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in

Katerji N. (ed.), Hamdy A. (ed.), van Hoorn I.W. (ed.), Mastrorilli M. (ed.).
Mediterranean crop responses to water and soil salinity: Eco-physiological and agronomic analyses

Bari : CIHEAM
Options Méditerranéennes : Série B. Etudes et Recherches; n. 36

2002
pages 87-103

Osmotic adjustment of sugar beets in response to soil salinity and its influence on stomatal conductance, growth and yield

N. Katerji[1], J.W. van Hoorn[2,*,1], A. Hamdy[3], M Mastrorilli[4], E. Mou Karzel[3]

Agricultural Water Management, 34 (1997) 57-69

Abstract

Sugar beets were grown in tanks filled with loam and clay, and were irrigated with waters of three different levels of salinity. Osmotic adjustment was determined by analyzing the pressure-volume curves at three growth stages. Sugar beets showed osmotic adjustment in two ways: with their phenological development and towards salinity. Owing to the latter adjustment sugar beets are able to maintain the turgor potential at the same value for lower values of the leaf water potential, to maintain stomatal conductance and photosynthesis and finally their production under severe water stress.

Salinity affected the pre-dawn leaf water potential, stomatal conductance and evapotranspiration on both soils, but leaf area and yield only on loam.

Soil texture affected stomatal conductance, evapotranspiration, leaf area and yield. As the latter was about 35% lower on clay, whereas the evapotranspiration decreased 10 to 15%, the water use efficiency was about 25% lower on clay compared with loam.

Keywords: Crop water stress; Crop water use efficiency; Leaf water potential; Osmotic adjustment, Stomatal conductance; Salt tolerance; Sugar beet

[1]*INRA, Station de Bioclimatologie, 78850 Thiverval-Grignon, France*
[2]*Department of Water Resources, Agricultural University, Wageningen, The Netherlands*
[3]*Istituto Agronomico Mediterraneo, 70010 Valenzano (Bari), Italy*
[4]*Istituto Sperimentale Agronomico, 70125 Bari, Italy*
*Corresponding author.
[1]Retired.

1. Introduction

Sugar beet is reputed to be a deep rooting crop and relatively insensitive to water stress (Salter and Goode, 1967). The insensitivity of sugar beet was observed for water stress caused by soil moisture deficit (Doorenbos and Kassam, 1979) or by soil salinity (François and Maas, 1993).

Among the hypotheses explaining the resistance of plants to drought, the literature often mentions the ability of certain plants for osmotic adjustment in the case of soil moisture deficit (Beeg and Turner, 1976) or soil salinity (Bernstein, 1961, 1963; Shalhevet and Hsiao, 1986). Many authors presume that turgor potential is the real variable that controls stomatal behaviour (Millar et al., 1971; Turner, 1974) and leaf elongation (Acevedo et al., 1971; Cutler et al., 1980). The leaf water potential, ψ_f (negative), equals the sum of the turgor potential, ψ_t (positive), and osmotic potential ψ_o (negative). During periods of water deficit the decrease of osmotic potential, due to net solute accumulation, maintains the turgor potential at a sufficiently high level to keep the stomata open.

Osmotic adjustment of sugar beets in the case of soil moisture deficit (Biscoe, 1972) or soil salinity (McCree and Richardson, 1987) was shown for plants grown in pots under controlled conditions. Experiments over a few days, like those of Oosterhuis and Wullshlerger (1989) and McCree and Richardson (1987), yielded conflicting results regarding the importance of osmotic adjustment, and do not give sufficient information about plants grown under natural conditions. More information is needed on the following subjects:

1. Development of osmotic adjustment under natural conditions for various growth stages, salinities and soils;
2. The physiological (gaseous exchanges) and agronomic (growth and yield) consequences;
3. Whether soil texture affects osmotic adjustment and plant reaction to this adjustment.

This paper discusses the osmotic adjustment at successive growth stages of sugar beets, together with observations of pre-dawn leaf water potential, stomatal conductance and growth and yield.

The study was carried out at the Mediterranean Agronomic Institute at Bari, southern Italy, where a long-term experiment on the use of saline water started in 1989. Previous papers (Katerji et al., 1992; van Hoorn et al., 1993; Katerji et al., 1996) described the effect of soil salinity on water stress, growth and yield of broadbeans, wheat, potatoes, maize and sunflower. A recent paper (van Hoorn et al., 1997) presents detailed information on soil properties, composition of irrigation water and soil salinity.

2. Experimental procedure

2. 1. Set-up

The set-up consisted of 30 tanks of reinforced fibre-glass with a diameter of 1.20 m and a depth of 1.20 m. A layer of coarse sand and gravel, 0.10 m thick, was overlain by a re-packed soil profile of 1 m. At the bottom of the tank, a pipe serving as a drainage outlet connected the tank to a drainage reservoir. The set-up was covered at a height of 4 m by a sheet of transparent plastic to protect the assembly against precipitation.

One series of 15 tanks was filled with loam and a second series of 15 tanks with clay.

The tanks were irrigated with water of three different qualities: the control treatment with fresh water containing 3.7 meq Cl l^{-1} and an electrical conductivity (EC) of 0.9 dS m^{-1} and two saline treatments containing 15 and 30 meq Cl l^{-1} and an EC of 2.3 and 3.6 dS m^{-1}, obtained by adding equivalent amounts of NaCl and $CaCl_2$ to fresh water. For each water quality, five tanks were available.

At each irrigation, surplus water was added to provide a leaching fraction of about 0.2. Irrigation water was applied when the evaporation of the Class A pan had attained about 80 mm. The evapotranspiration of the irrigation interval was calculated as the difference between the amounts of irrigation and drainage water.

For determining soil salinity, the average chloride concentration of soil water was calculated from the salt balance of irrigation and drainage water and converted into EC of soil water by the following equation, established after the first 3 years 1989-1992: In EC = 0.824 In Cl - 1.42. This EC-value of soil water was divided by two for the conversion into EC_e. Owing to leaching at each water application, soil salinity remained almost constant from the start until the end of the growing period. According to measurements with soil water samplers, soil salinity slightly increased with depth.

2.2. Crop

Sugar beet *(Beta vulgaris*, variety Suprema) was sown on 25 November 1994 (Day *t)* at a density of 15 clusters per tank, regularly distributed and each cluster containing seven to eight grains. After emergence the number of plants was reduced to 15, and later gradually to five at harvest time, because of the successive samplings to determine the growth parameters. The number of five plants per lysimeter corresponds with a normal field density of 50 to 60000 plants per ha.

Fertilizing was done twice: a nitrogen supply equivalent to 150 kg N ha^{-1} at the vegetative stage *(t* + 89) and a phosphate supply equivalent to 120 kg P_2O_5 ha^{-1} at the stage of beet formation *(t* + 178).

When 50% of the plants had attained a phenological stage, this date was noted: emergence *t* + 25; four to five leaves *t* + 89; 16 leaves (beet formation) *t* + 172; harvest *t* + 214.

2.3. Use of the pressure-volume curve for determining osmotic and turgor potential

The pressure-volume curve shows the relationship between the water potential of an organism, in general the leaf, and its relative water content. The graphical analysis of the curve yields several water parameters. The application of different procedures and mathematical expressions for curve analysis was carried out and discussed by Tyree and Hammel (1972) and by Schulte and Hinckley (1985).

The pressure-volume curve typically has two parts (Ritchie and Hinckley, 1975). In the first part turgor and osmotic potential are combined (Fig. 1). As the turgor potential falls to zero with decreased leaf water potential, the relationship becomes linear and represents only the osmotic potential at that relative water content. Extrapolation yields an estimate of the osmotic potential for maximum relative water content.

From the extrapolated values of the osmotic potential, ψ_o and the observed values of the leaf water potential, ψ_f the turgor potential, ψ_t can be calculated as $\psi_t = \psi_f - \psi_o$.

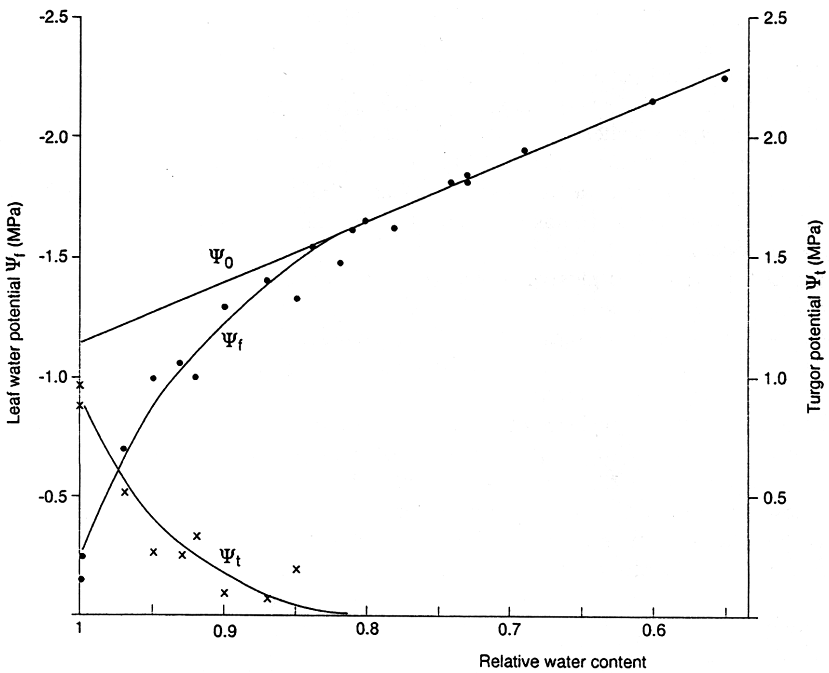

Fig. 1. *Pressure-volume curve established on Day t + 172 for fresh water on loam.*

In our experiment, the osmotic and turgor potentials were determined from the leaves of all six treatments at three dates (*t* + 118, *t* + 172, *t* + 211), following the experimental procedure proposed by Andersen et al. (1991). The leaves are cut at dawn and put in distilled water for 3-4 h. Then the leaf water potential at saturation is measured with a pressure chamber (Sholander et al., 1965) and the weight of the leaf is also measured, before putting it in a plastic bag to minimize water loss by transpiration. The two measurements, water potential and weight, are repeated at hourly intervals for about 12 h. After the last measurement the leaves are dried at 75°C for 36 h t o determine the dry weight, and to calculate the relative water content as (wet weight - dry weight)/(weight at saturation - dry weight).

The pressure-volume curves in our experiment were established from two replicates for all six treatments.

2.4. Water stress of the plant

Two parameters were used to characterize the water stress of the plant: the pre-dawn leaf water potential and the stomatal conductance.

Both parameters were determined on the upper leaf surface, the pre-dawn leaf water potential on one leaf per tank (five leaves per treatment), and the stomatal conductance at midday on the upper leaf surface, well-exposed to sunlight, of two leaves per tank (ten leaves per treatment).

2.5. Growth and yield

The leaf area and dry matter of leaf and stem were determined at the successive phenological stages.

At harvest, the dry matter of leaves and root of the remaining five plants were determined for each tank.

3. Results and discussion

3.1. Osmotic adjustment to salinity

Fig. 1 shows as an example the pressure-volume curve, determined on two leaves of the control treatment on loam at Day *t* + 172 and the decomposition of the leaf water potential in its two components, the turgor and the osmotic potential. From this curve we determine, following the procedure described earlier:

- The maximum osmotic potential at saturation (relative water content: 1);
- The leaf water potential for zero turgor potential;
- The relationship between turgor potential and relative water content or leaf water potential.

Table 1 presents the maximum values of the osmotic potential, measured at three dates, and shows that:

- The maximum osmotic potential of the control treatments decreases with time, which means an osmotic adjustment to the phenological stage. This change was observed for other crops, such as sunflower (Cruiziat, 1989*)* and sorghum (Hsiao et al., 1976*).*
- The maximum osmotic potential decreases with increasing salinity, on loam as well as on clay. The difference between the saline treatments and the control indicates an osmotic adjustment to salinity. The maximum decrease of the osmotic potential, observed at Day *t* = 211, equals about 0.4 M.Pa, a value near the one presented by McCree and Richardson (1987), but much higher than the decrease observed by Oosterhuis and Wullshlerger (1989).

Table 1

Maximum osmotic potential at three growth stages of suggar beet (M1)

Time	Loam			Clay		
	Fresh	15 meq l^{-1}	30 meq l^{-1}	Fresh	15 meq l^{-1}	30 meq l^{-1}
t + 118	-0.84	-0.89	-1.11	-0.88	-0.91	-1.09
t + 172	-1.13	-1.32	-1.50	-1.03	-1.15	-1.35
t + 211	-1.27	-1.45	-1.67	-1.36	-1.50	-1.73

F-values: time, 2958.3 > 18.00 = *F*(2,4; 0.01), highly significant; water quality, 1070.33 > 18.00 = *F*(2,4; 0.01), highly significant; interaction, 23.5 > 15.98 = *F*(4,4; 0.01), highly significant.

- The osmotic adjustment to salinity increases with the time of exposure to salinity. This phenomenon is clearly shown by comparing for *t* + 118, *t* + 172 and *t* + 211 the differences between the control treatments and the saline treatments. The differences in maximum osmotic potential of about 0.2 and 0.4 MPA at Day *t* + 211 are in the same order as the differences between the average osmotic potential of the soil water of the three water qualities.
- Soil texture does not show a clear effect on the maximum osmotic potential.

Fig. 2 presents an example of the relationship between the turgor potential and the relative water content or leaf potential at *t* + 172 for the three treatments on loam, and shows that:

- The higher the salinity, the lower the leaf water potential at which the turgor potential attains zero.
- The higher the salinity, the higher the turgor potential for the same value of the leaf water potential.

From these observations we can conclude that, owing to osmotic adjustment, the plant is able to maintain turgor potential at a similar level for lower values of leaf water potential.

3.2. Water stress of the plant

The pre-dawn leaf water potential (Fig. 3) shows, normally, an increase after each irrigation and then a decrease during the irrigation interval, with a clear difference due to salinity. The 15 meq l^{-1} treatment took an intermediate position. The largest difference between the treatments was always observed just before irrigation. Soil texture did not show a clear effect on the pre-dawn leaf water potential.

Fig. 4 shows the development of stomatal conductance during daytime at Day t + 144, just after irrigation at a high pre-dawn leaf water potential, and at Day t + 161, before the next irrigation at a low pre-dawn leaf water potential. At Day t + 144, the stomatal conductance clearly increases and decreases during the day, whereas at Day t + 161 the variation is small. The higher the salinity, the lower the pre-dawn leaf water potential and consequently the lower the stomatal conductance. Soil texture affects stomatal conductance, as the values on loam are always higher than the corresponding values on clay.

The stomatal conductance, shown in Fig. 5, also shows the effect of irrigation and salinity. The largest difference appears after irrigation, whereas the pre-dawn leaf water potential showed the largest difference before irrigation. Soil texture also affected stomatal conductance, especially between control treatments.

Fig. 6 presents a linear relationship between stomatal conductance at noon and the pre-dawn leaf water potential. The higher the salinity, the lower the slope, more than twice between the control and the most saline treatment. Loam shows a steeper slope than clay, especially for the control treatments, which corresponds with the effect of soil texture on stomatal conductance.

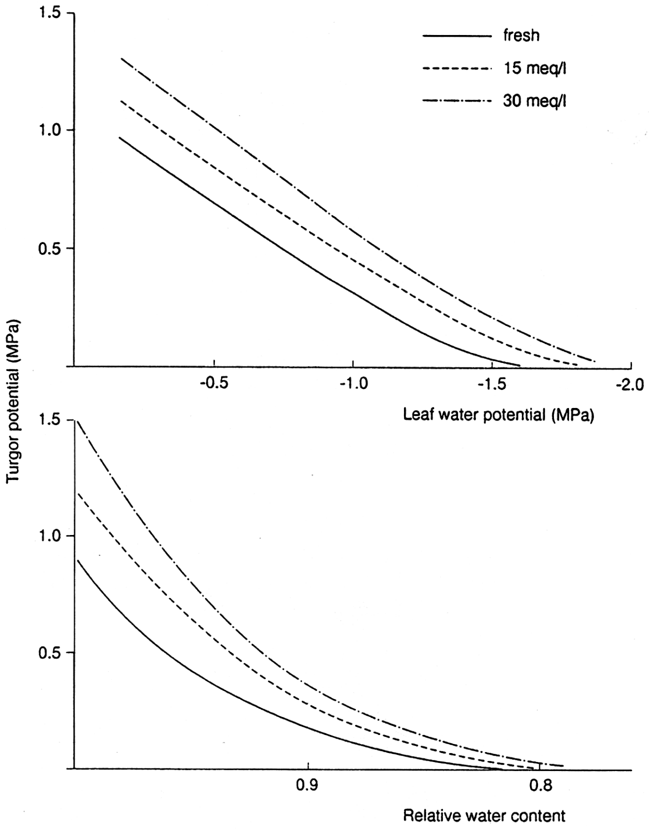

***Fig.* 2.** *Turgor potential vs. leaf 'water potential and relative water content on Day* t + 172 *on loam,*

If we take the pre-dawn leaf water potential corresponding to a stomatal conductance of 0.1 cm s^{-1} —this value corresponds to the cuticular conductance according to Milburn (1979), the stomata being completely closed— this value of the pre-dawn leaf water potential decreases with increasing salinity. In the case of good water supply (high pre-dawn leaf water potential) the lower the salinity, the higher the stomata] conductance. In the case of water stress (low pre-dawn leaf water potential) the plants, grown under saline conditions, are able to maintain the stomatal conductance at higher values than the control plants, owing to the osmotic adjustment that maintains the turgor potential, as was shown in Fig. 2.

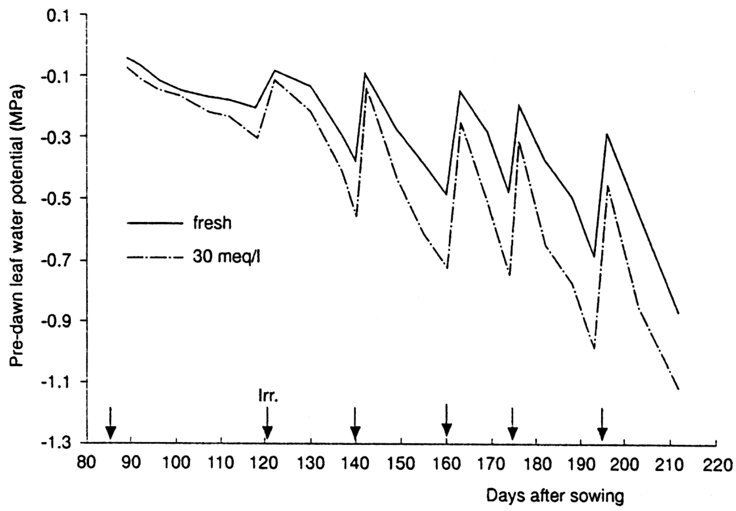

Fig. 3. *Pre-dawn leaf water potential vs. days after sowing on loam.*

3.3. Evapotranspiration

Evapotranspiration, presented in Table 2, showed the effect of salinity, a reduction of 10 to 12% between the control and the saline treatments, as well as the effect of soil texture, a decrease of 10 to 15% between loam and clay.

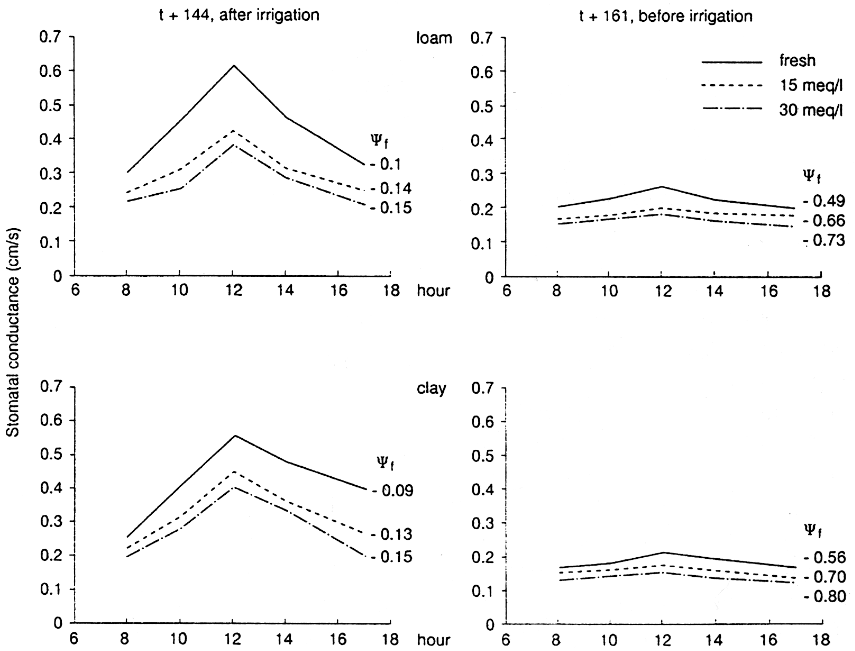

Fig. 4. *Stomatal conductance during day time.*

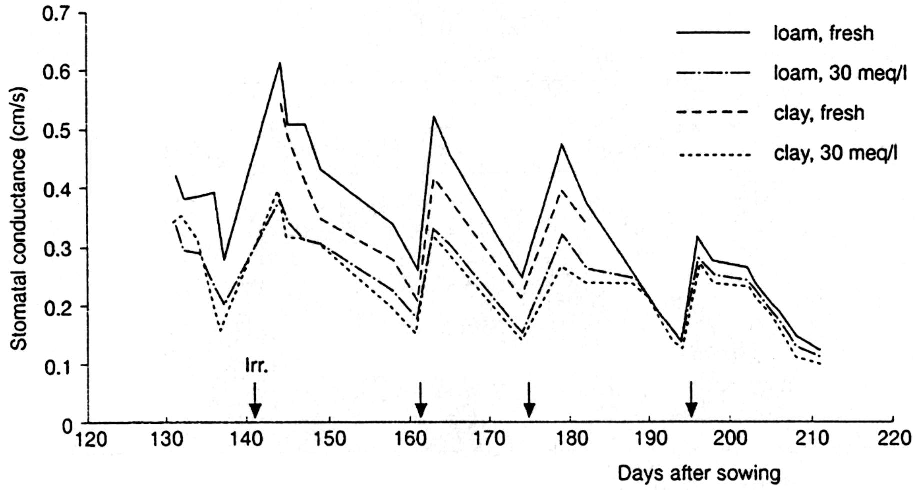

***Fig.* 5.** *Stomatal conductance vs. days after sowing..*

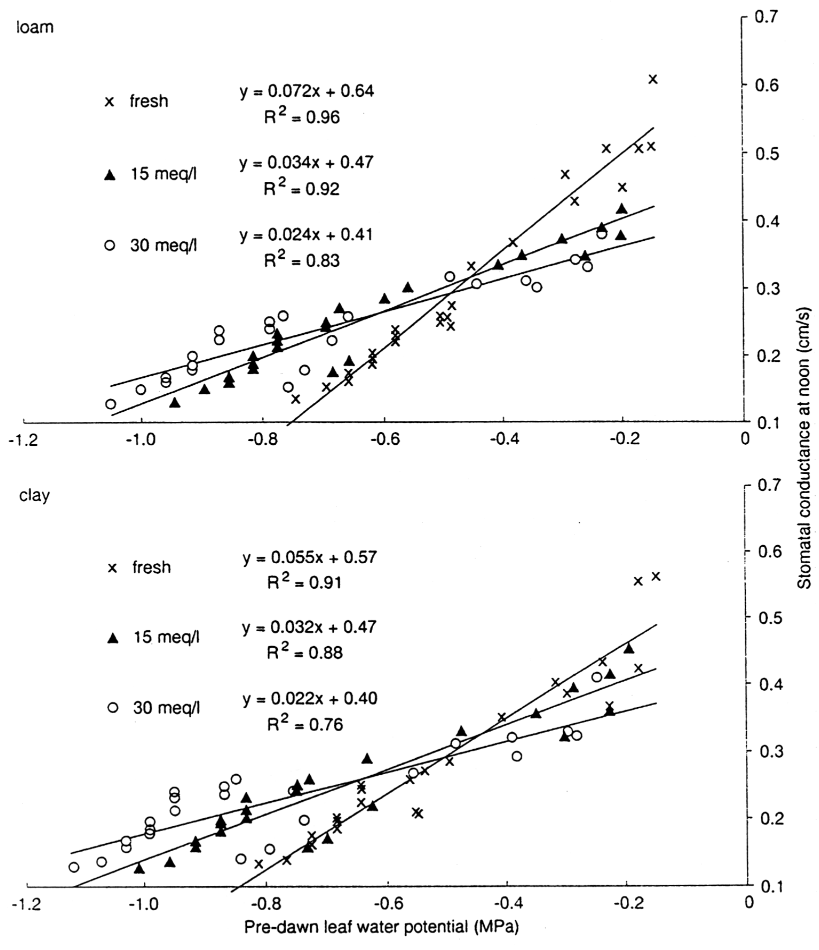

***Fig.* 6.** *Stomatal conductance vs. pre-dawn leaf water potential.*

Table 2

Evapotranspiration of sugar beet (mm day^{-1})

Period	Loam			Clay		
	Fresh	15 meq l^{-1}	30 meq l^{-1}	Fresh	15 meq l^{-1}	30 meq l^{-1}
25.11.94 - 17.02.95	1.0	1.0	1.0	1.0	0.9	0.9
17.02 - 15.04	2.3	2.3	2.2	2.3	2.0	2.1
15.04 - 06.05	5.7	5.2	4.8	4.9	3.9	4.0
06.05 - 19.05	8.3	7.6	7.2	6.7	6.0	6.5
19.05 - 08.06	8.6	7.2	7.2	6.7	5.7	6.1
08.06 - 26.06	9.9	8.2	8.2	8.4	7.6	7.2
Total period (mm)	836	753	734	731	642	657
(%)	100	90	88	100	88	90

F-values for total period: soil, 78.60 > 7.82 = F(1,24; 0.01), highly significant; water quality, 27.41 > 5.61 = F(2,24; 0.01), highly significant; interaction, 0.91 < 1.0, not significant.

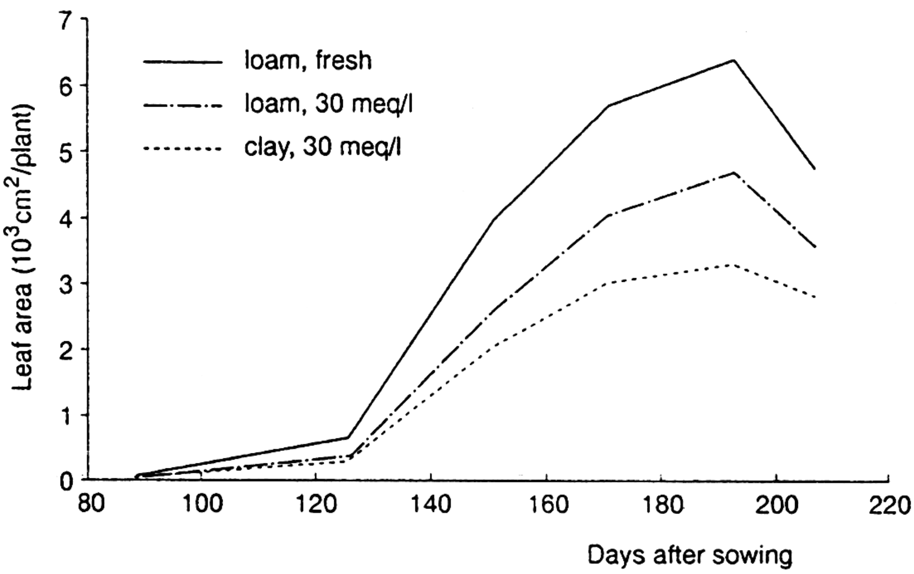

Fig. 7. *Leaf area vs. days akcr sowing.*

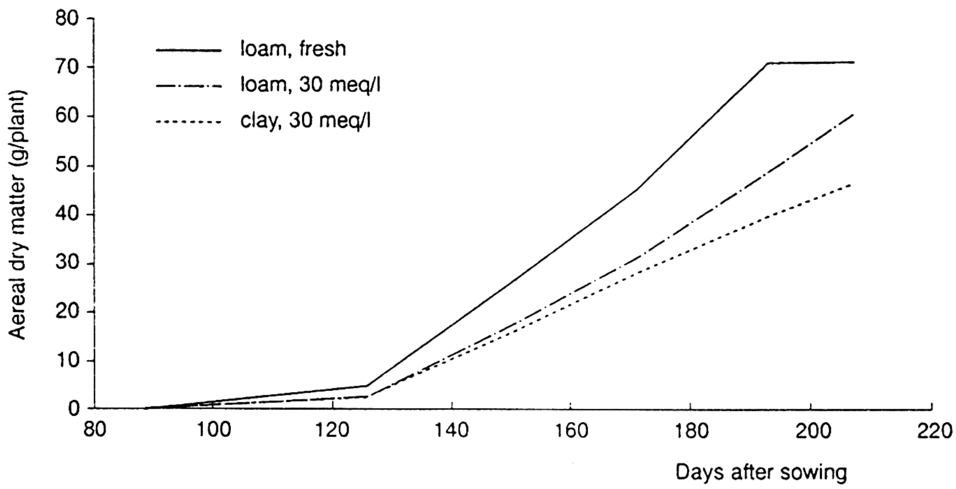

Fig. 8. *Aereal dry matter vs. days after sowing.*

Table 3

Yield of sugar beet and soil salinity

	Loam			Clay		
	Fresh	15 meq l^{-1}	30 meq l^{-1}	Fresh	15 meq l^{-1}	30 meq l^{-1}
Yield of beet (kg m^{-2})	6.56	5.84	5.53	4.47	3.57	3.68
Sugar (%)	15.5	16.1	14.5	14.3	15.0	16.7
Yield of sugar (kg m^{-2})	1.02	0.94	0.80	0.64	0.54	0.61
	A*	AB	BC	CD	D	CD
EC_e	0.8	3.5	6.3	0.8	3.4	5.8

*Values with a different letter differ significantly (95% probability level) according to the Student-Newman-Keuls test.

3.4. Growth and yield

The growth of leaf area (Fig. 7) and that of aereal dry matter (Fig. 8) show a similar development, slow until t + 120 due to low temperatures, followed by active growth until t + 200. The slight decrease in leaf area after Day t + 200 indicates leaf senescence. The salinity effect appeared on loam, but not clearly on clay. Soil texture also showed a systematic effect.

Table 3 shows the yield of beet and sugar, the sugar percentage, and the average soil salinity of the layer 0-100 cm, which remained nearly constant during the growing season. On loam, the sugar yield decreased with increasing salinity, but on clay the effect was not clear. Soil texture showed a systematic effect on sugar yield. This corresponds well with the observations of Fig. 7 and Fig. 8 on the growth parameters leaf area and aereal dry matter. Sugar beet is considered as a salt tolerant crop with a salinity threshold at EC_e 7 dS m^{-1} (Ayers and Westcot, 1985). In this experiment the salinity effect appears, at least on loam, at a lower level, which may be attributed to the variety. In a previous experiment (van Hoorn et al., 1993) the salinity effect on wheat also appeared at a lower level than the one mentioned by Ayers and Westcot (1985).

The average diameter and length of the beet were respectively 32.5 and 42 cm. Both diameter and length were unaffected by salinity and soil texture.

The water use efficiency of beet and sugar yield (Table 4) was not affected by salinity, whereas it reacted on soil texture.

Table 4
Water use efficiency for beet and sugar yield (kg m^{-3})

	Loam			Clay		
	Fresh	15 meq l^{-1}	30 meq l^{-1}	Fresh	15 meq l^{-1}	30 meq l^{-1}
Beet	7.8	7.8	7.5	6.1	5.6	5.6
Sugar	1.22	1.25	1.09	0.88	0.83	0.93

3.5. Effect of soil texture

For sugar beet, soil texture showed a stronger effect on yield than salinity, the average yield on clay being about 35% lower than on loam. This confirms the observations on all crops in this experiment, wheat, potatoes, maize and sunflower (van Hoorn et al., 1993; Katerji et al., 1996). Three hypotheses are possible to explain this phenomenon:

- The osmotic adjustment is stronger on loam than on clay;
- A mechanical effect of soil texture;

- The water supply to the plant is better on loam than on clay, notwithstanding the almost equal amount of available water between field capacity and wilting point.

This experiment does not confirm the first hypothesis, as was shown in Table 1. The second hypothesis does not seem probable, because of the homogeneous texture of the soil profile and the absence of a hard layer due to ploughing. Moreover, no difference was observed in the length of the beets between both soils.

The most probable explanation is the third hypothesis, a better water supply to the plant, owing to more aeration and a better developed root system, a higher capillary conductivity or a combination of both for the loamy soil.

4. Conclusions

The experiment shows that sugar beets are salt resistant owing to osmotic adjustment.

Two types of osmotic adjustment appeared: the first corresponds with the phenological development of the plant; the second is achieved by physiological adaptation to salinity. Owing to the latter adjustment the plant was able to lower the osmotic potential about 0.4 MPa in the case of the most saline treatment (EC_e ~ 6 dS m^{-1}) to maintain its turgor potential. This adjustment has two aspects: a physiological and an agronomic aspect.

Physiological adjustments enable the plant in a saline environment to maintain the turgor potential at a similar level as under non-saline conditions. In the case of sugar beet, a proportional relationship exists between stomatal conductance and photosynthesis (Bethenod et al., 1996). Therefore, sugar beet grown under saline conditions are able to maintain production under severe water stress.

The agronomic consequences are that sugar beet shows only a slight decrease in evapotranspiration and yield due to salinity, because of the slight decrease in leaf area and the maintenance of gaseous exchange under saline conditions.

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