Carbohydrate deposition and partitioning in elongating leaves of wheat under saline soil conditions

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Abstract. The objective of this study was to quantitatively evaluate the effect of salinity on the spatial distribution of glucose, fructose, sucrose, fructan and total C contents, as well as on their net deposition rates in the elongation and maturation zones of leaf 4 of the main stem of spring wheat (*Triticum aestivum* L.) during its linear growth phase. Plants were grown in growth chambers in 1.5-L pots containing an illitic–chloritic silty loam treated with or without 120 mM NaCl. 3 d after emergence of leaf 4, sampling started at 3 and 13 h into the 16 h photoperiod. The distribution of carbohydrates along the leaf axis showed distinct patterns that were altered by salinity and time in the photoperiod. Glucose and fructose concentrations were low at the base of the elongation zone and increased sharply up to the end of the leaf elongation zone in the two treatments. In contrast, sucrose concentration in the elongation zone was high at the leaf base and decreased sharply with distance from the base up to the end of the leaf elongation zone in both treatments. The main effect of salinity on the water-soluble carbohydrates (WSC) was that it significantly increased sucrose concentration in the elongation zone throughout the day and accumulation in the photosynthetically active zone during the photoperiod. Net deposition rates of sucrose and fructan in the elongation zone were enhanced by 120 mM NaCl. Salinity did not affect the sucrose import rate (g C kg^{-1} H_2O h^{-1}) in the sink (the elongation and secondary cell wall deposition zone). However, the partitioning of imported sucrose to WSC and structural C varied with salinity. In the basal part of the leaf (0–15 mm above the leaf base), net deposition of sucrose in the control treatment accounted for 7% of imported sucrose, compared with 17% at 120 mM NaCl. Eighty-seven percent of imported sucrose in the control treatment and 75% in the salinized treatment was used for synthesis of structural biomass (estimated as total C minus WSC-C). Conversely, in the 15–30 mm zone (i.e. in the distal part of the elongation zone and the secondary cell wall deposition zone), a greater fraction of imported sucrose was partitioned to synthesis of structural C under saline conditions. There was no significant effect of salinity on sucrose use in the region 30–60 mm.

Keywords: C deposition, leaf elongation, partitioning, soil salinity, *Triticum*, utilization, water-soluble carbohydrates.

Introduction

Since wheat leaf development largely determines the rate of plant growth (Williams 1975), and leaf elongation is restricted to a small region near the leaf base (Kemp 1980), the effects of salinity on leaf growth of wheat are logically much more closely associated with metabolic changes within the most actively growing tissues than in whole or non-growing tissue of leaves. Salinity depresses the leaf elongation rate, and alters the spatial distribution of relative elemental growth rates in the leaf elongation zone of sorghum (Bernstein *et al.* 1993) and wheat (Hu *et al.* 2000). Our early study (Hu *et al.* 2000) showed that the elongation rate of wheat leaves on the main stem was reduced by about 20–30% at 120 mM NaCl. Salinity did not only reduce leaf length, but also reduced the width of wheat leaves. For leaf 4 of wheat, for example, the average width was reduced by about 20% at 120 mM NaCl, and 90% of the reduction in the leaf width occurred at the base (Hu *et al.* 2000). However, the mechanism of salt effect on gramineous leaf growth is still poorly understood.

Water-soluble carbohydrates (WSC) are the major substrates for leaf growth. Most studies in the literature dealing with non-growing tissues of leaves showed that salinity generally increases the WSC accumulation (Poljakoff-Mayber and Lerner 1993). There was one report of the mean concentration of WSC in the elongation zone of barley leaves under saline conditions (Munns *et al.* 1982), which also showed higher WSC under saline conditions. Utilization of WSC for biosynthesis seems to be inhibited by salinity, but the metabolic steps by which this occurs are unknown. In wheat, carbohydrate translocation (Fisher and Gifford 1986; Hayashi and Chino 1986) and diurnal carbohydrate storage in the photosynthetically active tissue (Jenner and Rathjen 1972) are mainly in the form of sucrose. Therefore, it is

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important to understand how salinity affects sucrose storage in source tissue, transport from source to sink, and metabolism in sink.

During the period of most active elongation, the growing leaf of wheat presents three functionally distinct zones, i.e. the elongation (0–30 mm above the leaf base), the secondary cell wall deposition (30–60 mm), and the exposed photosynthetically active zone (> 60 mm) (Hu *et al.* 2000). The zones of elongation and secondary cell wall deposition are the regions of the highest biosynthetic activity, and are strong sinks for carbon photosynthate (Allard and Nelson 1991). Most of the assimilate used for the growth of grass leaves may be produced by its own exposed lamina (Allard and Nelson 1991; Bregard and Allard 1999). At present, however, there is no experimental data about the effect of salinity on spatial distribution of carbohydrates in those zones.

The continuity equation is a statement of the law of mass conservation. This equation can be used to calculate the local net deposition rate of substances in growing leaves of grasses and thus to investigate sink and source relationships (Gandar 1980; Silk 1984). This type of analysis was used to study carbohydrate metabolism in the elongation zone of tall fescue (*Festuca arundinacea* Schreb.) leaves (Schnyder and Nelson 1987; Schnyder *et al.* 1988). However, no experimental data has been reported on the spatial distribution and net deposition rates of carbohydrates in the elongation and mature zones of grass leaves under saline conditions. In this study, net deposition rates of carbohydrates, together with the net deposition rate of nitrogen in growing leaves of wheat (Hu and Schmidhalter 1998*a*), were used for the estimation of the rate of sucrose import and its use for the deposition of WSC components and structural C under saline conditions.

Materials and methods

Growth conditions

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona), pre-germinated for 2 d on filter paper wetted by tap water at 20°C, were sown in 1.5-L pots (10 cm in diameter and 20 cm high) containing an illitic–chloritic silty 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, which allowed for an optimum aeration) with full strength Hoagland solution for macronutrients, modified by increasing the phosphate concentration 10-fold to provide optimum phosphate concentration in the soil and by adding 0.5 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 level of 120 mM NaCl was obtained by adding NaCl to the nutrient solution. The soil was thoroughly mixed and kept in tightly closed plastic boxes for one week to facilitate equilibration. Thereafter, the soil was sieved and put into pots. Soil moisture content was maintained at the initial level by watering with tap water. In order to minimize water loss by evaporation, the pots were covered with a perforated plastic film, where plants could grow through small holes. 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 photon flux density (PPFD) was approximately 550 μmol photon m^{-2} s^{-1}, air temperature was 20°C (day/night) and the relative humidity was maintained at 55–65%.

Tissue sampling and analysis of carbohydrate concentration

Because salinity delays the development of grass leaves (Bernstein *et al.* 1993; Hu *et al.* 2000), plants in both treatments were harvested at the same development stage. Three d after leaf 4 emerged, sampling started at 3 h (0900 h) and 13 h (1900 h) into the 16 h photoperiod. Two replicates were harvested successively and harvest time recorded, all sampling being finished within 1 h. Elongating leaves 12–14 cm in total length were selected for sampling. Leaf elongation was approximately steady during this stage (Hu *et al.* 2000). The elongation zone was carefully freed from surrounding leaf sheaths, then cut from the base of the leaf with a razor blade. Beginning at the base, the leaf was then sectioned into six 5 mm long segments followed by three 10 mm and three 20 mm long segments. Segments from 20 leaves of control plants and 30 leaves of the salinized plants within one replicate were combined according to position and quickly placed in preweighed 15-mL test tubes, capped tightly and placed on ice for less than an hour. After the fresh weight (FW) was determined, tissue samples were extracted with 92% ethanol at 60°C for 20 min. According to Bergmeyer (1974), the enzymatic methods (Boehringer Mannheim, Germany) and a Kontron spectrophotometer (UVIKON 810, Tegimenta AG, Rotkreuz, Switzerland) were used to measure sucrose, glucose and fructose. The glucose concentration was determined before and after the enzymatic hydrolysis of sucrose; fructose was determined subsequently to the determination of glucose; the sucrose concentration was calculated from the difference of the glucose concentrations before and after enzymatic inversion. Because fructans in the leaf elongation zone of wheat predominantly have a degree of polymerization > 10 (Spollen and Nelson 1988), the sediment was extracted twice with 2.5 mL water at 60°C for the determination of fructans. We added 0.5 mL of 1 N H_2SO_4 to hydrolyse fructans into fructose and glucose at 100°C for 15 min. The sample was then neutralized with 0.5 mL of 1 N KOH. Fructose and glucose were determined enzymatically (see above). Total carbon was analysed with an elemental analyser (Carlo ERBA Strumentazione, NCS analyser 1500, Milan, Italy).

Numerical methods

Local net deposition rates (D, g C kg^{-1} H_2O h^{-1}) of carbohydrates such as sucrose, glucose, fructose, fructan, and total carbon were calculated using the one-dimensional version of the continuity equation as described by Silk (1984):

$$D = (\partial P/\partial t) + V_d \cdot (\partial P/\partial x) + (R_s \cdot P),$$

where P is substance density (g C kg^{-1} H_2O), t is time (h), x is distance (mm) from the base of the leaf, V_d is the displacement velocity of a segment (mm h^{-1}) and R_s is the segmental elongation rate (mm mm^{-1} h^{-1}). The calculation of the $\partial P/\partial t$, $V_d \cdot (\partial P/\partial x)$ and $R_s \cdot P$ on the right-hand side of the equation was performed as described in detail in a previous study (Hu and Schmidhalter 1998*b*). P in the terms of the $V_d \cdot (\partial P/\partial x)$ and $R_s \cdot P$ was obtained from averaging the two harvest times.

Statistical analysis

A randomized complete block design was used. Effects of salinity, harvest time (0900 h and 1900 h) and their interactions were evaluated by analysis of variance for each location along the leaf axis. Due to the larger number of plants and homogeneous growing conditions, the block effect was never significant. Hence, we assumed that the different batches of plants harvested within the treatments did not differ except for a change among treatments, and included the distance from the leaf base and the interaction with salinity and harvest time as sub-hierarchical effects in the model of analysis of variance. Because parameters such as P, V_d and R_s in the equation were from the experiments with the different replicates, the variance for the net deposition rates of

substances was in terms of a maximum standard error, which was estimated from a method described by Precht and Kraft (1992) and Precht *et al.* (1994). Terms were considered significant at $P \leq 0.05$.

Results and discussion

Spatial distribution of carbohydrate concentrations

In both treatments, glucose and fructose concentrations were low at the base of the leaf and increased to a maximum at the end of the elongation zone at both harvests (Figs 1 *A*, *B*).

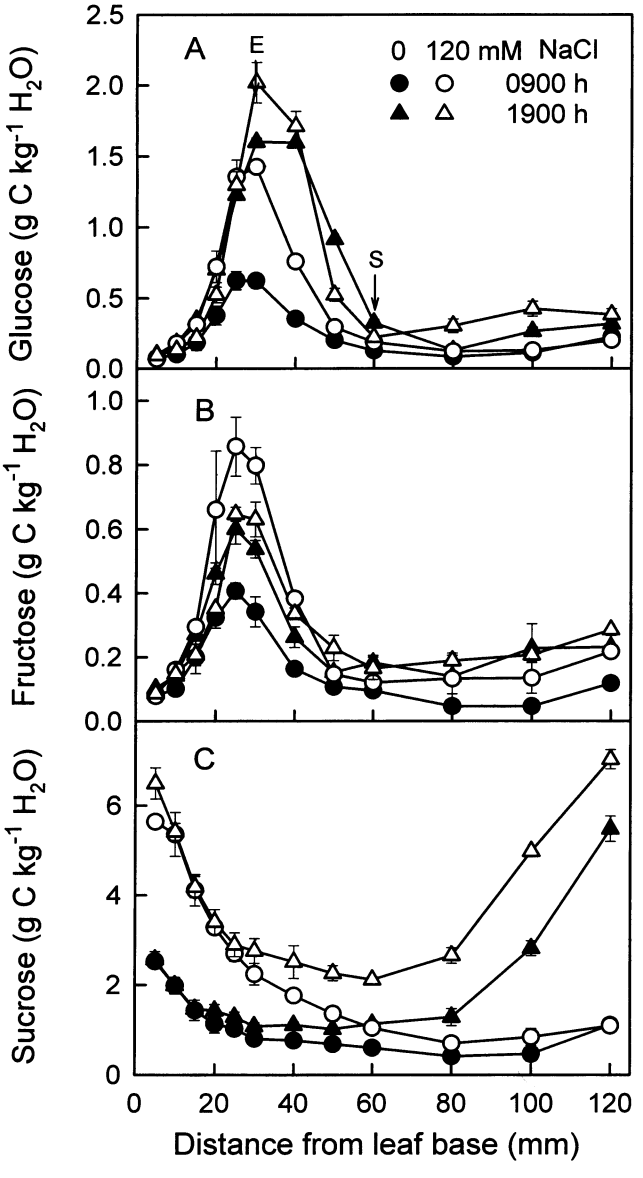

Fig. 1. Spatial distribution of glucose (*A*), fructose (*B*), and sucrose (*C*) concentrations in the growing leaf 4 on the main stem of wheat plants, grown in soil treated with no added or 120 mM NaCl, at two harvest times (at 0900 and 1900 h). Error bars ($n = 2$) represent standard errors and fit within the plot symbol if not otherwise shown. Arrows indicate the length of the elongation zone (E) and the position of the end of the leaf sheath (S).

According to Lüscher and Nelson (1995), the increase in the hydrolytic rate of sucrose with distance may lead to the increase in the concentrations of glucose and fructose from the leaf base to the end of the elongation zone. Beyond the elongation zone, a sharp decrease occurred up to 50–60 mm above the leaf base (near the point of emergence of the lamina tissue from the surrounding leaf sheaths). In the exposed zone, the concentrations were low and relatively constant. Salinity significantly increased glucose and fructose concentrations only between 20 and 50–60 mm above the leaf base at 0900 h. In both treatments, glucose concentration in the region 20–50 mm above the leaf base was higher at 1900 h than at 0900 h. Interestingly, fructose concentration under control conditions was higher at 1900 h than at 0900 h, whereas this was inverse under saline conditions.

In contrast to glucose and fructose, sucrose concentration was highest at the leaf base and decreased sharply towards the end of the elongation zone (Fig. 1*C*), which shows a similar pattern to that for tall fescue (Schnyder and Nelson 1987). Sucrose concentration in the elongation zone was consistently higher at 120 than at 0 mM NaCl. Previous studies also found the increased sucrose concentrations in the elongating tissues of leaves caused by drought (wheat, Munns and Weir 1981) and salinity (barley, Munns *et al.* 1982), which reported that only mean values of sucrose or WSC in the elongation zone were affected by stress conditions, but not their spatial distribution. There was no effect of harvest time on sucrose concentration in the elongation zone. Beyond the elongation zone, however, the spatial distribution of sucrose concentration changed during the light period (Fig. 1*C*). In the morning, the sucrose concentration was low in both treatments, but increased in the evening beyond 60 mm, i.e. in the exposed zone of the leaf. The highest sucrose concentration was attained in the most mature tissue near the leaf tip. Sucrose concentration in exposed tissue at 1900 h was consistently higher at 120 mM NaCl than in the control.

The spatial distribution of fructan resembled that of sucrose except for the control treatment at 0900 h (Fig. 2*A*). The fructan concentration was consistently higher at 120 than at 0 mM NaCl in the elongating tissue at both harvests and in the mature tissues at 1900 h. The mean fructan concentration in the elongation zone at 1900 h was about 4 times greater at 120 than at 0 mM NaCl. The increased fructan concentration may play a role in the regulation or storage of sucrose, especially under stress conditions (Pollock 1984; Spollen and Nelson 1994). Fructan concentration in the control treatment at 0900 h was almost zero, which was relatively low as compared with that in tall fescue (Schnyder *et al.* 1988). This may be due to conducting the experiment in the early tillering stages. Important variations in the amounts of fructans in wheat occur during the life cycle, and fructan levels are low at the early tillering stages (McGrath *et al.* 1997). Except for the fructan content at 0 mM

NaCl at 0900 h, the fructan levels decreased with distance in the sink tissues. The high fructan concentration at the leaf base may be due to the existence of high sucrose concentrations.

Carbon concentration decreased from the leaf base to reach a minimum at 25–30 mm, and then increased up to 120 mm from the leaf base (Fig. 2*B*). Carbon concentration was consistently higher at 120 mM NaCl than in the control. Diurnal changes in C concentration were small.

Net deposition rates of carbohydrates

In general, Figs 3–4 show that the net deposition rates of WSC were high in the elongation zone in both treatments, indicating that the elongation zone of wheat is a strong sink for the WSC. This is in agreement with results for inorganic nutrients in the elongation zone of grass leaves (Bernstein *et al.* 1995; Hu and Schmidhalter 1998*a*; Hu and Schmidhalter 2000). Net deposition rates of glucose and fructose in the two treatments increased from the leaf base to about 20–25 mm and then decreased sharply up to 50 mm (Figs 3*A*, *B*). Negative deposition rates were observed at about 40–80 mm for glucose and at 30–80 mm for fructose, indicating that there was a depletion of hexoses in this region since the negative net deposition rate describes the excess rate of utilization over import. Beyond 80 mm above the base, net deposition rates of both glucose and fructose were near zero in the two treatments. Net deposition rates of glucose and fructose were unaffected by salt addition except in the region 30–60 mm above the leaf base where secondary cell wall formation occurred. In this region, the net deposition rates of glucose and fructose at 120 mM NaCl became more negative as compared with that at 0 mM NaCl (Figs 3*A*, *B*).

The net deposition rate of sucrose increased from the leaf base to the location of most active elongation at 15 mm, and then decreased sharply to negative net rates at approximately 25 mm from the leaf base (Fig. 4*A*). Beyond 50 mm above the leaf base (i.e. in the exposed part of leaves), a steep increase in net sucrose deposition rate was observed in both treatments (Fig. 4*A*). In the region 0–15 mm above the leaf base, sucrose net deposition rate was considerably higher at 120 mM NaCl than at 0 mM NaCl.

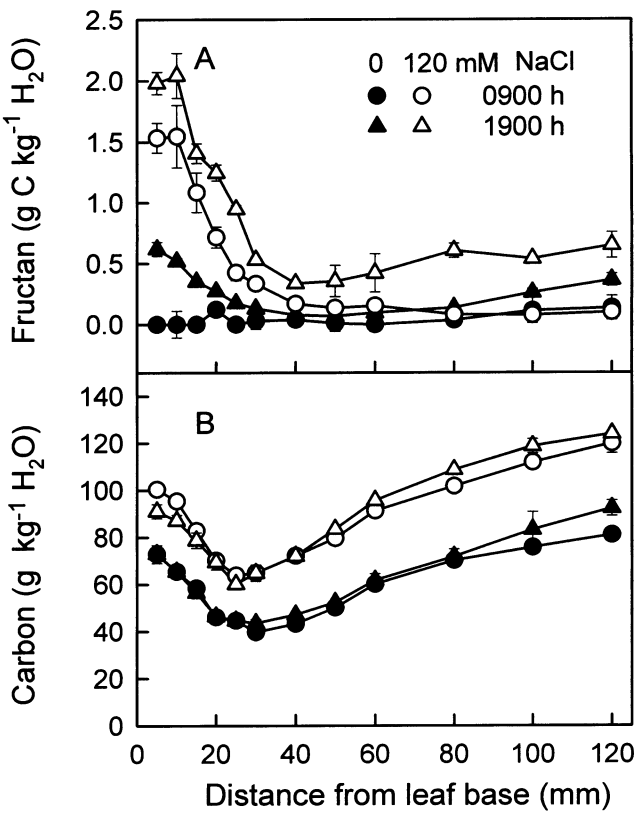

Fig. 2. Spatial distribution of fructan (*A*) and carbon (*B*) concentrations in the growing leaf 4 on the main stem of wheat plants, grown in soil treated with no added or 120 mM NaCl, at two harvest times (at 0900 and 1900 h). Error bars ($n = 2$) represent standard errors and fit within the plot symbol if not otherwise shown.

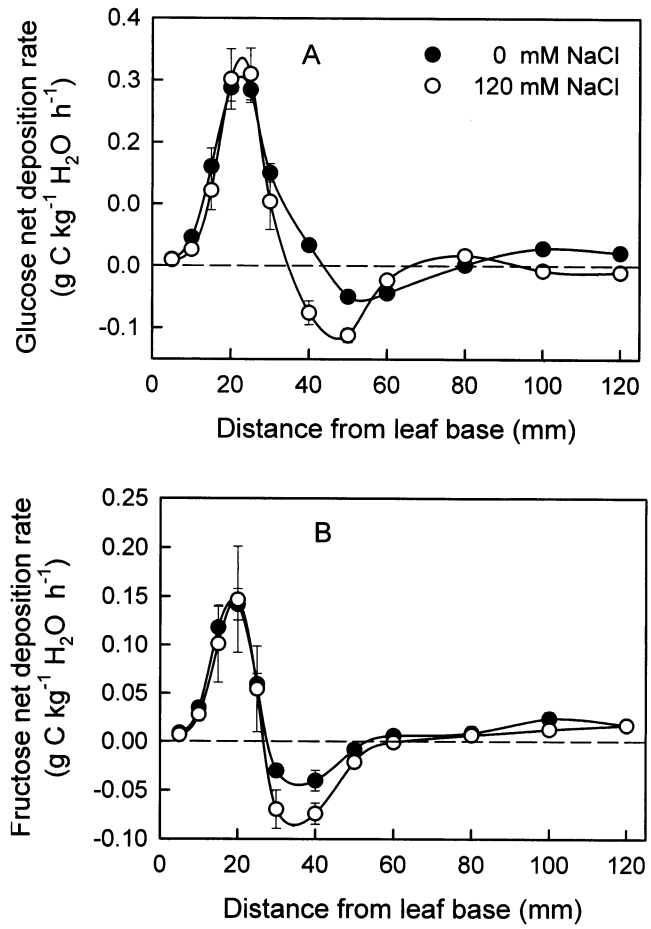

Fig. 3. Spatial distribution of glucose (*A*) and fructose (*B*) deposition rates in the growing leaf 4 of wheat plants grown in soil treated with no added or 120 mM NaCl between two harvest times (at 0900 and 1900 h). Error bars ($n = 2$–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

The spatial distribution of fructan net deposition rates was similar to that of sucrose in the 0–40 mm region (Fig. 4*B*). Beyond 40 mm above the leaf base, the deposition rate of fructan was very low in both treatments. Like sucrose, the deposition rate of fructans was higher at 120 than at 0 mM NaCl at 0–15 mm.

The net deposition rate of carbon increased sharply in the region between the leaf base and about 15 mm, followed by a sharp decrease to a minimum near 25 mm (Fig. 5). The C deposition rate was almost constant in the mature tissues (> 60 mm).

Sucrose import, partitioning and dilution by growth-associated water uptake

The main effect of salinity on WSC was that it increased sucrose concentration in sink regions, especially near the leaf base (0–15 mm) (Fig. 1*C*). Several mechanisms may influence sucrose concentration in expanding sink zones: (i) the rate of sucrose import; (ii) the rates of sucrose use for synthesis of structural biomass; (iii) the rates of sucrose use for deposition of non-sucrose WSC (fructose, glucose and fructan); and (iv) dilution by growth-associated water uptake in the expanding tissue (Fig. 6).

The net rate of sucrose import (D_S) (g C kg^{-1} H_2O h^{-1}), i.e. gross import minus consumption in respiration, was esti-

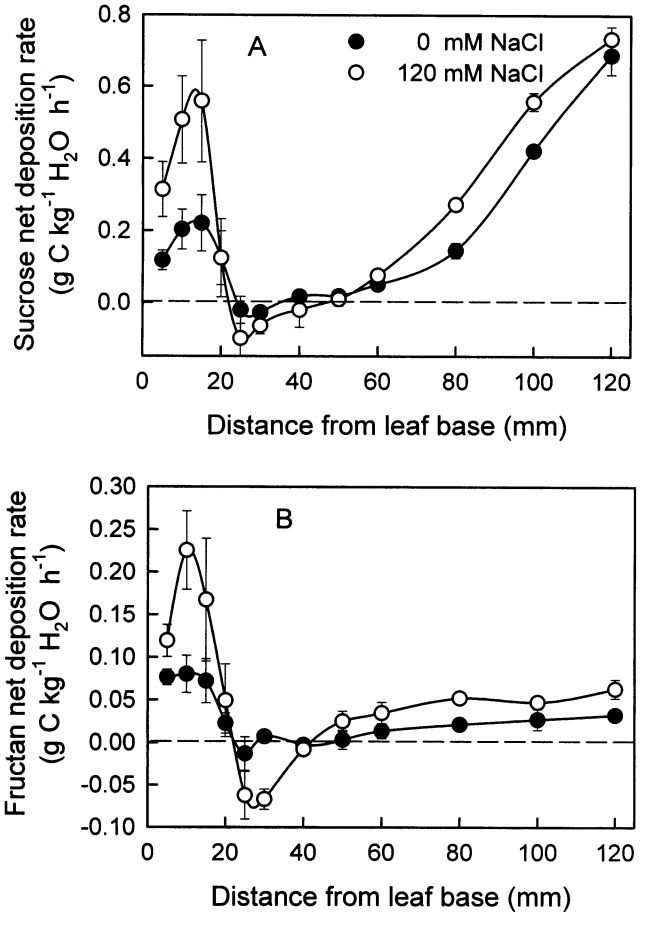

Fig. 4. Spatial distribution of sucrose (*A*) and fructan (*B*) deposition rates in the growing leaf 4 of wheat plants grown in soil treated with no added or 120 mM NaCl between two harvest times (at 0900 and 1900 h). Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

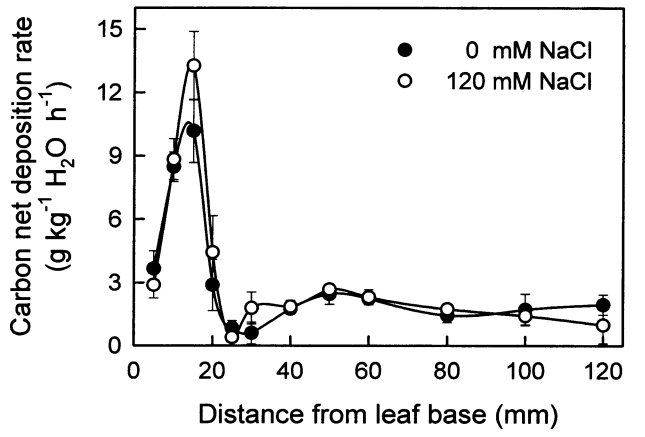

Fig. 5. Spatial distribution of carbon net deposition rates in the growing leaf 4 of wheat plants grown in soil treated with no added or 120 mM NaCl two harvest times (at 0900 and 1900 h). Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

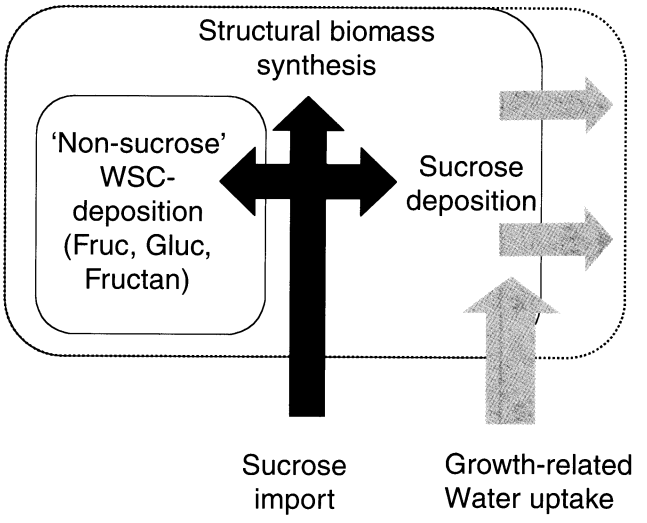

Fig. 6. Conceptual model of sucrose import, partitioning, and dilution by growth-associated water uptake in the growth zone of a wheat leaf. Net imported sucrose is used for three main activities: (i) synthesis of structural biomass (including cell wall material and cytoplasmic constituents), (ii) deposition of 'non-sucrose' WSC (fructose, glucose and fructan) and (iii) deposition of sucrose. The concentration (g C per g tissue water) of any component is dependent on both the rate of synthesis/deposition of the component and its 'dilution' by concurrent growth-related water uptake.

mated from the net rate of C import (D_C, Fig. 5) by subtracting C import in the form of amino-acids (D_N):

$$D_S = D_C - D_N.$$

N import in the leaf growth zone occurred in a reduced form, most likely as amino acids (Gastal and Nelson 1994). Thus, amino-C import was estimated as N deposition (Hu and Schmidhalter 1998*a*) multiplied by a factor of 3 (thus assuming a 3:1 (w/w) C to N ratio in amino acids supplied to growing tissue). Nitrate was only a minor fraction of total N (< 1%) (Hu and Schmidhalter 1998*a*).

The spatial patterns of the net rate of sucrose import were similar in the two treatments. Very similar patterns for tall fescue were also observed by Schnyder and Nelson (1987). The rate of sucrose import was relatively low near the leaf base, increased towards the position of most active expansion, and decreased to a relatively low level near the distal end of the growth zone (Fig. 7). Sucrose import rate remained almost constant in the zone of 30–60 mm from leaf base. In general, sucrose import in the growth zone was slightly higher under saline conditions. Near the leaf base, however, salinity caused a large increase in sucrose concentration (Fig. 1*C*) while sucrose import was virtually the same in the two treatments. Hence, sucrose import *per se* was not the cause for the enhanced sucrose accumulation in the basal part of expanding leaves.

However, it must be kept in mind that the concentrations of the substrates imported in growth zones are also related to the concomitant expansion (Fig. 6). The effect of salinity on this process can be analysed by using growth-associated water deposition as a measure of 3-dimensional expansion (Hu *et al.* 2000). Thus, the rate of sucrose import per unit growth-associated water deposition in Fig. 8 shows the relationship between sucrose import and concomitant dilution, and that net sucrose import per unit growth-associated water uptake was increased strongly by salinity. This was also true for all locations in the leaf growth zone (Fig. 8). High ratios of the net deposition rate of sucrose import to the water under saline conditions imply that the reduction in cell expansion was greater than in the net import rate of sucrose. This effect was due to lowered relative elemental growth rates along the entire length of the growth zone and the decreased cross-sectional area of leaves under saline conditions (Hu *et al.* 2000). Therefore, decreased expansion may clearly have been a primary cause for sucrose accumulation in the growth zone under saline conditions.

Furthermore, sucrose consumption in synthesis of structural biomass and in deposition of 'non-sucrose' WSC components may also influence sucrose concentration (Fig. 6). Fractions of utilization of sucrose import for the deposition of glucose, fructose, sucrose and fructan and for structural C were expressed as the ratios of their net deposition rate to the rate of imported sucrose (Table 1). Since net sucrose import was only used for the WSC and structural biomass, the fraction of the use for structural C was calculated by subtracting the sum of fractions of glucose, fructose, sucrose and fructan of WSC from 1 (Table 1). Synthesis of structural biomass was the most important sink for using sucrose in both treatments (Table 1). Near the leaf base, the fraction of sucrose partitioned to synthesis of structural biomass was lower in the saline treatment (75%) than in the control (87%). Still,

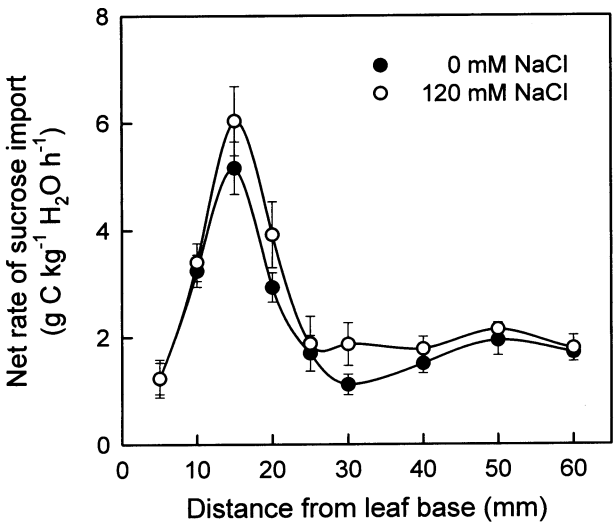

Fig. 7. Spatial distribution of the net rate of sucrose import in the region between the leaf base and 60 mm above the leaf base of wheat plants grown in soil treated with no added or 120 mM NaCl between two harvest times (at 0900 and 1900 h). Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

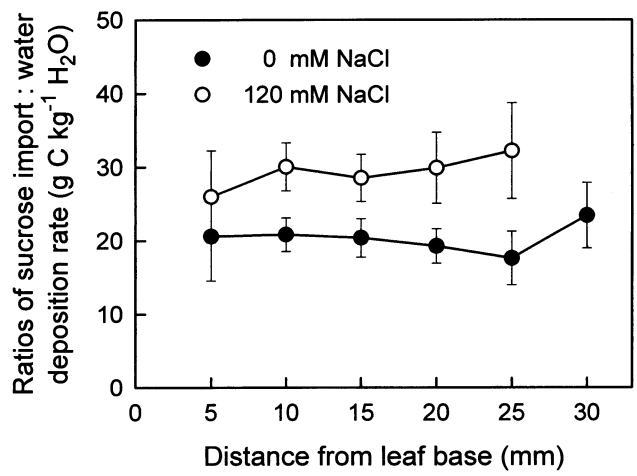

Fig. 8. Spatial distribution of the ratios of net deposition rate of sucrose import to water in the elongation zone in the leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Data was calculated by dividing sucrose import rate per unit length through water deposition rate per unit length. Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

Table 1. Water-soluble carbohydrates (WSC) and structural carbon derived from sucrose imported into in the sink zones between the leaf base and 15 mm, 15–30 mm, and 30–60 mm above the leaf base

	Fraction of sucrose partitioning					
	0–15 mm		15–30 mm		30–60 mm	
	0 mM	120 mM	0 mM	120 mM	0 mM	120 mM
Glucose	0.02	0.01	0.13	0.10	–0.01	–0.04
Fructose	0.01	0.01	0.02	0.01	–0.01	–0.02
Sucrose	0.07	0.17	0.00	–0.02	0.02	0.01
Fructan	0.03	0.06	0.00	–0.02	0.00	0.01
WSC[A]	0.13	0.25	0.15	0.07	0.00	–0.04
Structural C	0.87	0.75	0.85	0.93	1.00	1.04

[A]WSC = sum of glucose, fructose, sucrose and fructan

the decreased partitioning to structural biomass was not associated with a dilution of structural biomass in the saline treatment, i.e. when scaled to 3-dimensional expansion (as estimated by water deposition), synthesis of structural biomass was in fact the same near the leaf base in both treatments (data not shown). Beyond 15 mm above the base, synthesis of structural biomass was stimulated strongly under saline conditions. Thus, synthesis of structural biomass was not a factor explaining sucrose accumulation in growth zones under saline conditions.

The fraction of imported sucrose that was partitioned to 'non-sucrose' WSC components was quite low and similar in the two treatments. Near the leaf base (0–15 mm), 8% of the imported sucrose was used in deposition of 'non-sucrose' WSC components (fructose, glucose and fructan) in the saline treatment, and 6% in the control. Also, in this region the rates of fructose and glucose deposition per unit of growth-associated water uptake in tissue were virtually the same in the two treatments (Fig. 9). Conversely, the rate of fructan synthesis under saline conditions was twice that in the control. Sucrose is the immediate substrate for fructan synthesis (Pollock and Cairns 1991). There was a positive correlation between fructan and sucrose. Thus, increased fructan synthesis in saline conditions may be related to the increased sucrose concentration. Still, the effect on sucrose consumption for fructan synthesis was small since the fraction of imported sucrose used for fructan synthesis was low even in saline conditions.

Interestingly, sucrose concentration in the region at 15–30 mm was still increased by salinity even though the net rate of sucrose deposition was near zero in this zone in the control, and negative in the saline treatment (Fig. 4*A*). The increased sucrose concentration in this zone in the saline treatment was probably a result of the increased sucrose deposition that occurred when the tissue occupied a more proximal position (< 15 mm from leaf base). As tissue expands, cells at the basal part of the elongation zone containing high sucrose are displaced away. Thus, the concentration of sucrose in tissue at a particular position (x_i) of growing leaf and time (t_i) is a function of the sucrose concentration at an earlier position (x_{i-1}) and time (t_{i-1}), the rate of dilution by expansion during the interval ($t_i - t_{i-1}$), and the rate of sucrose deposition in the interval (which was zero or even negative).

Conclusions

Distribution patterns of accumulation of glucose, fructose, sucrose and fructan in the wheat leaf were distinct, and were altered by salinity and time. The elongation zone of wheat leaves is a strong sink for WSC in both treatments. The main effect of salinity on the WSC was that it increased sucrose

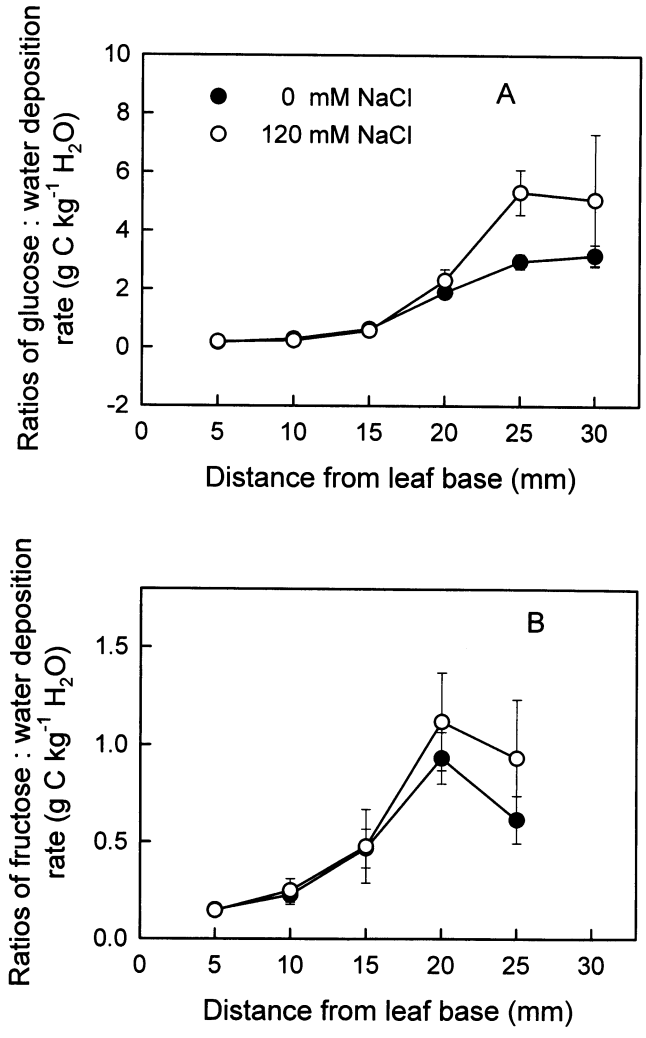

Fig. 9. Spatial distribution of the ratios of net deposition rates of glucose (*A*) and fructose (*B*) to water in the elongation zone in the leaf 4 of wheat plants grown in soil with no added NaCl and 120 mM NaCl. Data was calculated by dividing solute deposition rate per unit length through water deposition rate per unit length. Error bars (n = 2–14) represent maximum standard errors and fit within the plot symbol if not otherwise shown.

concentration in sink regions (0–60 mm above the base), especially near the leaf base (0–15 mm) where the net rate of sucrose deposition in the saline treatment was about 3 times higher than that of the control. This study suggests that the increase in sucrose concentration was not due to an effect of salinity on sucrose import *per se*, but was due to decreased water uptake during expansion. Also, other processes consuming sucrose for synthesis of structural biomass and for 'non-sucrose' WSC deposition (fructan synthesis, and glucose and fructose deposition) failed to show a significant positive response to the increased sucrose in this zone.

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