



International Journal of Botany

ISSN: 1811-9700

science
alert

ANSI*net*
an open access publisher
<http://ansinet.com>

Counteraction of Drought Stress on Soybean Plants by Seed Soaking in Salicylic Acid

A.M.A. Al-Hakimi

Department of Biology, Faculty of Science, Taiz University, Taiz, Yemen

Abstract: The interactive effects of drought stress (70, 50 and 30% field capacity) and salicylic acid (0.6 mM) were studied in soybean (*Glycine max* L.) plants. The content of pectin, cellulose, lignin and phospholipids of either shoots or roots and soluble sugars of shoots were significantly lowered with the rise of drought levels. On the other hand, the contents of hemicellulose, starch, total lipids, glycolipids and sterols of either shoots or roots, soluble sugars of roots were raised. It was found that application of salicylic acid enhanced pectin, cellulose, lignin and phospholipids contents of either shoots or roots and soluble sugars of roots. On the other side, the applied salicylic acid lowered hemicellulose, starch, total lipids, glycolipids and sterols of shoots and roots and soluble sugars of shoots. Soaking of soybean seeds in salicylic acid exhibited a favorable effect on the accumulation of some ions and antagonized or ameliorated the inhibitory effect of drought stress on some others.

Key words: Pectin, hemicellulose, cellulose, lignin, glycolipids, phospholipids, sterols, minerals, *Glycine max*

INTRODUCTION

The physiological and biochemical responses of plants to drought stress may be achieved by alteration of certain phases of the metabolic network mediated and directed by certain enzymes, which activate or retard particular metabolic activities. This may divert the perfect balance of the biochemical reactions with the accumulation of some metabolic intermediates or end products.

Salicylic acid, an ubiquitous plant phenolic, was recognized as an endogenous regulator in plants after the finding that it is involved in many plant physiological processes. In an extensive screening program using modern analytical technique, salicylic acid was detected in the leaves and reproductive organs of 34 agronomically important species (Raskin *et al.*, 1990).

One of the most studied functions of salicylic acid is that it is associated with its involvement in plant resistance response to different pathogen attacks (Yalpani and Raskin, 1993; Alvarez, 2000). It was also reported that salicylic acid accumulates during exposure to ozone or UV light (Sharma *et al.*, 1996). In this respect salicylic acid treatment was found to improve the chilling, heat-shock, drought and salt (Janda *et al.*, 1999; Guo-Zhang *et al.*, 2004; Dat *et al.*, 1998; 2000; Hamada and Al-Hakimi, 2001; Szalai *et al.*, 2005). Thus, in this study it seemed necessary to study the effects of various levels of drought on some metabolic processes (cell wall polysaccharides, soluble sugars, starch, total lipids,

glycolipids, phospholipids, sterols and mineral composition) and the role of salicylic acid in amelioration of the adverse effects of drought.

MATERIALS AND METHODS

The present study was conducted in greenhouse at Taiz University, Biology Department at summer 2005. The mean temperature was about 27°C and 70% relative humidity. Seeds of soybean (*Glycine max* L.) were grown in plastic pots (10 cm in diameter and 13.5 cm in height) lined with polyethylene bags and containing soil composed of clay and sand (2:1). The seeds of soybean before sowing were soaked for 6 h in solutions containing 0.6 mM salicylic acid and the other seeds soaked for 6 h in distilled water (regarded as control). After sowing seeds (5 seed in each pot), the pots then irrigated and the water content of the soil was adjusted regularly near to the field capacity and the plants were left to grow for 15 days. Thereafter, the pots (four replicate per treatment) were watered to the desired soil moisture content (70, 50 and 30% field capacity). Some pots were left untreated (100% field capacity and 0 salicylic acid) and regarded as absolute control. On the other side, droughted plants but non-treated with salicylic acid were regarded as reference control. At the end of the experimental period (30 days) cell wall fractionation was conducted essentially according to Dever *et al.* (1968) and Galbraith and Shields (1981). Tissue powder samples were extracted twice in distilled water, twice in 80% ethanol to

remove soluble sugars metabolites. The residue was then extracted in 2 mL 0.5 N NaOH for starch, 0.5% ammonium oxalate-oxalic acid (90°C for 24 h) for pectin, 17.5% NaOH for hemicellulose and in 72% H₂SO₄ (with 15 min autoclaving) for cellulose extraction. After that, the remaining precipitate was ascribed to the lignin fraction according to Dever *et al.* (1968). Contents of soluble sugars, starch and wall polysaccharides were determined by the anthrone sulfuric acid reagent using glucose as standard (Fales, 1951). Lipids were extracted three times for dried plant organs (each lasted for 24 h) with chloroform/methanol (2:1, v/v) at room temperature according to Navari-Izzo *et al.* (1989). Lipids (100 µg) were chromatographed on silica gel plates (silica gel G/60) using n-hexane-diethylether-glacial acetic acid (70: 30: 1) and the spots were visualized by I₂ vapor. According to Navari-Izzo *et al.* (1989) the Total Polar Lipids (TPL) were located at the origin of the chromatogram. These were scratched and redissolved in chloroform/methanol (2:1). Glycolipids were estimated as their monosaccharides content by the anthrone sulfuric acid reagent. Phospholipids were determined in lipid extracts according to Johnson (1971). Lipid phosphorus was estimated by the molybdate blue colour (Woods and Mellon, 1941). Phosphorus content was taken as an index for phospholipid contents. Total sterols were estimated according to the method described by Cook (1958). Sodium and potassium were determined by flame photometer method (Williams and Twine, 1960), calcium and magnesium by the versene titration method (Schwarzenbach *et al.*, 1948).

All data presented are the mean values. Statistical analysis was carried out by one-way ANOVA using Student's t-test to test significance of the difference between means. Means were considered significantly different at 5 or 1% level of probability.

RESULTS AND DISCUSSION

Cell wall metabolism is an important component in plant growth, not only because it represents a large proportions of the cell biomass, but also because determining wall extensibility for cell enlargement (Zhong and Läubli, 1988). In this investigation, pectin, cellulose, hemicellulose and lignin were determined in stressed soybean plants (Table 1 and 2). The contents of pectin, cellulose and lignin of shoots and of roots were significantly lowered by drought level. On the other side, hemicellulose contents of either shoots or roots were raised under all the drought levels. This could be important for preventing extension (Taiz, 1984; Volkenburgh and Boyer, 1985). Working with tobacco cell

Table 1: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of cell wall polysaccharides [(mg g⁻¹ (d.m.))] of shoots of soybean plants

Drought-SA (% FC-mM)	Pectin	Hemicellulose	Cellulose	Lignin
100+0	80.782	31.204	26.201	120.028
70+0	53.162**	40.993**	19.453**	98.997**
50+0	43.081**	49.603**	15.417**	84.744**
30+0	39.976**	60.947**	9.872**	76.269**
100+0.6	49.133**	20.947**	35.189**	136.318**
70+0.6	76.700**	19.115**	40.940**	140.772**
50+0.6	68.165**	17.142**	51.251**	143.799**
30+0.6	58.525**	14.880**	60.853**	156.088**
LSD at 5%	3.808	2.189	2.087	1.450
LSD at 1%	5.540	3.186	3.036	2.110

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

Table 2: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of cell wall polysaccharides [(mg g⁻¹ (d.m.))] of roots of soybean plants

Drought-SA (% FC- mM)	Pectin	Hemicellulose	Cellulose	Lignin
100+0	31.148	20.669	44.603	139.091
70+0	20.107**	32.025**	30.676**	122.191**
50+0	17.171**	39.205**	24.907**	116.015**
30+0	13.937**	40.808**	19.157**	91.973**
100+0.6	22.668**	17.771**	50.726**	148.937**
70+0.6	50.086**	28.227**	56.108**	155.951**
50+0.6	44.108**	30.704**	59.072**	162.997**
30+0.6	39.337**	32.162**	61.782**	169.267**
LSD at 5%	1.317	1.748	2.161	1.851
LSD at 1%	1.916	2.543	3.145	2.693

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

Table 3: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of soluble sugars and starch [(mg g⁻¹ (d.m.))] of shoots and roots of soybean plants.

Drought-SA (% FC-mM)	Shoot		Root	
	Soluble sugars	Starch	Soluble sugars	Starch
100+0	30.887	20.937	24.992	15.263
70+0	20.942**	25.648**	28.942**	16.801**
50+0	19.049**	27.997**	31.942**	18.038**
30+0	16.142**	30.682**	35.255**	20.848**
100+0.6	11.888**	18.331**	30.883**	11.592**
70+0.6	10.181**	14.197**	35.122**	6.692**
50+0.6	8.618**	11.942**	39.943**	7.527**
30+0.6	6.838**	10.553**	44.115**	8.514**
LSD at 5%	1.636	1.539	1.797	1.189
LSD at 1%	2.380	2.240	2.614	1.722

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

cultures in the presence of polyethylene glycol, Iraki *et al.* (1989) recorded a decrease in the percentage of cellulose and an increase in the hemicellulose percentage, whereas the pectic fraction remained more or less unchanged. Similar results were, also obtained by Wakabayashi *et al.* (1997). The possible mechanisms for the inhibitory effect of salinity on the incorporation of glucose into cell wall polysaccharides have been discussed (Zhong and Läubli, 1988; Hamada, 2001; Al-Hakimi, 2005).

Table 4: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of total lipids, glycolipids, phospholipids and sterols [(mg g⁻¹ (d.m.))] of shoots of soybean plants

Drought-SA (% FC- mM)	Total lipids	Glycolipids	Phospholipids	Sterols
100+0	31.229	10.976	1.117	3.153
70+0	39.221**	16.377**	0.572**	5.377**
50+0	42.136**	17.902**	0.444**	7.877**
30+0	49.170**	22.973**	0.316**	8.497**
100+0.6	21.083**	8.042**	1.612**	2.127**
70+0.6	18.972**	6.367**	1.472**	2.837**
50+0.6	20.808**	7.267**	1.803**	4.283**
30+0.6	23.861**	8.592**	1.972**	5.379**
LSD at 5%	1.853	1.180	0.097	0.155
LSD at 1%	2.696	1.171	0.141	0.226

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

Table 5: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of total lipids, glycolipids, phospholipids and sterols [(mg g⁻¹ (dm))] of roots of soybean plants

Drought-SA (% FC- mM)	Total lipids	Glycolipids	Phospholipids	Sterols
100+0	21.313	5.593	0.654	2.850
70+0	29.023**	7.632**	0.316**	4.702**
50+0	30.894**	8.681**	0.285**	5.752**
30+0	36.225**	9.797**	0.213**	7.389**
100+0.6	16.197**	3.773**	0.888**	1.957**
70+0.6	14.107**	3.118**	0.787**	1.705**
50+0.6	15.392**	2.587**	0.856**	3.394**
30+0.6	17.937**	2.122**	0.916**	4.617**
LSD at 5%	1.543	0.385	0.017	0.163
LSD at 1%	2.246	0.560	0.025	0.238

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

The adverse effects of soil moisture content on pectin, cellulose and lignin contents in shoots and roots were partially or completely alleviated by soaking seeds in salicylic acid. The applied salicylic acid inhibited the stimulatory role of water stress on the production of hemicellulose in shoots and roots. Salicylic acid could perhaps alleviate the inhibitory effects of drought on glucose incorporation into cell wall polysaccharides. Similarly cellulose biosynthesis was particularly enhanced (Zhong and Läuchli, 1988). These authors suggested that high Na⁺ concentrations reduced cellulose biosynthesis in cotton roots via disturbance of plasma membrane integrity. In this study treatment with salicylic acid, however, counteract this adverse effect (Table 1 and 2).

Drought stress stimulated soluble sugars accumulation in roots and retarded their biosynthesis in shoots (Table 3). The applied salicylic acid enhanced the stimulatory role of water stress on accumulation of soluble sugars in roots in drought stressed soybean plants. Also in this context, the applied salicylic acid retarded the accumulation of soluble sugars in shoots (Table 3). The starch was accumulated at all investigated drought levels in shoots and roots. The applied salicylic

Table 6: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of mineral composition [(mg g⁻¹ (d.m.))] of shoots soybean plants.

Drought-SA (% FC- mM)	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Na ⁺ /K ⁺	Ca ²⁺ /Mg ²⁺
100+0	17.389	41.577	16.247	8.282	0.418	1.962
70+0	25.046**	34.387**	17.111**	6.447**	0.728**	2.654**
50+0	40.778**	29.415**	19.337**	4.804**	1.386**	4.025**
30+0	65.280**	20.682**	22.734**	3.878**	3.158**	5.862**
100+0.6	15.389**	30.384**	18.403**	7.267**	0.506**	2.532**
70+0.6	18.718**	37.512**	20.519**	7.832**	0.499**	2.620**
50+0.6	26.169**	36.529**	22.789**	6.572**	0.716**	3.468**
30+0.6	45.745**	28.522**	26.525**	5.821**	1.604**	4.557**
LSD at 5%	1.085	0.490	0.151	0.138	0.080	0.117
LSD at 1%	1.579	0.713	0.220	0.201	0.117	0.170

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

Table 7: The action of Salicylic Acid (SA) treatment in ameliorating the adverse effects of drought stress on the content of mineral composition [(mg g⁻¹ (d.m.))] of roots soybean plants.

Drought-SA (% FC- mM)	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Na ⁺ /K ⁺	Ca ²⁺ /Mg ²⁺
100+0	28.384	15.878	11.280	6.871	1.788	1.643
70+0	32.787**	13.627**	16.784**	5.180**	2.406**	3.240**
50+0	58.527**	10.772**	18.380**	4.540**	5.433**	4.084**
30+0	76.303**	7.887**	20.187**	3.184**	9.675**	6.340**
100+0.6	20.390**	14.288**	12.174**	7.288**	1.427**	1.670
70+0.6	27.384**	16.373**	18.508**	6.144**	1.673**	2.850**
50+0.6	40.938**	13.268**	21.544**	5.888**	3.085**	3.660**
30+0.6	64.425**	10.399**	24.509**	4.621**	6.195**	5.255**
LSD at 5%	0.902	0.339	0.523	0.314	0.064	0.250
LSD at 1%	1.313	0.493	0.761	0.457	0.094	0.364

*Significant (p = 0.05), **highly significant (p = 0.01) as compared with control

acid was generally effective in antagonizing partially or completely the stimulatory effect of drought stress on starch accumulation in shoots and roots of test plants. Gordon *et al.* (1986) showed that regrowth of defoliated white clover was associated with a decrease in starch and other sugars of shoots and roots. It is accepted that with the demand for sugars starch degradation increased, but that was not strictly associated with low concentrations of sucrose, glucose and fructose (Baur-Hoch *et al.*, 1990). Water stress was found to affect the incorporation of internally available sugars into various fractions of cell wall in excised root segments or cell suspension cultures (Iraki and Carpita, 1986; Solomon *et al.*, 1987; Al-Hakimi and Hamada, 2001; Al-Hakimi, 2005).

Lipid and lipid fractions of the studied plants exhibited variable changes in response to the drought stress and their interaction with the applied salicylic acid (Table 4 and 5). Total lipid and glycolipid contents of shoots and roots were significantly increased with the decrease in soil moisture content. The phospholipid fraction was significantly lowered by drought stress. Total sterols were accumulated in drought-stressed shoots and roots. Salicylic acid treatment retarded the total lipid, glycolipid and total sterols of shoots and roots.

On the contrary, salicylic acid stimulated the phospholipids accumulation in shoots and roots of droughted plants. Similar decrease or increase in lipid contents by stress imposition was also recorded in plants (Peeler *et al.*, 1989; Dakhma *et al.*, 1995; Quartacci *et al.*, 1997; Al-Hakimi 2003, 2005).

The decrease in phospholipids may be due either to reduction in the power of hydrophobic proteins to bind phospholipids (Heber and Sanatarius, 1964) or due to lipid peroxidation on enhanced lecithinase (Harrison and Trevelyan, 1963). In this respect, Martin *et al.* (1986) and Al-Hakimi (2003) reported a general decrease in phospholipid and glycolipid contents with decreasing soil moisture content. The phospholipid loss is also known to occur under several adverse climatic conditions such as dehydration (Graziane and Livne, 1971; Quartacci *et al.*, 1997), chilling (Lurie *et al.*, 1994), freezing (Lea and Hawke, 1952), drought (Navari-Izzo *et al.*, 1993; Al-Hakimi, 2003) and senescence (Simon, 1974; Brown *et al.*, 1994). Sterols also play essential functions in the lipid core of cell membrane and they are also biogenetic precursors of numerous secondary metabolites including plant steroid hormones (Geuns, 1978). It has been shown that sterols could influence the structural and functional properties of biological membranes (Horvath *et al.*, 1981).

Significant response in connection with the interaction of drought and salicylic acid treatments was manifested in the present investigation with respect to ionic balance which is considered as one of the most complicated and integral parts of plant activities. The cation imbalance is one of the most basic disorders due to drought stress. The results of the present study (Table 6 and 7) reveal unequivocally that the applied drought stress was effectual in producing Na⁺ accumulation in the different organs of soybean plants; the highest Na⁺ accumulation was consistently displayed in plants subjected to the highest drought level. Serrano and Gaxiola (1994) reported that the high concentration of Na⁺ negatively affected the intercellular K⁺ accumulation, presumably either by competing for sites through which influx of both cations occurs (Jeschke and Wolf, 1988) or affecting membrane stability causing leakage of K⁺ (Watad *et al.*, 1991). The alterations in distribution and accumulation of mono- and divalent cations in the different organs of drought stressed plants may be an indication of the role of these cations in regulating the physiological activities of these plants (Benzioni *et al.*, 1992). The accumulation of K⁺ and Mg²⁺ decreased gradually with the rise of drought level stress and this trend was generally accompanied by reciprocal variations in the concentration of calcium. Variations in the

concentration of K⁺ and Mg²⁺ in soybean plants due to increased drought levels were generally accompanied by reciprocal variation in the concentration other mono (Na⁺) and divalent (Ca²⁺) cations, i.e., Na⁺/K⁺ and Ca²⁺/Mg²⁺ ratios increase along with drought level; a trend which is in accordance with some of the results of Garcia-Reina *et al.* (1988) and Torres-Schumann *et al.* (1989) using other plant tissues.

Seed soaking in salicylic acid had an inhibitory effect on the accumulation of sodium in the different organs under various level of drought. Furthermore, their application ameliorated the inhibitory effects of drought on K⁺ and Mg²⁺ accumulation in the different organs of the test plants. Also, this treatment enhanced the stimulatory effect of drought stress on the accumulation of Ca²⁺ in soybean organs. The salicylic acid and ubiquitous plant phenolic compound, was recognized as an endogenous regulator in many plant physiological processes (Enyedi *et al.*, 1992; Yalpani and Raskin, 1993). In this context, Janda *et al.* (1999) observed that salicylic acid pretreatment at normal growth temperature induced protection against low-temperature stress in young maize plants, probably due to increased antioxidant activity. Also, Mishra and Choudhuri (1999) found that deterioration at heavy metal stress was partially alleviated by the exogenous application of salicylic acid in *Oryza sativa*.

REFERENCES

- Al-Hakimi, A.M.A. and A.M. Hamada, 2001. Counteraction of salinity stress on wheat plants by grain soaking in ascorbic acid, thiamin or sodium salicylate. *Biol. Plant.*, 44: 253-261.
- Al-Hakimi, A.M.A., 2003. Physiological responses of sunflower-seedlings growing under drought stress. *F.S.B.*, 16: 169-176.
- Al-Hakimi, A.M.A., 2005. Salinity-calcium interactions on growth, cell wall polysaccharides, proteins, amino acids and some lipids of *Kirchmeriella lunaris*. *Assiut. Univ. J. Bot.*, 34: 99-209.
- Alvarez, M.E., 2000. Salicylic acid in the machinery of hypersensitive cell death and disease resistance. *Plant Mol. Biol.*, 44: 429-442.
- Baur-Hoch, B., F. Machler and J. Nosberger, 1990. Effect of carbohydrate demand on the remobilization of starch in stolons and roots of white clover (*Trifolium repens* L.) after defoliation. *J. Exp. Bot.*, 41: 573-578.
- Benzioni, A., A. Nerd, Y. Rosengartner and D. Mills, 1992. Effect of NaCl salinity on growth and development of jojoba clones: 1. Young plants. *J. Plant Physiol.*, 139: 731-736.

- Brown, J.H., J.A. Chambers, S. Ghosh, C.D. Froese, A.M. Huff and J.E. Thompson, 1994. Phospholipid metabolism in membranes of senescing bean cotyledons. *J. Exp. Bot.*, 45: 1513-1522.
- Cook, R.O., 1958. Cholesterol (Chemistry, Biochemistry and Pathology). Academic Press. New York, pp: 484.
- Dakhma, W.S., Z. Moktar and C. Abdel Kader, 1995. Effects of drought-stress on lipids in rape leaves. *Phytochemistry*, 40: 1383-1386.
- Dat, J.F., H. Lopez-Delgado, C.H. Foyer and I.M. Scott, 1998. Parallel changes in H₂O₂ and catalase during thermotolerance induced by salicylic acid or heat acclimation in mustard seedlings. *Plant Physiol.*, 116: 1351-1357.
- Dat, J.F., H. Lopez-Delgado, C.H. Foyer and I.M. Scott, 2000. Effects of salicylic acid on oxidative stress and thermotolerance in tobacco. *J. Plant Physiol.*, 156: 659-665.
- Dever, J.E., Jr., R. S. Bandurski and A. Kivilaan, 1968. Partial chemical characterization of corn root cell walls. *Plant Physiol.*, 43: 50-56.
- Enyedi, A., N. Yalpini, P. Silverman and I. Raskin, 1992. Localization, conjugation and function of salicylic acid in tobacco during the hypersensitive reaction to tobacco mosaic virus. *Proc. Natl. Acad. Sci. USA.*, 89: 2480-2484.
- Fales, F.W., 1951. The assimilation and degradation of carbohydrates by yeast cells. *J. Biol. Chem.*, 193: 113-118.
- Galbraith, D.W. and B.A. Shields, 1981. Analysis of the initial stages of plant protoplast development using 33258 Hoechst: Re-activation of the cell cycle. *Physiol. Plant.*, 51: 380-386.
- Garcia-Reina, G., V. Moreno and A. Luque, 1988. Selection for NaCl tolerance in cell culture of three Canary Island tomato land races. I. Recovery of tolerant plantlets from NaCl-tolerant cell strains. *J. Plant Physiol.*, 133: 1-6.
- Geuns, J.M.C., 1978. Steroid hormones and plant growth and development. *Phytochemistry*, 17: 1-14.
- Gordon, A.I., G.J.A. Ryle, D.F. Mitchell, K.H. Lowry and C.E. Poweel, 1986. The effect of defoliation on carbohydrate, protein and leghaemoglobin content of white clover nodules. *Ann. Bot.*, 58: 141-154.
- Graziane, Y. and A. Livne, 1971. Dehydration, water fluxes and permeability of tobacco leaf. *Plant Physiol.*, 48: 575-579.
- Guo-Zhang, K., Z. Guo-Hui, P. Xin-Xiang, S. Gu-Chou and W. Zheng-Xun, 2004. Isolations of salicylic acid-induction-expressed genes in chilling-stressed banana seedling leaf using mRNA differential display. *J. Plant Physiol. Mol. Biol.*, 30: 225-228.
- Hamada, A.M., 2001. The biochemical adaptive strategies for drought-salt resistance of wheat plants. *Rostlinná Viroba*, 47: 247-252.
- Hamada, A.M. and A.M.A. Al-Hakimi, 2001. Salicylic acid versus salinity-drought-induced stress on wheat seedling. *Rostlinná Viroba*, 47: 444-450.
- Harrison, J.S. and W.P. Trevelyan, 1963. Phospholipid breakdown in baker's yeast during drying. *Nature*, 200: 1189-1190.
- Heber, U. and K.A. Sanatarius, 1964. Loss of adenosine triphosphate synthesis caused by freezing and its relationship to frost hardiness problems. *Plant Physiol.*, 39: 712-719.
- Horvath, I., L. Vigh, T. Farkas, L.I. Horvath and D. Dudits, 1981. The manipulation of polar head group composition of phospholipids in the wheat miranovskaja 808 affects frost tolerance. *Planta*, 153: 476-482.
- Iraki, N. and N. Carpita, 1986. Extracellular polysaccharides of *Nicotiana tabacum* cell cultures in relation to adaptation to drought and saline stress. *Plant Physiol.*, 80: 500-511.
- Iraki, N.M., N. Singh, R.A. Bressan and N.C. Carpita, 1989. Alteration of the physical and chemical structure of the primary cell wall of growth-limited plant cells adapted to osmotic stress. *Plant Physiol.*, 91: 39-47.
- Janda, T., G. Szalai, I. Tari and E. Páldi, 1999. Hydroponic treatment with salicylic acid decreases the effects of chilling injury in maize (*Zea mays* L.) plants. *Planta*, 208: 175-180.
- Jeschke, E.O. and O. Wolf, 1988. Effect of NaCl salinity on growth, development, ion distribution and ion translocation in castor bean (*Ricinus communis* L.). *J. Plant Physiol.*, 132: 45-53.
- Johnson, D.L., 1971. Simultaneous determination of arsenate and phosphate in natural waters. *Environ. Sci. Technol.*, 5: 411-414.
- Lea, C.H. and J.C. Hawke, 1952. The influence of water on the stability of lipovitellin and effects of freezing and drying. *Biochem. J.*, 52: 105-114.
- Lurie, S., R. Ronen, Z. Lipsker and B. Aloni, 1994. Effects of paclobutrazol and chilling temperatures on lipids, antioxidants and ATPase activity of plasma membrane isolated from green cell pepper fruits. *Physiol. Plant.*, 91: 593-598.
- Martin, B.A., J.B. Schoper and R.W. Rinne, 1986. Change in Soybean (*Glycine max* L. Merr) glycerolipids in response to water stress. *Plant Physiol.*, 81: 798-801.
- Mishra, A. and M.A. Choudhuri, 1999. Effect of salicylic acid on heavy metal-induced membrane deterioration mediated by lipoxygenase in rice. *Biol. Plant.*, 42: 409-415.

- Navari-Izzo, R., M.F. Quaracci and R. Izzo, 1989. Lipid changes in maize seedlings in response to field water deficits. *J. Exp. Bot.*, 40: 675-680.
- Navari-Izzo, F., M.F. Quatacci, D. Melfi and R. Izzo, 1993. Lipid composition of plasma membranes isolated from sunflower seedlings grown under water-stress. *Physiol. Plant.*, 87: 508-514.
- Peeler, T.C., M.B. Stephenson, K.J. Einspahr and G.A. Thompson, 1989. Lipid characterization of an enriched plasma membrane fraction of *Dunaliella salina* grown in media of varying salinity. *Plant Physiol.*, 89: 970-976.
- Quartacci, M.F., M. Forli, N. Rascio, F. Dalla Vecchia, A. Bochicchio and F. Navari-Izzo, 1997. Desiccation-tolerant *Sporobolus stapfianus*: Lipid composition and cellular ultrastructure during dehydration and rehydratoin. *J. Exp. Bot.*, 48: 1269-1279.
- Raskin, I., Z. Skubatz, W. Tang and B.J.D. Meeuse, 1990. Salicylic acid levels in thermogenic and non-thermogenic plants. *Ann. Bot.*, 66: 369-373.
- Schwarzenbach, G., W. Biedermann and X. Complexons, 1948. Alkaline earth complexes of O, O-dihydroxyazo dyes. *Helv. Chim. Acta*, 31: 678-687.
- Serrano, R. and R. Gaxiola, 1994. Microbial models and salt stress tolerance in plants. *Crit. Rev. Plant Sci.*, 13: 121-128.
- Sharma, Y.J., J. Leon, I. Raskin and K.R. Davis, 1996. Ozone-induced responses in *Arabidopsis thaliana*: the role of salicylic acid in the accumulation of defense related transcripts and induced resistance-Pro. *Nat. Acad. Sci. USA.*, 93: 5099-5104.
- Simon, E.W. 1974. Phospholipids and plant membrane permeability. *New Phytol.*, 73: 377-420.
- Solomon, M., R. Ariel, M.J. Hodson, A.M. Mayer and A. Poljakoff-Mayber, 1987. Ion absorption and allocation of carbone resources in excised pea roots growin in liquid medium in absence or presence of NaCl. *Ann. Bot.*, 59: 387-398.
- Szalai, G., E. Páldi and T. Janda, 2005. Effect of salt stress on the endogenous salicylic acid content in maize (*Zea mays* L.) plants. *Acta Biol. Szeged.*, 49: 47-48.
- Taiz, L., 1984. Plant cell expansion: regulation of cell wall mechanical properties. *Annu. Rev. Plant Physiol.*, 35: 585-657.
- Torres-Schumann, S., J.A. Godoy, J.A. Pentor-Toro, F.J. Moreno, R.M. Rodrigo and G. Garcia-Herdugo, 1989. NaCl effects on tomato seed germination, cell activity and ion allocation. *J. Plant Physiol.*, 135: 228-232.
- Volkenburgh, E. and J.S. Boyer, 1985. Inhibitory effects of water deficit on maize leaf elongation. *Plant Physiol.*, 77: 190-194.
- Wakabayashi, K., T. Hoson and S. Kamisaka, 1997. Osmotic stress suppresses cell wall stiffening and the increase in cell wall-bound ferulic and diferulic acids in wheat coleoptiles. *Plant Physiol.*, 113: 967-973.
- Watad, A.E., M. Reuveni, R.A. Bressan and P.M. Hasegawa, 1991. Enhanced net K⁺ uptake capacity of NaCl adapted cells. *Plant Physiol.*, 95: 1265-1269.
- Williams, V. and S. Twine, 1960. Flame Photometric Method for Sodium, Potassium and Calcium. In: Peach, K. and M.V. Tracey (Eds.), *Modern Methods of Plant Analysis*. Springer Verlag, Berlin.
- Woods, J.T. and M.G. Mellon, 1941. Chlorostannous Reduced Molybdophosphoric Blue Colour Method, in Sulfuric Acid System. In: *Soil Chemical Analysis*, by M.L. Jackson, 1958. Printico-Hall International, Inc., London.
- Yalpani, N. and I. Raskin, 1993. Salicylic acid: a systematic signal in induced plant decrease resistance. *Trends Microbiol.*, 1: 88-92.
- Zhong, H. and A. Läuchli, 1988. Incorporation of [¹⁴C] glucose into cell wall polysaccharides of cotton roots: Effects of NaCl and CaCl₂. *Plant Physiol.*, 88: 511-514.