Int. J. Plant Sci. 161(4):575–582. 2000.

1058-5893/2000/16104-0004$03.00

KINETICS AND SPATIAL DISTRIBUTION OF LEAF ELONGATION OF WHEAT (*TRITICUM AESTIVUM* L.) UNDER SALINE SOIL CONDITIONS

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Leaf development of wheat largely determines the rate of plant growth in the early growth stages and is most sensitive to salinity. The objectives were to investigate the shoot growth, area of leaves, and kinetics of leaf elongation of wheat seedlings (*Triticum aestivum* L.) grown in illitic-chloritic silt loam with four salinity levels from 0 to 120 mM NaCl in growth chambers. Shoot fresh mass (FM) and leaf area were measured at days 12 and 18 after sowing. Instantaneous measurements of the leaf elongation rate (LER) of leaves 3, 4, and 5 of the main stem were carried out by using linear variable differential transducers (LVDT). Spatial distribution of relative elemental growth rate (REGR) and the length of the leaf elongation zone were determined by measuring displacement rates with a pricking method. Shoot FM per plant linearly decreased with increasing salinity levels. Leaf area under saline conditions was significantly correlated to the shoot FM during vegetative stages, indicating that leaf growth most sensitively responds to salinity. Salinity delayed leaf emergence and affected leaf growth longitudinally and laterally. Reduction in the final length of leaves 3, 4, and 5 was mainly a result of a decrease in their LER. The decreased LER under saline conditions was more pronounced during the steady growth phase and during the light period compared to later stages and to the dark period, respectively. Salinity affected the LER more severely with increasing leaf number, probably as a result of the longer exposure to salinity and longer elongation zones for higher leaf numbers. The reduction in LER resulted from decreasing the REGR but did not result from shortening the length of the leaf elongation zone during the linear phase of leaf growth.

Keywords: leaf elongation rate (LER), leaf elongation zone, linear variable differential transducer (LVDT), saline soil, relative elemental growth rate (REGR), *Triticum aestivum* L.

Introduction

Salinity affects wheat growth during all growth stages. However, the vegetative stage, which establishes the final yield potential in wheat plants and is characterized by the sequential appearance of leaves and tillers and leaf elongation on tillers, is most sensitive to salinity (Munns and Termaat 1986; Maas and Poss 1989; Arif and Tomos 1993). In the early stages of wheat development, leaf development largely determines the rate of plant growth. Limitation of salinity to leaf development may cause tiller reduction and irreversible yield reduction. Therefore, a better understanding of the effect of salinity on wheat growth requires detailed studies of leaf development under saline conditions.

A visible leaf of a monocotyledonous species increases only its length because the width remains unchanged once it has emerged from the sheath bundle (Dale 1988). The increase in the length of leaves is a dynamic process. The final leaf length is a function of leaf elongation rate (LER) and the duration of leaf elongation. Under the given conditions, the LER varies with leaf age and day/night cycle (Christ 1978*a*, 1978*b*). Different LER with time may characterize the distinct stages during leaf development, i.e., increasing elongation rate, steady elongation rate, and decreasing elongation rate (Skinner and Nelson 1995). The change in the leaf elongation of wheat in a day/night cycle includes a number of physical and physiological activities (Christ 1978*a*, 1978*b*). At present, however, there is no information available about the effects of salinity on the elongation rates during steady and decreasing growth stages and on the diurnal course of leaf elongation.

The elongation of a growing leaf of grasses is restricted to a small region at the base of the blade enclosed by sheaths of older leaves, and the leaves only grow in the longitudinal direction (Kemp 1980*b*). The LER is a function of the length of the elongation zone (LEZ) and the relative elemental growth rate (REGR). The REGR is a parameter to compare the efficiency of cell elongation in the growing zone for the different leaves and under different conditions Kemp (1980*a*). Data on the effect of salinity on the spatial distribution of REGR will also provide the fundamental information on the further physiological study. For example, Silk (1984) discussed and demonstrated that the local net deposition rate of substances (such as nutrients and water) in growing leaves of grasses, which may be regarded as a useful means of describing physiological and morphological aspects of the growth process, can be calculated by using the continuity equation. Data of the spatial distribution of REGR are required for this calculation. Moreover, in the literature the studies on the effect of salinity on

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Manuscript received November 1999; revised manuscript received December 1999.

the LEZ of gramineous leaves are inconsistent. For example, Delane et al. (1982) and Arif and Tomos (1993) reported that salinity did not affect the LEZ of growing leaves for wheat, whereas Bernstein et al. (1993*b*) found that the LEZ of sorghum leaves was reduced by salinity.

Leaf growth of wheat reacts mostly to salinity and plays such an important role in plant growth during the early growth stages. Thus, the parameters such as leaf area, final leaf length, leaf width, kinetic process of leaf elongation, and the distribution profile of leaf elongation in the growing zone, which characterizes the leaf growth, were chosen for the study of the effect of salinity on leaf growth. In this study, the effect of salinity on the relationships between leaf development and shoot growth during the early stages and on leaf elongation diurnally and developmentally were demonstrated. By considering the distribution profile of REGR, more insight can be gained into the involvement of limitation of salinity to leaf elongation in the growing tissues of grass leaves. Effects of salinity on the distribution profiles of leaf elongation in the growing zone would indicate that the decreased leaf elongation of wheat by salinity should be much more closely associated with metabolic/nutritional changes within the growing regions of leaves than in whole or nongrowing regions.

Material and Methods

Growth Conditions

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona) per pot, pregerminated for 2 d on filter paper moistened by tap water at 20°C, were sown in 1.5-L pots (10-cm diameter and 20-cm height) containing an illitic-chloritic silt loam (fine, mixed, mesic Aquic Ustifluvent) (Schmidhalter et al. 1994). The soil was initially watered to 0.25 g H_2O g^{-1} dry soil (soil matric potential: $\Psi_m = -0.03$ MPa) with one strength Hoagland solution for macronutrients and half-strength micronutrients as recommended by Epstein (1972). The composition of the modified Hoagland nutrient solution was (in mol m^{-3}): 6.05 K^+, 15.0 NO_3^-, 5.0 Ca^{2+}, 2.0 Mg^{2+}, 10.0 $H_2PO_4^-$, and 2.0 SO_4^{2-}. The salt levels of 40, 80, and 120 mM NaCl were obtained by adding NaCl to the nutrient solution. The soil was mixed thoroughly and kept in tightly closed plastic boxes for 1 wk to facilitate equilibration. Thereafter, the soil was sieved and placed into pots. Soil moisture content was maintained at the initial content by adding tap water. In order to avoid water losses by evaporation, the pots were covered with a perforated plastic foil, and plants grew through small holes in the foil. One week after sowing, the seedlings were thinned to four plants per pot. The experiment was conducted in a growth chamber with a 16-h photoperiod. The light intensity was ca. 550 μmol photon m^{-2} s^{-1} (PPFD). The air temperature was 20°C day/night and the relative humidity was maintained at 55%–65%.

The following three experiments were conducted to determine the growth of wheat seedlings, leaf length, LER, the length of elongation zone, and REGR. The number of replications are reported individually in following sections.

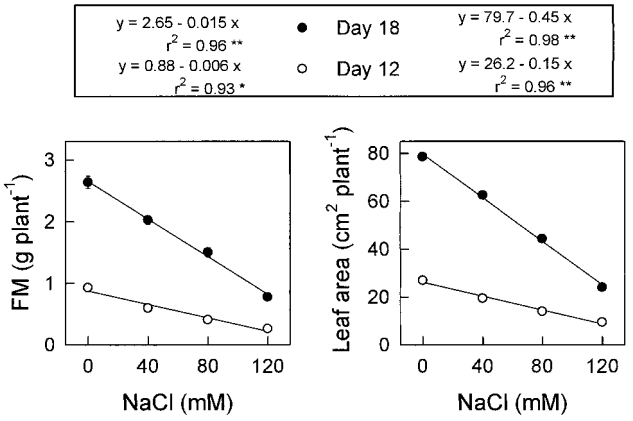

Fig. 1 Effect of salinity on shoot fresh mass (FM) and leaf area of wheat seedlings grown in soil with 0, 40, 80, and 120 mM NaCl on days 12 and 18 after sowing. Error bars represent standard errors ($n = 4$) and fit within the plot symbol if not shown.

Determination of the Growth of Seedlings

Four replicate plants were harvested on days 12 and 18 after sowing. Shoot fresh mass (FM) was determined. Tiller number per plant was recorded. Leaf length, average leaf width, and leaf area were determined with a portable leaf area meter (Model LI-3000A, Li-Cor, Lincoln, Nebr.).

After each harvest, the soil was carefully removed from the pots and cut horizontally into three 5-cm sections. Gravimetric soil water content (θ_g) of each section was determined by weighing before and after drying at 105°C for 36 h. The electrical conductivity of the soil solution in a 0.25 : 1 water-soil extract ($EC_{0.25:1}$) was measured with a conductometer (Conductometer, E 518, Metrohm, Herisau, Switzerland) on days 0, 12, and 18 after sowing. In general, there was no significant change in the salt concentration for any treatment. Only a decrease in $EC_{0.25:1}$ on day 18 after sowing was observed in the top section of the pot; e.g., $EC_{0.25:1}$ at 0 mM NaCl was 1.0 dS m^{-1} at 0–5 cm and 1.6 dS m^{-1} at 5–10 and 10–15 cm, respectively; $EC_{0.25:1}$ at 120 mM NaCl was 11.6 dS m^{-1} at 0–5 cm, 15.0 dS m^{-1} at 5–10, and 16.0 dS m^{-1} at 10–15 cm, respectively.

Instantaneous Measurements of Leaf Elongation Rate and Leaf Length

Instantaneous measurements of leaf growth were conducted by using linear variable differential transducers (LVDT) when the visible part of leaves 3, 4, and 5 of the main stem was 1–2-cm long (ca. 1 d after leaf emergence) in all treatments. The tip of the leaf was connected to the LVDT by a fishing line (0.22-mm diameter) that was attached to the leaf tip using a small clamp cushioned with rubber to avoid damaging the leaf. The force on the fishing line was 10 *g* to eliminate oscillations in LVDT output resulting from slipping and friction in the measurement system. According to our preexperiment, this force did not affect LER during measurements. One reading was taken from each transducer every 30 min. During this period of 30 min, six values were averaged, and the average values were stored in a logger (Delta-T Device, Cambridge,

Table 1

Time of Leaf Emergence, Leaf Length, and Average Leaf Width of Fully Developed Leaves 3, 4, and 5 on the Main Stem of Wheat Grown in Soil with 0, 40, 80, and 120 mM NaCl

Leaf number	0	40	80	120
Emergence at day after sowing:				
3	8	9	10	11
4	12	13	14	16
5	16	17	19	20
Final leaf length (cm):				
3	30.9 ± 0.6	30.4 ± 1.7	28.6 ± 0.7	27.6 ± 1.3
4	33.9 ± 0.6	30.7 ± 1.4	28.5 ± 1.0	26.9 ± 0.7
5	33.1 ± 1.5	27.1 ± 1.1	23.2 ± 1.7	22.1 ± 1.4
Final average leaf width (cm):				
3	0.40 ± 0.00	0.33 ± 0.03	0.30 ± 0.03	0.30 ± 0.03
4	0.68 ± 0.03	0.60 ± 0.00	0.60 ± 0.00	0.48 ± 0.03
5	0.60 ± 0.00	0.60 ± 0.00	0.53 ± 0.03	0.43 ± 0.03

Note. Means ± SE; n = 4–8.

United Kingdom). The measurements of leaf elongation rate were completed when the elongation rate (mm h^{-1}) was ca. 0. LER was calculated by dividing the increase in length by the time interval. All measurements of the LER were performed with eight replications.

Leaf length can be viewed as the integral of LER. Once the measurement of each leaf was finished, the final leaf length was also recorded by means of a ruler in order to compare the results of the LVDT method.

Determination of the LEZ and REGR

The position of the growth zones of the third, fourth, and fifth leaves of the main stem was determined by measuring displacement rates along the leaf axis by the pricking method (Kemp 1980*b*). Each treatment had 16 replications. The first pinhole was made at 2 mm above the node between shoot and roots. In total, 15 pinholes were made at 3-mm intervals by inserting a small needle (0.2-mm diameter) through the enclosing leaf sheaths 3 h after the photoperiod was initiated. Ten hours after pricking, the leaf was removed from the plant and displacement of pinholes was measured with a binocular microscope. All measurements were performed ca. 2–3 d after leaf emergence; i.e., measurements were taken during the steady phase of leaf growth. The effect of pricking on the rate of leaf elongation was evaluated during a 10-h period by comparing the elongation rate in pricked leaves with that of nonpricked leaves on other plants. Measurements from the nonpricked leaves were made with a ruler.

Relative elemental growth rate (REGR) (mm mm^{-1} h^{-1}) is the relative elongation rate of a leaf segment in one dimension, i.e., the change that occurs in the length of a leaf segment per unit length per unit time. The $REGR_i$ was calculated according to the following equation:

$$REGR_i = (D_{i2} - D_{i1}) \times D_{i1}^{-1} \times (t_2 - t_1)^{-1},$$

where D_{i1} represents the initial distance in millimeters between neighboring holes defining segment i (i = 1, 2, ... , 15) at the time (t_1) of making punctures, and D_{i2} represents the distance between these same punctures after an elongation period ($t_2 - t_1$). According to Schnyder et al. (1987, 1990), the pricking results in the reduction in LER result from a uniform reduction in the REGR along the elongation zone. Therefore, data of LER for nonpricked leaves 3, 4, and 5 were used to correct the REGR in the elongation zone (cf. also Bernstein et al. 1993*b*). The length of the elongation zone (LEZ) was defined as the distance from the leaf base to the middle of the last segment where REGR was <0.002 mm mm^{-1} h^{-1}.

Statistical Analysis

A completely randomized design was used with four to 16 replications for all experiments. Effects of salinity on shoot FM and leaf area were evaluated by steady regression analysis (n = 4). Data were also analyzed by analysis of variance (ANOVA) to test the significance of the main effects. Terms were considered significant at $P \leq 0.05$.

Results

Shoot FM and Leaf Area

Mean values of shoot FM and leaf area per plant of wheat decreased linearly with an increase in external NaCl concentration at days 12 and 18 after sowing (fig. 1). Differences in shoot FM and leaf area between control and saline treatments increased over time. At 120 mM NaCl, for instance, shoot FM decreased by 66% and 70.5% at days 12 and 18, respectively, and leaf area decreased by 65% and 69% at days 12 and 18, respectively, as compared with the control.

Time of Appearance, Final Length, and Average Width of Leaves on the Main Stem

Leaf appearance was significantly delayed with increasing salinity (table 1). The final leaf length from the integral of mean LER by LVDT and the average width in the main stem decreased as the external NaCl concentration increased (table 1). With an increase in leaf number, the reduction in the final leaf length of plants grown in soil with 120 mM NaCl became more pronounced. The final leaf lengths of leaves 3, 4, and 5 of the main stem with 120 mM NaCl were reduced by 11%, 21%, and 33%, respectively. The final leaf areas of leaves 3,

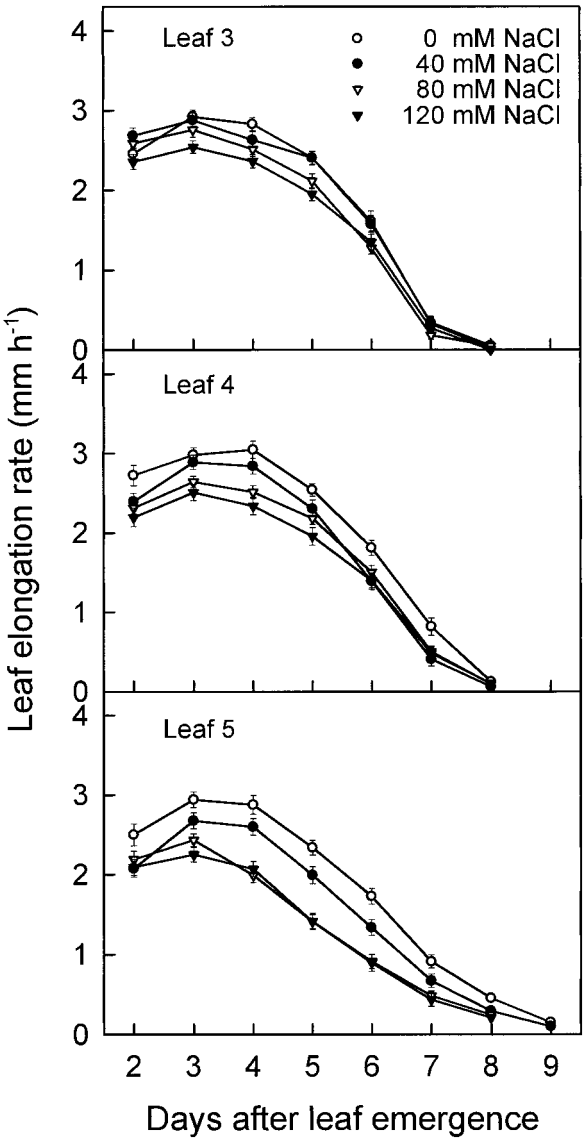

Fig. 2 Average daily rates of leaf elongation of leaves 3, 4, and 5 of the main stem of wheat plants grown in soil with 0, 40, 80, and 120 mM NaCl. Error bars represent standard errors (n = 8) and fit within the plot symbol if not shown.

4, and 5 of the main stem at 120 mM NaCl were reduced by 35%, 45%, and 51%, respectively.

Kinetics of Leaf Elongation

The results of the LER for leaves 3, 4, and 5 on the main stem in all treatments show a similar pattern of the kinetics of leaf elongation (fig. 2). The LER remained nearly unchanged from 2 to 4 d after the leaf emerged, i.e., steady growth phase, and then decreased with time until the end of leaf elongation, i.e., decreasing growth phase. The decrease in LER by salinity increased with an increase in leaf number. At 120 mM NaCl, the average LER during the entire period of leaf growth decreased by ca. 14%, 22%, and 33% for leaves 3, 4, and 5, respectively. The decreases in the LER of leaves 3 and 4 resulting from salinity were more pronounced during the steady growth phase than during the decreasing phase (fig. 2). However, the strong effect of salinity on the LER of leaf 5 continued after the steady phase of leaf growth. During the period of 2–4 d after the leaf emerged, for example, the reduction in LER by 120 mM NaCl contributed to ca. 60% of the total reduced length of leaves 3 and 4 as compared with only 45% in leaf 5. No difference in the duration of leaf elongation after leaf emergence was observed between control and salinized treatments (fig. 2).

Leaves 3, 4, and 5 exhibited a distinct diurnal variation during the entire period of leaf elongation. As a representative, the LER data of leaf 4 are shown in figure 3. In a diurnal cycle, the LER changed between the light and dark period and when the lights were turned off and on through the entire period of leaf growth. The LER was not quite constant during light and dark periods (fig. 3). During the steady phase of growth, LER was slightly lower in the second part of the light period. The LER was significantly higher during the light period than during the dark period for days 2–5 ($P < 0.001$) (table 2). The decrease in LER by salinity was less pronounced during the dark period than during the light period (table 2). At 120 mM NaCl, for instance, the mean LER of leaf 4 for the first 3-d measurements decreased by 22% during the light period and only 16% in the dark period.

Spatial Distribution of Leaf Elongation and LEZ

The spatial distribution of leaf elongation was characterized by REGR and displacement velocity (DV), the rate of displacement of a particle from the leaf base. At any given location of the elongation zone, cells of leaves 3, 4, and 5 elongated faster in control treatments than in salinized treatments (fig. 4). At 120 mM, the average REGR within the elongation zone decreased by 29.9%, 19.9%, and 23.3% for leaves 3, 4, and 5, respectively, as compared with the control. The maximum

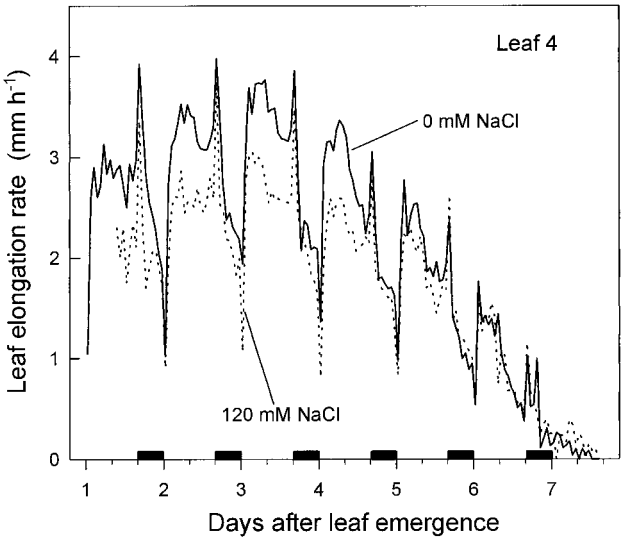

Fig. 3 Diurnal course of the rate of leaf elongation of leaf 4 of the main stem of wheat plants grown in salinized soil with 0 and 120 mM NaCl. Mean values presented are based on eight observations.

Table 2

Average Elongation Rate of Leaf 4 on the Main Stem of Wheat Plants Grown in Soil with 0 and 120 mM NaCl during the Light and Dark Period and Percentage of the Leaf Elongation Rate (LER) at 120 mM NaCl to That at 0 mM NaCl during Light (PL) and Dark Periods (PD)

Time after leaf emergence (days)	Light			Dark		
	NaCl (mM)		PL	NaCl (mM)		PD
	0 (mm h^{-1})	120 (mm h^{-1})	(%)	0 (mm h^{-1})	120 (mm h^{-1})	(%)
2	2.77	2.10	75.8	2.62	2.01	76.7
3	3.13	2.52	80.5	2.65	2.29	86.4
4	3.32	2.58	77.7	2.44	2.18	89.3
5	2.85	2.21	77.5	1.93	1.74	90.2
6	2.30	1.80	78.3	1.20	1.40	116.7
7	0.94	1.02	108.5	0.49	0.55	112.2
8	0.14	0.16	114.3	...	...	...

Note. Means are based on eight measurements.

REGR decreased with increasing leaf number ($P < 0.001$), e.g., at 0 mM NaCl the maximum REGR of leaf 3 was 0.17 mm mm^{-1} h^{-1} compared to 0.12 mm mm^{-1} h^{-1} for leaf 5.

The LEZ was ca. 2.7 cm for leaf 3, 3.0 cm for leaf 4, and 3.3 cm for leaf 5, respectively, regardless of the treatments. The LEZ was not affected by salinity, whereas it increased with leaf number.

Displacement velocity (DV) increased with distance from the leaf base to the end of the elongation zone, where DV became constant (fig. 5). In figure 5, DV beyond the elongation zone is equal to LER.

Discussion

Correlation analysis showed that the leaf areas per plant at the two harvest times were significantly and positively correlated to shoot FM ($r > 0.98***$). The rates of leaf growth and appearance determine the rate of production of potential tiller sites, i.e., axillary buds (Davies 1974). An important effect of the rate of leaf emergence on yield is its effect on the rate of tiller initiation because early formed tillers are more likely to produce heads (Rawson 1971; Kirby and Riggs 1978). Studies have shown that the reduced final grain yield of wheat by salinity is mainly correlated to a decreased tiller number per plant (Maas and Grieve 1990; Maas et al. 1994; Hu et al. 1997). In this study, leaves 3, 4, and 5 emerged ca. 3–4 d later at 120 mM NaCl than at 0 mM NaCl (table 1), which also contributes to the reduction in the shoot FM on a given day of harvest.

A visible leaf of wheat increases only its length because the width remains unchanged once it has emerged from the sheath bundle (Dale 1988). The final leaf length is a function of LER and duration of leaf elongation. In this study, salinity did not affect the duration of leaf elongation, regardless of leaf numbers. Thus, the reduction in the leaf length by salinity resulted from the effect of salinity on the LER. The decreases in the LER of leaves 3 and 4 as a result of salinity were more pronounced during the steady growth phase than during the decreasing phase (fig. 2), which was in agreement with the study on the effect of salinity on the leaf growth of sorghum (Bernstein et al. 1993*b*). In this study, however, the strong effect of salinity on the LER of leaf 5 continued after the steady phase of leaf growth. The LER is a function of LEZ and REGR. During the steady phase of leaf elongation, the LEZ, which reaches its maximum, remains unchanged (Skinner and Nelson 1995). Results here did not show the effect of salinity on the LEZ during the steady phase of growth for a given leaf. Therefore, the reduction in leaf elongation by salinity can only result from a decrease in the REGR during the steady growth phase. This finding is consistent with other reports of salt effects on wheat leaves (Delane et al. 1982; Arif and Tomos 1993). It differs, however, from one study in which salinity inhibited the leaf growth of sorghum by shortening the LEZ and by reducing the REGR (Bernstein et al. 1993*a*, 1993*b*).

The REGR is a parameter to compare the efficiency of growth for the different leaves and under different conditions, i.e., where the more efficient leaves are those elongating more per unit of growing tissue. The decrease in the REGR with leaf number in the control conditions during the steady phase (fig. 4) was in agreement with an earlier study of wheat leaf growth by Kemp (1980*a*). He found that the decrease in the efficiency of leaf growth with an increase in the number of leaves was associated with tiller emergence and a decline in protein concentration in leaves. In other words, the increase in the LEZ with increasing the leaf number would increase demand for the nutrients, resulting in competition between the leaves. However, the causes for the lowered efficiency of leaf elongation under saline conditions are still unclear. The direct causes may result from either decreases in the turgor pressure and cell wall extensibility or increase in yield threshold. The recent studies revealed that no decrease in turgor pressure (measured with a pressure probe) occurred in the elongating cells for wheat under saline conditions (Arif and Tomos 1993). Our previous study of osmotic adjustment in the elongating tissue of wheat leaves showed that turgor pressure of elongating tissues was maintained under saline conditions in the steady growth phase (Hu and Schmidhalter 1998*b*). However, reports in the literature demonstrated that under saline conditions, decreases in the cell wall extensibility of maize leaves (Cramer and Bowman 1992; Neumann 1993) and increases

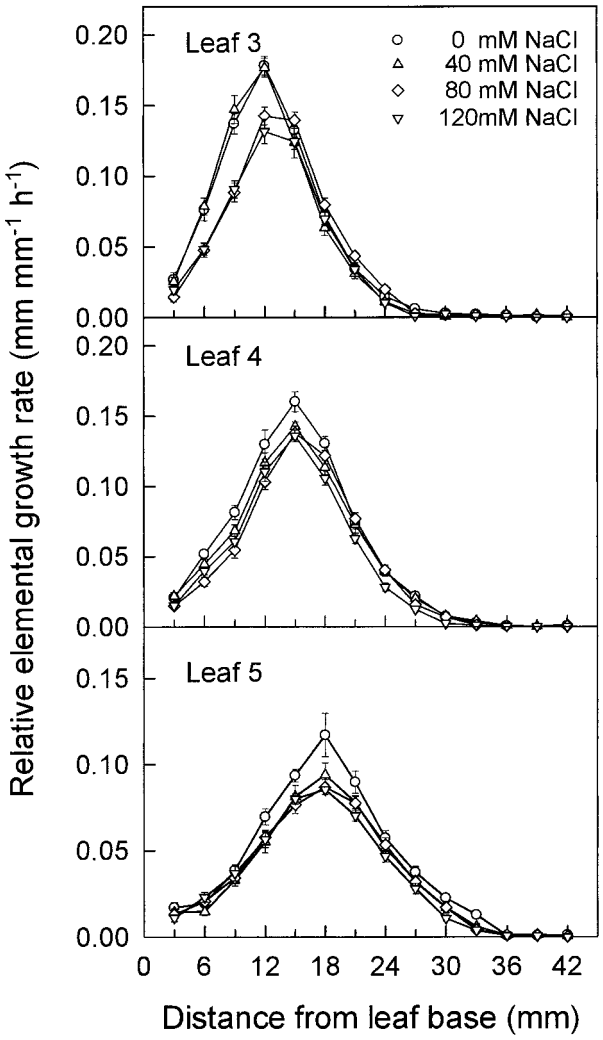

Fig. 4 Distribution of relative elemental growth rate in the elongation zone of leaves 3, 4, and 5 of the main stem of wheat plants grown in soil with 0, 40, 80, and 120 mM NaCl during the linear phase of leaf elongation. Error bars represent standard errors (n = 16) and fit within the plot symbol if not shown.

in the yield threshold of maize leaves (Cramer and Bowman 1992) may be responsible for the reduction in leaf elongation. Some additional likely mechanisms are that salinity causes ionic imbalance and disturbance of carbon metabolism in the elongation zone of grass leaves under saline conditions (Munns et al. 1982, 1988; Bernstein et al. 1995; Hu et al. 2000; Hu and Schmidhalter 1998*a*).

The decreased LER by salinity during the decreasing phase of growth is probably also associated with the reduction in the REGR because the duration of the leaf elongation did not change with salinity. The phase of decreasing elongation occurs when cell division ceases at the leaf base (Skinner and Nelson 1995). As the supply of new cells for leaf growth ceases and older cells reach their final length, the LEZ shrinks, causing the LER to decrease until all cells reach their final length. Schnyder et al. (1990) observed that the cell elongation rate throughout the elongation zone of ryegrass decreased progressively during the phase of decreasing leaf development. A reduction in the length of the elongating region when leaf elongation is no longer linear with time was also found for sorghum under both control and saline conditions (Bernstein et al. 1993*b*). If a faster shrinkage of the LEZ under saline conditions occurs, the duration of leaf elongation must be shorter.

The greater reduction in the LER of leaf 5 under saline conditions may result from the longer exposure of plants to salinity after sowing compared to leaves 3 and 4. The duration of elongation of leaf 5 in the decreasing phase was 1 d more than those of leaves 3 and 4. Effects of salinity on plant growth generally become more severe with increasing length of exposure to saline conditions. Since the development of leaf 5 occurred during the tillering, higher competition for nutrients by tillers under saline conditions may occur at this stage (Williams 1975). The final leaf size not only depends on the cell

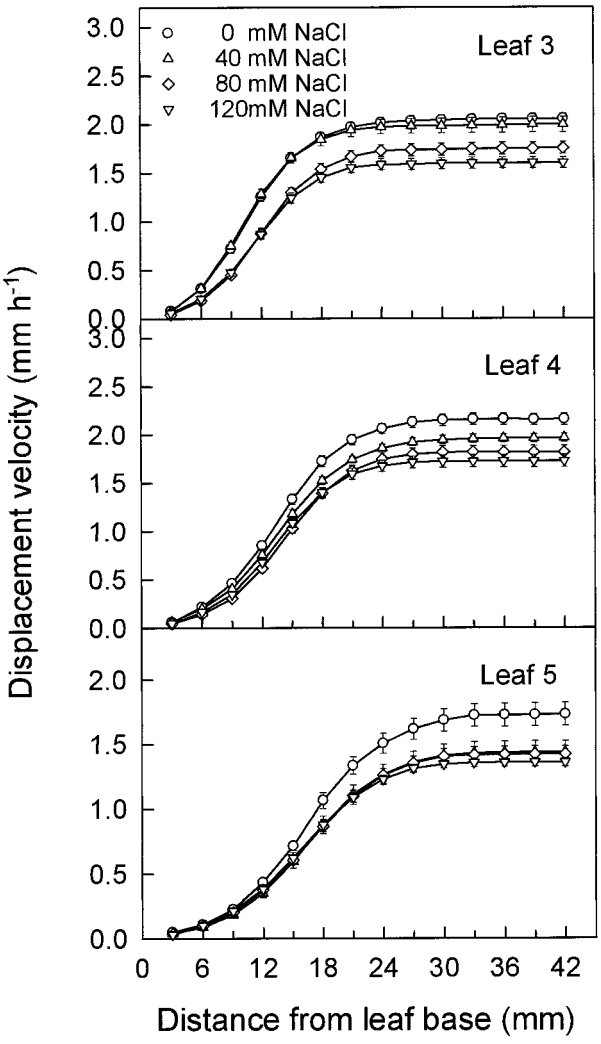

Fig. 5 Spatial distribution of displacement velocity in the elongation zone of leaves 3, 4, and 5 of the main stem of wheat plants grown in soil with 0, 40, 80, and 120 mM NaCl during the linear phase of leaf elongation. Error bars represent standard errors (n = 16) and fit within the plot symbol if not shown.

expansion, but it also depends on the number of cells. Final cell numbers in grass leaves were significantly reduced by salinity (Munns and Termaat 1986). Some biochemical work on effects of salinity on cell division has been reported in the literature. Rapid effects of salinity or drought on polyribosome formation in the whole shoot might also be taken as circumstantial evidence that protein synthesis may be inhibited crucially in meristematic cell division where rates of protein synthesis are most intensive (Rhodes and Matsuda 1976). Decreases in root tip protein synthesis as a result of salinity were found for *Pisum sativum* and *Glysine max* (Rauser and Hanson 1966; Kahane and Poljakoff-Mayber 1968). Thus, the greater reduction in the area of leaf 5 may also result from the severe reduction in the cell division. However, the further study on the effect of salinity on cell division in the meristematic zone of leaves is required.

Kinetic studies of leaf elongation rate show a distinct diurnal pattern (fig. 3). Christ (1978*a*, 1978*b*) reported a similar daily oscillation in wheat leaves. He found that during the steady growth phase, the mean LER during the night was ca. 66%–73% of that during the day, which is in agreement with the findings in this study. Interestingly, there was a greater effect of salinity on the LER during the light period than during the dark period (table 2). During the dark period, leaf growth, to a certain degree, is maintained by the consumption of carbohydrates stored during the previous light period, and there may be a process competing with growth for carbohydrates that caused the lower LER during the dark period than during the light period (Gordon et al. 1980). In other words, under control conditions, the lowered LER during the darkness compared with light period may result from the limitation of supply of water-soluble carbohydrates like sucrose. It was found that the sucrose content in leaves of wheat and barley in the salinized treatments is higher than in control treatments (Munns et al. 1982; Hu et al. 2000). The higher level of sucrose in salinized leaves from the previous light period may indicate the higher level of sucrose availability under saline conditions, which may be a reason why the LER was less affected during the dark period than during the light period.

In conclusion, the reduction in the leaf growth by salinity results in the decrease in whole-plant growth during the vegetative stages because the decreased number of tillers is related to the effect of salinity on leaf development. The reduced leaf area occurred longitudinally and laterally, regardless of leaf number. The reduced leaf growth by salinity became more severe with increasing leaf number, which may result from the plants being exposed to the salinity for a longer time. Salinity reduced the final length of leaves 3, 4, and 5 as a result of a decrease in their LER but not the duration of elongation. Effect of salinity on the LER varied with the growth stages of leaves and the diurnal course. Because there was no effect of salinity on the length of leaf elongation zone, reduced REGR is responsible for a decrease in LER during the linear phase of leaf growth under saline conditions.

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