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Effect of Waterlogging and Kinetin on the Stability of Leaf Membranes, Leaf Osmotic Potential, Soluble Carbon and Nitrogen Compounds and Chlorophyll Content of *Ricinus* Plants

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Summary

GADALLAH M. A. A. 1995. Effect of waterlogging and kinetin on the stability of leaf membranes, leaf osmotic potential, soluble carbon and nitrogen compounds and chlorophyll content of *Ricinus* plants. – Phyton (Horn, Austria) 35 (2): 199–208. – English with German summary.

Plants of castorbean (*Ricinus communis* L.) were waterlogged for 15 days and were sprayed with 0, 10, 50 and –100 mgL^{-1} of kinetin. The stability of leaf membranes was assessed by determining leakage of electrolytes from leaf discs exposed to heat (51° C) and dehydration (40% PEG) stress. The membranes of waterlogged plants were more stable than control plants. Discs taken from waterlogged plants were less injured by heat than by dehydration stress. The reverse was true in control plants. Waterlogging increased proline and total free amino acids content but decreased leaf osmotic potential, chlorophyll, soluble sugars, hydrolysable carbohydrates, soluble proteins and dry matter content. Application of kinetin increased the stability of leaf membranes, chlorophyll, soluble sugars, soluble proteins and dry matter content. Statistical treatments of data show that waterlogging (WL), Kinetin (K) and their interaction significantly affected the parameters tested. The only statistically non significant effect was waterlogging on total free amino acids content. The single factors (K and WL) and their interaction (WL × K) have dual roles in their dominant and subsidiary effect (as indicated by η^2 values). The results proved that kinetin can alleviate the effect of waterlogging on the parameters tested.

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Zusammenfassung

GADALLAH M. A. A. 1995. Der Einfluß von Wasserstreß und Kinetin auf die Stabilität der Membranen von Laubblättern, des osmotischen Potentials und den Gehalt an löslichen Kohlenhydraten und Stickstoffverbindungen sowie Chlorophyll von Ricinus-Pflanzen. – Phyton (Horn, Austria) 35 (2): 199–208. – Englisch mit deutscher Zusammenfassung.

Töpfe und Pflanzen von *Ricinus communis* L. wurden 15 Tage lang vollständig in Wasser getaucht und mit 0, 10, 50 und 100 mg L^{-1} Kinetinlösung besprüht. Als Maß für die Membranstabilität von Blättern wurde die Durchlässigkeit von Blattscheibchen gegenüber Elektrolyten nach Hitzeexposition (51° C) und Austrocknung (40 % PEG) bestimmt. Die Membranen gewässerter Pflanzen waren stabiler als bei Kontrollen und die Blattscheibchen wurden durch Hitzebehandlung weniger geschädigt als durch Trockenstreß. Umgekehrt war es mit den Kontrollpflanzen. Der Wasserstreß der Pflanzen führte zu einem Anstieg des Gehaltes an Prolin und den freien Aminosäuren, aber zu einem verhinderten osmotischen Potential der Blätter, geringeren Gehalt an Chlorophyll, löslichen Zuckern, hydrolysierbaren Kohlenhydraten, löslichen Proteinen und Trockensubstanz. Die Behandlung mit Kinetin erhöhte die Stabilität der Blattmembranen, den Chlorophyllgehalt, die löslichen Zucker, die löslichen Proteine und den Trockensubstanzanteil. Die statistische Überprüfung der Daten ergab, daß die Überflutung mit Wasser (WL), sowie Kinetin (K) und ihre Wechselbeziehungen die überprüften Parameter signifikant beeinflußten. Einzig nicht signifikant war der Einfluß des Wasserstresses auf den Gehalt freier Aminosäuren. Die einzelnen Faktoren (K und WL) und ihre Wechselbeziehungen (WL × K) haben zweierlei Rollen in ihren Haupt- und Nebeneffekten (wie durch die η^2-Werte angegeben). Die Ergebnisse belegen, daß Kinetin die Einflüsse des Wasserstresses auf die untersuchten Parameter mindern kann.

Introduction

Waterlogging, an important water related stress, depresses plant growth (JONES 1972), inhibits the rate of photosynthesis in many species (REGEHR & al. 1975, WAMPLE & THORNTON 1984), decreases leaf water potential and increases stomatal resistance (KRAMER 1969) and reduces chlorophyll content (JACKSON 1979, BISHNOI & KRISHNAMOORTHY 1992).

Waterlogging decreases the cytokinin content (BURROWS & CARR 1969, BRADFORD 1983a) which is reported to influence plant growth and the activity of many physiological processes. Application of kinetin a cytokinins, is reported to increase the rate of transpiration (BENGTSON & al. 1979), enhance chlorophyll synthesis and reduce chlorophyll degradation by either stress or heat (BANERJI & LALORAYA 1967, SABATER & RODRIQUEZ 1978), promote plant growth and the activity of many physiological reactions (ZERBE & WILD 1980) and affect membrane permeability and the uptake of ions (WILLIAMS & HESTER 1983).

The present biochemical and physiological knowledge of the mechanisms controlling stress resistance of plants suggests that the membrane is one of the main cellular targets common to different stresses (LEVITT 1980).

The extent of membrane damage is commonly used as a measure of tolerance to various stresses in plants (BLUM & EBERCON 1981).

Proline has been implicated as an anti-stress organic molecule in some higher plants (GREENWAY & MUNNS 1980) and is known to accumulate in tissues/organs of plants subjected to drought, salt, temperature, heavy metals stress and/or infected by some pathogens (NIKOLOPOULOS & MANETAS 1991, ALIA & PARDHA SARDAHI 1991).

The present study was conducted to investigate the combined effect of waterlogging and kinetin on the stability of the leaf membranes, cell sap osmotic potential, chlorophyll and dry matter content and soluble carbon and nitrogen in *Ricinus* plants.

Materials and Methods

Castorbean plants (*Ricinus communis* L.) were grown from seeds in plastic pots containing 1400 g air dry soil (sand/clay 2:1 v/v) under field conditions at the experimental farm of the Faculty of Science, Assiut University. The plants (five per pot) were twice watered with 100 ml portions of full nutrient solution prepared according to DOWNS & HELLMERS 1975. Plants grown for 20 d in soil, the water content of which was maintained at field capacity, were subjected to 15 d of waterlogging as described by WAMPLE & THORNTON 1984. Plants were flooded by immersing the pot in water and maintaining the water level 1 to 2 cm above the soil surface by periodically adding water. Control plants were watered periodically to field capacity. Soon after the end of the stress treatment, the plants were sprayed with 0, 10, 50 and 100 mgL^{-1} of kinetin. Kinetin solutions were applied three times at 3d intervals by spraying the shoot. Three pots were assigned at random to each treatment combination. The plants were sampled 7 d after the last kinetin application.

Membrane stability test:

A method used by BLUM & EBERCON 1981 on wheat was modified for use with *Ricinus*. Leaf discs of 10 mm in diameter were punched out of the upper fully-expanded leaves and washed with deionized water to remove surface electrolytes. Five discs of each treatment were placed in each of (a) wetted test tubes (heat test), (b) test tubes with 10 ml deionized water (controls) and (c) test tubes with 10 ml 40% PEG 6000 (drought test). These were either a) heated to 51° C for 20 min in a water bath then incubated for 20 h at 10° C or b) and c) incubated for 20 h at 10° C, washed three times with deionized water, and reincubated with 10 ml deionized water for a further 20 h at 10 C. The samples were equilibrated at 25° C in a water bath and the conductance measured. Following autoclaving at 100° C for 15 min and re-equilibration at 25° C the conductance was measured a second time. Conductance measurements were made with an YSI, Model 35 conductance meter.

The degree of injury was calculated according to the following formula:

$$\% \text{ injury} = 1 - [1 - (T_1/T_2)/1 - (C_1/C_2)] \times 100$$

where T_1 and T_2 represent the first and second measurements on the treatment samples and C_1 and C_2 the first and second measurements on the control.

Measurement of proline

Leaf tissue (0.5 gm) was homogenized with 10 ml 3% sulphosalicylic acid. The extract was centrifuged and the supernatant was used for proline quantification. Proline was determined by the method of BATES & al. 1973.

Measurement of leaf osmotic potential

Leaf osmotic potential was determined by a cryoscopic method. Leaves were sampled at noon. The freezing point of the extract was determined by using a special ether evaporation device and a Beckman differential thermometer calibrated to 0.01° C. The osmotic potential was calculated as described by EL-SHARKAWI & ABDEL-RAHMAN 1974.

Chlorophyll a and b contents were measured spectro-photometrically according to TOOD & BASLER 1965. For dry matter determination the fresh plants were dried in an aerated oven at 70° C to constant weight. Soluble sugars (SS), hydrolysable carbohydrates (HC), total free amino acids (AA) and soluble proteins (SP) were determined according to procedures described by DUBOIS & al. 1956, PUCHER & al. 1957, LEE & TAKAHASHI 1966 and LOWRY & al. 1951 respectively.

Statistical inferences necessary to evaluate the effects and relative roles (shares) of single factors and their interaction on the parameters tested included:analysis of variance (F values) and coefficient of determination (η^2) respectively (OSTLE 1963). The latter (η^2) has been devised to evaluate the relative effect of each single factor and interaction in contributing to the total response.

Results

A solution of 40% P.E.G. applied to leaf discs excised from leaves of unflooded control plants caused leakage of electrolytes (Table 1). Discs of waterlogged plants were less leaky (low percent injury) than those of control plants. Discs derived from kinetin-treated plants were less injured than discs isolated from plants not treated with kinetin.

Heat stress (51° C) also caused leakage in discs taken from control plants. Leakage from these discs was however higher than that from discs excised from waterlogged plants. Generally, kinetin treatment decreased the percent of injury in both control and waterlogged plants compared to plants not treated with kinetin (0 mg kinetin).

Table 1

Dehydration and heat injury in leaf discs excised from unlogged (cont) and waterlogged (WL) *Ricinus* plants in the presence and absence of kinetin.

Kin. ($mg\ L^{-1}$)	Dehydration injury (%) (40% PEG)		Heat injury (%) (51° C)	
	Cont	WL	Cont	WL
0	19.55±0.98	16.48±1.96	24.82±1.67	13.36±1.32
10	3.75±0.20	4.81±0.93	10.78±0.63	7.43±1.68
50	6.00±0.60	10.28±1.50	15.44±1.53	9.56±2.02
100	8.81±0.58	7.48±0.70	17.16±1.93	8.98±1.39

In the absence of kinetin, waterlogging depressed plant growth (measured as dry mass production) and reduced chlorophyll a and b contents, soluble sugars, hydrolysable carbohydrates and soluble protein content compared to control plants (Tables 2 and 3). Leaf osmotic potential was decreased markedly by waterlogging, to about -1.35 MPa compared to -0.85 MPa in control. Waterlogged plants accumulated more proline and free amino acids than the controls. Proline content of flooded plants was nearly twice that in controls.

Kinetin application increased chlorophyll a and b contents in both control and flooded plants. Kinetin at 50 mg L^{-1} was the most effective concentration for increasing chlorophyll content. Kinetin-treated plants had higher soluble sugars and soluble proteins than untreated analogues. Generally, the highest kinetin concentration was the most effective. Control plants receiving kinetin solutions accumulated fewer hydrolysable carbohydrates, but the reverse was true in waterlogged plants. A lower kinetin concentration (Table 4) reduced proline content in both control and flooded plants as well. A moderate kinetin concentration (50 mgL^{-1}) enhanced proline accumulation in the control and decreased its content in waterlogged plants but the reverse was noticed with higher kinetin doses (100 mgL^{-1}). All three kinetin concentrations decreased leaf osmotic po-

Tabel 2

Effect of waterlogging (WL) and application of kinetin on chlorophyll (Chl.) content (mg g FW^{-1}) and absolute dry matter content (g) of *Ricinus* plants.

Kin	Chl a		Chl b		Dry matter	
(mg L^{-1})	Cont	WL	Cont	WL	Cont	WL
0	1.78±0.14	1.14±0.07	1.30±0.22	0.82±0.29	1.05±0.05	0.69±0.05
10	2.31±0.06	1.61±0.03	1.55±0.08	1.05±0.06	1.52±0.06	1.78±0.03
50	2.50±0.02	2.14±0.03	1.71±0.09	1.45±0.06	1.46±0.08	1.69±0.07
100	2.13±0.05	2.07±0.05	1.46±0.13	1.51±0.10	1.30±0.03	1.59±0.05

Tabel 3

Effect of waterlogging (WL) and application of kinetin on soluble sugars (SS), hydrolysable carbohydrates (HC), Soluble proteins (SP) content (mg g DM^{-1}) of *Ricinus* plants.

Kin	SS		HC		SP	
(mg L^{-1})	Cont	WL	Cont	WL	Cont	WL
0	32.34±0.69	26.57±0.83	4.22±0.23	2.05±0.14	79.26±0.86	64.45±1.35
10	43.81±1.11	36.76±0.85	2.80±0.16	4.01±0.11	98.82±1.32	89.13±1.15
50	35.17±0.62	36.56±0.96	0.78±0.13	9.44±0.57	90.62±1.17	86.76±0.69
100	36.15±1.65	41.28±1.15	1.25±0.15	5.56±0.34	100.28±1.48	94.11±1.82

tential in control plants. This was not the case, however with flooded plants. Only 50 mgL^{-1} kinetin decreased leaf osmotic potential but lower and higher concentrations increased it. Plants receiving kinetin solution, whether waterlogged or not tended to contain higher concentrations of free amino acids than untreated plants (waterlogged plants treated with 10 mg L^{-1} were exception).

Statistical analyses (Tables 5, 6) show that waterlogging (WL) and kinetin (K) have highly significant effects (as indicated by F values) on the parameters tested. Only the effect of waterlogging on free amino acids was not statistically significant ($P > 0.05$). Bifactorial interaction (WL × K) was significant for most parameters tested, indicating that the effect of increasing kinetin was not the same for the control and waterlogged plants. For example, for waterlogged plants, chlorophyll b content increased with increasing amounts of kinetin, but with the control plants, chlorophyll content only increased with kinetin up to 50 mgL^{-1}, and then decreased with 100 mgL^{-1} .The magnitude of the relative effects of single factors and their interactions (as indicated by η^2 values) is quite versatile.

Table 4

Effects of waterlogging (WL) and application of kinetin (Kin.) on proline content (µg/g FM^{-1}), total free amino acids (AA) content (mg g DM^{-1}) and cell sap osmotic potential (– MPa) in *Ricinus* plants.

Kin (mg L^{-1})	Proline		A. A.		Osmotic potential	
	Cont	WL	Cont	WL	Cont	WL
0	770.30±65.1	1342.75±11.5	74.42±0.97	89.,95±1.23	0.85±0.03	1.35±0.04
10	710.87±41.3	682.39±10.4	79.90±1.10	32.87±1.14	1.11±0.03	1.25±0.03
50	1027.53±76.4	824.64±47.9	81.62±0.65	100.39±1.6	1.02±0.04	1.48±0.03
100	755.07±40.0	1565.21±71.7	88.80±1.08	105.14±1.4	0.95±0.03	0.98±0.04

Table 5

F and η^2 values for the effect of waterlogging (WL), kinetin (K) and their interaction (WL × K) on the stability of leaf membranes, chlorophyll content (Chl.), cell sap osmotic potential (OP) of *Ricinus* plants.

Source of variance	Membrane stability				Chl a		Chl b		OP	
	Dehydration		Heat							
	F	η^2	F	η^2	F	η^2	F	η^2	F	η^2
WL	114.07**	0.29	61.77**	0.08	40.67**	0.30	80.13**	0.47	4.09.15**	0.50
K	74.45**	0.57	136.36**	0.57	26.67**	0.59	24.23**	0.43	73.43**	0.27
WL×K	18.35**	0.14	83.31**	0.35	5.33*	0.11	6.58**	0.10	62.80**	0.23

**) Significant at 1% confidence level.
*) Significant at 5% confidence level.

Table 6

F and η^2 values for the effect of waterlogging (WL), kinetin (K) and their interaction on proline (P), soluble proteins (SP), total free amino acids (AA), soluble sugars (SS), hydrolysable carbohydrates (HC) and dry matter content (DM) of *Ricinus* plants.

Source of variance	P F	P η^2	S. P. F	S. P. η^2	A. A. F	A. A. η^2	D. M. F	D. M. η^2	S. S. F	S. S. η^2	H. C. F	H. C. η^2
WL	74.15**	0.22	118.33**	0.16	2.05	–	17.50**	0.03	6.49**	0.03	225.88**	0.33
K	35.79**	0.32	201.79**	0.81	415.81**	0.55	187.50**	0.82	59.65**	0.71	20.58**	0.09
WL × K	51.82**	0.46	9.02**	0.03	336.77**	0.45	35.00**	0.15	22.06**	0.26	132.50**	0.58

**) Significant at 1% confidence level.
*) Significant at 5% confidence level.

The relative role of kinetin is predominant in affecting the stability of cell membranes, SS, SP, AA, chlorophyll a and dry matter content but that of waterlogging and interaction is subdominant. The share of (WL × K) interaction is predominant in proline and H. C. accumulation. Waterlogging has a dominant effect on cell sap osmotic potential only. However, the relative share of both waterlogging and kinetin in affecting chlorophyll b content is nearly equally dominant (η^2 = 0.47 and 0.43 respectively) and the effect of interaction is subsidiary (η^2 = 0.10).

Discussion

Exposure of *Ricinus* plants to waterlogging (Table 1) increased the stability of leaf membranes to either heat or dehydration stress, with discs taken from flooded plants being less injured than those taken from control plants.Such an effect means that membrane resistance to solute leakage was increased in response to waterlogging.The differences in the permeability of cell membranes may result from changes in the degree of saturation of fatty acids in the phospholipids of cell membranes (YAMADA & al. 1980).

Waterlogging depressed growth (dry matter production) of *Ricinus* plants. The reduction in growth could probably be a consequence of the inhibition of a number of metabolic processes associated with normal development, especially (i) various photosynthetic processes like chlorophyll content (JACKSON 1979, BISHNOI & KRISHNAMOORTHY 1992), reduction in photosynthetic enzymes (BRADFORD 1983b) and inhibition of photosynthetic transport resulting from reduced sink demand (WAMPLE & THORNTON 1984). (ii) depletion of phytohormones such as cytokinins (BRADFORD 1983a) and gibberellin (REID & CROZIER 1971).

Waterlogging decreased chlorophyll content in *Ricinus,* confirming earlier results on other plants (JACKSON 1979, BISHNOI & KRISHNAMOORTHY 1992). Contents of soluble sugars and hydrolysable carbohydrates were lower in flooded plants compared to controls. Such a reduction is probably a result of stomatal closure and a reduced rate of photosynthesis in waterlogged plants (BRADFORD 1983b, BISHNOI & KRISHNAMOORTHY 1992). On the other hand, waterlogged plants had a markedly lower osmotic potential, this may be due to either accumulation of solutes and/or increased root resistance to water flow owing to anaerobiosis (KRAMER 1969). This would reduce replenishment of transpired water leading to decreased leaf osmotic potential. Waterlogging reduced soluble proteins and enhanced free amino acids accumulation. The increase in free amino acids could be due to increased synthesis, decreased utilization in waterlogged plants and/or inhibition of amino acids incorporation in protein synthesis.

Leaf discs derived from kinetin-treated plants were less injured than those excised from untreated parallels (0 mgL^{-1} kinetin), probably due to effects of kinetin on cell membrane permeability to solutes (WILLIAMS & HESTER 1983). Enhancement of membrane stability (low % injury) by kinetin can improve the tolerance of *Ricinus* plants to anaerobiotic conditions.

Kinetin-treated plants had higher chlorophyll and dry matter content, in agreement with the findings of GADALLAH 1994. Kinetin enhanced soluble sugars and hydrolysable carbohydrates especially in flooded plants. Such an enhancement may be the result of an increase in chlorophyll content and photosynthetic activity by kinetin. Soluble protein content was much higher in both control and flooded plants receiving kinetin, presumably through enhancement by kinetin of protein synthesis (SUGIURA & al. 1962).

Both kinetin and waterlogging synergize to increase proline content. However proline has been reported to play an important role in osmoregulation (AHMED & HELLEBUST 1988, LALIBERTE & HELLEBUST 1989), protection of enzymes against denaturation (NIKOLOPOULOS & MANETAS 1991), acting as a reservoir of carbon and nitrogen sources (FUKUTAKU & YAMADA 1984), stabilizing the machinery of protein synthesis (KADPAL & RAO 1985).

Statistical analysis showed an interaction between waterlogging and kinetin. In certain cases (e. g., proline and H. C. content) the relative role (share) of this interaction is quite large to the extent that the role of single factors could be considered minor, though significant. It is suggested that such an interaction could play a role in the adaptive response to flooding conditions. The results proved that kinetin relieved the effects of waterlogging on the parameters tested.

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