

NaCl salt stress and PEG water stress differentially affect germination and early seedling growth of two sesame (*Sesamum indicum* L.) cultivars

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3 Abstract

4 Drought stress and salt stress are serious challenges to crop productivity in the arid lands. This work investigates the impact of
5 NaCl-salt stress and PEG-water stress on germination and embryo growth of two sesame cultivars. The red seeds of Sohg were
6 larger with oblong appearance and lower density relative to the white seeds of Shnd. Seeds were germinated in the dark in
7 isosmotic solutions of NaCl and PEG-6000 at 0, -0.103, -0.205, -0.410 and -0.615 MPa. The time-based parameters, e.g. velocity,
8 uniformity and synchrony of germination were more reliable measures of germination efficiency than the final germination
9 percentage. The impact of PEG was more severe than that of NaCl particularly on Sohg. The peaks of daily germination
10 percentage were lowered and delayed under stress. The genotypic variability in germinability became evident under stress in
11 favor of Shnd. Radicle length was the most reliable measure of seedling growth but was subjected to stronger impact of NaCl
12 than PEG. Although Na⁺ mobilization from the seed to the emerging embryo was indifferent in the two cultivars in PEG solutions,
13 Shnd exhibited higher Na⁺ uptake from NaCl solutions. Whereas K⁺ mobilization was restricted by NaCl only in Sohg, it was
14 hastened by PEG equally in the two cultivars. The stress-vulnerable cv. (Sohg) recovered with higher magnitude than Shnd,
15 particularly from the more stressing osmoticum (PEG). The indices of germination recovery were highest in PEG-pretreated Sohg
16 while the fresh weight of recovered seedlings was highest in NaCl-pretreated Sohg.

17 **Key words:** Sesame . Genotype . NaCl . PEG-6000 . Germination speed . Germination uniformity . Seedling growth . Mineral
18 content . Recovery

19 1 Introduction

20 The current episode of climate disturbance has altered the amount and pattern of precipitation all over the world, leading to
21 increasing durations and severity of drought [15]. In arid regions, soil moisture is too low to secure satisfactory seed germination
22 which results in delayed and poor establishment of crop stands. The scarcity of fresh water resources forced farmers to use poor-
23 quality water in irrigation, thus raising the problem of secondary salinization.

24 Plant species exhibit differential tolerance to water stress and salt stress. Both stresses involve water deficit but salt stress
25 is characterized by the specific ion effect of Na⁺ or Cl⁻ [10]. Therefore, it is reasonable to assume that plants can adapt more easily
26 to water stress than to salt stress. But, better tolerance of some species and cultivars to salt stress than to water stress [25] raises
27 the probability that salt ions can ameliorate the adverse effect of low water potential of salt solutions. In addition to water deficit
28 and specific ion effect, the adverse effect of salt stress and drought stress on plant performance can be attributed to disturbance
29 of mineral nutrition and induction of oxidative stress. Sensitivity of plant species to abiotic stress can vary according to the plant
30 developmental stage. Salt tolerance of rice is particularly evident at germination [32] but the reverse seems true for salt tolerance

of sugar beet [11] as well as for salt tolerance and drought tolerance of sesame [4, 8]. Nevertheless, drought resistance at germination of rapeseed [14] and maize [3] matched the crop response at maturity.

Sesame (*Sesamum indicum* L.) is one of the most valuable oil cash crops in Africa and Asia [31]. The oil content and nutritional value of sesame seeds differ considerably according to the genotype, plant vigor and physiology. The black sesame cultivars are drought-resistant with low oil content of inferior quality but high protein and lignan contents relative to the white cultivars [6]. The high oil content of sesame seeds is characterized with high proportion of unsaturated fatty acids, particularly omega 3 and γ -tocopherol [30]. Sesame seeds are also rich in human-compatible proteins, most vitamins, dietary fibers and dietary minerals [17, 22] as well as the bioactive polyphenols, lignans, phytosterols, quinones and triterpenoids [19].

The decline in sesame productivity can be attributed to several constraints including drought episodes, improper cultural practices and selection of inferior cultivars. Therefore, research should be directed towards selection of the high performing and stress-resistant cultivars in addition to monitoring the consequences of abiotic stress on plant performance [16]. The present work investigates the differential impact of salt stress (induced by NaCl) and water stress (induced by polyethylene glycol, PEG-6000) on germination and early seedling growth of two Egyptian sesame cultivars (Sohag 1 and Shandaweel 3). Being particularly sensitive to water deficit at germination, sesame germination represents a critical stage that can be utilized as a quick and reliable indicator of plant performance under abiotic stress. The white-seeded Shandaweel 3 is more vigorous with higher yield potentiality than the yellow-seeded Sohag 1 [1, 12]. Our hypothesis is that: do NaCl-salt stress and PEG-water stress differentially affect germination of sesame in interaction with the genotype? The germination performance of seeds under stress will be evaluated in terms of the final germination percentage as well as the speed, uniformity, synchrony and lag of germination to identify the most reliable germination index.

2 Materials and methods

2.1 Plant material and stress solutions

Seeds of cultivars Sohag 1 (Sohg) and Shandaweel 3 (Shnd) of sesame (*Sesamum indicum* L.) were obtained from Oil Crops Research Department, Field Crops Research Institute (FCRI), Agricultural Research Center (ARC), Ministry of Agricultural and Land Reclamation, Egypt. The two experimental sesame cultivars are national cultivars, produced and released by Oil Crops Research Department, Field Crops Research Institute (FCRI), Agricultural Research Center (ARC), Ministry of Agricultural and Land Reclamation, Egypt according to The International Union for the Protection of New Varieties of Plants (UPOV) guideline (Egypt is a member of UPOV) and the Intellectual Property Rights (IPR) national law. The acquired names "Sohag 1" and "Shandaweel 3" are given by the breeder program of ARC and are related to national districts of Egypt. Seeds of the two cultivars exhibit distinct appearance; therefore, seed morphology was assessed. Seed length and width were measured using a 1-mm micrometer and seed volume was estimated by water displacement using 10-ml volumetric flask.

61 To prepare isosmotic solutions of NaCl and PEG, the following formulae [21] were adopted:

62 For NaCl $\psi_w = -4.1 \times C$

63 For PEG 6000 $\psi_w = -12.1 \times C + 980 \times C^2$

64 where ψ_w is the water potential (MPa) and C is the molarity of the solution.

65 According to these equations, water potentials of 0, -0.103, -0.205, -0.410 and -0.615 MPa correspond to 0, 25, 50, 100 and 150
66 mM NaCl, respectively and 0, 108.7, 131.4, 165.2 and 191.8 g PEG-6000 L⁻¹, respectively.

67 **2.2 Germination conditions**

68 Seeds were germinated in the dark between filter papers saturated with the test solutions in Petri dishes at 30 ± 2 °C; 50 uniform
69 seeds per dish. Seeds were frequently transferred to new Petri dishes lined with filter papers saturated with fresh test solutions to
70 prevent buildup of solutes. Seeds were considered germinated with the emergence of radicle up to 2 mm; and the number of
71 germinated seeds was counted daily for a period of 9 days. The recovery of germination from abiotic stress was assessed by
72 transfer of non-germinated seeds to distilled water and recovery was monitored for a period of 4 days. The recovery percentage
73 was estimated by calculating the number of germinated seeds after transfer to water as a percentage of the number of seeds
74 transferred.

75 **2.3 Seedling harvest and assay of minerals**

76 Upon approaching steady germination in treatment solutions, the emerged embryos were transferred to large plastic pots lined
77 with filter papers moistened with the test solutions under irradiance of 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ from white fluorescent tubes and
78 temperature of 30/20 °C at 14/10 h day/night periods, respectively for further three days. Seedlings were harvested, washed gently
79 with distilled water to remove the extraneous solutes where root length and fresh weight of the whole seedlings were recorded.
80 Dry weights were recorded after drying at 80 °C for 48 h. The dried seedlings were extracted in hot distilled water at 95 °C for
81 2 hours [13]. The debris was removed by centrifugation at 9500 rpm for 5 min. and the extract was used for determination of
82 soluble K⁺ and Na⁺ using a Jenway PFP7 flame photometer.

83 **2.4 Definitions and calculations**

84 According to [29], germination of sesame seeds was assessed in terms of the final germination percentage, speed, lag period,
85 uniformity and synchrony of germination.

86 1. Germinability is the final cumulative germination percentage, calculated by expressing the final number of germinants as a
87 percentage of the total number of seeds.

88 2. Germination lag

89 T₁₀ or time to 10% germination is a measure of germination lag that is the period between imbibition and onset of germination.

90 3. Speed of germination was estimated in terms of two indices as follows:

a) Timson index of germination velocity was calculated as:

$$\text{Timson index} = \frac{\sum G_i}{T} = \frac{G_1 + G_2 + G_3 + \dots + G_n}{T} \quad (\% \text{ day}^{-1})$$

where G_1, G_2, G_3, G_i and G_n are the cumulative germination % at the first, second, third, i^{th} and n^{th} time, respectively and T is the total germination period.

b) Weighted mean germination rate (WMGR) was calculated using the mean germination rate ($\bar{V}$) of each treatment and its variance (S^2_v) as follows:

$$\text{WMGR} = \frac{\sum (W_j \times \bar{V}_j)}{\sum W_j} \quad (\text{day}^{-1})$$

$$\text{where } W_j = \frac{n_j}{S^2_{j}} \quad S^2_{j} = (\bar{V})^4 \times S^2_t \quad n_j = \sum g_i \quad \text{and} \quad \bar{V} = \frac{1}{\bar{t}} \quad (\text{day}^{-1})$$

In the present work, WMGR was calculated using the equation $\text{WMGR} = \frac{W_j \times \bar{V}_j}{W_j}$ for each replicate in order to allow doing

ANOVA of WMGR, and this equation yielded very close values to the original equation.

4. Uniformity of germination

a) The coefficient of uniformity of germination (CUG) is a direct measure of germination uniformity that is high values indicate concentrated germination in time.

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

where g_i is the daily germination % at time t_i from sowing and $\bar{t}$ is the mean germination time.

$$\bar{t} = \frac{\sum g_i \times t_i}{\sum g_i} \quad (\text{day})$$

b) The coefficient of variation of germination time (CV_t) is an inverse measure of germination uniformity or the variability in the mean germination time and was calculated as:

$$CV_t = \frac{(S_t) \times 100}{\bar{t}} \quad \%$$

where S_t is the standard deviation of germination time and $\bar{t}$ the mean germination time.

The variance of germination time (S^2_t) was calculated according to the following formula:

$$S^2_t = \frac{\sum g_i (t_i - \bar{t})^2}{\sum g_i - 1} \quad (\text{day}^2)$$

5. Synchrony of germination was estimated using the synchronization index ($\bar{E}$) which is an inverse measure of germination uniformity:

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

where f_i is the relative frequency of germination, and g_i the daily germination % at day i .

118 **2.5 Experimental design and statistical analysis**

119 The experiment was factorial with three factors and three replications in a completely randomized design. The main factors were:
120 1) cultivar with two levels: Sohg and Shnd, 2) type of osmoticum with two levels: NaCl and PEG-6000 and 3) water potential
121 with five levels: 0, -0.103, -0.205, -0.410 and -0.615 MPa. Data were analyzed using SPSS version 22, and the effects of the main
122 factors and their interactions were assessed using three-way ANOVA. Mean separation was performed using the Duncan's
123 multiple range test at $P < 0.05$. Final germination percentage was arcsine-transformed prior to ANOVA to ensure homogeneity of
124 variance. The correlation among the different germination indices was assessed using Principal Component Analysis (PCA).

125 **3 Results**

126 The red seeds of Sohg were significantly longer and narrower, with larger volume, greater seed index and lower density relative
127 to the white seeds of Shnd (Table 1). ANOVA revealed that the most reliable germination parameters, based on the P value, were
128 germination velocity and germination synchrony whereas the least sensitive one was the final germination percentage. Also,
129 WMGR was a more reliable index of germination velocity than Timson index (Table 2).

130 **3.1 Time course of germination**

131 The cumulative germination percentage exhibited a sigmoid pattern with a brief lag followed by sharp increase and finally a
132 tendency to a plateau. The timing of transition between these phases and the final germination percentage varied according to
133 sesame genotype, type of osmoticum and water potential of the medium. Generally, the impact of PEG was more severe than that
134 of NaCl and the stress-susceptibility was more evident in Sohg than Shnd (Fig. 1). The daily germination percentage showed
135 peaks of different magnitudes and timing depending on the treatments. Generally, the daily germination peak was considerably
136 lowered and delayed as the water potential of the medium became more negative; and this pattern was more evident in Sohg than
137 Shnd and under the impact of PEG than NaCl. In Sohg, the daily germination peak was shifted from 54.4% by the 2nd day of
138 germination for the control to 12.3% at -0.615 MPa by the either the 5th day (NaCl) or the 6th day (PEG). In Shnd, the daily
139 germination peak was shifted from 52.2% by the 2nd day for the control to either 17.2% at -0.615 MPa NaCl by the 5th day or
140 12.2% at -0.615 MPa PEG by the 6th day (Fig. 2).

141 **3.2 Final germination percentage, germination lag and germination speed**

142 The final germination percentage (FGP) of Sohg exhibited a threshold of -0.410 MPa NaCl followed by mild reduction of 38%
143 at -0.615 MPa versus a less negative PEG threshold (-0.205 MPa) and a subsequent severe reduction of 57%. For Shnd, the
144 thresholds were less negative (-0.205 MPa NaCl and -0.103 MPa PEG), and also the subsequent reductions at -0.615 MPa were
145 less severe than those of Sohg (33% and 53% for NaCl and PEG, respectively) (Fig. 3a). Thus, the severe stress (-0.615 MPa)
146 cleared the genotypic difference in FGP in favor of Shnd and the adverse effect of osmoticum in favor of PEG.

Germination lag (T_{10}) was mildly affected by genotype but markedly lengthened with the severity of stress. Lowering water potential of the medium from 0 to -0.615 MPa increased T_{10} ; and the increase was more evident in Sohg than Shnd and under the impact of PEG than NaCl (Fig. 3b). Speed of germination was generally higher in Shnd than Sohg and under the impact of NaCl than PEG. Lowering water potential of NaCl and PEG solution from 0 to -0.615 MPa reduced the weighted mean germination rate (WMGR) of the two cultivars by an average of 53% and 57%, respectively (Fig. 3c) and Timson index (TI) by 61% and 76%, respectively (Fig. 3d).

3.3 Uniformity and synchrony of germination

The CV_t (an inverse measure of germination uniformity) was significantly higher in Sohg than Shnd, and in NaCl than PEG at mild stress (-0.103 MPa) but the reverse was true under severe stress (-0.615 MPa). Lowering water potential of NaCl solutions from 0 to -0.205 MPa led to 28% and 61% increases in CV_t of Sohg and Shnd, respectively followed by 14% average reduction at -0.615 MPa. Similarly, lowering water potential of PEG solutions from 0 to -0.103 MPa led to 59% average increase in CV_t of Sohg and Shnd, followed by 34% average reduction at -0.615 MPa (Fig. 4a).

The CUG—a direct index of germination uniformity—was significantly higher in Shnd than Sohg and under the impact of NaCl than PEG. Lowering water potential of NaCl solutions from 0 to -0.205 MPa led to an average 74% reduction in CUG of the two cultivars followed by steady low values at lower water potentials. Similarly, lowering water potential of PEG solutions from 0 to -0.103 MPa led to an average 80% reduction in CUG of the two cultivars followed by steady low levels at lower water potentials (Fig. 4b).

The $\bar{E}$ (an inverse index of germination synchrony) was significantly greater in Sohg than Shnd and in PEG than NaCl. Lowering water potential of NaCl solutions from 0 to -0.615 MPa increased $\bar{E}$ by 93% and 170% in Sohg and Shnd, respectively. Lowering water potential of PEG solutions from 0 to -0.103 MPa increased $\bar{E}$ by 88% and 96% in Sohg and Shnd, respectively with a tendency to a plateau at lower water potentials (Fig. 4c).

3.4 Growth and mineral composition of seedlings

ANOVA revealed that radicle length was more sensitive to treatments than seedling biomass and that seedling Na^+ content was more sensitive than K^+ content (Table 3). Lowering water potential of NaCl and PEG solutions from 0 to -0.615 MPa reduced seedling fresh weight of the two cultivars by an average of 86% and 72%, respectively (Fig. 5a). A different pattern was exhibited by seedling dry weight, where it was reduced in the two cultivars by moderate NaCl stress then increased under severe stress; meanwhile, moderate PEG stress markedly increased seedling dry weight of the two cultivars with a tendency towards steady values at severe stress (Fig. 5b).

Seedling water content exhibited changes that were more related to type of osmoticum than to genotype. Lowering water potential of NaCl solutions from 0 to -0.410 MPa led to an average 7% reduction in water content of Sohg and Shnd seedlings

177 followed by an average 41% reduction for the two cultivars with further lowering in water potential down to -0.615 MPa.
178 Lowering water potential of PEG solutions from 0 to -0.615 MPa led to a progressive moderate reduction of 26.5% in seedling
179 water content of the two cultivars (Fig. 5c). In contrast to seedling water content, the changes in radicle length were more related
180 to genotype than to type of osmoticum. Radicle length of Sohg exhibited progressive reduction with the lowering in water
181 potential of the medium from 0 to -0.615 MPa, and the reduction amounted to 97% and 73% in NaCl and PEG solutions,
182 respectively. By contrast, radicle length of Shnd was increased by moderate stress then reduced by severe stress; the initial
183 increase amounted to 12% at -0.103 MPa NaCl and 100% at -0.205 MPa PEG above the control and was followed by 93% and
184 65% reductions with further lowering in water potential to -0.615 MPa NaCl and PEG, respectively (Fig. 5d).

185 Lowering water potential of the medium from 0 to -0.615 MPa NaCl increased Na⁺ content of Sohg and Shnd seedlings
186 by 5.2 and 7.5 folds, respectively with non-significant effect of PEG (Fig. 6a). Lowering water potential of NaCl solutions post
187 a threshold of -0.103 MPa down to -0.615 MPa led to 70% reduction in K⁺ content of Sohg seedlings with non-significant effect
188 on Shnd seedlings. By contrast, lowering water potential of PEG solutions from 0 to -0.615 MPa increased seedling K⁺ content
189 of both cultivars (Fig. 6b). As a consequence of the changes in K⁺ and Na⁺ contents, K⁺/Na⁺ ratio of the seedlings experienced
190 an average 90% reduction in the two cultivars with the lowering in water potential of NaCl solutions from 0 to -0.615 MPa;
191 meanwhile it was increased by an average of four folds in PEG solutions (Fig. 6c).

192 **3.5 Recovery of germination from abiotic stress**

193 The stronger impact of PEG relative to NaCl on sesame germination allowed monitoring of recovery from the top NaCl solution
194 (-0.615 MPa) and the two highest PEG solutions (-0.410 and -0.615 MPa). Upon release of stress, seeds of the two cultivars
195 germinated readily without lag, with high speed and final germinability compared with the native seeds (Fig. 7a, b). The peak of
196 daily recovery of Sohg coincided with the first day of recovery for all stress pretreatments but, in contrast to germination of native
197 seeds, with markedly lower values in NaCl than in PEG (Fig. 7c). By contrast, the peak of Shnd recovery, being in accordance
198 with germination of its native seeds, moved from high value by the first day in NaCl solution to slightly lower comparable values
199 by the second day in PEG solutions (Fig. 7d).

200 The final recovery percentage from the top NaCl and PEG solutions (-0.615 MPa) was comparable in the two cultivars
201 but genotypic variability emerged in favor of Sohg only in -0.410 MPa PEG. Also, recovery was better from PEG (the more
202 stressing osmoticum) than from NaCl, particularly that of Sohg. The speed of recovery from NaCl stress was slightly higher for
203 Shnd than Sohg, but the reverse was true for recovery from PEG stress (Table 4). Uniformity of recovery was generally
204 comparable in the two cultivars (being in favor of Sohg only in -0.615 MPa PEG) and was generally higher from PEG than from
205 NaCl, particularly in Sohg. Synchrony of recovery from NaCl was comparable in the two cultivars but that from PEG was
206 significantly higher in Sohg than Shnd (lower $\bar{E}$) (Table 4). Fresh weight and water content of seedlings recovered from PEG

were comparable in the two cultivars but those of seedlings recovered from Na Cl were in favor of Sohg. Dry weight and radicle length of recovered seedlings were non-significantly affected neither by genotype nor by stress pretreatment (Table 5).

4 Discussion

The present findings suggest that the time-based parameters such as velocity, uniformity and synchrony of germination are more reliable measures of germination efficiency than the final germination percentage; that is the sesame cultivars Sohg and Shnd can attain the same final germination percentage but with different velocity, uniformity and synchrony. Whereas the genotypic difference was non-significant in final germination percentage it was highly significant in velocity, uniformity and synchrony of germination. Similarly, salinity has been reported to induce marginal reductions in germination capacity versus marked reductions in germination speed of four faba bean cultivars [7]. Furthermore, the weighted mean germination rate (WMGR) seems more sensitive index of germination velocity than Timson index. In this regard, **Ranal and Santana [29]** claimed that WMGR is a more representative index of germination velocity than the unweighted rates.

The stronger impact of PEG than NaCl on sesame germination raises several hypotheses: 1) sesame germination is more tolerant to salt stress than to drought stress; 2) the salt ions can partly alleviate the consequences of water deficit; 3) the molecules of PEG-6000 can exert a toxic effect that is more aggressive than that of Na⁺ and Cl⁻. The first hypothesis seems likely in view of the claim that sesame is more resistant to salt stress than to drought stress at germination and seedling stage [8]. Similarly, a stronger impact of PEG relative to NaCl on germination of *Mentha pulegium* [2] and different cultivars of sweet sorghum [28] has been reported. Thus, it is probable that inducing water stress using PEG have different consequences than the physical drought induced by water withholding. Although PEG, a high molecular weight osmoticum, is assumed not to cross cellular membranes; yet, it can exert a specific toxic effect on seed germination and seedling growth. The more aggressive effect of PEG relative to NaCl on maize growth has been attributed either to the presence of toxic contaminants, reduced oxygen availability or impeded water uptake by the root from the viscous PEG solutions [5].

Although sesame is sorted as salt- and drought-tolerant crop, it is sensitive to both stresses at germination and early seedling stage in a genotype-dependent pattern, where the yellow and brown sesame seeds of high germination potentiality were less-affected by salt stress and PEG stress than the white and black seeds of lower germination potentiality [8]. The present work reveals that the red large-sized seeds of Sohg, of low germination potentiality, seem more susceptible to NaCl and PEG stress than the white small-sized and highly germinable seeds of Shnd. Genotypic variability in tolerance to PEG-drought stress has been reported among 60 barley cultivars [23] and several maize cultivars [3]. The present findings suggest also that abiotic stress can maximize the rather vague genotypic variability in seed germinability (in favor of the vigorously germinating Shnd) with a more distinct role of PEG than NaCl. In accordance with the present work, the weak genotypic variability among four faba bean cultivars in germination potential became clearly evident under the impact of salt stress [7]. In addition to the genotypic

237 differences in speed, uniformity and synchrony of germination, the daily germination pattern differed in the two sesame cultivars.
238 The peak of daily germination was progressively lowered in magnitude and delayed in timing with the lowering of water potential
239 of the bathing solution, and this pattern was most evident in the sensitive cv. (Sohg) under the impact of the aggressive osmoticum
240 (PEG).

241 In accordance with the final germination percentage, speed of germination was faster in Shnd than Sohg and was
242 subjected to less reduction under the impact of NaCl than PEG. However, the presence of -0.103 MPa threshold for Timson index
243 of germination speed in NaCl-treated Sohg does not imply better resistance of Sohg than Shnd to stress. Meanwhile, the
244 percentage reduction in germination velocity of NaCl-treated Sohg post the threshold was comparable to that of NaCl-treated
245 Shnd. Sorting of crop salt tolerance is routinely based on threshold salinity and the critical salinity that is the salinity level
246 corresponding to 50% reduction in performance [11]. However, the threshold salinity rather than the critical salinity has been
247 recommended as the most reliable parameter for screening of barley germplasm for salt tolerance during germination [20].

248 The present findings suggest also that CUG is a more sensitive measure of germination uniformity than CV_t , since CUG
249 resolved the effect of osmoticum on germination uniformity while CV_t could not. Germination has been claimed as a high-risk
250 event in plant life because of the extreme delicacy of the emergent seedlings. Therefore, modulation of timing, uniformity and
251 synchrony of germination represent an adaptive strategy to adjust seedling emergence in the due time and under the favorable
252 circumstances for seedling establishment. The shorter germination lag (T_{10}) along with the higher uniformity and synchrony of
253 germination of Shnd than Sohg particularly under the impact of NaCl are other aspects of the superiority of germination efficiency
254 of Shnd and the less severe impact of NaCl on its germination efficiency. These findings support the claim that abiotic stress in
255 general and the more impacting osmoticum (PEG) in particular can maximize the genotypic variability in germination efficiency.
256 The final germination percentage, germination velocity, peak of daily germination, germination uniformity and germination
257 synchrony are significantly positively correlated with each other but negatively correlated with germination lag and timing of
258 daily germination peak (Fig. 8).

259 In accordance with the pattern of sesame germination, the adverse effect of abiotic stress was more evident on seedling
260 growth of Sohg than Shnd. However, the severity of stress was more pronounced in seedling fresh weight than in seed germination
261 with stronger impact of NaCl than PEG. This implies that the response pattern of sesame to abiotic stress during germination
262 might differ than the response of seedling growth, where sesame germination can be considered relatively salt-resistant while
263 seedling growth is drought-resistant. In this regard, the contradiction between salt tolerance of seed germination and early
264 vegetative growth has been reported for nine barley [18] and four faba bean [7] genotypes. Stronger impact of abiotic stress on
265 seedling growth than on seed germination have been reported for salt stress and water stress on sesame [8] and for salt stress on
266 sweet sorghum [27]. However, the stronger impact of PEG-water stress than that of NaCl-salt stress on seed germination of
267 *Mentha pulegium* was maintained during seedling growth [2].

268 The severe stress-induced reductions in seedling fresh weight along with the limited changes in seedling dry weight
269 suggests that the impact of NaCl and PEG stresses on seedling growth is mainly performed via an osmotic effect. It seems that
270 the osmotic effect of NaCl on seedling growth surpassed that of PEG despite the fact that the severe osmotic effect of NaCl
271 occurred post a threshold in front of the progressive but moderate effect of PEG. Again, as encountered in seed germination, the
272 emergence of a NaCl threshold does not ensure better resistance of seedling growth to salt stress. Another aspect of the more
273 stress-resistance of Shnd than Sohg and the more aggressive impact of NaCl than PEG on seedling growth can be found in the
274 beneficial effect of mild NaCl (-0.103 MPa) and moderate PEG (-0.205 MPa) on radicle length of only Shnd. In accordance with
275 the present findings, mild drought stress induced by PEG has been reported to improve radicle growth of several sesame cultivars,
276 with pronounced genotypic variability [4]. The differential stress-induced changes in seedling fresh weight and radicle length led
277 to altered specific weight of seedlings, that is the fresh weight/radicle length ratio which increased with the lowering in water
278 potential of the medium particularly in NaCl-treated Sohg. This implies that NaCl can lead to shorter and thicker seedlings,
279 particularly in Sohg while PEG can either lead to the opposite effect (in Shnd) or was without effect (in Sohg).

280 Since sesame seeds were germinated in aqueous solutions of NaCl and PEG without exogenous nutrient supply, the
281 changes in K^+ and Na^+ contents of PEG-treated seedlings and those in K^+ content of NaCl-treated seedlings can be attributed to
282 mobilization of minerals from the storage pool of seed to the emerging embryo. The moderate reduction in K^+ concentration of
283 seedlings, along with the severe reduction in seedling fresh weight by salinity suggest that NaCl can restrict K^+ mobilization from
284 the storage pool of seed to the emerging embryo. Meanwhile the substantial increase in seedling K^+ concentration by PEG
285 suggests that PEG can accelerate K^+ mobilization from the storage pool to the emerging embryo particularly in Shnd. On the
286 other hand, the non-significant effect of PEG on Na^+ concentration of seedlings along with the reduction in seedling biomass
287 implies that PEG can restrict Na^+ mobilization from the seed to the embryo. The overall higher Na^+ content of Shnd seedlings
288 than Sohg seedlings under the impact of salinity suggests that Shnd has greater capacity for Na^+ uptake from NaCl solutions than
289 Sohg.

290 The present finding suggests that subjecting sesame seeds to abiotic stress for a period of time can enhance their
291 subsequent germinability, and this priming effect was manifested as faster germination with no lag compared with the native non-
292 treated seeds. This priming effect which was most evident in the more sensitive cv. (Sohg) under the more stressing osmoticum
293 (PEG) can be manipulated to improve seed germination of inferior seeds under abiotic stress as has been claimed by **Nerson [24]**.
294 However, the pattern of daily recovery was genotype-dependent, where in Shnd PEG-pretreatment led to lowering and delaying
295 in peak of daily germination recovery relative to NaCl-pretreatment but in Sohg the peak was higher in PEG with the same timing
296 in both osmotica.

297 The genotypic pattern of recovery indices was modified by the stress pretreatment in contrast to the consistent superiority
298 of Shnd over Sohg in germination indices of native seeds. Whereas the magnitude, speed, uniformity and synchrony were better

in Shnd than Sohg for recovery from salinity stress, the reverse was true for recovery from PEG stress. The more aggressive effect of PEG on sesame germination along with better subsequent recovery relative to NaCl suggests that the more aggressive treatment (e.g. PEG on Sohg) can lead to better recovery upon release of stress. The lower final percent recovery and speed of recovery of Sohg from NaCl compared to PEG might refer to a toxic ion effect on seed viability, particularly in the more stress-susceptible cultivar Sohg. It has been postulated that improved germination efficiency upon release of stress points to an osmotic effect whereas low recovery refers to specific ion toxicity as has been reported for rice [9]. In this regard, the reduced germination recovery of barley from saline solutions was related to uptake of Na⁺ and loss of K⁺ from the seeds [26].

5 Conclusions

The time-based parameters such as velocity, uniformity and synchrony of germination are more reliable measures than the final germination percentage. The response of sesame to abiotic stress during germination differs than the response of seedlings; where germination is relatively salt-resistant but seedling growth is relatively drought-resistant. The seed lot of low germination potentiality were more susceptible to abiotic stress than the highly germinable seeds. Abiotic stress, particularly the severe PEG-induced stress maximizes the genotypic variability in seed germination. The lowered germinability under stress was associated with lowered and delayed daily germination peaks. The presence of stress threshold for germination rate does not ensure better resistance to stress. The final germination percentage, germination velocity, peak of daily germination, germination uniformity and germination synchrony are positively correlated with each other but negatively correlated with germination lag and the delay of daily germination peak. The impact of abiotic stress on seedling growth is mainly performed via an osmotic effect, with stronger effect of NaCl which produced shorter and thicker seedlings compared with PEG. Whereas K⁺ mobilization from seed storage pool to the embryo was restricted by NaCl, it was enhanced with restricted Na⁺ mobilization by PEG. Subjecting seeds to abiotic stress can enhance subsequent germinability, with ready recovery and no lag. This priming effect was most evident in the more sensitive genotype under the more stressing osmoticum (PEG). Salt ions exert toxic effect on seed viability, particularly in the more susceptible genotype.

Author contributions

Conceptualization: TME, NMH and SNA; Material preparation, data collection and analysis: SHA and SNA; Formal data analysis: TME and SHA; Writing—review and editing: TMS, SNA and NMS; Supervision: NMS and TME. All authors read and approved the final manuscript.

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329 **Declarations**

330 **Competing interests**

331 The authors declare that they have no competing interests.

332 **Data availability**

333 The data that support the findings of this study are available from the authors upon request.

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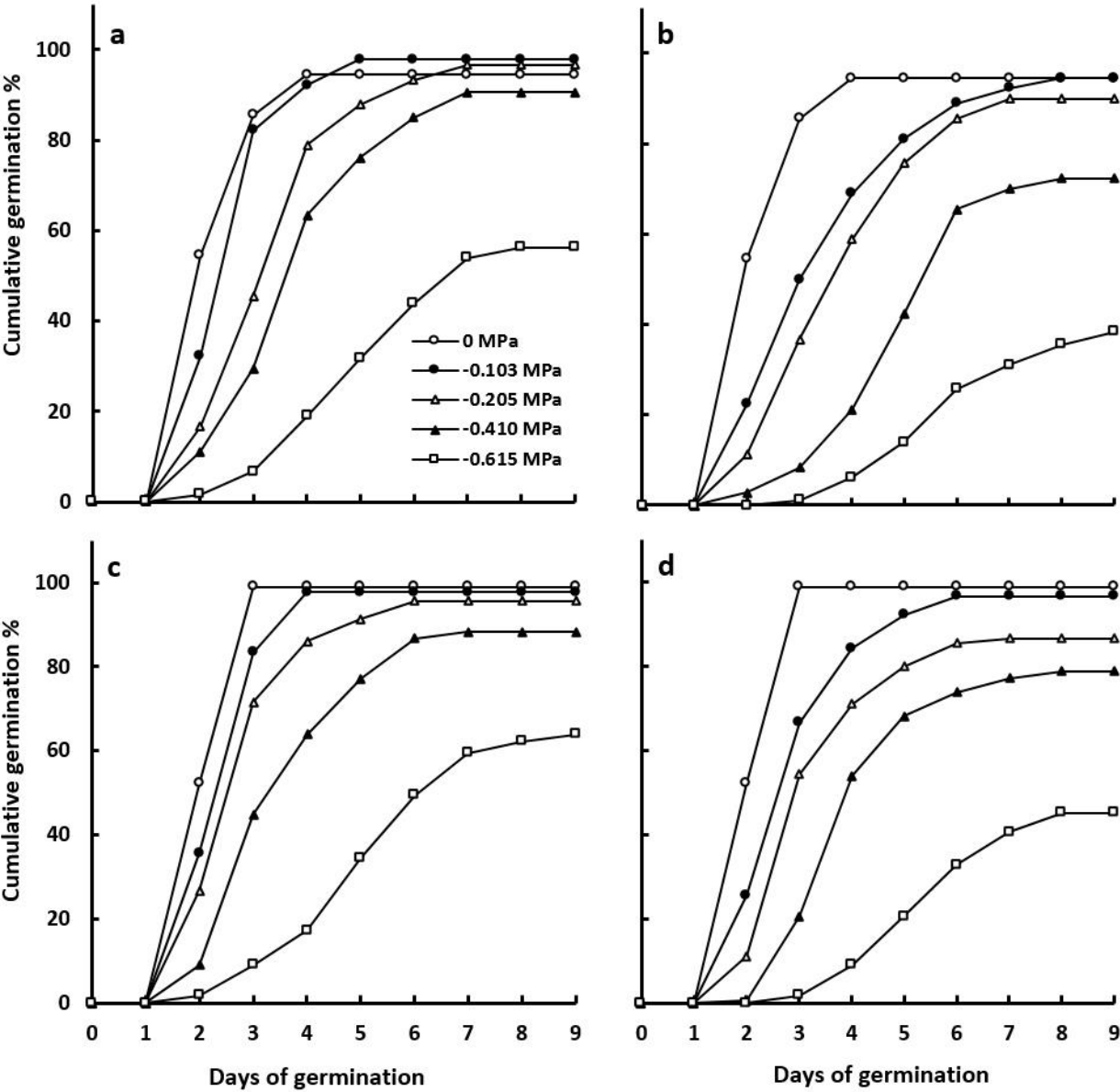
Figure captions

420

Fig. 1 Time course of cumulative germination of cvs. Sohg and Shnd of sesame in isosmotic solutions of NaCl and PEG-6000.

421

(a): Sohg NaCl, (b): Sohg PEG, (c): Shnd NaCl, (d): Shnd PEG. Each value is the mean of three replicates



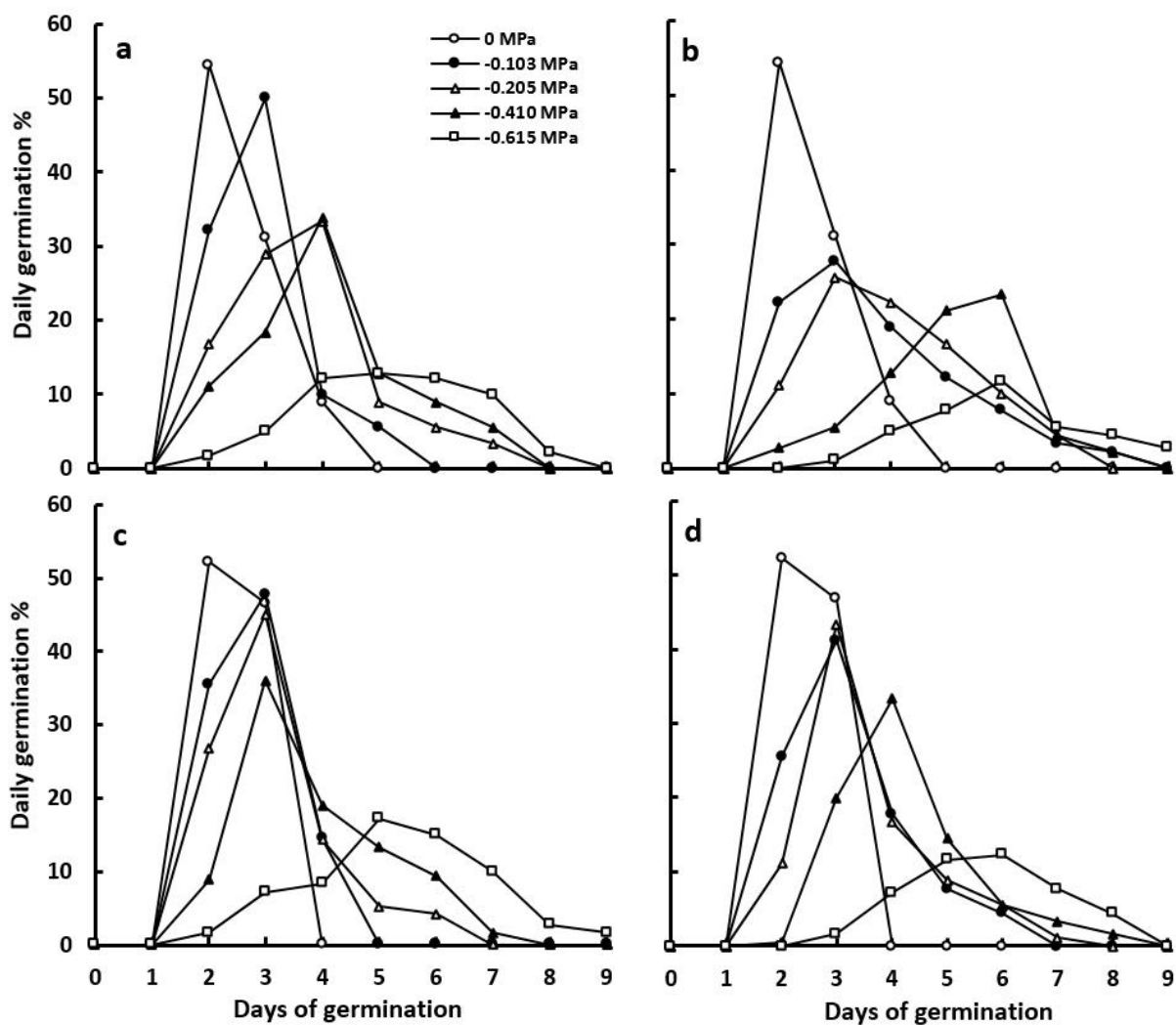
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Fig. 2 Time course of daily germination of cvs. Sohg and Shnd of sesame in isosmotic solutions of NaCl and PEG-6000. (a):

424

Sohg NaCl, (b): Sohg PEG, (c): Shnd NaCl, (d): Shnd PEG. Each value is the mean of three replicates



425

426 **Fig. 3** Final germination percentage (a), germination lag (T_{10} , b), WMGR (c) and Timson index (d) of cultivars Soh and Shnd
 427 of sesame in isosmotic solutions of NaCl and PEG-6000. Each value is the mean of three replicates $\pm$ SE. T_{10} was
 428 calculated from the time-course of germination curves, therefore, their means have no SE

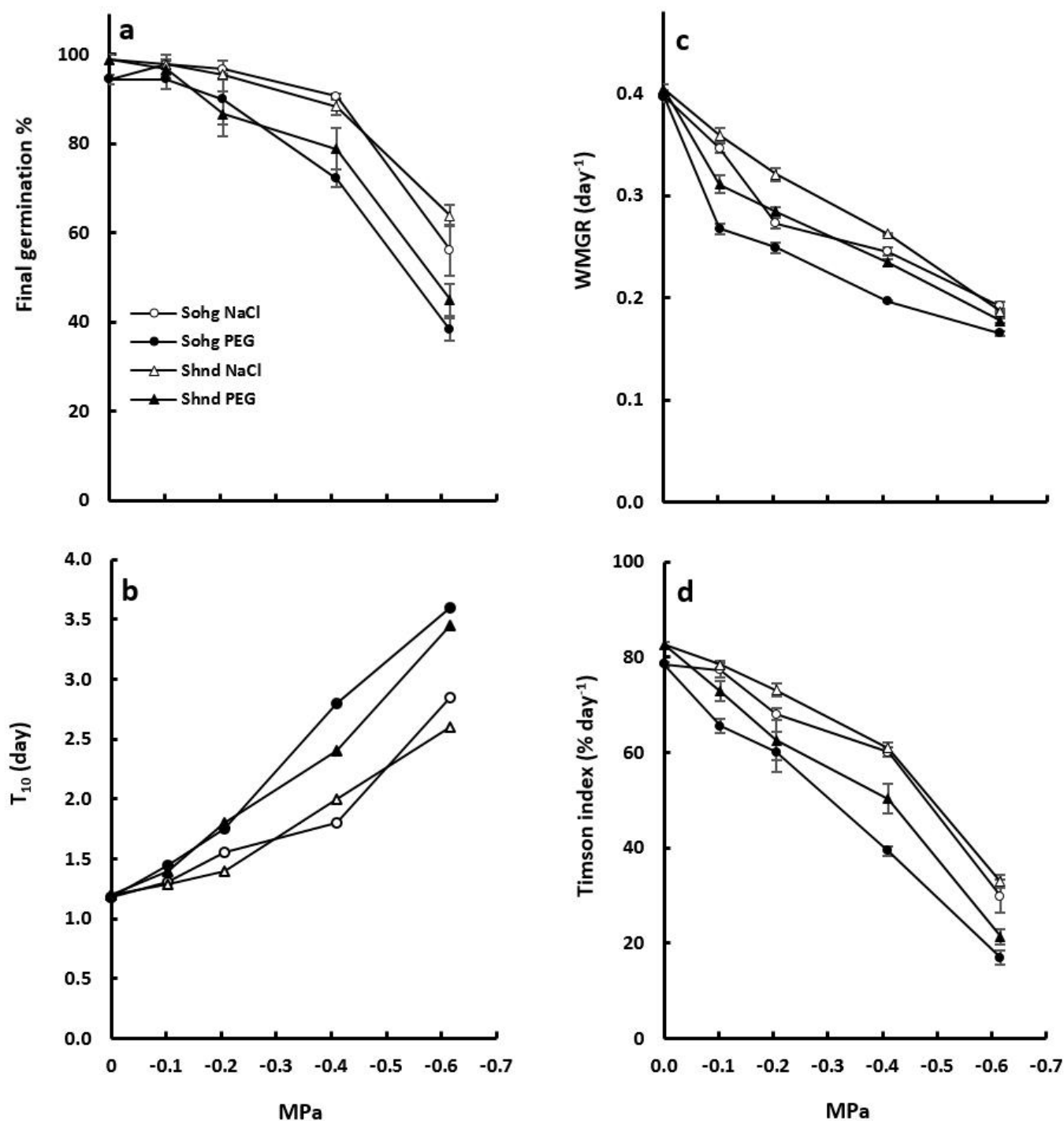
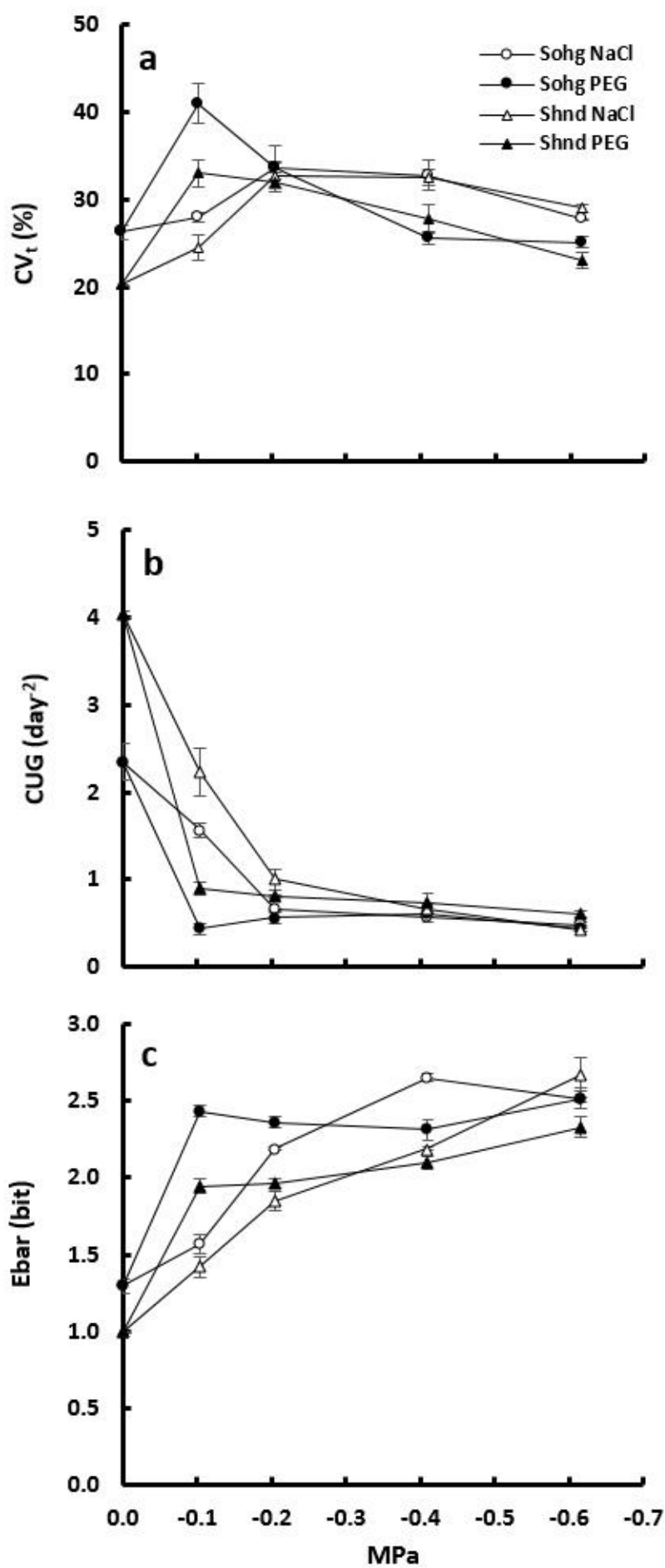
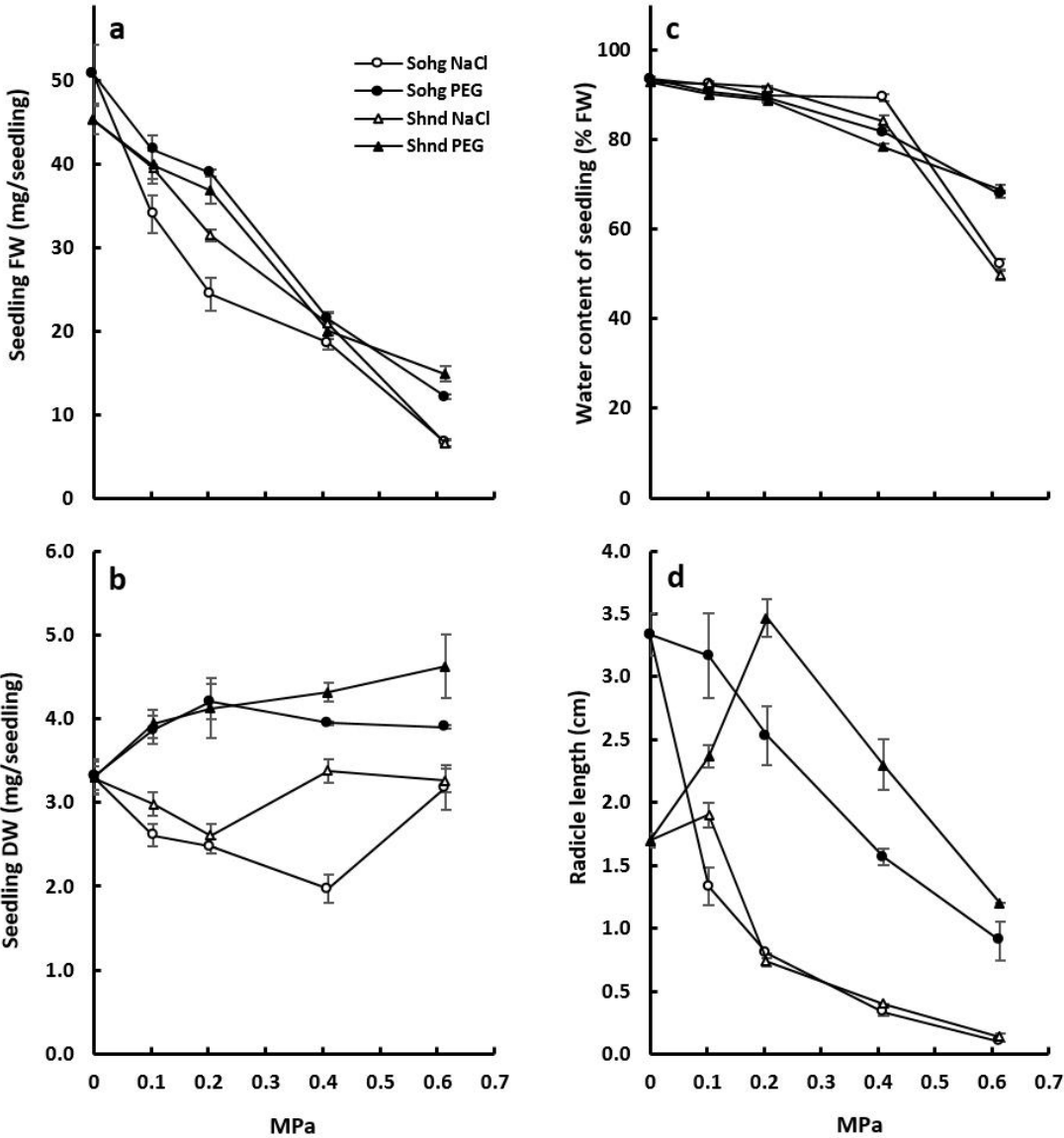


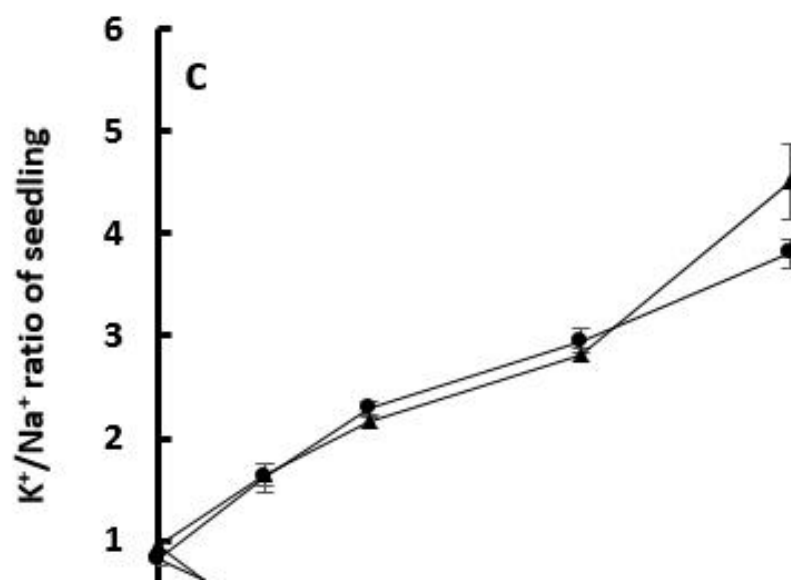
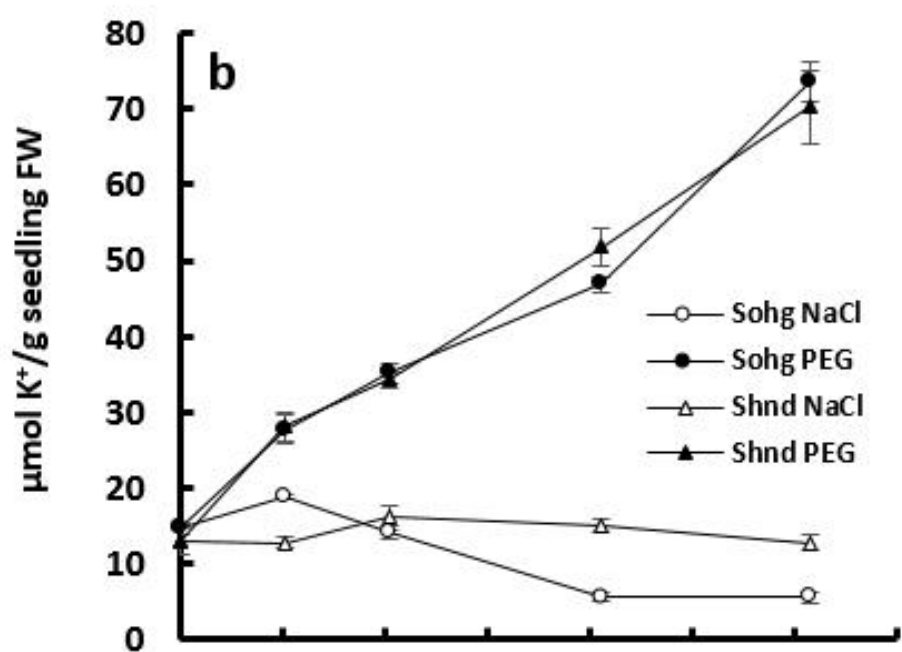
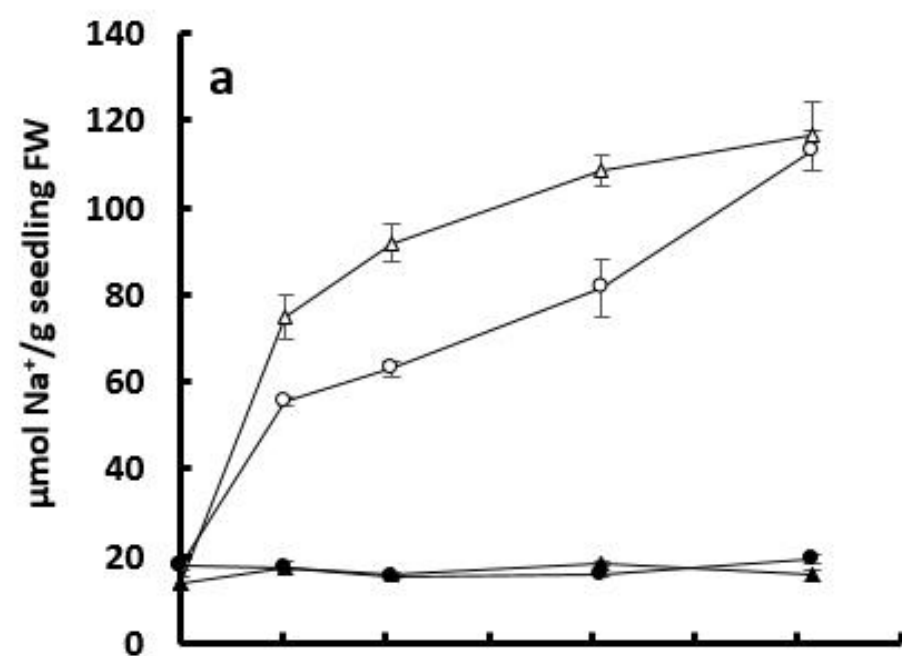
Fig. 4 The coefficient of variation of germination time (CV_t , a), coefficient of uniformity of germination (CUG, b) and Synchronization index of germination ($\bar{E}$, c) of cultivars Sohg and Shnd of sesame in isosmotic solutions of NaCl and PEG-6000. Each value is the mean of three replicates $\pm$ SE



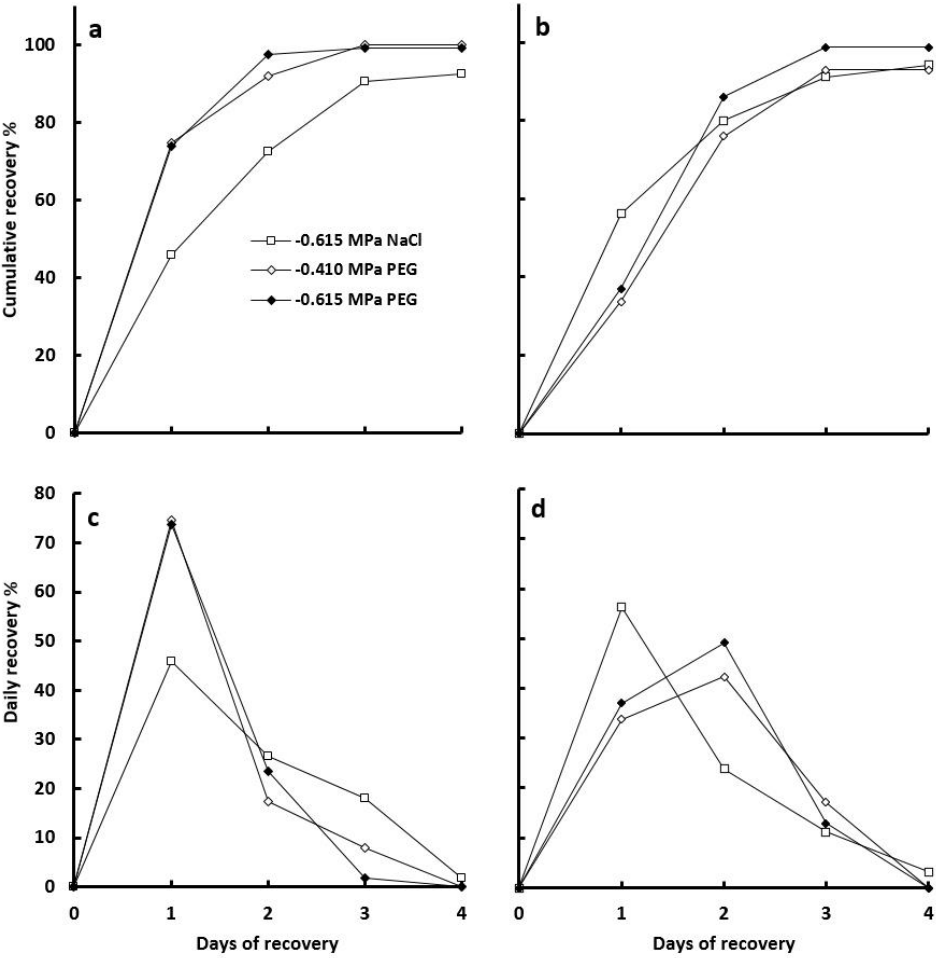
434 **Fig. 5** Fresh weight (a), dry weight (b), water content (c) and radicle length (d) of seedlings of Sohg and Shnd cultivars of sesame
 435 in isosmotic solutions of NaCl and PEG-6000. Each value is the mean of three replicates $\pm$ SE



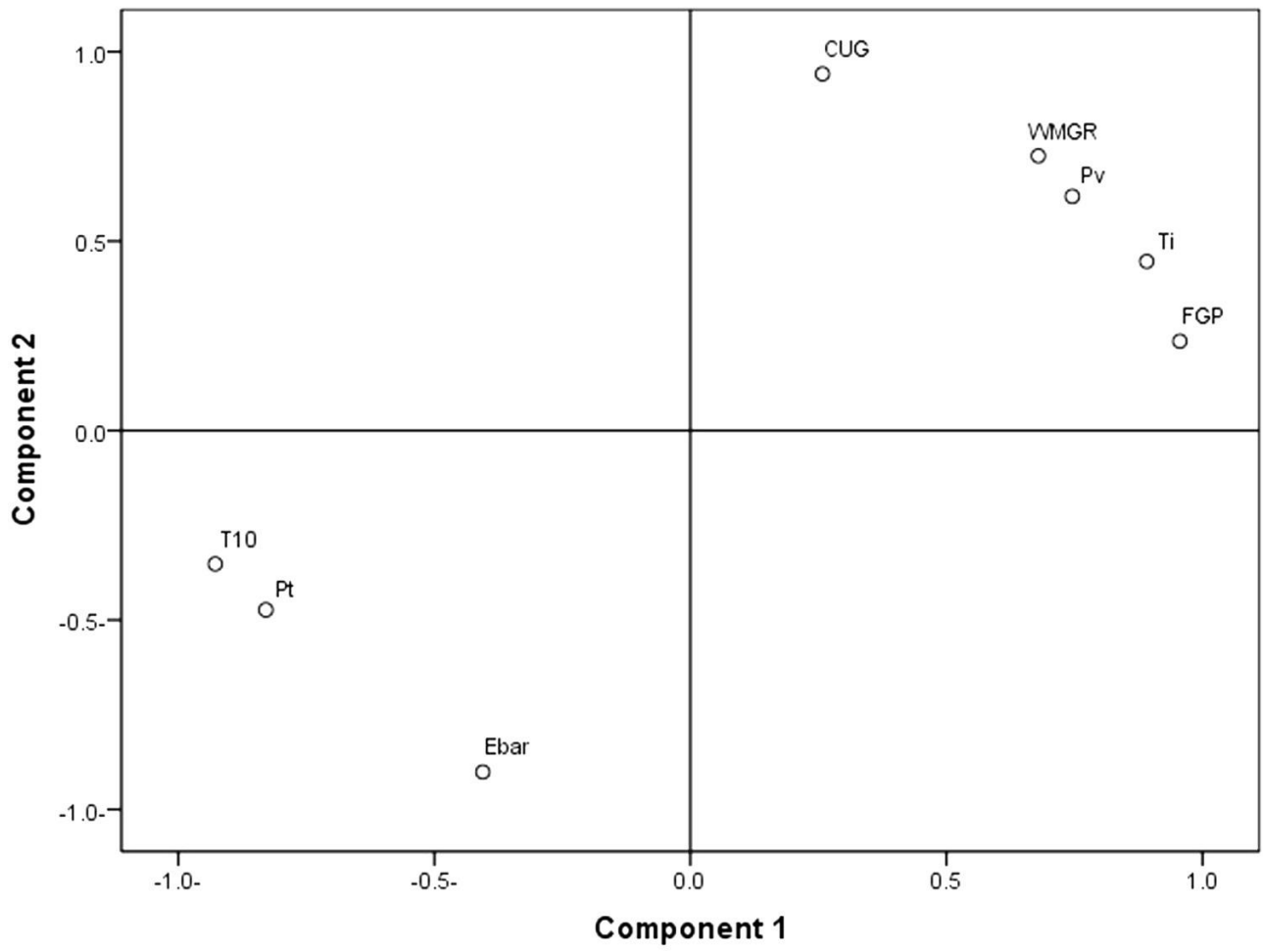
436
 437 **Fig. 6** Concentrations of K⁺ (a) and Na⁺ (b) and the K⁺/Na⁺ ratio (c) of seedlings of Sohg and Shnd cultivars of sesame in
 438 isosmotic solutions of NaCl and PEG-6000. Each value is the mean of three replicates $\pm$ SE



440 **Fig. 7** Time course of cumulative germination recovery of cultivars Sohg (a) and Shnd (b) of sesame and time course of daily
 441 germination recovery of Sohg (c) and Shnd (d) from isosmotic solutions of NaCl and PEG-6000. Each value is the mean
 442 of three replicates $\pm$ SE



443
 444 **Fig. 8** PCA abstracting the relationships between germination indices of Sohg and Shnd cultivars of sesame under NaCl and PEG
 445 stresses. FGP: Final germination percentage, WMGR: Weighted mean germination rate, Ti: Timson index, CUG:
 446 Coefficient of uniformity of germination, T10: Germination lag (time to 10% germination), Ebar: Synchronization index
 447 of germination, Pv: Value of daily germination peak, Pt: Timing of daily germination peak



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