip irrigation (DI); red lines with diamonds, maternal furrow irrigation (FI); CK denotes the control (0 mmol L^{-1}). Values are mean ± SE (n = 3). (b) Germination potential (GP), germination rate (GR), and germination index (GI) for cultivar A (upper row) and cultivar B (lower row). Within each subplot, blue-toned bars indicate DI-derived seeds and red-toned bars indicate FI-derived seeds. Values are mean ± SE (n = 3). Different lowercase letters above bars indicate significant differences among concentrations within the same maternal irrigation treatment (LSD test with Bonferroni correction, $P < 0.05$).

3.3 Transgenerational effects of maternal irrigation on F_1 seedling growth and biomass allocation under saline-alkali stress

Root length declined progressively with increasing stress intensity in both cultivars. Nevertheless, DI-derived seedlings maintained significantly greater root elongation than FI-derived counterparts at all concentrations beyond the control in cultivar B (Fig. 4; $P < 0.05$, independent-samples t-test). This DI advantage intensified as environmental pressure increased: in cultivar A, the root length superiority expanded from approximately 26 % under control conditions to approximately 73 % under 180 mmol L^{-1} alkaline stress, whereas under salt stress the same cultivar showed a less pronounced yet consistent DI lead. In cultivar B, the DI advantage in root elongation was significant at all stress levels above the control, though the magnitude was smaller than in cultivar A. At equivalent concentrations, alkaline stress imposed a stronger inhibitory effect on root elongation than salt stress; yet DI-derived progeny consistently outperformed FI-derived progeny across both stress regimes. Biomass allocation patterns revealed sharply divergent strategies programmed by maternal seed source (Fig. 5). Under mild-to-moderate stress (60 to 120 mmol

L^{-1}), FI-derived seedlings exhibited a marked surge in root-to-shoot ratio (R/S), with R/S peaking at approximately 4.0 to 4.5 in both cultivars under alkaline and salt stress. This indicates a compensatory root-foraging response at the expense of shoot biomass. In striking contrast, DI-derived seedlings maintained a relatively stable, low R/S across the entire stress gradient (approximately 0.5 to 1.5), reflecting a balanced growth architecture that prioritised sustained root elongation without sacrificing shoot development. Under severe stress (180 mmol L^{-1}), R/S converged between the two progeny types as overall growth was severely suppressed, erasing the allocation divergence observed at lower concentrations.

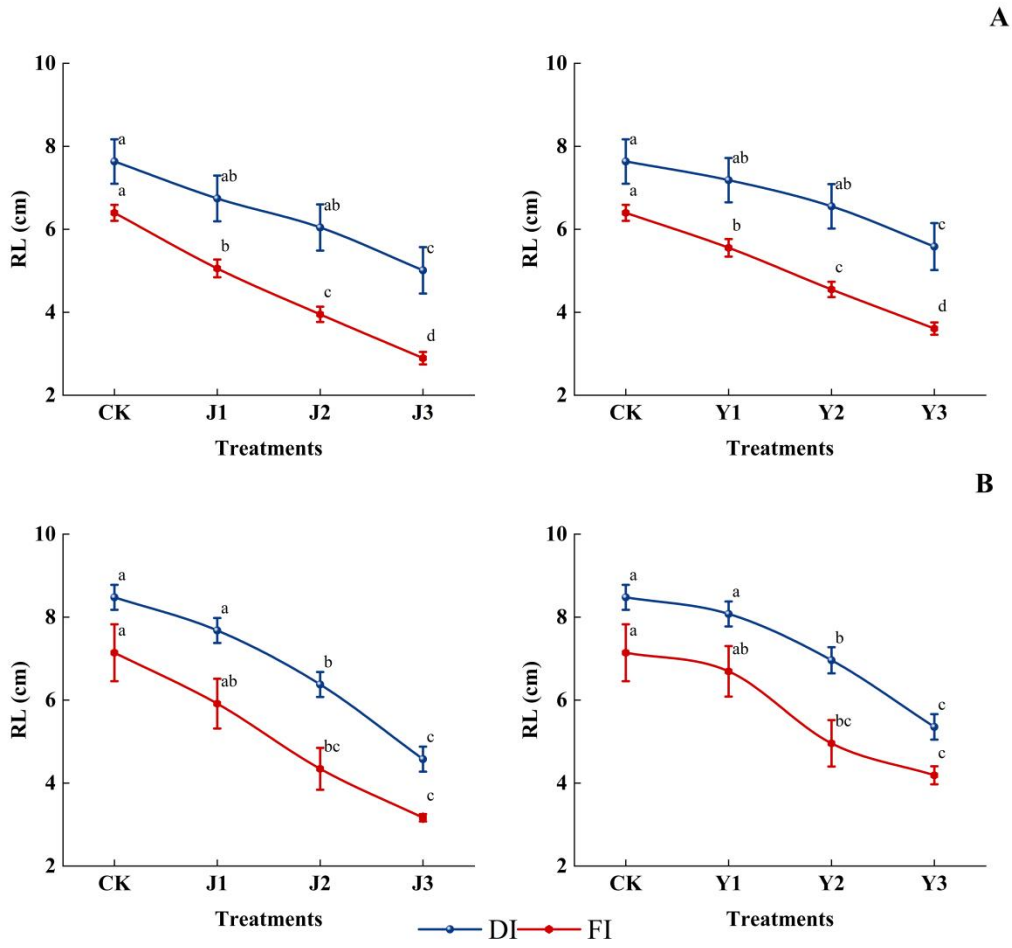


Fig. 4 Root length of F_1 seedlings under saline–alkali stress as affected by maternal irrigation method. Blue lines with circles, drip irrigation (DI); red lines with diamonds, furrow irrigation (FI). Values are mean ± SE (n = 3). Lowercase letters indicate significant differences among concentrations within the same maternal irrigation regime (LSD test with Bonferroni correction, $P < 0.05$). DI vs. FI comparisons at the same concentration were performed by independent-samples t-test (see Results for statistics).

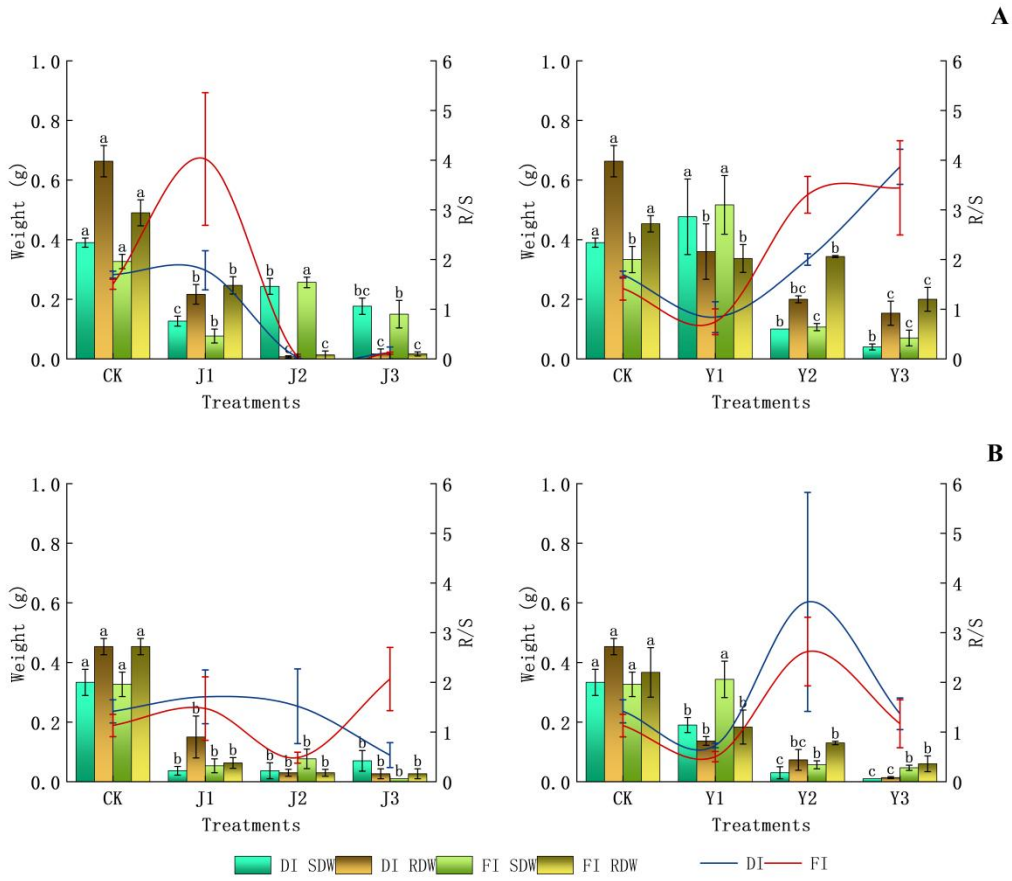


Fig. 5 Biomass allocation and root-to-shoot ratio (R/S) of F_1 seedlings under saline–alkali stress. Values are mean ± SE (n = 3). Different lowercase letters above bars indicate significant differences among concentrations within the same tissue and maternal irrigation regime (LSD test with Bonferroni correction, $P < 0.05$).

3.4 Multidimensional phenotypic divergence in F_1 maize under severe saline–alkali stress

To integrate the multi-dimensional transgenerational effects identified in preceding sections, radar profiling was applied to evaluate the relative performance of six key traits under severe saline-alkali stress (180 mmol L^{-1}). Under alkaline stress, DI-derived progeny of cultivar A exhibited a markedly expanded polygon driven by superior root length (124.3 % of control), vigour index (43.1 %), and stress tolerance index (43.1 %), whereas FI-derived progeny displayed a contracted profile with only marginal competitiveness in germination potential and germination rate (Fig. 6a). This pattern indicates that maternal drip irrigation conferred a broad-spectrum transgenerational enhancement encompassing both growth vigour and root elongation capacity. Under salt stress, the DI advantage in root length was further amplified (138.5 %), yet FI-derived progeny outperformed DI counterparts in germination rate (97.2 % vs. 92.0 %) and seedling dry weight (33.1 % vs. 20.2 %), revealing a decoupling whereby the maternal furrow irrigation legacy shifted progeny resource allocation toward germination completion and biomass retention at the expense of root expansion (Fig. 6b).In cultivar B under alkaline stress, the transgenerational divergence was attenuated; FI-derived seeds achieved higher germination rate (74.7 % vs. 63.9 %),

while DI-derived seeds maintained advantages in root length (86.0 %), stress tolerance index (45.4 %), and vigour index (45.5 %) (Fig. 6c). The most pronounced strategy divergence occurred in cultivar B under salt stress: FI-derived progeny dominated germination potential (84.9 % vs. 69.5%), germination rate (97.2 % vs. 86.1 %), and seedling dry weight (15.4 % vs. 3.3 %), effectively encircling the DI polygon in the upper-left phenotypic space, whereas DI-derived progeny retained competitiveness exclusively in root length (100.4 %), stress tolerance index (36.6 %), and vigour index (36.4 %) (Fig. 6d). Again, because cultivar and production site are fully nested, these contrasting patterns between Longyu 168 and Leidan No. 1 should be interpreted as cultivar–site combination effects.

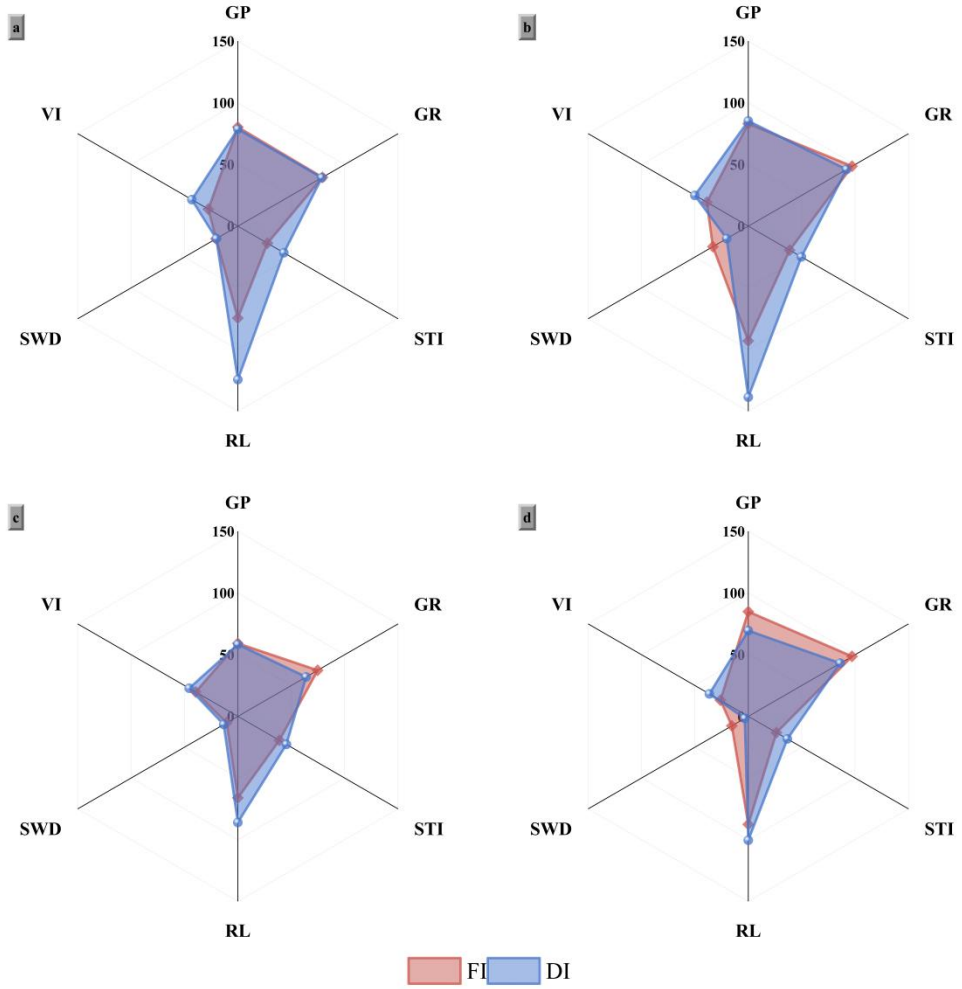


Fig. 6 Radar profiling of transgenerational stress-coping strategies in F_1 maize progeny under severe saline-alkali stress (180 mmol L^{-1}). (a) Cultivar A under alkaline stress (Na_2CO_3/$NaHCO_3$, 5:1 molar ratio), (b) cultivar A under salt stress (NaCl), (c) cultivar B under alkaline stress, and (d) cultivar B under salt stress. Six axes represent: GP, germination potential; GR, germination rate; SWD, seedling dry weight; VI, vigour index; STI, stress tolerance index; RL, root length. Relative performance for each trait was calculated as (value at 180 mmol L^{-1} / value at 0 mmol L^{-1}) × 100 % within the same maternal irrigation regime and cultivar. Blue solid polygons with circles,

maternal drip irrigation (DI); red dashed polygons with diamonds, maternal furrow irrigation (FI).

3.5 Correlation analysis of transgenerational trait networks

Pearson correlation matrices constructed separately for each cultivar by pooling alkaline and salt stress data (n = 48 per cultivar) revealed that maternal irrigation effects propagated through integrated trait networks rather than acting on isolated parameters (Fig. 7). In both cultivars, germination potential (GP) and germination rate (GR) were tightly coupled (r = 0.81 in A, 0.87 in B, P < 0.001). Thousand-seed weight (TSW) correlated positively with baseline germination rate (BaseGR; r = 0.52, P < 0.01) and root length (RL; r = 0.35 in A, 0.43 in B, P < 0.05), while BaseGR itself was positively associated with RL (r = 0.31, P < 0.05) in both backgrounds. These associations indicate that maternal resource provisioning and metabolic priming converged on belowground foraging capacity. Germination speed and completion were further linked to post-germination growth, but the coupling strength differed genetically: in cultivar B, GP correlated with RL (r = 0.65), shoot dry weight (SDW; r = 0.67), and vigour index (VI; r = 0.68) (all P < 0.001), whereas in cultivar A the corresponding coefficients were lower (r = 0.40–0.61, P < 0.05–0.01). The most consequential divergence concerned root-to-shoot ratio (R/S). In cultivar A, R/S was strongly negatively correlated with VI (r = –0.78, P < 0.001) and SDW (r = –0.78, P < 0.001), and negatively associated with GP (r = –0.49, P < 0.05), confirming that the compensatory root-foraging surge in FI-derived progeny was achieved through a zero-sum reallocation of carbon away from shoot development. In cultivar B, however, R/S showed no significant correlation with VI, SDW, or germination parameters (all $|r|$ < 0.30, P > 0.05), indicating that elevated root allocation was not tightly constrained by aboveground trade-offs in this genetic background. In both cultivars, VI was strongly driven by RL (r = 0.85 in A, 0.97 in B, P < 0.001) and SDW (r = 0.95 in A, 0.76 in B, P < 0.001), with SDW and RL also significantly linked (r = 0.61–0.65, P < 0.01).

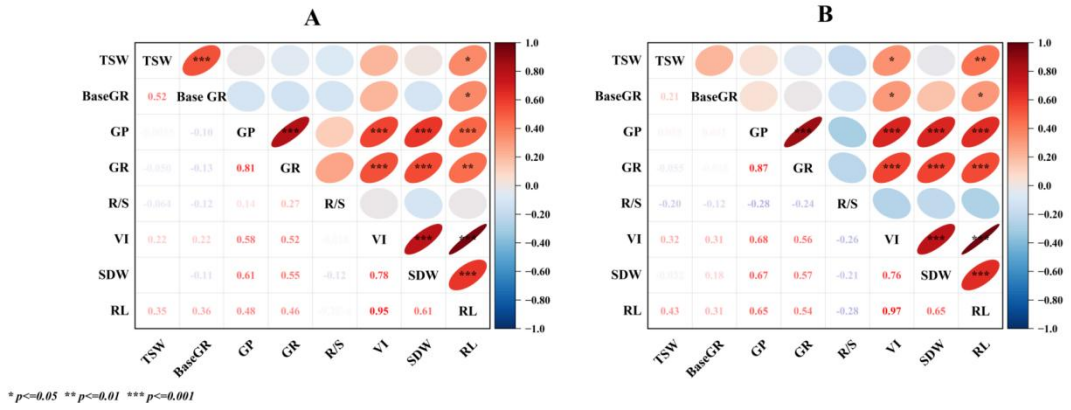


Fig. 7 Pearson correlation matrices of seed intrinsic traits and stress-response indicators in F_1 maize progeny. (a) Cultivar A (Longyu 168, n = 48); (b) Cultivar B (Leidan No. 1, n = 48). Data from alkaline (Na_2CO_3/$NaHCO_3$, 5:1 molar ratio) and salt (NaCl) stress treatments were pooled within each cultivar. Colour intensity and ellipse shape indicate the strength and direction of Pearson correlation coefficients (r). Asterisks denote significance levels (* P < 0.05, ** P < 0.01, *** P < 0.001). TSW, thousand-seed weight; BaseGR, baseline germination rate; GP, germination potential; GR, germination rate; R/S, root-to-shoot ratio; VI, vigour index; SDW, shoot dry weight;

RL, root length.

4 Discussion

4.1 Maternal irrigation imprints on F_1 seed intrinsic traits and germination dynamics

Maternal irrigation regime during seed production generated measurable transgenerational imprints on F_1 seed yield, size, physicochemical traits and germination dynamics, and these intrinsic differences propagated into divergent germination trajectories under saline-alkali stress. Crucially, these divergent outcomes were achieved under an identical seasonal water quota of 4800 m^3 hm^{-2}, isolating the pure effect of water delivery mode. The transgenerational effects extended beyond individual seed mass to whole-seed yield and grain dimensions. Seed yield per unit area was markedly elevated under maternal DI relative to FI, with the advantage most pronounced in cultivar A (14 073.50 vs. 10 264.72 kg hm^{-2}, a 37.1 % increase) compared with cultivar B (11 207.69 vs. 10 095.36 kg hm^{-2}, an 11.0 % increase). The significant cultivar × irrigation interaction (P = 0.040) indicates a genotype-dependent yield response. Consistent with this, individual seed size and thousand-seed weight were also significantly greater under DI (P = 0.025 and P = 0.011, respectively), corroborating that DI enhanced both grain number and plumpness. These data establish that maternal DI confers a comprehensive transgenerational benefit to seed provisioning, programming offspring biomass and early vigour Donohue(2009). Seed pH responded in a cultivar-specific manner: maternal DI significantly elevated seed pH in cultivar B relative to FI ($P < 0.01$), whereas no difference was detected in cultivar A. Electrical conductivity showed inconsistent trends between cultivars and did not differ significantly between irrigation regimes, suggesting that membrane-integrity readouts are more strongly modulated by genetic background than by the maternal water regime. Even under benign water-only conditions, maternal irrigation history left a detectable imprint on offspring germination capacity. FI-derived seeds exhibited a statistically significant reduction in baseline germination percentage relative to DI-derived seeds (P = 0.024), with the depression more pronounced in cultivar B (0.91 vs. 0.95). This subtle difference suggests that the maternal FI environment may have compromised embryo membrane integrity or metabolic preparedness, consistent with the directionally higher EC values observed in FI-derived seeds of cultivar A. This baseline germination divergence foreshadows the more pronounced speed-completion trade-off under saline-alkali stress: the slightly lower vigour of FI progeny under optimal conditions expanded into a delayed but ultimately more complete germination phenotype under severe stress, whereas the DI advantage in speed became amplified under osmotic challenge. These intrinsic trait differences translated into a pronounced decoupling of germination speed from final germination percentage. Under severe alkaline stress (180 mmol L^{-1}), cultivar B exhibited a striking temporal dichotomy: DI-derived seeds reached 50 % cumulative germination approximately 1 day earlier than FI-derived seeds, recording an approximately 8 % advantage in germination potential by day 4. Between days 4 and 7, however, the FI curve continued to rise while the DI curve plateaued, and by day 7 FI had achieved an approximately 15 % higher final germination rate and an approximately 13 % greater germination index. This pattern does not indicate a functionally equivalent "robust-survival" strategy; rather, it reveals a germination speed–completion trade-off in which the maternal FI legacy imposed a delayed-emergence penalty. Under field conditions, where early uniform stand establishment is

critical for competitive canopy development and resource capture, a one-day delay in reaching 50 % emergence can significantly compromise maize establishment. Thus, while FI progeny eventually attained marginally higher final counts, this was achieved through a slower, less synchronous germination process that is agronomically disadvantageous. This speed-completion trade-off indicates that maternal DI programmes progeny for rapid stand establishment, whereas maternal FI imprints a delayed-emergence phenotype that sacrifices synchrony for marginal gains in final count. Such environment-dependent shifts in offspring germination behaviour are consistent with the adaptive transgenerational plasticity framework, wherein maternal conditions act as predictive cues that adjust progeny phenotype to anticipated stress (Galloway and Etterson 2007; Herman and Sultan 2011). The direction of this trade-off was strictly cultivar-dependent. Under identical alkaline stress (180 mmol L^{-1}), DI-derived seeds of cultivar A outperformed FI-derived seeds in germination index by approximately 7 %—a direction completely reversed from that observed in cultivar B. Under salt stress, cultivar A DI seeds maintained a modest but consistent lead from day 3 onwards, whereas the two curves remained nearly coincident until day 5 before diverging marginally in favour of DI. Stress chemistry further modulated the magnitude of transgenerational divergence: when cultivar B was subjected to 180 mmol L^{-1} NaCl stress, the FI advantage in germination index expanded to approximately 21 %, exceeding the approximately 13 % divergence recorded under alkalinity. Notably, alkaline stress suppressed germination more strongly than salt stress; the final germination rate of DI-derived seeds in cultivar B under 180 mmol L^{-1} alkaline stress was approximately 26 % lower than under equivalent NaCl stress. Four-way ANOVA confirmed that stress concentration was the dominant driver of variation (P <0.001), while maternal seed source contributed significantly to germination rate and germination potential ($P < 0.05$), and significant seed source × concentration interactions (P<0.05) confirmed that transgenerational effects were strongly stress-severity-dependent. Collectively, these germination dynamics demonstrate that, under an equal water quota, maternal DI programmes F_1 progeny for rapid, synchronous stand establishment—a trait of paramount agronomic value—whereas maternal FI imprints a delayed and asynchronous germination phenotype.

4.2 Transgenerational divergence in root elongation and biomass allocation

Maternal irrigation regimes programmed contrasting root-system ideotypes in F_1 seedlings, with root length representing the most sensitive transgenerational indicator. DI-derived seedlings maintained significantly greater root elongation than FI-derived counterparts at all concentrations beyond the control in cultivar B ($P < 0.05$), and this DI advantage amplified progressively as environmental pressure intensified. In cultivar A, the root-length superiority of DI expanded from approximately 26 % under control conditions to approximately 73 % under 180 mmol L^{-1} alkaline stress; under salt stress, the same cultivar exhibited a consistent yet less pronounced DI lead. In cultivar B, the DI advantage was statistically significant across all stress levels above the control, though the magnitude remained smaller than in cultivar A. At equivalent concentrations, alkaline stress imposed a stronger inhibitory effect on root elongation than salt stress, yet DI-derived progeny consistently outperformed FI-derived progeny across both chemistry regimes. The primacy of root elongation as a transgenerationally plastic trait is supported by studies in *Polygonum* and barley, where drought-stressed parents produced offspring with longer, more

rapidly extending root systems that conferred a measurable growth advantage under water limitation (Sultan et al. 2009; Nosalewicz et al. 2016). Deep root systems under salinity serve as a critical component of the ion-exclusion strategy that restricts toxic ion accumulation in surface horizons Munns and Tester (2008). Under an identical water quota during seed production, maternal DI imprinted a fundamentally superior root-system architecture that became increasingly advantageous as stress severity escalated. Biomass allocation patterns revealed sharply divergent coping ideotypes. Under mild-to-moderate stress (60 to 120 mmol L^{-1}), FI-derived seedlings exhibited a marked surge in root-to-shoot ratio (R/S), peaking at approximately 4.0 to 4.5 in both cultivars under alkaline and salt stress. While this pattern superficially resembles a compensatory root-foraging response, the concomitant suppression of shoot dry weight and vigour index indicates that it operated as a stress-induced carbon reallocation away from aerial growth—a metabolic compromise rather than an adaptive optimization. In contrast, DI-derived seedlings maintained a stable, low R/S across the entire stress gradient (approximately 0.5 to 1.5), reflecting a balanced growth architecture that sustained root elongation without sacrificing shoot development. This capacity to simultaneously invest in both belowground exploration and aboveground growth represents a more efficient resource-use strategy, enabling DI progeny to maintain photosynthetic capacity while accessing deeper, less saline soil horizons. Under severe stress (180 mmol L^{-1}), R/S converged between the two progeny types as overall growth was severely suppressed, erasing the allocation divergence observed at lower concentrations. Four-way ANOVA corroborated these patterns: maternal seed source exerted a significant main effect on root dry weight ($P < 0.01$), and the seed source × concentration interaction was significant for root dry weight ($P < 0.05$), confirming that maternal irrigation effects on belowground biomass were contingent on stress intensity. The contrasting R/S trajectories mirror transgenerational drought-memory responses in barley, where maternal drought decreased the shoot-to-root mass ratio and enhanced thin-root growth in offspring, thereby maintaining relatively long roots at lower carbon cost (Nosalewicz et al., 2016). However, in the present study, the maternal FI legacy imposed a far more severe shoot-growth penalty (R/S up to 4.5) than reported in prior drought-memory studies, suggesting that the saline–alkali environment programmed by furrow irrigation during seed production imposes a particularly costly transgenerational reallocation burden. Whether the divergent R/S patterns observed here under saline–alkali stress are mediated by epigenetic regulation of auxin–TOR signalling, which is known to control root–shoot allocation under stress (Zhu 2016; Karalija et al. 2025), remains to be tested.

4.3 Maternal irrigation programmes divergent transgenerational stress-coping strategies

Transgenerational effects manifested as cultivar-specific phenotypic integration patterns within multidimensional trait space; however, across all cultivar × stress chemistry combinations, DI progeny consistently maintained superior root elongation and a balanced biomass allocation, whereas FI progeny exhibited a compensatory root-foraging surge that was invariably coupled with suppressed shoot development. Radar profiling under severe stress (180 mmol L^{-1}) revealed distinct polygons for each cultivar × stress chemistry combination, yet a consistent asymmetry

emerged. In cultivar A under alkaline stress, DI-derived progeny displayed broad-spectrum superiority, driven by higher relative performance in root length (124.3 % of control), vigour index (43.1 %), and stress tolerance index (43.1 %), whereas FI-derived progeny showed only marginal competitiveness in germination potential and germination rate (Fig. 6a). Under NaCl stress in the same cultivar, this pattern decoupled: DI retained dominance in root length (138.5 % of control), yet FI outperformed DI in germination rate (97.2 % vs. 92.0 %) and seedling dry weight (33.1 % vs. 20.2 %). Nevertheless, even in this scenario, DI progeny still maintained root length at 138.5 % of control, markedly outpacing FI counterparts whose root expansion was compromised—a trait that is arguably the primary determinant of long-term saline–alkali tolerance under field conditions. In cultivar B under alkaline stress, transgenerational divergence was attenuated: FI-derived seeds achieved a higher germination rate (74.7 % vs. 63.9 %), while DI-derived seeds maintained advantages in root length (86.0 %), stress tolerance index (45.4 %), and vigour index (45.5 %) (Fig. 6c). The most pronounced strategy divergence occurred in cultivar B under salt stress: FI-derived progeny dominated germination potential (84.9 % vs. 69.5 %), germination rate (97.2 % vs. 86.1 %), and seedling dry weight (15.4 % vs. 3.3 %), effectively encircling the DI polygon in the upper-left phenotypic space, whereas DI-derived progeny retained competitiveness exclusively in root length (100.4 %), stress tolerance index (36.6 %), and vigour index (36.4 %) (Fig. 6d). Yet this apparent FI 'dominance' must be interpreted cautiously: both progeny types suffered extreme growth suppression under severe salt stress (note the low absolute values of 15.4 % and 3.3 % for seedling dry weight). FI's marginally higher relative retention of germination metrics reflects a diversion of residual resources toward completion at the expense of root expansion, rather than a genuine resilience advantage; indeed, the absolute values for both progeny types were severely depressed, and DI's retention of root-length competitiveness suggests a survival mechanism that prioritizes belowground exploration over ephemeral shoot biomass under catastrophic stress. Contrary to the interpretation that these contrasting patterns indicate equally valid alternative strategies, the data collectively support the superiority of the DI-programmed phenotype for sustainable maize establishment. Genotype-dependent transgenerational plasticity has been documented across multiple species, where identical parental environments produce divergent offspring responses depending on genetic background (Vu et al. 2015; Aycan et al. 2021), and maternal genotype can contribute substantially to offspring salinity tolerance (Aycan et al., 2021). Epigenetic mechanisms such as DNA methylation and histone modifications are implicated in establishing persistent chromatin states that record maternal stress episodes (Bilichak et al. 2012; Brunel-Muguet et al. 2025). Because the two hybrids were produced at separate locations (Regiment 64 and Regiment 69), cultivar identity is confounded with site-specific conditions; consequently, observed

cultivar-specific patterns should be interpreted as cultivar–site combination effects. Nevertheless, the present data establish maternal irrigation as a management-level determinant of F_1 seed stress resilience, and critically, they demonstrate that under an equal water quota, drip irrigation programmes a transgenerational phenotype that combines rapid germination, superior root elongation, and balanced biomass allocation—a profile that is agronomically more robust than the delayed-emergence, shoot-suppressed phenotype programmed by furrow irrigation. This provides a basis for tailoring irrigation protocols during seed production to match anticipated target environments, contributing to the emerging concept of climate-smart seed production (Brunel-Muguet et al., 2025). In arid regions where irrigation water quotas are strictly regulated, the choice of delivery method under a fixed volume becomes a critical management lever.

4.4 Maternal irrigation legacy programmes transgenerational trait-integration networks

The correlation analyses demonstrate that maternal drip (DI) and furrow (FI) irrigation during hybrid seed production did not merely alter isolated trait means, but reshaped the covariance architecture among F_1 offspring traits. This pattern aligns with the concept of phenotypic integration, whereby environmental cues experienced by the maternal plant rewire relationships among offspring traits rather than shifting single parameters in isolation (Pigliucci 2003; Murren 2012). Across both genetic backgrounds, thousand-seed weight (TSW) correlated positively with baseline germination rate (BaseGR; $r = 0.52$, $P < 0.01$) and root length (RL; $r = 0.35$–0.43, $P < 0.05$), while BaseGR itself was positively associated with RL ($r = 0.31$, $P < 0.05$). These converging pathways indicate that maternal irrigation transmitted transgenerational effects through at least two partially independent yet complementary mechanisms—resource provisioning (TSW) and metabolic priming (BaseGR)—both funnelling into belowground foraging capacity (Herman and Sultan, 2011; Donohue, 2009). The positive link between seed size and seedling vigour echoes the widespread seed-size–seedling-performance relationship documented across angiosperms (Moles and Westoby 2004; Rees and Brown 1991), yet our data extend this classical framework by showing that the maternal water regime can modulate the strength of this coupling in the F_1 generation. Importantly, under an identical water quota, maternal DI strengthened these positive couplings, whereas maternal FI disrupted them. The most functionally significant network divergence concerned the root-to-shoot ratio (R/S) and its coupling with integrated vigour. In the network topology of FI-derived progeny, elevated R/S was consistently associated with depressed shoot dry weight (SDW) and vigour index (VI; $r = -0.78$, $P < 0.001$) and negatively associated with GP ($r = -0.49$, $P < 0.05$), confirming that the compensatory root-foraging surge observed under mild-to-moderate stress (R/S peaking at 4.0–4.5) operated as a zero-sum carbon reallocation

strategy. This trade-off is not merely an alternative allocation scheme; it represents a metabolic compromise in which the maternal FI legacy forces progeny to divert carbon from photosynthetic tissues to root maintenance, thereby constraining overall growth potential. This pattern is consistent with biomass partitioning theory predicting allocation conflicts between root acquisition and shoot growth under resource limitation (Poorter et al. 2012). By contrast, DI-derived progeny maintained a low, stable R/S (0.5–1.5) while sustaining positive correlations among germination speed (GP), shoot biomass, and root length, reflecting a balanced growth architecture that preserved aboveground development without sacrificing belowground exploration. The DI network state is therefore characterized by functional synergy: seed size, metabolic priming, root elongation, and shoot growth operate as mutually reinforcing modules. The FI network state, by contrast, is characterized by functional antagonism: root allocation and shoot vigour are locked in a zero-sum relationship that depresses integrated performance. Root length emerged as the dominant driver of the vigour index across irrigation regimes (r = 0.85–0.97, $P < 0.001$), reinforcing the view that deep root systems serve as the primary transgenerational vehicle for saline–alkali tolerance by restricting toxic ion accumulation in surface horizons Munns and Tester (2008). Because DI progeny excelled specifically in this network-central trait while simultaneously preserving positive correlations with shoot biomass, they occupy a superior position in the transgenerational fitness landscape. Collectively, these correlation profiles demonstrate that DI programmes a functionally superior transgenerational network state characterized by coordinated positive linkages among TSW, BaseGR, RL, and SDW, enabling rapid germination initiation coupled with balanced seedling growth. The FI state shifts the network toward elevated R/S and anticorrelated shoot vigour, reflecting a stress-avoidance response that prioritizes root foraging at the expense of aerial biomass—a pattern indicative of metabolic compromise rather than adaptive resilience. Because these network topologies are programmed by a management-level decision—irrigation method under an equal water supply—rather than by genetic modification, they identify maternal drip irrigation as a practical, non-genetic lever for enhancing F_1 seed resilience in saline–alkali-prone environments (Brunel-Muguet et al., 2025). Tailoring irrigation protocols during seed production to programme the DI-type synergistic trait network, rather than simply maximizing mean yield or accepting the FI-type compromise network, represents an actionable and agronomically superior step toward climate-smart seed systems for salt-affected agriculture.

5.Conclusions

Maternal irrigation during hybrid maize seed production determines transgenerational saline–alkali tolerance in F_1 progeny. Critically, under an identical seasonal water quota of 4800 $m^3\ hm^{-2}$, drip irrigation (DI) consistently outperformed furrow irrigation (FI) across yield, seed quality, and stress-tolerance indicators. DI significantly increased seed yield per unit area, with a 37.1 % advantage in cultivar A (14 073.50 versus 10 264.72 kg hm^{-2}) and an 11.0 % advantage in cultivar B (11 207.69 versus 10 095.36 kg hm^{-2}). DI-derived seeds were significantly larger and heavier, as reflected by greater individual seed size and thousand-seed weight. Under saline–alkali stress, DI progeny displayed superior germination speed and amplified root elongation that expanded from approximately 26 % under control to approximately 73 % under 180 mmol L^{-1} alkalinity. DI progeny also sustained a balanced root-to-shoot ratio (0.5–1.5), preserving shoot biomass while simultaneously exploring deeper soil profiles. By contrast, FI progeny exhibited a compensatory surge in root-to-shoot ratio (peaking at 4.0–4.5), reflecting stress-induced carbon reallocation to root foraging at the expense of shoot development. Correlation analyses further revealed that DI programmed coordinated positive linkages among seed size, germination, and root length, whereas FI induced a zero-sum network state in which elevated R/S was strongly negatively correlated with shoot vigour (r = -0.78 in cultivar A). Although FI progeny occasionally recorded marginally higher final germination percentages under severe stress, this was invariably offset by delayed emergence and substantially suppressed shoot growth, yielding lower integrated seedling vigour and compromising field establishment potential. Collectively, these findings establish drip irrigation as the superior management strategy for maize hybrid seed production under equal water supply, delivering higher yield, better seed fill, and transgenerationally programmed F_1 progeny with faster germination, stronger root systems, and balanced biomass allocation. For saline–alkali-prone regions where water quotas are fixed, transitioning from furrow to drip irrigation during hybrid seed production offers a non-genetic, immediately implementable pathway to enhance both seed lot productivity and the inherent stress resilience of the resulting F_1 maize.

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Data Availability Statement: The datasets obtained during this study are accessible from the corresponding author upon reasonable request.

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Conflicts of Interest: The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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