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Involvement of polyamines in the contrasting sensitivity of chickpea (*Cicer arietinum* L.) and soybean (*Glycine max* (L.) Merrill.) to water deficit stress

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Abstract. Chickpea (*Cicer arietinum* L. cv. GPF2) and soybean (*Glycine max* (L.) Merrill cv. Brag) genotypes were subjected to varying water stress levels of -0.2 to -0.8 MPa to assess their relative sensitivity towards water stress. Soybean seedlings experienced significantly more stress injury (as electrolyte leakage) than chickpea at all stress levels. LD_{50} in terms of percent germination, root length, and root growth rate occurred at -0.4 MPa in soybean and at -0.6 MPa in chickpea. In chickpea, the root water content was higher than in soybean during stress. Endogenous levels of individual as well as total polyamines (PAs) in roots of 7-d-old seedlings subjected to -0.8 MPa stress increased to a significantly greater extent in chickpea than in soybean. The stress injury was accentuated as the PA levels declined in both the plant types. The reduced levels of PAs in soybean, especially putrescine (PUT) and spermidine (SPD) relative to chickpea, were related to higher stress injury and decreased water content. Exogenous PUT and SPD markedly mitigated the stress-induced effects, particularly in soybean. Inhibitor studies involving α-Difluromethylarginine (DFMA) and α-difluromethylornithine (DFMO), the biosynthetic inhibitors of PUT, as well as cyclohexylamine (CHA), biosynthetic inhibitor of SPD and SPM, corroborated the role of PAs in mediating the differential sensitivity of chickpea and soybean to water stress.

Keywords: *Cicer arietinum*; *Glycine max*; Polyamines; Putrescine; Spermidine; Spermine; Water stress.

Abbreviations: CHA, Cyclohexylamine; **DFMA,** α-Difluromethylarginine; **DFMO,** α-difluromethylornithine; **EL,** Electrolyte leakage; **PAs,** Polyamines; **PUT,** Putrescine; **SPD,** Spermidine; **SPM,** Spermine.

Introduction

Chickpea (*Cicer arietinum* L.) and soybean (*Glycine max* (L.) Merrill), the two most important pulses of India are grown as rainfed crops in the country, and consequently they experience water deficit stress at one or the other growth stage(s). A distinctive variation exists between the two plant types in their sensitivity to water stress (Grzesiak et al., 1996). Chickpea is considered relatively more tolerant, possibly because its root system is deeper, its leaves and canopy smaller than soybean (Serraj et al., 2004). The metabolic reasons governing their differential sensitivity towards water stress are not known. Moreover, the contrasting responses of different plant types to water stress offer an excellent model to elucidate the underlying causes of stress sensitivity, which can be employed to develop better stress tolerance in sensitive crops.

Several adaptive mechanisms are evoked by plants in response to water stress (Chaves et al., 2003). Interest has been growing in the possible involvement of polyamines (PAs) in the defense reaction of plants to various environmental stresses (Kao, 1997; Bouchereau et al., 1999; Kakkar and Sawhney, 2003). PAs are polycationic cellular molecules that play an essential role in cell growth and differentiation (Evans and Malmberg, 1989), and at a physiological pH, PAs can bind strongly to the negative charges in cellular components such as nucleic acids, proteins, and phospholipids (Smith, 1985). Interactions of PAs with membrane phospholipids may stabilize the membranes under conditions of stress (Roberts et al., 1986). It has been found that stress-tolerant plants increase their endogenous PAs levels to a much greater extent than sensitive ones (Lee, 1997). Furthermore, transgenic plants overproducing PAs possess greater stress tolerance (Galston et al., 1997), and exogenous PAs confer protection from a variety of abiotic stresses (Basra et al., 1997; Nayyar and Chander, 2004). In the present study, we tested the hypothesis that the variation in water stress sensitivity between chickpea and soybean plants is related to changes in the levels and functioning of endogenous PAs.

Materials and Methods

Plant Material and Growth Conditions

Seeds of chickpea (*Cicer arietinum* L. cv. GPF2) and soybean (*Glycine max* (L.) Merrill cv. Brag) procured from Panjab Agricultural University, Ludhiana, India, were surface sterilized with 0.1% mercuric chloride for 2 min and subsequently washed thoroughly with distilled water.

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Seeds were kept in 10 cm petri dishes lined with a double layer of filter papers (Whatman no. 1) under controlled conditions (Chickpea-24/21°C, soybean - 30/28°C; Light/ dark; 16/8 h; irradiance 250 µmol m^{-2} s^{-1}). Water stress was applied by subjecting the seeds to polyethylene glycol-6000 (SRL, India) with an osmotic potential of -0.2 to -0.8 MPa. Germination was observed after 7 days while stress injury (electrolyte leakage) and the growth of roots and shoots were measured in 15-d-old seedlings.

PA Treatments

Seven-day old seedlings of both the plant types were grown hydroponically in half strength Hoagland's solution and subjected to water deficit stress of -0.8 MPa for 8 days in the presence of PAs (Sigma, USA), putrescine (PUT), sperimidine (SPD), or spermine (SPM) (0.1 mM each), or in the presence of one of the inhibitors, α-Difluromethylarginine (DFMA) and α-difluromethylornithine (DFMO), the biosynthetic inhibitors of PUT (Merrell Dow Research Institute, USA) or cyclohexylamine (CHA; Sigma, USA), a biosynthetic inhibitor of SPD and SPM (0.01 mM each). These concentrations were chosen based upon a preliminary experiment involving a range of 0.1 to 1 mM of PAs and their inhibitors.

Electrolyte Leakage and Water Content

The electrolyte leakage (EL) and root water content were measured everyday for 8 days. For EL, samples were washed thrice with deionised water to remove surface adhered electrolytes (Lutts et al., 1996). These were placed in closed vials containing 10 ml of deionised water and incubated at 25°C on a rotary shaker for 24 h, and subsequently electrical conductivity of the solution (L_1) was determined. Samples were then autoclaved at 120°C for 20 min, and the final electrical conductivity (L_2) was obtained after equilibration at 25°C. The EL was defined as follows: EL (%) = $(L_1/L_2) \times 100$. Water status of the roots was determined by measuring relative water content (RWC) calculated as follows (Weatherley, 1950): RWC = (FW - DW)/(TW - DW) × 100, where FW is the fresh weight, DW is dry weight, and TW is turgid weight of tissue after being soaked in water for 4 h at room temperature.

Analysis of Endogenous PAs

Endogenous PAs were analyzed in the uppermost leaves of the main shoot (7-d-old) during a stress period of 8 days using a modified method of Goren et al. (1982) and elaborated previously (Nayyar and Chander, 2004). Briefly, the tissue was extracted in 5% perchloric acid (PCA) on ice using 100 mg ml^{-1} tissue. The homogenates were kept on ice for 60 min and centrifuged at 27,000 *g* for 20 min. The supernatant contained free amines, and the bound amines in soluble form while the pellet contained insoluble (bound) amines. The bound amines in the supernatant were released by treating the fractions with 6 N HCl at 110°C for 18 h in a sealed ampule. After heating, the sample was filtered through glass wool, dried under a stream of air at 80°C, and resuspended in PCA. The fractions were used for PA analysis and stored in plastic tubes at -20°C. PCA extracts were analysed for free PAs following dansylation. Dansyl polyamines were quantified in duplicate on silica gel plates using a fluorescence spectrophotometer with excitation at 360 nm and emission at 500 nm. Observations were recorded in replications, and mean values were pooled, standard error (S.E.) calculated, and the data subjected to analysis of variance (ANOVA). The differences between the mean values of treatments were estimated using least significant difference (L.S.D.) at a 0.05 level of significance.

Results

Effect of Water Stress on Stress Injury, Water Content, and Growth of Seedlings

The roots of soybean experienced higher stress injury, assessed as electrolyte leakage (EL) than chickpea at all stress levels except -0.2 MPa (Table 1). At -0.8 MPa, soybean showed 79% stress injury compared to 63% in case of chickpea. This might be due to relatively less water content in roots of soybean than chickpea at comparable stress levels (Table 1). Consequently, soybean had greater inhibition of seed germination, as well as root and shoot growth compared to chickpea (Table 1). Near LD_{50} values in terms of percent germination, root length, and root growth rate (RGR) occurred at -0.4 MPa in the case of soybean and at -0.6 MPa in the case of chickpea. The root and shoot lengths at -0.8 MPa were inhibited by 78 and 83%, respectively, over the controls in soybean while chickpea experienced corresponding reductions of 63 and 76%. Likewise, at the same stress level the growth rate of roots and shoots in soybean declined by 88 and 92%, respectively, over controls while in chickpea they showed a matching decreases of 70 and 78%, respectively. These results indicated higher sensitivity of soybean seeds and seedlings to water stress than chickpea.

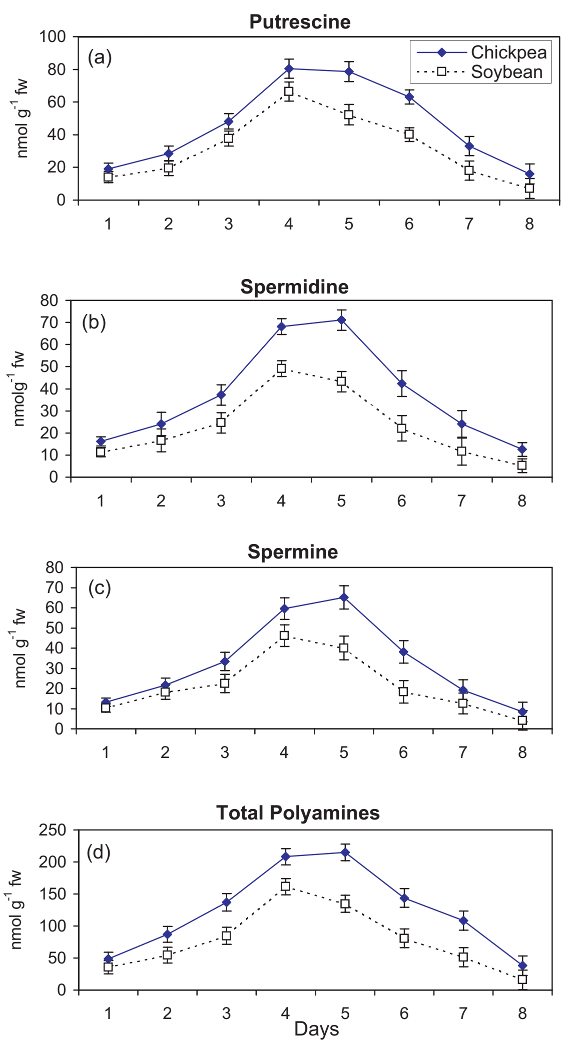
Endogenous PAs

Seedlings (7-d-old) of both plant types exposed to the highest stress level (-0.8 MPa) for 8 days were analyzed for endogenous PAs and assessed for stress injury and root water content. PUT, SPD, and SPM began to rise on the 2nd day of stress in both plant species (Figure 1a-c) and peaked on the 4th day in soybean and 5th day in chickpea. Thereafter, PA levels began to decline significantly and reached their nadir at the end of the assay in both plant types. In general, chickpea seedlings possessed a significantly higher level of total PAs than soybeans during stress (Figure 1d). In chickpea, the maximum level of PUT was 80.4, SPD-71 and SPM-65.2 nmol g^{-1} fw while in soybean, it was 66.4, 49.1 and 46.2 nmol g^{-1} fw, respectively.

Stress injury (Figure 2a) began to increase rapidly on the 4th day in soybean and 5th day in chickpea while root water content decreased gradually in both the species and was significantly less in soybean (36%) than in chickpea (47%) at the end of stress period (Figure 2b).

Table 1. Effects of varying water deficit stress levels (-0.2 to -0.8 MPa) on various parameters of chickpea and soybean seedlings. Seed germination was recorded after 7 days. Electrolyte leakage, root water content, root and shoot growth were recorded in 15-d-old seedlings. For the rate of root and shoot growth, observations were recorded between 9 and 15 d. Values presented are means ± SE, n =3 for EL, n=9 for others.

Parameter	Stress levels (MPa)					
	Control	-0.2	-0.4	-0.6	-0.8	LSD (0.05)
Chickpea						
Electrolyte leakage (%)	5.5±2.3	17.2±3.1	40.1±3.6	48.7±2.5	62.8±3.2	6.1
Root water content (%)	96.2±3.1	90.1±4.2	79.3±2.4	55.3±3.1	48.2±3.4	5.1
Seed germination (%)	100±8.3	100±3.2	80±2.8	52±3.4	48±3.6	8.9
Root length (cm)	11.2±1.1	8.9±1.3	7.2±1.4	5.4±1.1	4.1±0.8	1.2
Shoot length (cm)	6.2±1.2	5.0±1.3	3.7±1.2	2.5±0.87	1.4±0.8	1.1
Root growth rate (cm/week)	3.2±0.8	2.6±0.4	2.1±0.5	1.4±0.3	0.8±0.3	0.3
Shoot growth rate (cm/week)	2.7±0.3	2.1±0.24	1.5±0.2	0.9±0.2	0.5±0.15	0.3
Soybean						
Electrolyte leakage (%)	8.4±2.4	20.2±3.5	58.2±3.5	64.6±2.7	79.2±4.1	8.2
Root water content (%)	92.6±2.4	82.4±3.4	62.2±4.1	45.1±5.1	31.4±2.8	6.3
Seed germination (%)	100±3.7	82.5±2.8	54.2±2.3	42.1±2.6	32.1±3.1	6.2
Root length (cm)	10.4±1.2	7.0±1.1	5.0±1.4	3.7±1.0	2.3±0.6	1.1
Shoot length (cm)	5.3±1.2	3.8±0.6	2.0±0.4	1.7±0.4	0.9±0.5	0.63
Root growth rate (cm/week)	2.3±0.3	1.7±0.4	1.2±0.3	0.92±0.20	0.27±0.16	0.28
Shoot growth rate (cm/week)	2.1±0.4	1.5±0.2	0.88±0.21	0.58±0.16	0.17±0.12	0.25



Effect of Exogenous PAs and their Inhibitors on Stress Response

In water-stressed chickpea plants (-0.8 MPa), exogenous PUT, SPD and SPM (at 0.1 mM each) reduced the stress injury (as EL) in roots (Table 2) to 38, 52 and 61%, respectively, over control (65%) while in soybean a corresponding decrease of 43, 59 and 65%, respectively, was observed over its control (78%). The water content of roots rose significantly in the presence of PUT and SPD in chickpea while soybean showed an appreciable increase with all the PAs (Table 2). In PA-treated chickpea plants, the length of roots increased by 39 and 26% with PUT and SPD, respectively, over stressed controls while soybean showed a corresponding increase of 53 and 35%, respectively. SPM was less effective in both species for root growth. An increase of 36, 20 and 23% over control occurred in shoot growth of chickpea with PUT, SPD and SPM, respectively, with corresponding increases of 43, 30 and 21% in soybean. In contrast, in the presence of DFMA, DFMO and CHA (0.01 mM each), the stress injury intensified, and growth was severely inhibited in both the plant types, and water content of roots was significantly decreased (Table 2).

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Figure 1. Endogenous levels of PAs, PUT (a), SPD (b), SPM (c) and total PAs (d) in chickpea and soybean seedlings subjected to -0.8 MPa level of water deficit stress. 7-d-old seedlings were exposed to stress for 8 days, and observations were recorded in three replications. Mean ± S.E. (vertical bars). Control values (unstressed) in chickpea (PUT: 18.1-19.3; SPD: 13.1-14.6; SPM: 10.2-11.4; total: 38.6-40.1) and soybean (PUT: 12.4-13.6; SPD: 9.6-10.4; SPM: 8.6-9.3; total: 32.1-34.3).

Table 2. Effect of exogenous PUT, SPD and SPM and their inhibitors DFMO, DFMA and CHA on various parameters of water stressed (-0.8 MPa) chickpea and soybean seedlings. 7-d-old seedlings of both the plant species were subjected to water stress in the absence (control) or presence of PAs (0.1 mM each) or their inhibitors (0.01 mM each) for 8 days and observations were recorded in 15-d-old seedlings. For measurement of growth rate of root and shoot, observations were recorded between 9 and 15th day. Values presented are means ± SE, n =3 for EL, n = 9 for others.

Parameters	Control	PUT	SPD	SPM	DFMO	DFMA	CHA	LSD (0.05)
Chickpea								
Electrolyte leakage (%)	65±4.2	38±2.3	52±2.5	61±3.1	72±2.6	78±2.4	68±2.1	2.6
Root water content (%)	51±3.2	62±2.4	58±2.1	54±3.1	39±3.5	38±3.2	46±2.4	2.4
Root length (cm)	4.9±1.1	6.8±1.4	6.1±1.0	5.7±1.2	3.9±1.1	2.9±0.8	4.0±1.1	1.0
Shoot length (cm)	1.8±0.4	2.4±0.3	2.1±0.2	2.2±0.2	1.4±0.3	1.2±0.2	1.4±0.2	0.17
Root growth rate (cm/week)	0.8±0.1	1.1±0.2	1.0±0.1	0.9±0.1	0.6±0.1	0.5±0.14	0.7±0.11	0.16
Shoot growth rate (cm/week)	0.56±0.08	0.72±0.07	0.68±0.06	0.66±0.05	0.43±0.05	0.34±0.07	0.48±0.06	0.06
Soybean								
Electrolyte leakage (%)	78±3.1	43±2.4	59±2.6	65±2.5	86±2.1	91±2.2	82±3.1	3.2
Root water content (%)	34±2.3	49±3.1	42±2.5	40±2.5	25±3.1	21±2.4	31±2.3	3.4
Root length (cm)	2.3±0.8	3.5±0.7	3.1±0.6	2.7±0.6	1.2±0.3	0.92±0.3	1.6±0.2	0.3
Shoot length (cm)	0.92±0.3	1.7±0.2	1.5±0.2	1.1±0.3	0.7±0.1	0.5±0.1	0.8±0.1	0.12
Root growth rate (cm/week)	0.3±0.1	0.46±0.08	0.40±0.06	0.38±0.06	0.16±0.04	0.11±0.04	0.22±0.03	0.03
Shoot growth rate (cm/week)	0.22±0.05	0.30±0.03	0.27±0.04	0.25±0.03	0.16±0.03	0.12±0.03	0.19±0.02	0.03

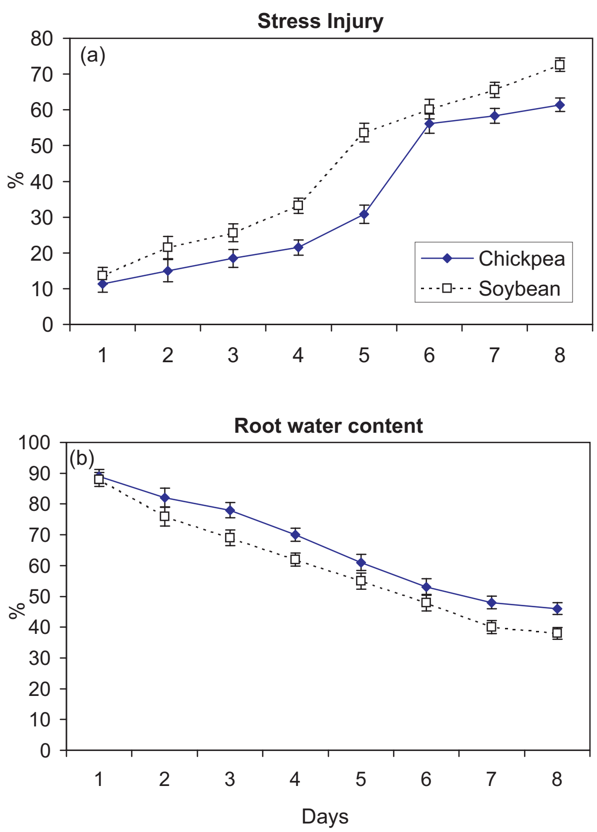

Figure 2. Stress injury (as electrolyte leakage-a) and root water content (RWC-b) in Chickpea and Soybean seedlings subjected to -0.8 MPa level of water deficit stress. 7-d-old seedlings were exposed to stress for 8 days, and observations were recorded in three replications. Mean ± S.E. (vertical bars). Control values (unstressed) in chickpea (Stress injury: 10.4-13.6; RWC: 94.3-96.1) and in soybean (Stress injury: 12.3-14.1; RWC: 92.6-93.4).

Discussion

The present findings show that chickpea seedlings experienced considerably less water stress injury to its membranes, as determined by EL, and to growth compared to soybean. These differential responses could be related to significantly more endogenous PAs in chickpea than in soybean since high PAs accumulation has been related to acquisition of stress tolerance (Lazcano-Ferrat and Lovatt, 1999). Though the exact cause of variation in PAs levels between the two plant types was not determined, earlier reports ascribe it to differences in the expression of PAs biosynthetic enzymes, e.g., arginine decarboxylase (ADC) and ornithine decarboxylase (ODC) (Benavides et al., 1997; Lee et al., 1997). In rice, Lee et al. (1997) observed that both PUT and ADC increased to a higher magnitude in a chilling-tolerant cultivar upon exposure to cold than its susceptible counterpart while ODC activity did not differ between the two cultivars.

One of the primary reasons affecting the difference in the PAs levels of two plant types might be their water status (Figure 2b). Chickpea seedlings might support a higher content of PAs during water stress due to their better capacity to maintain turgor than soybean. Alternatively, it is possible that accumulation of PAs itself affects the osmoregulation and thus contributes towards improved water status (Chen and Kao, 1993; Erdei et al., 1996). In a related study, we found chickpea to accumulate more osmolytes like proline and glycine betaine than soybean during similar conditions of water stress (unpublished data), which might explain its superior water content. It should be noted that at similar levels of root water content e.g., 60%, chickpea had more PAs content than soybean (Figures 1 and 2b) indicating the existence of a relatively tolerant PAs metabolism in the former genotype.

Exogenous PAs resulted in significant decrease in stress injury, improvement in water content and growth of both the plant types supporting the role of PAs in the stress response. Our results are in agreement with previous studies (Wang, 1993; Basra et al., 1997), where exogenous PAs were reported to alleviate stress-induced growth inhibition possibly due to protection of membranes (Xu et al., 1995) and minimization of oxidative damage (Kim et al., 2000; Nayyar and Chander, 2004). The participation of PAs in stress response was further corroborated by use of their biosynthetic inhibitors like DFMA, DFMO and CHA, which increased the stress injury and severely impaired the growth. Moreover, the water content of roots in inhibitor-treated plants was significantly decreased suggesting a role of PAs in turgor maintenance. The effects of exogenous PAs and their inhibitors were more pronounced in soybean than in chickpea seedlings, which might be related to lower endogenous PAs in the former plant type than the latter.

In conclusion, this study has revealed that soybean is more sensitive to water deficit stress than chickpea, and this is probably due to its reduced ability to accumulate PAs. Manipulation of endogenous PAs levels through genetic or exogenous means might enhance the capability to improve stress tolerance in both the plant species, especially in soybean. In a recent study (Capell et al., 2004), a transgenic rice expressing ADC of Datura (water stress tolerant) was found to accumulate PAs to a much higher degree than its wild type, thus achieving higher tolerance to water stress.

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多胺涉及鴨豆及大豆對缺水之靈敏度

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使鴨豆（*Cicer arietinum* L. cv. GPF2）及大豆（*Glycine max* (L.) Merrill cv. Brag）處於不同程度之缺水逆境（-0.2 到 -0.8 MPa）以評估它們對缺水之不同靈敏度。大豆顯然較鴨豆易受缺水傷害（在所有供試情形下，以電解質之流失作判斷）依發芽百分率，根長度及根生長率為測定項目所定出之 LD_{50}（達 50% 時之劑量）在大豆為 -0.4 MPa 而鴨豆為 -0.6 MPa（表示後者較耐缺水逆境）。當處於缺水逆境時，鴨豆根部之水含量較大豆高。以發芽後七天之細菌為例，當處於 -0.8 MPa 時，根部之多胺（個別或總量）的增加鴨豆顯著地高於大豆。不論那一種豆類，當內在之多胺含量下降時，受缺水之傷害會加重。大豆根部，相對於鴨豆根部，多胺之減少（尤其是 putrescine 及 spermidine）和它的較易受缺水傷害及較少之水含量息息相關。外加之 putrescine 及 spermidine 大大地減緩缺水造成之傷害（尤其是大豆較明顯）。分別以 putrescine 及 spermidine 之生合成抑制劑做試驗証實了上述觀點。

關鍵詞：*Cicer arietinum*；*Glycine max*；多胺；Putrescine；Spermidine；Spermine；缺水逆境。