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Architectural Space Modulates the Response of Rice to Abiotic Stress during Germination

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Abstract: The effect of space architecture on the performance of living organisms is poorly investigated. This work investigates the effect of a container shape on seed germination of rice. Seeds of rice (*Oryza sativa* cv. Sakha 101) were germinated under water potential (ψ_w) of 0, -0.205, -0.41, and -0.615 MPa, using either NaCl or PEG 6000 in wooden boxes of the same volume but with different base shape, viz. square, rectangle, pentagon, and hexagon. The Pentagon, which powered full germinability, with more uniformity and shorter lag of germination, was superior to other shapes, particularly the square which secured only 82% germinability. The differential adverse effect of osmoticum, in favor of PEG, was most evident at moderate stress (-0.410 MPa). The advantage of the Pentagon was more evident on embryo growth than on seed germination, but the reverse was true for the adverse effect of abiotic stress. The advantage of the Pentagon on embryo growth was related to improved membrane integrity and *vice versa* for the adverse effect of abiotic stress. Abiotic stress beyond ψ_w of -0.205 MPa progressively increased the thickness (the fresh weight/length ratio) of the embryo, with a greater effect on radicle than plumule and due to PEG than NaCl.

Keywords: Embryo growth, Germination speed, Membrane leakage, NaCl, PEG 6000, Pentagon.

1 Introduction

Shape, color, and sound can induce similar responses in living systems, via interaction with energy fields, to produce a balancing effect at multiple levels. Therefore, Gin [1] considered shapes as frozen qualities that affect the performance of living organisms. In addition to the major determinants of plant growth (including the supply of water and nutrients), plant performance can be modulated by a multitude of mild effectors such as type, size, color and shape of the container in the nursery as well as plant spacing and orientation in the field. Plant productivity can be affected by planting geometry in the field. The better growth of *Phaseolus vulgaris* [2] in the north-south than the east-west direction has been attributed either to the higher soil temperature and radiation interception or the perception of higher FR/R light ratio by plants of the north-south direction. Likewise, the higher harvest index of drought-stressed *Sorghum bicolor* planted in clumps above that of evenly-spaced plants was attributed to fewer tillering and lower vapor pressure deficits of clump plants [3].

In nursery beds, in addition to the size of the container, type and shape of a container are also important. The advantage of hard plastic containers over paper pots [4], of root trainers over plastic pots [5] and smooth-sided containers over rough-textured containers [6] has been reported. The height of tomato seedling increased as the container shape was changed from a square to a rectangle, but narrower cells decreased seedling height [6]. Because roots of transplants in plug tray cells proliferate at the growing medium-cell interface, seedling growth of Chinese cabbage [7] was better in square cells than round cells. The advantage of pyramidal cells over square or round cells has been recorded for lettuce and leek [8] and sweet potato [9]. Chen et al. [7] demonstrated that even with the same substrate volume and plant density, cell shape affected growth and performance of Chinese cabbage seedlings, with marked interference from the developmental stage. Geometrically, with equivalent volume, the interior surface area of the round, pentagonal, square and triangular cells is of increasing order, while cell angles exhibit the reverse order. Cell shape can affect the water-holding capacity of the growing medium; the larger the interior surface area of cells the greater will be the water-holding capacity. Because water is held by the growing medium as well as on its periphery adjacent to the inner cell wall due to surface tension, round containers have the minimum exposed surface area, the lowest water-holding capacity and the greatest ability to induce water stress compared with the square containers [10, 11].

The influence of pyramidal shape, in particular, on biological systems has been manifested as inhibition of microbial growth of milk and increased water and food safety and quality [12]. This effect was attributed either to energy trapping by the pyramid or alteration of the crystallization mode of water's mineral content, via induction of a low-frequency magnetic field. Furthermore, the pyramid structure has been reported to alter the pH of the solution, promote moisture loss of biological samples and decomposition of H_2O_2 [13] and probably might reduce tumor size in mice [12].

Rice is an important cereal crop, with numerous cultivars of divergent yield potentiality. In spite of the importance of rice as a daily food for a great sector of the world's population, consumption of huge amounts of water by rice plantations puts a heavy demand on water supplies, particu-

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larly in the arid regions. Furthermore, the reduced supply, along with a deteriorated quality of water, necessitates evaluating abiotic stress tolerance, particularly salt stress and water stress, of rice to find out safe and economic practices to enhance crop yield under stress conditions. The present work aims to investigate the effect of the geometry of container on the response of cv. Sakha 101 of rice to abiotic stress during germination. Among several Egyptian rice cultivars, Sakha 101 was the most productive one [14]. Because germination is usually carried out in the dark and presents the earliest stage in plant development, any possible effects related to radiation interception as well as the complications arising from root proliferation and circling within the container can be excluded.

2 Materials and Methods

2.1 Plant material and germination conditions

Seeds of *Oryza sativa* L. cv. Sakha 101 were obtained from the Experimental Station of Agricultural Research at Giza, Egypt. Uniform seeds were germinated at 35 °C in the dark in 12 cm Petri dishes lined with filter papers moistened with the test solutions, 50 seeds per dish. At intervals seeds and emerging seedlings were transferred, under dim light, to fresh solutions to prevent a buildup of solutes. Seeds were considered germinating with the emergence of radicle up to 2 mm.

2.2 Container shape × abiotic stress interaction on germination of rice

Petri dishes, with seeds, were placed in wooden containers of the same volume (11,370 cm^3) and height (28.5 cm) but with different base shape, viz. rectangular, square, pentagonal and hexagonal. The specifications of the four shapes are summarized in the following table:

Base shape	Base dimensions (cm)	Internal Surface area	Head angle (°)	Central angle (°)
Square	20	3080	90	90
Rectangle	25.4 × 15.7	3140	90	64.5 × 115.5
Pentagon	15.2	2961	108	72
Hexagon	12.4	2919	120	60

Within each shape, seeds were germinated in isosmotic solutions of NaCl and PEG 6000 at a water potential (ψ_w) of 0, -0.205, -0.410 and -0.615 MPa. To prepare iso-osmotic solutions of NaCl and PEG, the following formulae of Money [15] were used:

for NaCl $\Pi = 4.1 \times C$ $r^2 = 0.9997$

for PEG 6000 $\Pi = -12.1 \times C + 980 \times C^2$ $r^2 = 0.9990$

where Π is ψ_w in MPa and C is the molarity of the solution.

The experiment was factorial with three factors and three replications in a completely randomized design. The main factors were 1) shape of the container with four levels: square, rectangular, pentagonal, and hexagonal, 2) osmoticum type (Osm.) with 2 levels: NaCl and PEG 6000, 3) ψ_w of the medium with four levels: 0, -0.205, -0.410 and -0.615 MPa.

Seed germination was monitored daily for 8 days. By the end of the germination period, lengths and fresh weights of radicles and plumules were measured. Membrane leakage of the emerging radicle was estimated by measuring electrical conductivity (EC) according to Shalata and Neumann [16]. Radicles were rinsed for 5 min. in a large volume of 0.5 mM $CaCl_2$ and then in distilled water prior to incubation under dim light in 5 ml deionized water for 1 h, and EC of the bathing solution was measured. Tissues were then immersed in 5 ml fresh water at 95 °C for 5 min., cooled and incubated for 1 h prior to measurement of EC. Membrane leakage was estimated as ion leakage from live tissues expressed as % of the total EC (EC of live tissues + EC of killed tissues).

2.3 Germination parameters

Germination parameters were estimated according to Ranal and Santana [17] as follows:

1. Germinability is the final cumulative germination percentage (FGP).

2. Rate or speed of germination was estimated in terms of the germination value of Czabator (GV)

$$GV = PV \times \text{final } MDG \quad (\% \text{ day}^{-1})$$

where PV is the peak value or the maximum mean daily germination (MDG).

$$MDG = \frac{\text{cumulative germination \% at time } t_i}{t_i} \quad (\% \text{ day}^{-1})$$

3. Germination times:

Time to 10% germination (T_{10}) is a measure of the lag period between imbibition and onset of germination.

4. Uniformity of germination:

The coefficient of uniformity of germination (CUG) measures the variability among seeds in relation to the mean germination time and was calculated as:

$$CUG = \frac{\Sigma g_i}{\Sigma(\bar{t}-t_i)^2 \times g_i} \quad (\text{day}^{-2})$$

High values of CUG indicate concentrated germination in time.

5. Synchrony of germination was estimated using the synchronization index ($\bar{E}$), calculated as follows:

$$\bar{E} = -\Sigma f_i \times \log_2 f_i \quad \text{bit} \qquad \text{and } f_i = \frac{g_i}{\Sigma g_i}$$

Low values of $\bar{E}$ indicate more synchronized germination.

2.4 Statistical analysis

The final germination percentage and the percentage of membrane leakage were arcsine-transformed before performing ANOVA to ensure homogeneity of variance. Data were ana-

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lyzed using SPSS version 22. Mean separation was performed using the Duncan's multiple range test at P<0.05. T_{10} was calculated using the mean germination percentages of the times course of germination curves; therefore, they were not subjected to ANOVA and their values were not followed by SE. Correlation analysis was performed using Microsoft Excel, and linear and polynomial trend lines were tried to give the best fit.

3 Results

ANOVA reveals a highly significant effect (P<0.01) of the main factors and their interactions on most of the germination parameters of rice. However, based on values of the F ratio the most reliable parameter of rice germination was the final germination percentage, followed by germination speed, whereas the least sensitive parameters were germination uniformity and germination synchrony (Table 1).

Table 1 Three-way ANOVA showing the effect of the main factors (container shape, Osm., and ϕ w of the medium) and their interactions on germination parameters, embryo growth and membrane leakage of the radicle of *Oryza sativa* L. cv. Sakha 101.

Variable and source of variation	df	F	P	Variable and source of variation	df	F	P
Germinability (deg.)				**Radicle length**			
Shape	3	301.9	0.000	Shape	3	175.9	0.000
Osm.	1	879.3	0.000	Osm.	1	91.36	0.000
ψ_w	3	10728	0.000	ψ_w	3	2262	0.000
Shape × Osm.	3	0.553	0.650	Shape × Osm.	3	0.471	0.705
Shape × ψ_w	9	87.93	0.000	Shape × ψ_w	9	13.72	0.000
Osm. × ψ_w	3	303.4	0.000	Osm. × ψ_w	3	20.62	0.000
Shape × Osm. × ψ_w	9	1.607	0.155	Shape × Osm. × ψ_w	9	0.219	0.990
Germination value (GV)				**Plumule length**			
Shape	3	19.15	0.000	Shape	3	389.4	0.000
Osm.	1	33.03	0.000	Osm.	1	180.5	0.000
ψ_w	3	810.8	0.000	ψ_w	3	4306	0.000
Shape × Osm.	3	0.323	0.809	Shape × Osm.	3	1.083	0.370
Shape × ψ_w	9	6.126	0.000	Shape × ψ_w	9	27.01	0.000
Osm. × ψ_w	3	10.31	0.000	Osm. × ψ_w	3	45.60	0.000
Shape × Osm. × ψ_w	9	0.214	0.990	Shape × Osm. × ψ_w	9	0.354	0.948
Coefficient of germination uniformity				**Radicle FW**			
Shape	3	4.161	0.013	Shape	3	62.39	0.000
Osm.	1	6.599	0.015	Osm.	1	208.6	0.000
ψ_w	3	4.126	0.014	ψ_w	3	845.0	0.000
Shape × Osm.	3	2.916	0.049	Shape × Osm.	3	0.075	0.973
Shape × ψ_w	9	1.262	0.295	Shape × ψ_w	9	0.688	0.717
Osm. × ψ_w	3	1.643	0.199	Osm. × ψ_w	3	23.71	0.000
Shape × Osm. × ψ_w	9	1.383	0.237	Shape × Osm. × ψ_w	9	0.058	1.000
Synchronization index ($\bar{E}$)				**Plumule FW**			
Shape	3	7.852	0.000	Shape	3	29.79	0.000
Osm.	1	1.122	0.297	Osm.	1	158.7	0.000
ψ_w	3	1.450	0.247	ψ_w	3	379.4	0.000
Shape × Osm.	3	2.134	0.115	Shape × Osm.	3	0.097	0.961
Shape × ψ_w	9	1.728	0.123	Shape × ψ_w	9	0.395	0.933
Osm. × ψ_w	3	0.144	0.933	Osm. × ψ_w	3	18.00	0.000
Shape × Osm. × ψ_w	9	0.471	0.883	Shape × Osm. × ψ_w	9	0.066	1.000
Membrane leakage (deg.)							
Shape	3	6.262	0.001				
Osm.	1	13.15	0.001				
ψ_w	3	375.1	0.000				
Shape × Osm.	3	0.501	0.683				
Shape × ψ_w	9	0.837	0.585				
Osm. × ψ_w	3	3.839	0.014				
Shape × Osm. × ψ_w	9	0.592	0.799				

The FGP and the GV were in the order: pentagon > hexagon > rectangular > square. The advantage of the pentagon was more evident in terms of the GV than the FGP, with 48% and 22% higher values, respectively in the pentagon above the square in absence of stress. Furthermore, the advantage of the pentagon emerged more convincingly under abiotic stress, particularly water stress, under which the GV of the pentagon was 186% higher than that of the square versus only 87% increase under salt stress (Table 2). The adverse effect of abiotic stress on rice germination was more severe under the impact of water stress (PEG) compared with salt stress (NaCl), and this differential effect was more evident at the moderate depression of ψ_w (-0.41 MPa) than at severe stress (-0.615 MPa). Lowering ψ_w of the medium from 0 to -0.415 MPa reduced GV in the four containers by an average of 75% and 96%, under salt stress and water stress, respectively; but further lowering in ψ_w down to -0.615 MPa led to sharp comparable reduction of 98%, in the average, under salt stress and water stress (Figs. 1-2).

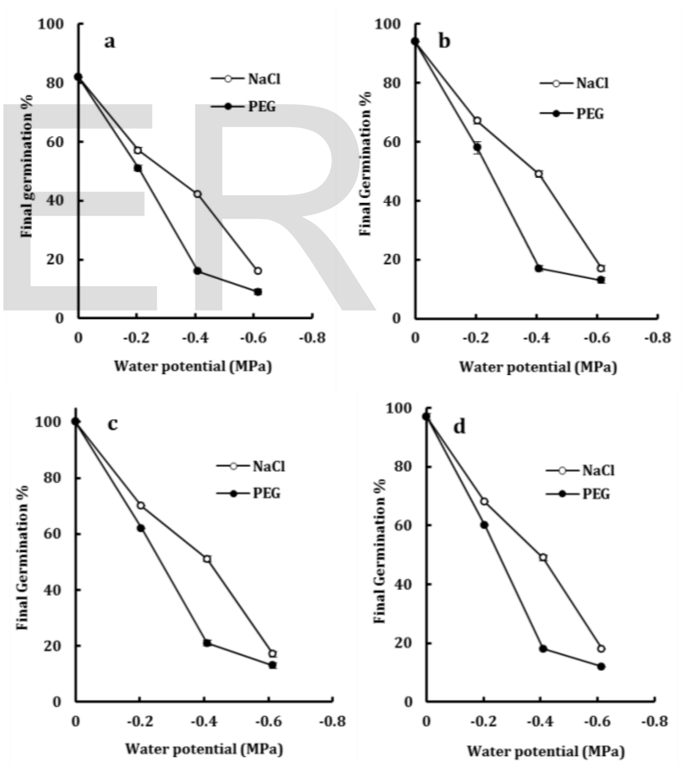

Fig. 1 Final germination percentage of *O. sativa* L. cv. Sakha 101 seeds under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

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Table 2 Summary of the effects of container shape on germination parameters of *O. sativa* L. cv. Sakha 101 in absence of stress and under the impact of top abiotic stress (ψ_w of -0.615 MPa) imposed either as salt (NaCl) stress or water (PEG 6000) stress. Each value is the mean of 4 replicates ± SE. Means with common letters are non-significantly different at P<0.05.

Stress	Container shape				Container shape			
	Square	**Rectangular**	**Pentagon**	**Hexagon**	**Square**	**Rectangular**	**Pentagon**	**Hexagon**
	Final germination %				**GV (% day^{-1})**			
Ctrl	82 ± 0.0^{d}	94 ± 0.0^{c}	100 ± 0.0^{a}	97 ± 1.0^{b}	328 ± 20^{c}	387.8 ± 20^{b}	487.5 ± 37^{a}	448.3 ± 31^{a}
NaCl	16 ± 0.0^{e}	17 ± 1.0^{e}	17 ± 1.0^{e}	18 ± 0.0^{e}	8.0 ± 0.00^{d}	7.9 ± 1.15^{d}	15 ± 3.00^{d}	15.8 ± 2.25^{d}
PEG	9 ± 1.0^{g}	13 ± 1.0^{f}	13 ± 1.0^{f}	12 ± 0.0^{f}	2.9 ± 0.90^{d}	5.2 ± 0.65^{d}	8.3 ± 2.25^{d}	4.3 ± 0.25^{d}
	T_{10} (day)				**CUG (day^{-2})**			
Ctrl	0.30	0.30	0.25	0.28	0.54 ± 0.08^{cde}	0.41 ± 0.06^{cde}	0.51 ± 0.03^{cde}	0.41 ± 0.06^{cde}
NaCl	3.00	2.80	1.60	1.75	0.30 ± 0.03^{e}	0.39 ± 0.02^{de}	0.85 ± 0.02^{ab}	0.42 ± 0.02^{cde}
PEG	10	3.60	3.00	4.00	0.88 ± 0.04^{a}	0.60 ± 0.05^{bcd}	0.66 ± 0.04^{abc}	0.58 ± 0.02^{cd}
	$\bar{E}$ (bit)							
Ctrl	2.14 ± 0.10^{bc}	2.33 ± 0.06^{ab}	2.16 ± 0.04^{bc}	2.25 ± 0.04^{abc}				
NaCl	2.21 ± 0.05^{abc}	2.51 ± 0.00^{a}	1.83 ± 0.04^{d}	2.24 ± 0.02^{abc}				
PEG	1.97 ± 0.04^{cd}	2.25 ± 0.01^{abc}	2.05 ± 0.04^{cd}	2.26 ± 0.00^{abc}				

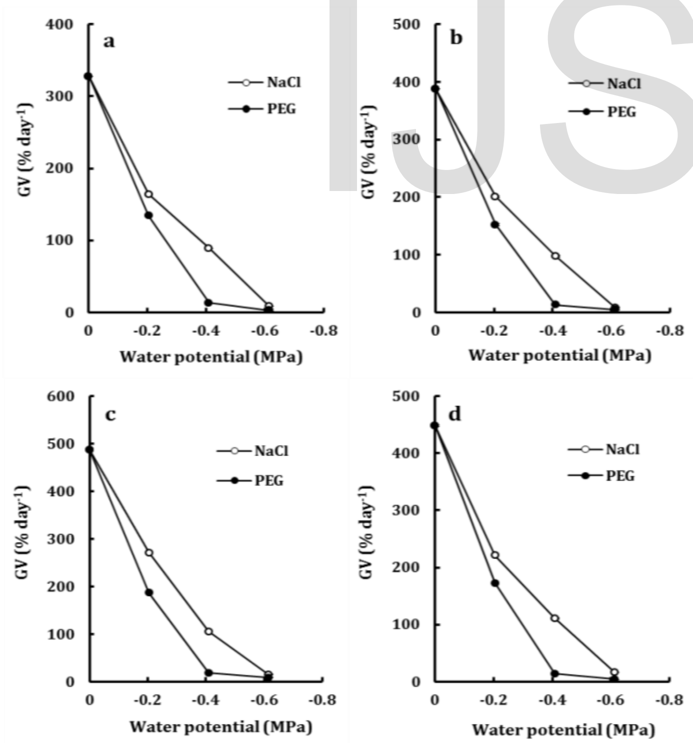

Fig. 2 Germination value (GV) of *O. sativa* L. cv. Sakha 101 seeds under the influence of container shape, Osm., and ψ_w of the medium Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

Uniformity of germination (CUG) was comparable in the four containers in absence of stress, but the effect of container shape emerged quite convincingly under abiotic stress, in favor of the pentagon under salt stress and of the square under water stress (Table 2). In the square, lowering ψ_w of the medium, post a threshold of -0.205 up to -0.615 MPa led to 44% reduction in CUG under salt stress but to 56% increase under water stress. In the rectangle and hexagon, a non-significant increase in CUG was found across the whole range of ψ_w. In the pentagon, CUG experienced transient non-significant reduction at -0.410 MPa, followed by 124% and 84% increases under salinity stress and water stress, respectively as ψ_w was further lowered down to -0.615 MPa (Fig. 3). Germination synchrony was non-significantly affected by treatments (Table 2 and Fig. 4); but it approached relatively high values (the lowest $\bar{E}$) in the pentagon under the impact of salt stress (Fig. 4). In absence of stress, T_{10} was comparable in the four containers; but, the effect of container shape emerged clearly under the impact of abiotic stress, at which T_{10} was shortest in the pentagon, followed by the rectangle and hexagon and was longest in the square (Table 2). Lowering ψ_w of the medium led to a sharp progressive increase in T_{10}, and the increase was more evident under the impact of water stress than salt stress and was most evident in the square but least evident in the pentagon (Fig. 5).

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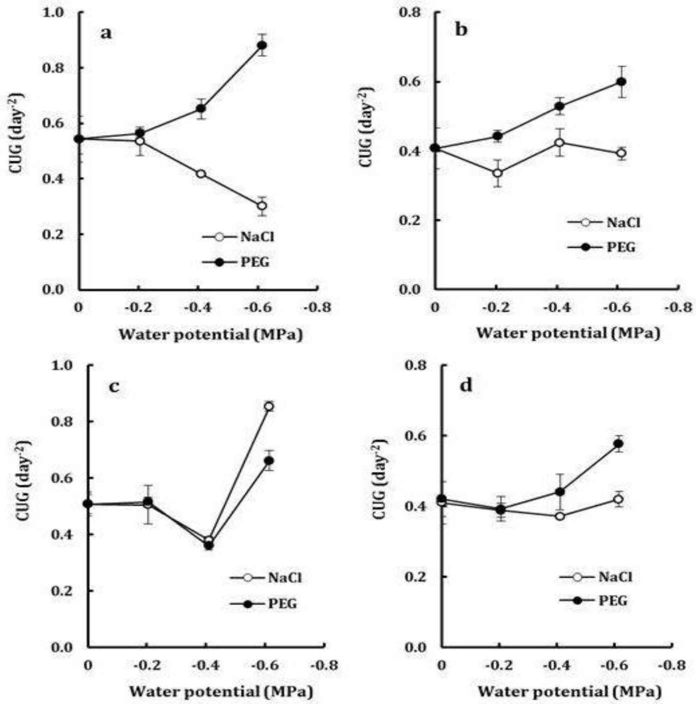

Fig. 3 Coefficient of uniformity of germination (CUG) of *O. sativa* L. cv. Sakha 101 seeds under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

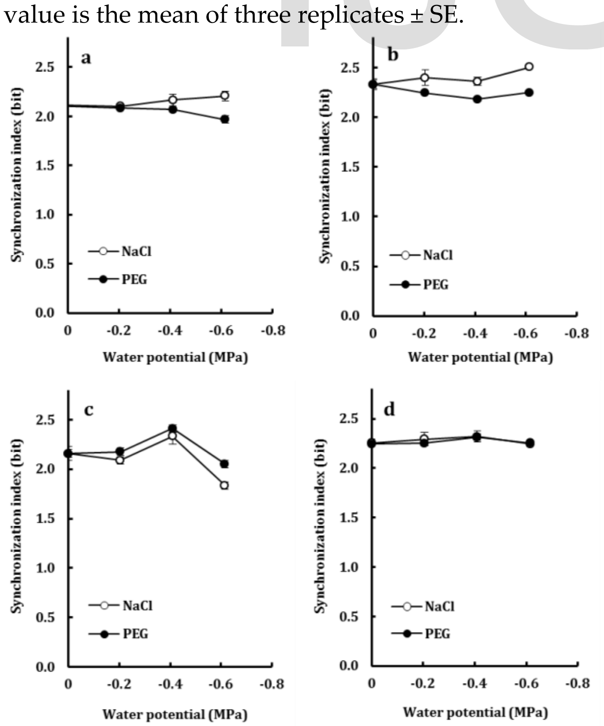

Fig. 4 Synchronization index of germination of *O. sativa* L. cv. Sakha 101 seeds under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

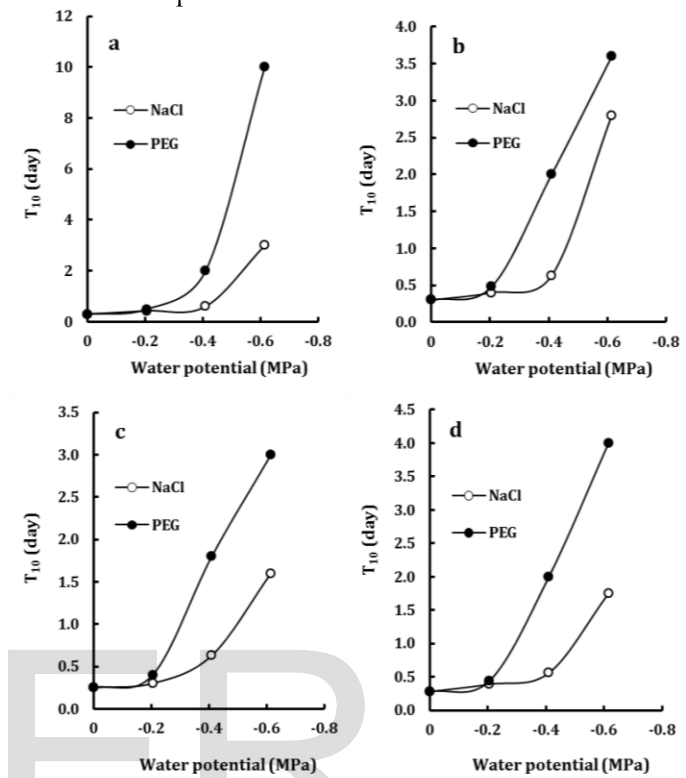

Fig. 5 Germination lag (T_{10}) of *O. sativa* L. cv. Sakha 101 seeds under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d).

The length and fresh weight of the embryonic axis were highest in the pentagon, moderate in the hexagon and rectangle and lowest in the square; and this pattern was maintained irrespective of the stress regime (Table 3). In the four containers, lowering ψ_w of the medium post a threshold of - 0.205 MPa down to - 0.615 MPa comparably reduced embryo extension, with more severe effect on radicle length (an average 77% reduction) than on plumule length (73% reduction) and under the impact of water stress (an average 79% reduction in radicle and plumule length) than salt stress (an average 72% reduction) (Fig. 6). Lowering ψ_w of the medium from 0 to -0.615 MPa progressively reduced fresh weights of plumule and radicle by an average of 40% under water stress and 30% under salt stress, irrespective of shape of the container (Fig. 7). The differential effect of treatments on biomass (fresh weight) and length of the embryonic axis led to a progressive increase in the fresh weight/length ratio as ψ_w of the medium was lowered beyond -0.205 MPa up to -0.615 MPa, with a greater effect on radicle than plumule and due to PEG than NaCl.

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Table 3 Summary of the effects of container shape on embryo growth and membrane leakage of the radicle of *O. sativa* L. cv. Sakha 101 in absence of stress and under the impact of top abiotic stress (ψ_w of -0.615 MPa) imposed either as salt (NaCl) stress or water (PEG 6000) stress. Each value is the mean of 4 replicates ± SE. Means with common letters are non-significantly different at P<0.05.

Stress	Container shape				Container shape			
	Square	**Rectangular**	**Pentagon**	**Hexagon**	**Square**	**Rectangular**	**Pentagon**	**Hexagon**
	Plumule length (mm)				**Radicle length (mm)**			
Ctrl	5.45 ± 0.05[d]	6.3 ± 0.10[c]	7.95 ± 0.05[a]	6.8 ± 0.00[b]	4.10 ± 0.10[d]	4.70 ± 0.10[c]	5.95 ± 0.15[a]	5.15 ± 0.15[b]
NaCl	1.65 ± 0.05[gh]	1.9 ± 0.10[fg]	2.4 ± 0.10[e]	2.05 ± 0.05[f]	1.05 ± 0.05[fghi]	1.20 ± 0.10[efg]	1.50 ± 0.10[e]	1.30 ± 0.10[ef]
PEG	1.30 ± 0.00[i]	1.5 ± 0.00[hi]	1.9 ± 0.00[fg]	1.65 ± 0.05[gh]	0.75 ± 0.05[i]	0.85 ± 0.05[hi]	1.10 ± 0.10[fgh]	0.95 ± 0.05[ghi]
	Plumule FW (mg plant^{-1})				**Radical FW (mg plant^{-1})**			
Ctrl	140 ± 4.51[b]	148 ± 4.51[a]	157.7 ± 5.36[a]	152.7 ± 4.33[a]	161.0 ± 2.52[c]	170.0 ± 2.52[b]	182.0 ± 2.52[a]	176.3 ± 2.73[ab]
NaCl	101.7 ±	107.7 ±	113.3 ± 2.37[c]	110.0 ± 2.08[cd]	111.7 ± 2.03[fg]	118.3 ± 2.33[ef]	126.3 ± 2.33[d]	122.7 ± 2.40[de]
PEG	85.7 ± 2.03[h]	90.3 ± 2.03[gh]	95.0 ± 2.31[fg]	94.0 ± 1.73[gh]	97.3 ± 2.33[i]	103.3 ± 2.40[hi]	108.7 ± 1.20[gh]	107.3 ± 2.40[h]
	Membrane leakage (%)							
Ctrl	25.5 ± 0.84[a]	24.2 ± 0.47[a]	23.2 ± 0.81[a]	24.0 ± 0.67[a]				
NaCl	61.3 ± 0.12[bc]	58.4 ± 1.65[bc]	54.6 ± 1.74[b]	57.9 ± 1.94[bc]				
PEG	65.5 ± 0.66[c]	62.6 ± 1.53[c]	58.1 ± 1.65[bc]	71.5 ± 1.13[d]				

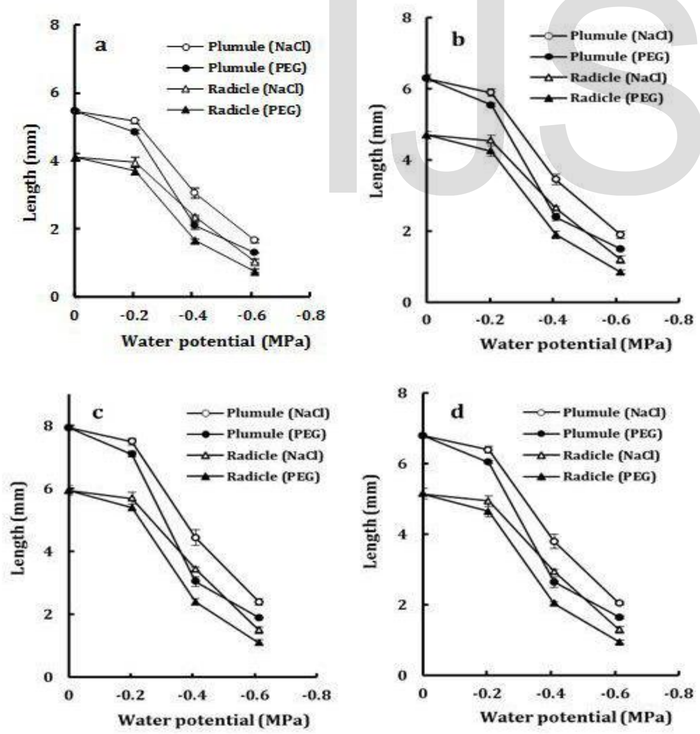

Fig. 6 Length of the embryonic axis of the emerging embryo of *O. sativa* L. cv. Sakha 101 under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

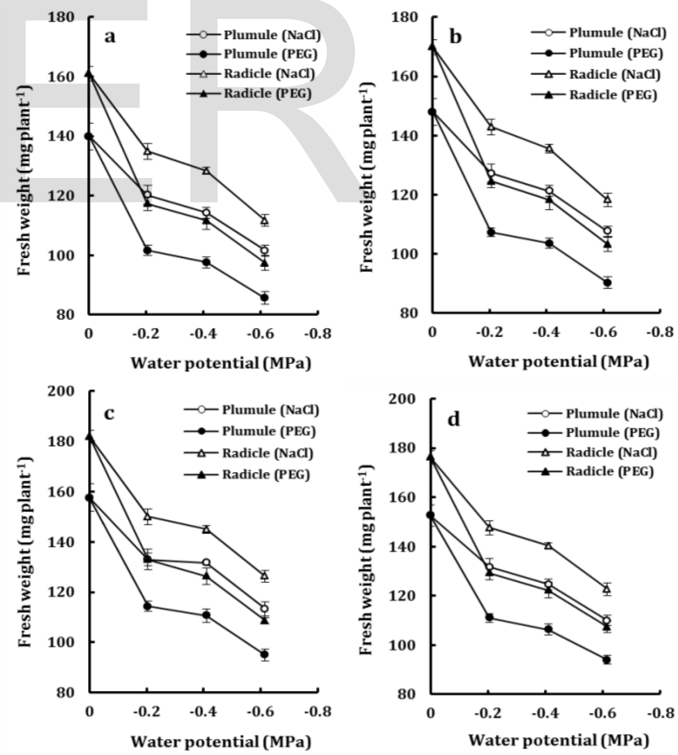

Fig. 7 Fresh weight of the emerging embryo of *O. sativa* L. cv. Sakha 101 under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

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Membrane leakage was very low, with comparable magnitude, in the four containers in absence of stress; but the effect of container shape emerged clearly under abiotic stress, with markedly lower membrane leakage in the pentagon relative to other containers (Table 3). Lowering ψ_w of the medium from 0 to -0.614 MPa progressively increased membrane leakage by an average of 167% under water stress and 140% under salt stress, irrespective of container shape (Fig. 8).

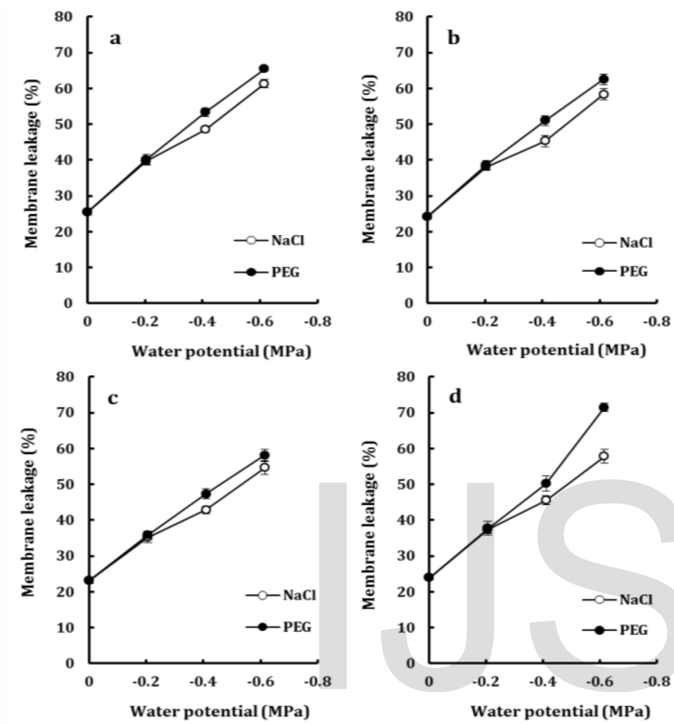

Fig. 8 Membrane leakage of the radicle of *O. sativa* L. cv. Sakha 101 under the influence of container shape, Osm., and ψ_w of the medium. Seeds were germinated under salt stress (NaCl) and water stress (PEG 6000) in wooden boxes of the same volume but with base shape either square (a), rectangular (b), pentagonal (c) or hexagonal (d). Each value is the mean of three replicates ± SE.

4 Discussion

Full germinability of the well-domesticated rice crop is expected in absence of abiotic stress. Failure of cv. Sakha 101 of rice to achieve full germinability (only 82% germination in the square container) suggests that a considerable proportion of the seed population of this cultivar possesses enforced or conditional dormancy, rather than being non-viable; since the pentagon container can power full germinability with enhanced speed, brief lag, and good embryo growth. Domestication of wild species in agriculture involves selection against the impeding trait of dormancy [18]. The superiority of the pentagon over the other three containers in enhancing rice germination can be related to several characteristics other than container volume, which was similar the same in the four containers. Container characteristics such as interior surface area and head angle can be considered to control rice germination. In this regard, Chen et al. [7, 10] postulated that the advantage of round cells above square cells in growth enhancement of Chinese cabbage seedlings is related to the small surface area and great angle of the square cells. They claimed that, with equivalent volume, the interior surface area of the round, pentagonal, square, and triangular cells is of increasing order, while cell angle exhibits the reverse order [7, 10]. Regarding the surface area of the four used containers, the square and rectangle, on one hand, shared comparable higher values than those of the pentagon and hexagon on the other hand. Likewise, the square and rectangle, on one hand, shared comparable smaller head angle (90°) than that of the pentagon (108°) and the hexagon (120°). In addition, the rank of the central angle, square (90°) > pentagon (72°) > rectangle (the smaller angle, 64°) > hexagon (60°), bears no relationship with germination performance of rice, which was in the order: pentagon > hexagon > rectangular >> square. The most appropriate characteristic of the four shapes, that may govern germination efficiency of rice, is probably the head angle/central angle ratio, which returned a significant quadratic relationship with most of the germination parameters (Fig. 9). Nevertheless, the direct relationship between this ratio and the energy-mediated impact of container shape on seed germination still to be resolved. The golden ratio governs the shape of a pentagon, and for Pythagoreans, it symbolizes the generation of the cosmos, spirit or ether [19]. The effect of container shape on plant performance can be modified according to the plant developmental stage [7].

The advantage of the pentagon over other containers as well as the differential impact of osmoticum (the more aggressive effect of PEG compared with NaCl) on rice germination was more evident in terms of the FGP than germination speed. Nevertheless, greater reliability of germination rate than germination magnitude in the evaluation of the impact of salt stress has been reported for quinoa [20] and *Vicia faba* [21]. The stronger impact of PEG relative to NaCl on rice germination at moderate stress (-0.410 MPa) rather than at severe stress (-0.615 MPa) is in accordance with the postulation of George et al. [22] that in salt-sensitive plants, growth inhibition and injury of the foliage occur at too low levels of NaCl to induce water deficit. Dominance of the osmotic component of salt stress on germination of chicory at high salinity was observed. It seems that at severe abiotic stress, the low ψ_w of the medium becomes too strong to allow a differential effect of NaCl and PEG on rice germination.

The beneficial influence of the pentagon in the enhancement of rice germination was associated with more uniform germination and shorter lag, with no effect on germination synchrony. However, El-Katony et al. [23] demonstrated

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that germination improvement due to a nutrient amendment of *Elymus farctus* seeds had no consequences on uniformity, synchrony, and lag of germination. However, the effect of abiotic stress on uniformity and synchrony of rice germination seems to vary according to the type of Osm. and shape of the container.

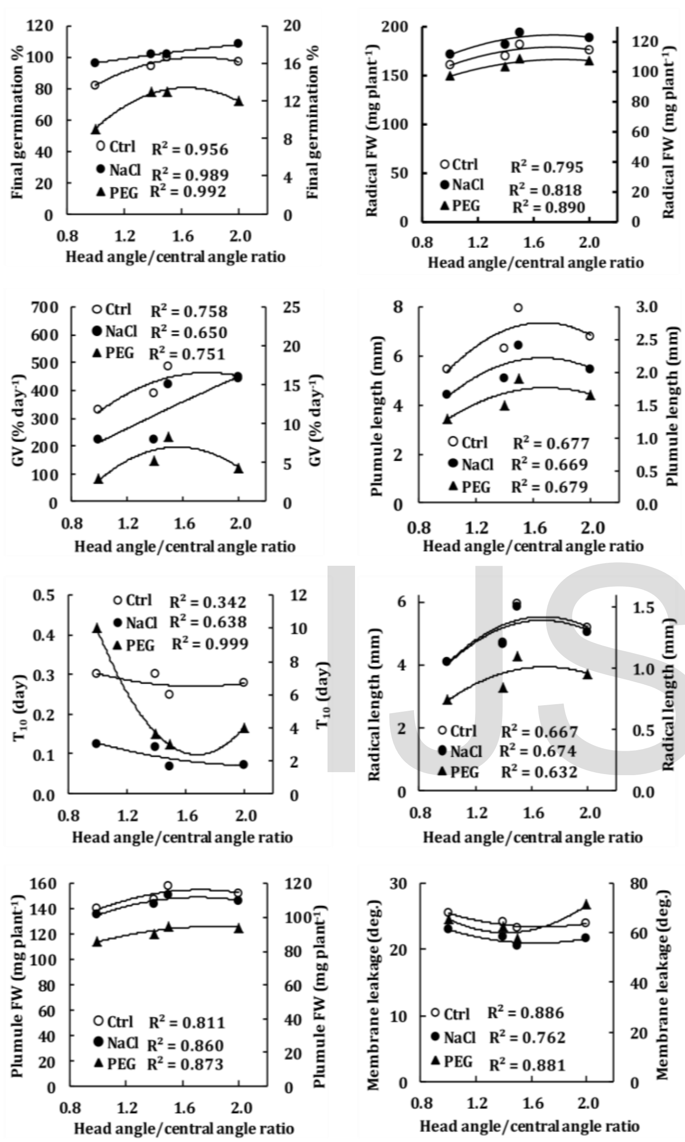

Fig. 9 Relationship between the head angle/central angle ratio of the base of container and germination parameters and membrane leakage of the radicle of *O. sativa* L. cv. Sakha 101 under the influence of -0.615 MPa induced either by NaCl or PEG 6000. The angle ratio was 1, 1.4, 1.5 and 2.0 for the square, rectangle, pentagon, and hexagon, respectively. The primary vertical axis was devoted for control and the secondary axis for stressed plants.

The species-specific effect of salinity on germination uniformity varied from a non-significant effect in *Physalis peruviana* [24] to a significant reduction in *Moringa oleifera* [25]. Similarly, Jeller and Perez [26] demonstrated reduced germination synchrony of *Senna spectabilis* seeds by salinity; whereas El-Katony et al. [23] reported increased germination synchrony by salinity only in non-amended *Elymus farctus* seeds, versus negligible effect in nutrient-amended seeds. The inhibitory effect of abiotic stress on magnitude and speed of rice germination, with prolongation of germination lag, coincides with the postulation of Hilhorst and Toorop [27] that stress conditions led to the restoration of the wild trait of dormancy in crop species. The sharp reduction in germination of rice under the fairly moderate stress of -0.614 MPa (equivalent to 150 mM NaCl) indicates that rice is salt-sensitive during germination, which is in agreement with the characterization of rice as a natrophobic and salt-sensitive species by Broadley et al. [28].

The advantage of the pentagon was, generally, more evident on the subsequent embryo growth than on seed germination. By contrast, the adverse effect of abiotic stress was more severe on seed germination than on embryo growth, with comparable effect on radicle and plumule and greater impact on embryo biomass than on its length. However, whereas the length of the embryonic axis exhibited -0.205 MPa threshold, beyond which it was severely reduced, the reverse was true for embryo biomass, where most of the reduction occurred within the -0.205 MPa threshold of embryo length. This results in the production of slightly thinner embryos (with negligibly lower biomass/length ratio) under mild stress versus markedly thicker embryos under severe stress, compared with the control. In contrast to the present findings, greater salt sensitivity of embryo growth than of seed germination has been reported for *Elymus farctus* [23], along with greater damage to plumule than radicle growth. The beneficial effect of the pentagon over the other shapes on embryo growth was associated with improved membrane integrity; and vice versa, retardation of embryo growth under abiotic stress, with a more adverse effect of PEG over NaCl, was associated with increased membrane leakage. Increased membrane leakage has been suggested as a likely cause of the damage induced by salinity stress in tomato [29] and *Brassica juncea* [30] as well as drought stress in rice [31]. However, no information is available concerning the effect of container shape on the membrane integrity of plants.

With the same ψ_w, the deleterious effect of salt stress on plant performance is expected to surpass the effect of water stress (induced by physical withholding of water); since the former involves an extra specific ion effect in addition to the osmotic effect shared by the two types of stress. Nevertheless, the present work suggests a more deleterious effect of water stress than that of salt stress on germination of rice. This can be resolved to assuming a beneficial role of salt ions, as cheap osmotic, in germinating rice seeds, particularly at moderate stress (-0.415 MPa = 100 mM NaCl), where the differential effect of NaCl and PEG was most pronounced. This hypothesis

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seems, however, unlikely in light of the fact that rice is a natrophobic and salt-sensitive species [28]. Alternatively, it seems that inducing water stress, manipulating PEG 6000, might yield a different response than the physical drought induced by the mere withholding of water from the soil. Although PEG 6000 is virtually assumed not to cross cellular membranes because of its high molecular weight, yet it seems to penetrate rice cells and to exert a specific toxic effect which is even stronger than that of NaCl. This toxic effect of PEG might arise from the polymer molecules themselves or, more likely, from some contaminants such as traces of the monomers or the chemicals used in the manufacture of the polymer. In support to our hypothesis, the more toxic effect of PEG on maize growth than that of NaCl [32] has been assigned either to the presence of toxic contaminants, reduced oxygen availability or inhibition of water uptake by as a result of the greater viscosity of PEG solutions compared with NaCl. However, the contribution of reduced oxygen availability is not likely for rice since paddy rice is well-adapted for anaerobic conditions.

5 Conclusion

The cv. Sakha 101 of rice has appreciable enforced dormancy which can be fully broken with high speed and uniformity of germination simply by using pentagon containers. The advantage of the pentagon over other shapes in the restoration of rice germinability and alleviation of abiotic stress can be related to the head angle/central angle ratio, which might have a role in the maintenance of membrane structure and functioning, particularly under abiotic stress. The toxicity of PEG 6000 on rice germination exceeded that of isosmotic NaCl. From an architectural point of view, pentagram containers can be manipulated to enhance germination and early seedling growth of rice and to alleviate the impact of abiotic stress on seed germination.

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