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An Analysis of Leaf Growth under Osmotic Stress

¹B.T. Yasseen, ¹M.A. Abu-Al-Basal and ²F.A. Alhadi

¹Department of Biological Sciences, Faculty of Science,
Al-al-Bayt University, Mafraq, Jordan

²Department of Biology, Faculty of Science, Sana'a University, Sana'a, Yemen

Abstract: The need to develop plants with higher resistance to environmental stresses has increased tremendously in the last forty years. Drought (water stress) and salinity are major problems facing agriculture all over the world. Much work has been done to determine the anatomical, physiological and biochemical features that are consistently associated with the response and resistance to water stress and salinity during different stages of growth and development and because leaf area is a major determinant of photosynthesis and yield of crop plants, it should be considered in any serious program to improve the resistance of crop plants under stress conditions. Thus, the present review focuses on the analysis of plant and leaf growth and the growth variables and processes that might be affected by osmotic stresses; which could be considered as parameters for screening drought and salinity traits in crop plants, thereby can be used in the breeding programs and/or in the modern technology to improve resistance to those environmental conditions. Also, the recent efforts of drawing the perspectives of improving plant adaptation under osmotic stress through the linking of leaf growth variables and the genetic approach are discussed.

Key words: Cell growth, genetic approach, growth processes, growth variables, leaf growth, plant structure

INTRODUCTION

Osmotic stress caused by drought (water stress) or salinity is a major problem facing agriculture and the wildlife all over the world and especially in the developing countries. These environmental factors affect plants at various stages of growth and development from germination, seedling stage, vegetative growth and productivity (Yasseen, 1983; Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995). The need to develop plants with higher resistance to environmental stresses has increased tremendously in the last forty years by adopting genetic manipulation through three main methods: (1) breeding and hybridization, (2) biotechnological and tissue culture techniques and (3) genetic engineering techniques. Genetic variability in sensitivity to these conditions exists within many plant species and crop species such as barley, wheat, rice, tomato and could be in other crop plants (Epstein *et al.*, 1980; Yasseen and Al-Omary, 1994). Much work has been done to determine the anatomical, physiological and biochemical features that are consistently associated with the response and resistance to water stress and salinity during different stages of growth and development (Manikandan and Desingh, 2009;

Corresponding Author: B.T. Yasseen, 3 Petunia Court, Dorrington Close, Luton, Beds, LU3 1XT,
UK Tel: 00441582486672

Singh and Prasad, 2009) and since leaf area as determinant of photosynthesis and yield of crop plants is well recognized (Monteith, 1977; Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995; Muhling and Lauchli, 2002), it should be considered in any serious program to improve the resistance of crop plants under stress conditions. In fact, during the last decade many serious attempts have been made for linking physiological variables and genetic analysis of the control of leaf growth under stress conditions (Tardieu *et al.*, 2005). Thus, the present review focuses on the analysis of leaf growth and the growth variables that might be affected by osmotic stresses and could be considered as parameters for screening drought and salinity in crop plants (Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995; Yasseen and Abu-Al-Basal, 2010), thereby can be used in the breeding programs and/or in the modern technology to improve resistance to drought and salinity (Flowers, 2004). Also, the recent efforts of drawing the perspectives in improving plant adaptation under osmotic stress through the linking of leaf growth variables and the molecular and genetic approaches are discussed.

GROWTH ANALYSIS

Water stress and salinity cause series of changes in plant growth and development; these include reduction in plant height, number of leaves, leaf size (Table 1) and plant productivity (Yasseen and Al-Maamari, 1995). These changes have been attributed to disturbances in many physiological and biochemical activities (Yasseen, 1992; Munns *et al.*, 2006).

The reduction in the size of plant organs such as leaves (leaf area) can be attributed mainly to a reduction of the growth processes (Schuppler *et al.*, 1989; Maggio *et al.*, 2006), which includes cell division and cell expansion. The possible reasons behind the reduction in the growth processes due to osmotic stress include: (1) reduction in the synthesis of DNA, RNA and protein (Jaleel *et al.*, 2008), (2) reduction in the activity of Auxins (that promote cell expansion) and cytokinins (that promote cell division) (Wang *et al.*, 2008). and (3) changes in the structural characteristics of cells (Mustard and Renault, 2004). These parameters have been used successfully to distinguish the different cultivars in response to osmotic stress, since resistant cultivars proved to have leaves of more cells and these cells were bigger than those of susceptible ones (Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994; Maggio *et al.*, 2006). However, other studies have concluded that cell volume might not be reliable parameter in the process of selecting drought resistant plants because no clear differences were observed between cultivars in those experiments (Yasseen and Al-Maamari, 1995). Such conclusion was based on a particular method of measuring cell volume (Yasseen, 1983), however, other factors might have contributed to such conclusion like: (1) different

Table 1: The effect of salinity on the growth parameters in a Mexican wheat Cultivar (Cajeme), after 40 days of treatment

Growth parameters	NaCl concentration (mol m ⁻³)	
	0	150
Tillers number	8.7	2.3
Total leaf area (cm ² plant ⁻¹)	468	94
No. of leaves on the main tiller	8.4	8.0
Area of leaves on the main tiller (cm ² plant ⁻¹)	107	48
Area of leaf 6 of the main tiller (cm ² leaf ⁻¹)	28.3	14.3
Cell number (10 ⁶)	5.010	3.726
Cell volume (mm ³)	122	69

Yasseen (1983)

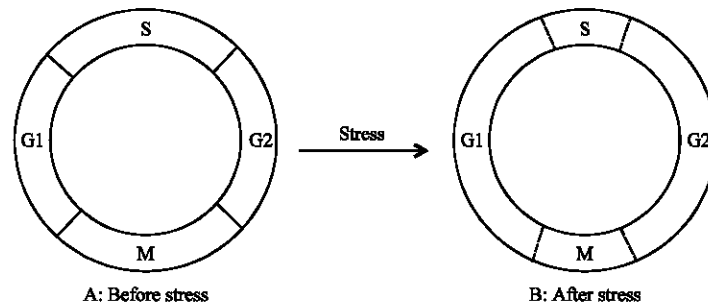


Fig. 1: Cell cycle under osmotic stress (Adopted from Rost, 1977)

experimental conditions, (2) various methods of estimation with no reliable technique has been used and adopted and (3) different tissues and plants may respond differently to osmotic stresses and (4) no consensus about the role of cell volume in evaluating osmotic resistance of plants (Yasseen, 1983; Lorences and Fry, 1991). Therefore, improvement the techniques of the estimation of cell volume could be useful to make clear conclusion (Godoy-Hernandez and Vazquez-Flota, 2005).

Cell Division

Early studies (Rost, 1977) have shown that water stress causes great changes in the stages of the cell cycle: (1) cells are arrested in G1 and G2 stages. This means that the duration of both stages becomes longer, (2) reduction in DNA synthesis or DNA replication (Fig. 1) and (3) Mitosis is inhibited. Mitosis can be studied quantitatively by studying the Mitotic Index (MI). The above conclusions were obtained from events of seed maturation of *Vicia faba* before harvesting (during the period 39 days up to 5 days before harvesting). During this period water content is reduced from 91 to 55% and the Mitotic Index (MI) decreased in the radicle from 10.5 to 2.7. From these data, it can be concluded that water stress affects almost all stages of cell cycle depending on the degree of the reduction in the water content of the cell.

Gould *et al.* (1981) have studied the effect of nutrient starvation on the cell cycle of suspension cultures of *Acer pseudoplatanus*. They found that cells suffering from phosphorus or carbohydrate starvation arrest in the G1 and G2 phases. Other studies have shown that osmotic stress decreased the Mitotic Index (MI) considerably in the root tip during seed germination and seedling growth, thereby reducing the germination percentage and radicle lengths (Abu-Al-Basal and Yasseen, 2009) (Table 2). In a study of the mitotic activity of mesophyll cells and the enzymes involved in DNA replication in wheat (*Triticum aestivum*) plants, water stress caused a reduction in H1 histone kinase activity to one-half of the control level and as a result the leaf-elongation rate was reduced by one-half and the mitotic activity of mesophyll cells was reduced to 42% of well-watered controls within 1d. after imposing mild water stress (water potential of -0.3 MPa). There was also a reduction in the length of the zone of mesophyll cell division to within 4 mm from the base compared with 8 mm in control leaves (Schuppler *et al.*, 1989).

Cell Enlargement

The reduction in cell volume is a common response to osmotic stress causing adverse effect on cell growth. As osmotic stress increases in the growth medium of plants, volume of cells shows gradual reduction thereby decreasing the area of leaves and the size of the plant as a whole (Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994; Yasseen and

Table 2: Germination, mean radicles length, Mitotic Index (MI) and cell volume of the barley cultivar Arivat in response to salt stress

Growth parameters	NaCl concentration (mol m ⁻³)		
	0	200	400
Germination %	100	97	71
Radicle length (mm radicle ⁻¹)	84	30	6
Mitotic index (MI)	16.7	13.1	7.5
Cell volume (mm ³ ×10 ⁶)	95	72	33

Abu-Al-Basal and Yasseen (2009)

Al-Maamari, 1995; Alhadi *et al.*, 1999). Such reduction in cell volume involves changes in both biophysics (Fricke and Peters, 2002) and biochemistry (Navari-Izzo *et al.*, 1989; Wu *et al.*, 2005) of plants under stress, changing the structure and function of cell wall and plasma membranes (Berube *et al.*, 1999). Deformation of the cell surface is a major response to osmotic stress causing a reduction in cell volume. In severely stressed and damaged plants, a range of cell shapes and deformations occur which are characteristics of particular cell types (Pearce and Beckett, 1987) and the cell walls relax (Gosgrove, 1997), thereby lowering turgor pressure (Pessarakli, 1999). As water deficit progresses and cells contract further which accompanied with changes in the physical and chemical characteristics of plasma membranes, their ability to maintain a semipermeable barrier is impaired (Navari-Izzo *et al.*, 1993). In fact, all activities that are dependent upon turgor are very sensitive to water stress, for example, cell expansion is turgor-driven process is extremely sensitive to water deficit (Gosgrove, 1997; Pessarakli, 1999; Taiz and Zeiger, 2006). The solutes under such conditions become more concentrated (Buhl and Stewart, 1983); these solutes include proline (Yasseen, 1992). Looking at the biophysics of cell expansion; growth expansion rate (GR) is described by the relationship:

$$GR = m (\Psi_p - Y)$$

where, *m* is wall extensibility, Ψ_p is pressure potential, *Y* is yield threshold, ($\Psi_p - Y$) is called the effective pressure on leaf expansion (Taiz and Zeiger, 2006). Under osmotic stress, both *m* and the effective pressure are reduced (Gosgrove, 1997; Pessarakli, 1999) and elimination of cell expansion totally could be taken place when Ψ_p is reduced to the value of *Y*. Thus, it could be imagined that osmotic stress not only decreases turgor, but also decreases *m* and might increase *Y* (Pessarakli, 1999; Evered *et al.*, 2007). The reduction of *m* under such environmental conditions could come from the inhibition of proton transport across the plasma membrane into the cell wall, raising the cell wall pH (Neves-Piestun and Bernstein, 2001; Lew, 2004). On the other hand, the mechanism of the effect of osmotic stress on *Y* seemed not so clear (Cramer and Bowman, 1991), however, since the last two decades, efforts have fruited in clarifying the mechanism of the effects osmotic stress on the physical and chemical properties of cell wall. *Y* response to stress may involve complex changes and modifications in the cell wall structure and composition; these changes include modifications in the cell wall polysaccharides underlie the process of cell expansion. The contents of cellulose, hemicelluloses and pectic substances in the cell walls are reduced by osmotic stress due to drought and salinity (Mustard and Renault, 2004). Such modifications in cell wall components could cause changes in the structure of plant as a whole (Pearce and Beckett, 1987; Yasseen, 1992). Auxin activity, on the other hand, is reduced due to osmotic stress as earlier studies have revealed and the level of growth inhibitors in the leaves might be increased (Fig. 2), which completely neutralized by the presence of growth promoting substances (Khan *et al.*, 1976). From the above discussion it worth to hypothesize a model for the possible effect of osmotic stress on cell expansion components as can be seen in Fig. 3.

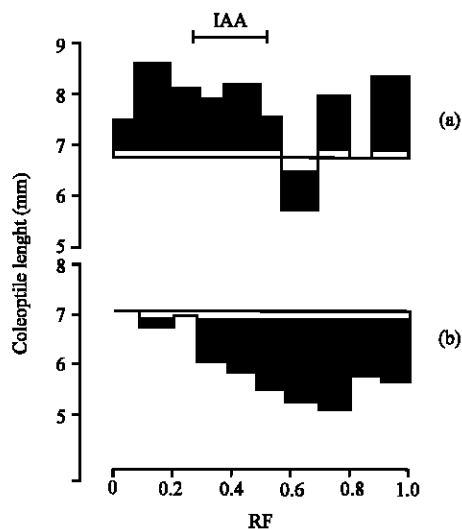


Fig. 2: Bioassay of endogenous hormones in shoots of *Zea mays* in non-saline (A) and saline; 150 mM NaCl and (B) soil. Dark areas are significantly different ($p < 0.001$) from the control (Khan *et al.*, 1976)

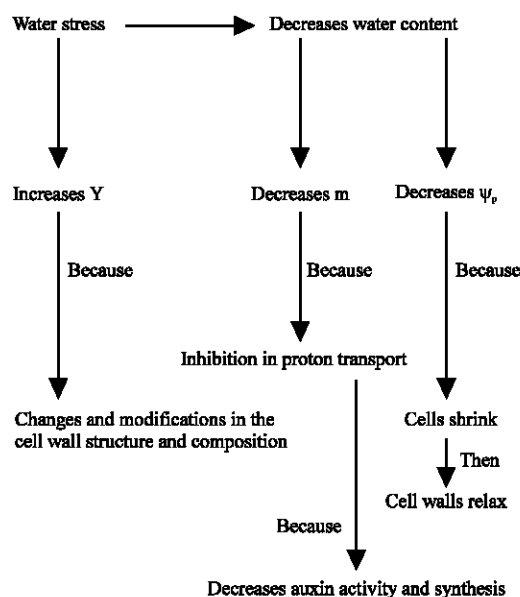


Fig. 3: The hypothetical possible effect of osmotic stress on the components of the cell expansion as described by the equation: $GR = m (\Psi_p - Y)$

The hormonal imbalance is one of the most important metabolic disturbances that take place when plants are exposed to saline or drought conditions. Changes include increasing or decreasing the synthesis or activity of growth regulators (retardants and promoters). The early works of Kahn *et al.* (1957) on the seed germination of lettuce (*Lactuca sativa*) demonstrated that the inhibition of seed germination by the osmotic agent of mannitol can

be alleviated using gibberellins. Also, Nieman and Bernstein (1959) found that the plant dry weight of dwarf beans growing under saline conditions increased by GA₃ application. Moreover, other studies have shown that there is a possibility of using plant growth hormones to alleviate the adverse effect of salts or other non-ionic agents on germination and growth of many plants. Many reports confirm such conclusion in many plants such as potato, *Brassica campestris*, *Pisum sativum*, fenugreek and corn (Alhadi *et al.*, 1999; Wang *et al.*, 2008). Such results might be useful in the field of soil water deficits reclamation efforts by using plant growth regulators (Jaleel *et al.*, 2008) and to improve drought and salinity tolerance by adopting modern techniques (Wang *et al.*, 2008).

Description of Leaf Growth

Two main mathematical methods have been adopted to describe leaf growth in order to get information of biological meanings to be used by physiologists, geneticists, breeders, molecular biologists and biotechnologists.

Logistic Equations

Logistic equations have been used to describe the growth of leaves under stress (Yasseen, 1983), or other empirical equations for calculating the growth variables which had good performance in predicting leaf growth in various plants (Yan *et al.*, 2006).

Linear Description of Leaf Growth

Linear description of leaf growth adopted by Gallagher (1979) has been used to describe the linear leaf growth in some cereals such as barley and wheat (Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995). Gallagher equation has been then adopted in many other plants with new approach and vision (Clouvel *et al.*, 2008). During the past three decades many studies have been published on the analysis of leaf growth under various environmental conditions such as temperature, water stress and salinity (Yasseen, 1983). Those studies were aimed to determine the growth variables that can distinguish the crop cultivars under salt stress (Yasseen *et al.*, 1987), water stress (Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995; Pereyra-Irujo *et al.*, 2008), or any other factor.

Analysis of leaf growth under osmotic stress using both logistic equations and linear description showed clearly that the great reduction in the size of leaves (in terms of area or length) was attributed to the reduction in the growth rate, while the duration of growth was not affected very much (Table 3, 4). Thus, it can be concluded that the great reduction

Table 3: Effect of salinity on growth rate, duration of growth and final area of leaf 6 in two Mexican wheat cultivars

NaCl (mol m ⁻³)	Growth rate (cm ² day ⁻¹)		Growth duration (days)		Area at the point of inflexion (cm ²)		Final area (cm ²)	
	Cajeme	Yecora	Cajeme	Yecora	Cajeme	Yecora	Cajeme	Yecora
0	3.15	3.33	9.1	8.4	11.5	11.2	28.3	27.8
75	2.80	2.43	7.8	7.2	9.1	7.4	21.8	17.3
150	1.87	1.80	7.7	6.6	6.4	5.3	14.3	11.8

Yasseen (1983)

Table 4: The effect of NaCl on the rate (R_L), duration (D_L) of growth and final length (F_L) of leaf 6 of two barley cultivars

NaCl (molm ⁻³)	Growth rate (R _L) (cm day ⁻¹)		Growth duration (D _L) (days)		Final length (F _L) (cm)	
	Black	Arivat	Black	Arivat	Black	Arivat
0	4.8	4.1	7.1	4.0	36.2	17.7
50	4.7	3.6	6.9	3.9	36.3	15.3
100	4.3	2.4	7.1	4.0	34.2	10.9
200	3.8	1.7	7.6	4.2	31.1	8.1

Yasseen *et al.* (1987)

in the size of leaves was attributed mainly to the reduction in the rate of growth processes (cell division and cell expansion). Looking at the genetic variability in sensitivity to osmotic stress which exist within crop species such as barley, wheat, sorghum and pearl millet (Yasseen, 1992). Faster rates and longer duration of growth of individual leaves were found in Mexican wheat of the long season cultivars; salt tolerant as compared to the short season cultivars; salt susceptible (Yasseen, 1983). Also, this has been considered as an important criterion in selecting barley cultivars suitable for the cultivation in water stressed soils and for breeding programs to develop salt tolerant cultivars (Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995).

The hypothesis of increasing the length of growing season and if leaves are able to expand rapidly under stress conditions, may lead to considerable maintenance of yield under these conditions (Monteith, 1977). Moreover, the varietal differences in those crop plants could come from the differences in the duration of growth as well, since crops of long season cultivars like a Mexican wheat cultivar (Cajeme) and local Black barley (long season cultivars) proved to have long growth duration of individual leaves as compared to those like a Mexican wheat cultivar (Yecora) and barley cultivars like CM-72 and Arivat (short season cultivars) under both drought and saline environments (Yasseen, 1983; Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995). In fact, since 1980 there have been serious efforts by many scientists to peruse genetic manipulation to improve the salt resistance of crop plants and these attempts proved fruitful in determining some features associated with drought or saline resistance in plants; focusing on wild plants (Yasseen and Al-Thani, 2007; Yasseen and Abu-Al-Basal, 2008) and on many cultivated crops such as barley, wheat, rice and tomatoes (Yasseen and Al-Omary, 1994; Yasseen and Al-Maamari, 1995; Hasegawa *et al.*, 2000; Flowers, 2004; Abu-Al-Basal and Yasseen, 2009). Such findings could be considered as experimental materials for plant breeders, geneticists and molecular biologists, to improve osmotic resistance of crop plants.

Genetic Approach

In the last decade, our understanding of the processes underlying plant response to drought or salinity at the molecular and the whole plant levels has rapidly progressed. To start with, the reduction of leaf growth at stressed growth conditions has been considered as a complex response, since the small area of leaf can be seen in two points of view: (1) an adaptation feature to reduce the water lost by transpiration process, (2) stomata of less number and less efficiency due to partial or complete closure, might have adverse effect on gas exchange and photosynthesis (Pereyra-Irujo *et al.*, 2008), thereby decreasing the biomass; a variable of great importance in the determining of productivity (Monteith, 1977). Thus, breeding for resistance to osmotic stress can therefore involve two opposite strategies: either select plants with reduced leaf area under water deficit in order to avoid plant water stress, or select plants with maintained leaf area in order to maximize light interception under water deficit (Tardieu *et al.*, 2005). However, the first strategy should involve improving stomatal efficiency, while the second strategy might involve improvement of the efficiency of water absorption by roots (Spollen *et al.*, 2000). It is difficult to judge which of these strategies is determinant in plant adaptation and / or which one of these is feasible in dealing with resistance genes and proteins. Among such proteins is water transporters, their roles in the regulation of plant water status and transport of other metabolites are the subject of intense investigation (Vinocur and Altman, 2005). Long-distance chemical signalling, as an early response to drought, started to be unraveled more than a decade ago. Modern technologies might be able to engineer plants for many

physiological and biochemical aspects including: easier absorption of water and nutrients, osmotic adjustment or protection, water transporters and C_4 traits, as well as for more efficient stomata under osmotic stress (Vinocur and Altman, 2005). In fact, a balance is required between maintaining the water content of the plant and maintaining the efficiency of photosynthesis. Increasing water absorption efficiency by roots to improve water status under osmotic stress (drought or salinity) could be one of the major topics to be addressed in the current century (Shao *et al.*, 2009). Moreover, the argument that plants with more suberin-which decreased transpiration-used the water they able to absorb more efficiently. So, plants could be genetically engineered for specific amounts of suberin to enable these plants to absorb beneficial nutrients and use less water in a more efficient manner (Wallheimer, 2009). There have been some attempts to describe the source of genetic variability in response of leaf growth and its growth variables; growth rate and duration to osmotic stress. Several mechanisms have been suggested to drive the reduction in leaf growth rate under osmotic stress: (1) reduction in leaf carbon balance, (2) incomplete turgor maintenance, (3) decrease in cell wall plasticity, (4) decrease in cell division rate, (5) contributions of hormones, abscisic acid and ethylene, which are known to increase under stress (Tardieu *et al.*, 2005). Each of these mechanisms is still controversial and involves several families of genes and it was argued that gene regulatory networks are not feasible for modeling such complex systems (Vinocur and Altman, 2005). Also, much attention has been paid to the role of potassium under osmotic stress, since maintaining high potassium concentration in leaves of crops could increase their salt tolerance (Rascio *et al.*, 2001). Scientists are trying to develop crop plants (like cereals) that have efficient mechanisms to maintain high levels of potassium in leaves under salt stress (Shabala and Cuin, 2008). So far, a considerable number of studies have presented two possible mechanisms to maintain optimal cytosolic K^+/Na^+ ratio by either: (1) restricting Na^+ accumulation in plant tissues, (2) preventing K^+ loss from the cell. Some recent studies (Abu-Al-Basal and Yasseen, 2009) have shown that potassium accumulated in leaves of a local barley cultivar (Black) as NaCl increased in the growth medium, which was explained by activation of high-affinity potassium uptake transporters (HKT) (Rubio *et al.*, 1995). Also, it has been recognized that K^+/Na^+ ratio is a determinant factor in the ability of a plant to survive saline environments (Botella *et al.*, 1997). Black barley proved superior over other cultivars during vegetative growth (Yasseen *et al.*, 1987; Yasseen and Al-Omary, 1994) and yield stages (Yasseen and Al-Maamari, 1995) under water stress conditions because of a faster rate and longer duration of leaf growth, which was accompanied by potassium accumulation as soil matric potential decreased. It is very likely that the ability of Black barley to accumulate K^+ might provide this cultivar with traits of improved growth variables (i.e., faster rate and longer duration of growth processes) under osmotic stress (Itoh *et al.*, 1997). This needs further investigation to explore the activity of plant K^+ - permeable cation transporters (Maser *et al.*, 2002) under salt stress in such cultivars (Yasseen and Al-Maamari, 1995; Abu-Al-Basal and Yasseen, 2009) to draw clear conclusion about the mechanism of effect of sodium salts on growth parameters (variables and processes).

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