

EFFECTS OF SALINITY AND WATERLOGGING ON PHYSIOLOGICAL PROCESSES AND IONIC REGULATION IN *ATRIPLEX AMNICOLA*

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Abstract

The effects of salinity (EC: 0, 10 and 20 dS.m⁻¹) and waterlogging levels of 75, 100 and 125 % of soil water holding capacity on some physiological processes and ionic regulation were studied in *Atriplex amnicola* Paul G. Wilson in sandy loam and silty loam soils. Stomatal conductance of plants grown on sandy loam soil exhibited significant variations under the waterlogging treatments of 10 and 20 dS.m⁻¹ salinity levels. At low waterlogging level (75% WHC), significant differences were recorded at different salinity levels for stomatal conductance, transpiration rate and quantum yield. In silty loam soil, non-significant variation was observed for both salinity and waterlogging treatments when analyzed one day after irrigation, but after three days, there were significant variations in stomatal conductance and transpiration rate in different salt treatments.

Sodium showed maximum accumulation in leaves followed by roots and minimum in stem in both sandy and silty loam soils at different salinity and waterlogging levels. Concentration of Na⁺ varied with time and exhibited higher amount after 8 weeks as compared to 4 weeks growth period. Chloride also showed the same pattern, however, plants grown on silty loam soil exhibited higher amount as compared to sandy loam soil. Salinity did not have any pronounced effect on the oxalate content, whereas, waterlogging did affect the oxalate concentration after 4 weeks of growth with non-significant effects after 8 weeks growth. Increase in salt concentration of the irrigation medium increased the electrical conductivity of both sandy and silty loam soils at different growth periods and with different waterlogging levels.

Introduction

Salinity and waterlogging are the factors which significantly reduce productivity in many parts of the world. Generally, these two factors are found in conjunction and affect growth due to hypoxic conditions and greater influx of sodium and chloride ions into the plant cells. Glycophytes can tolerate salinity and waterlogging upto a certain extent. On the other hand, halophytes are plants that can grow upto a high level of salinity. Various species and lines grow naturally that through natural process have adapted themselves to different levels of waterlogging as well. Of the halophytic plants the genus *Atriplex* is well known for its tolerance to salinity, higher productivities and economical proposition as fodder/forage plants. The quality of forage/fodder is usually determined by the quality and proportion of organic matter, percentage of salt and the concentration of individual ions. Sodium and chloride are the dominating ions which not only alter the normal metabolism, thus affecting quality, but also affect the health of

browsing animals. Sodium and chloride ions are reported to show a substantial accumulation in a number of halophytic species (Albert, 1975). Higher absorption of Na^+ and localization in salt bladders and leaves has also been reported in *Atriplex amnicola* (Aslam *et al.*, 1986).

The present report describes the interactive effects of salinity and waterlogging on some physiological processes, ion uptake and regulation, and oxalate content in *A. amnicola*. Growth and biomass productivities of the plants have been reported earlier (Ala *et al.*, 1994).

Materials and Methods

Fifteen cm long vegetatively propagated seedlings of *Atriplex amnicola* Paul G. Wilson (obtained from Western Australian Department of Agriculture, Perth, Australia) were transplanted in plastic pots of 30 cm diameter and 45 cm height. These pots were filled with sandy loam (EC: 4.98 $\text{dS}\cdot\text{m}^{-1}$, Na^+ 16 $\text{Meq}\cdot\text{L}^{-1}$, Cl^- 52 $\text{Meq}\cdot\text{L}^{-1}$) and silty loam (EC: 8.45 $\text{dS}\cdot\text{m}^{-1}$, Na^+ 170 $\text{Meq}\cdot\text{L}^{-1}$, Cl^- 156 $\text{Meq}\cdot\text{L}^{-1}$) soil.

The experiment was conducted using a CRD design with three different salinity levels (EC: 0, 10 and 20 $\text{dS}\cdot\text{m}^{-1}$) and three waterlogging levels (W_1 , W_2 and W_3 corresponding to 75, 100 and 125% water holding capacity) of irrigation water. Saline water were prepared by dissolving dry sea salts in tap water to obtain the desired EC of the water. A summary of analyses of the irrigation water used is given in Table 1. Pots for both salinity and waterlogging levels were randomized with three replicates for each treatment. The whole set-up was replicated twice for plant harvest at 4 and 8 weeks, respectively. Other details of the experimental design have been reported earlier (Ala *et al.*, 1994).

Physiological Measurements: Stomatal conductance, transpiration rate and quantum yield of all the plants were measured at 7 weeks of growth using a LICOR (Li-1600) porometer. Measurements were recorded on 1 and 3 days after irrigation to find out the variation with soil moisture depletion. The temperature was more or less equal on both the days, whereas, relative humidity was set at 40%.

Ionic Content: After 4 and 8 weeks of growth, when the plants were harvested for biomass productivity, fresh samples of leaf, stem and roots were collected, oven-dried and then a unit weight of the samples was ashed in a furnace at 600°C for 4 h. The ashed samples were then dissolved in deionized water for the estimations of Na^+ and

Table 1. Analysis of saline irrigation solution used in the experiment.

Parameters Studied	Salt Treatment 1	Salt Treatment 2	Salt Treatment 3
Electrical Conductivity ($\text{dS}\cdot\text{m}^{-1}$)	0.34	10.00	20.00
pH	8.00	8.10	8.25
Na^+ ($\text{Meq}\cdot\text{L}^{-1}$)	0.91	395.65	840.00
Cl^- ($\text{Meq}\cdot\text{L}^{-1}$)	0.74	63.50	136.20

Cl⁻ as described by Karimi & Ungar (1986). Sodium was determined by atomic absorption spectrophotometry (Jarrell Ash AA-782 A), and chloride by chloridometry (Haake Buchler Chloridometer).

Oxalate Content: The oxalate content was determined in leaf samples at both harvests as described by Moir (1953) and modified by Karimi & Ungar (1986). The method involves extraction of oxalate in 0.25N HCl and precipitation overnight in a mixture of sodium acetate, calcium acetate and acetic acid. The precipitate was then redissolved in HCl and washing reagent (ethanol + ammonium hydroxide), oven dried and finally redissolved in 2N H₂SO₄. The solution was then titrated with 0.02N KMnO₄.

Soil Analyses: Soil samples at both harvests were obtained from each pot. Oven dried samples were used for the estimation of electrical conductivity of the saturation extract using a Canterbury conductivity meter (AGB-1000).

Results

Physiological Measurements: Stomatal conductance in plants grown on sandy soil showed significant variation to waterlogging treatments at 10 and 20 dS.m⁻¹ salt concentrations on both periods of measurements (Table 2). Measurements taken one day after irrigation showed non-significant effect for both salinity and waterlogging treatments. At low waterlogging level (75% WHC), significant differences were observed at different salinity treatments for stomatal conductance, transpiration rate and quantum yield when measurements were made after three days.

Plants grown in silty-loam soil exhibited non-significant differences in stomatal conductance and transpiration rate for both salinity and waterlogging treatments when measured one day after irrigation (Table 3). Quantum yield showed significant differences at W₁ and W₂ waterlogging treatments at 0 and 10 dS.m⁻¹ salt levels. The plants showed significant differences for stomatal conductance to both salinity and waterlogging treatments 3-days after irrigation, whereas, transpiration rate showed variation for salinity treatments only at given waterlogging levels. Quantum yield showed non-significant variation to both salinity and waterlogging treatments.

Ionic Contents: The absorption and accumulation of sodium and chloride in different plant parts under the influence of salinity and waterlogging treatments are shown in Figs.1 and 2.

Sodium: Both salinity and waterlogging treatments had significant effects on sodium concentration in all parts of the plants grown on sandy soil (Fig.1). Comparative studies of different plant parts showed maximum concentration in leaves followed by roots with minimum amount in stem. In general, increase in both salinity and waterlogging increased the concentration of sodium ions in all plant parts with some exceptions.

Plants grown on silty-loam soil also exhibited variation in sodium absorption like those of sandy soil. The same trend of sodium accumulation was also evident with increase in salinity and waterlogging levels. Apparently, plants harvested at two different time periods did not seem to exhibit significant variations in the ionic contents of different plant parts.

Chloride: More or less similar pattern of chloride accumulation was evident in plants grown on both soil types. No variation was evident in chloride concentrations due to

Table 2. Some physiological measurements recorded in *Atriplex amnicola* under various degrees of salinity and waterlogging treatments grown in sandy soil.

PARAMETERS STUDIED	WATERLOGGING LEVELS (% OF MWHC)	SALINITY LEVELS (EC _{1w} in dS.m ⁻¹)			LSD _{0.05}
		0	10	20	
1-Day After Irrigation					
Stomatal	75	13.360±2.920	13.270±0.670	13.830±2.200	n.s.
Conductance (m.mol.m ⁻² .s ⁻¹)	100	15.860±3.790	9.250±0.570	9.790±0.600	n.s.
	125	14.560±1.790	13.830±1.370	15.470±3.330	n.s.
	LSD _{0.05}	n.s.	3.319	n.s.	
Transpiration Rate (m.mol.m ⁻¹ .s ⁻¹)	75	1.120±0.140	1.110±0.080	1.190±0.230	n.s.
	100	1.190±0.230	0.850±0.050	0.870±0.040	n.s.
	125	0.950±0.310	0.940±0.190	1.050±0.090	n.s.
	LSD _{0.05}	n.s.	n.s.	n.s.	
Quantum Yield (μmol.s ⁻¹ .m ⁻²)	75	1666±57	1513±18	1766±26	n.s.
	100	1616±11	1553±24	1439±18	n.s.
	125	1736±18	1523±13	1766±24	n.s.
	LSD _{0.05}	n.s.	n.s.	n.s.	
3-Days After Irrigation					
Stomatal	75	14.830±3.040	19.430±1.840	8.360±1.680	7.87
Conductance (m.mol.m ⁻² .s ⁻¹)	100	16.160±2.880	17.090±0.190	14.730±0.800	n.s.
	125	10.020±3.000	10.940±2.650	12.520±1.720	n.s.
	LSD _{0.05}	n.s.	6.458	5.070	
Transpiration Rate (m.mol.m ⁻¹ .s ⁻¹)	75	0.990±0.170	1.460±0.080	0.780±0.080	0.42
	100	1.220±0.100	1.390±0.120	1.030±0.060	n.s.
	125	0.930±0.190	0.870±0.260	0.980±0.210	0.77
	LSD _{0.05}	n.s.	n.s.	n.s.	
Quantum Yield (μmol.s ⁻¹ .m ⁻²)	75	1753±38	1680±77	1693±89	n.s.
	100	1566±71	1620±17	1586±16	n.s.
	125	1546±10	1653±33	1790±36	228.29
	LSD _{0.05}	n.s.	n.s.	n.s.	

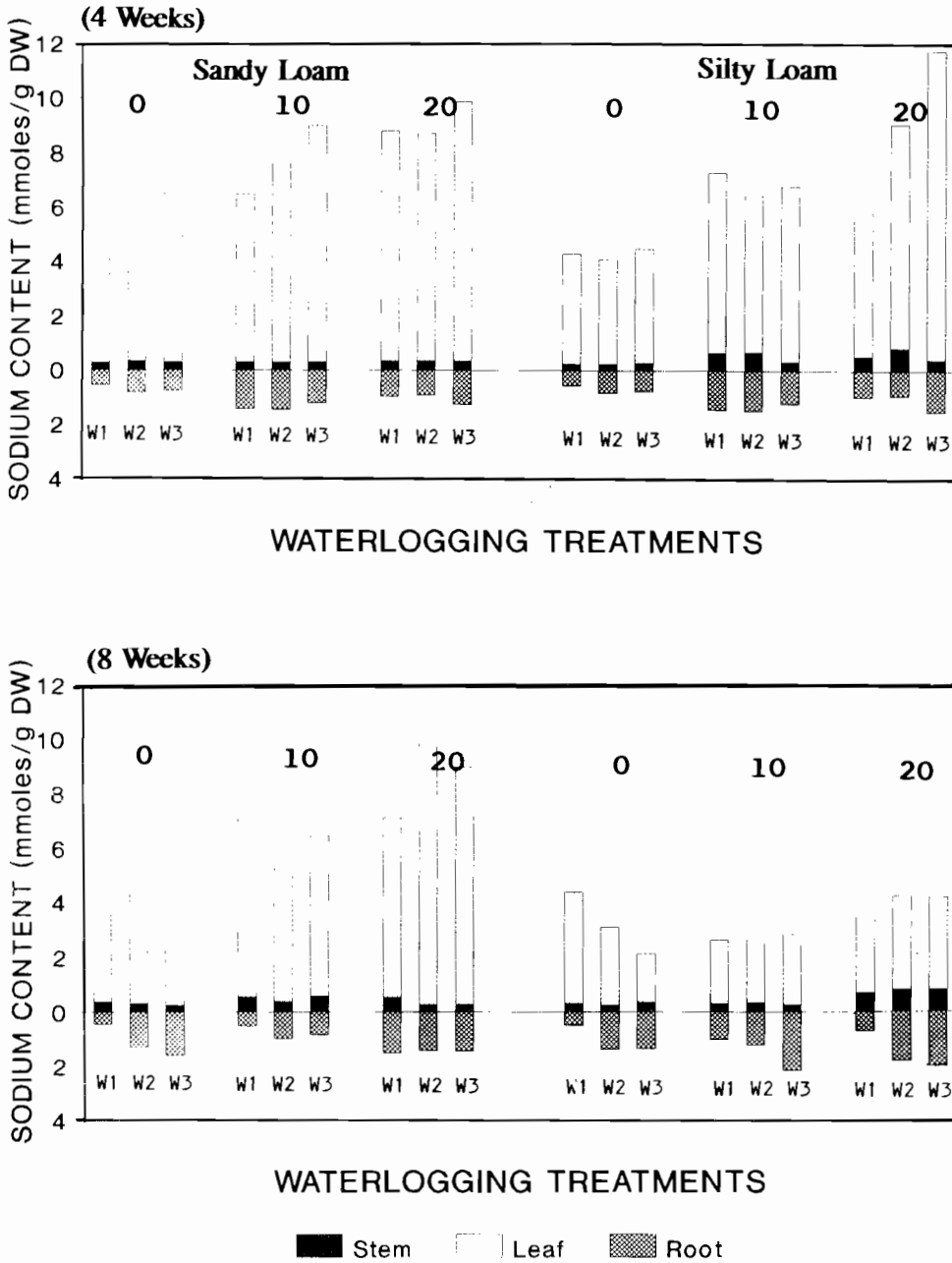


Fig.1. Sodium content in different plant parts of *Atriplex amnicola* subjected to various degrees of salinity and waterlogging in sandy- and silty-loam soils at two different growth periods.

LSD_{0.05} : Leaves 3.45; Stem 0.98; Roots 1.42

Table 3. Some physiological measurements recorded in *Atriplex amnicola* under various degrees of salinity and waterlogging treatments grown in silty loam soil.

PARAMETERS STUDIED	WATERLOGGING LEVELS (% OF MWHC)	SALINITY LEVELS (EC _{iw} in dS.m ⁻¹)			LSD _{0.05}
		0	10	20	
1-Day After Irrigation					
Stomatal	75	9.980±1.310	11.280±0.890	13.200±2.090	n.s.
Conductance (m.mol.m ⁻² .s ⁻¹)	100	12.290±2.120	15.130±1.340	9.810±2.160	n.s.
	125	12.600±1.590	12.780±4.910	8.160±0.260	n.s.
	LSD _{0.05}	n.s.	n.s.	n.s.	
Transpiration Rate (m.mol.m ⁻¹ .s ⁻¹)	75	0.910±0.080	1.180±0.070	1.170±0.220	n.s.
	100	1.240±0.190	1.150±0.040	0.890±0.150	n.s.
	125	1.130±0.110	1.100±0.090	0.790±0.020	0.296
	LSD _{0.05}	n.s.	n.s.	n.s.	
Quantum Yield (μmol.s ⁻¹ .m ⁻²)	75	1320±26	1386±14	1616±8	287.147
	100	1343±68	1543±53	1543±52	202.77
	125	1640±85	1603±44	1403±13	n.s.
	LSD _{0.05}	224.369	314.005	n.s.	
3-Days After Irrigation					
Stomatal	75	10.830±0.860	16.600±0.980	19.130±0.130	2.637
Conductance (m.mol.m ⁻² .s ⁻¹)	100	19.650±2.740	14.030±0.770	11.470±1.660	5.322
	125	15.650±1.920	8.600±0.800	11.270±0.260	3.229
	LSD _{0.05}	5.047	2.973	3.375	
Transpiration Rate (m.mol.m ⁻¹ .s ⁻¹)	75	0.950±0.060	1.420±0.070	1.440±0.140	0.338
	100	1.360±0.280	1.190±0.080	1.060±0.210	n.s.
	125	1.210±0.060	0.870±0.140	0.990±0.080	0.569
	LSD _{0.05}	n.s.	n.s.	n.s.	
Quantum Yield (μmol.s ⁻¹ .m ⁻²)	75	1339±28	1593±67	1663±57	n.s.
	100	1586±11	1446±37	1233±69	273.947
	125	1656±38	1606±64	1596±56	n.s.
	LSD _{0.05}	n.s.	n.s.	211.759	

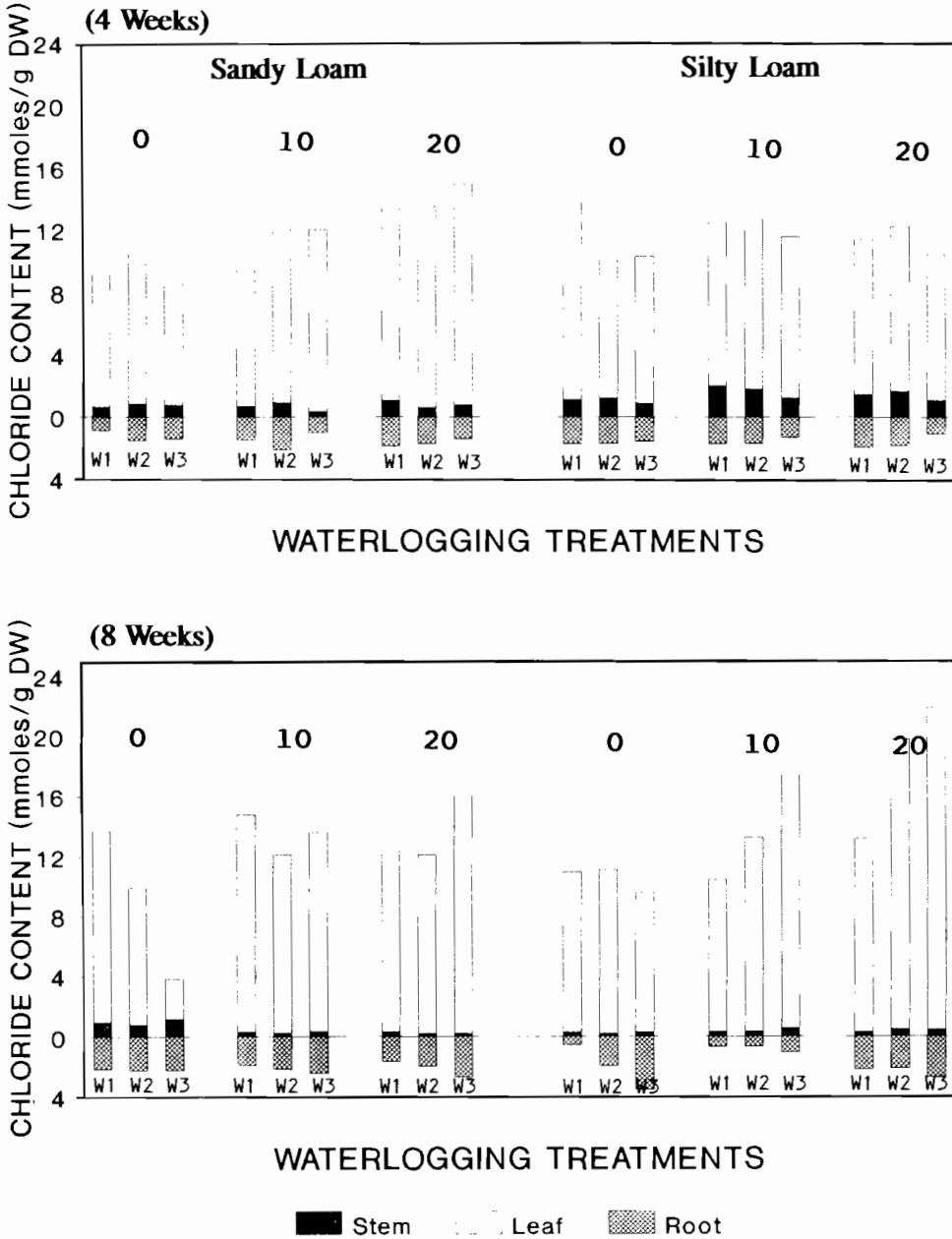


Fig.2. Chloride content in different plant parts of *Atriplex amnicola* subjected to various degrees of salinity and waterlogging in sandy- and silty-loam soils at two different growth periods.

LSD_{0.05}: Leaves 1.78; Stem 0.36; Roots 0.25

growing time. Effects of both salinity and waterlogging were more significant for chloride contents in leaves as compared to stem and roots (Fig.2). Plants grown on silty-loam showed higher concentrations of Cl^- in all plant parts as compared to plants grown in sandy soils. Most of the differences due to salinity and waterlogging were found to be significant.

A decrease in sodium concentration was observed as compared to chloride after eight weeks of growth in both the soil types and plant parts. There appears to be higher absorption of sodium as compared to chloride ions upto 10 dS.m^{-1} of salinity after which this absorption relatively decreased at 20 dS.m^{-1} . Waterlogging increased the absorption and accumulation of both the ions in the plant parts. No significant difference was evident in leaves and stem after eight weeks of growth due to waterlogging treatments. On the other hand, roots did exhibit significant variation due to waterlogging treatments only.

Oxalate Content: Oxalate content varied between 4-9% in plants grown at different levels of salinity and waterlogging in both types of soil. In sandy soil, salinity did not have any pronounced effect on oxalate content, however, waterlogging did influence oxalate accumulation after 4 weeks of growth (Fig.3). No significant variation was evident for both salt and waterlogging treatments after 8 weeks of growth. Silty loam soil exhibited variations to both salt and waterlogging treatments after 4 weeks of growth, with non-significant effects at 8 weeks growth period. Percentage of oxalate was low after 8 weeks as compared to 4 weeks growth.

Changes in Soil Characteristics: Irrigation with saline solution at different watering rates had a marked effect on both the types of soil and harvest period in respect to change in electrical conductivity (Fig.4). Increase in salt concentrations in the irrigation medium increased the EC_e in both types of soil and growth periods at all waterlogging levels. Waterlogging levels from 75-125% WHC, however, decreased salt accumulation in the upper soil depth of 0-20 cm (Fig.4). This trend was observed for all the salt levels.

Sandy soil showed non-significant differences in EC_e at both growth periods for all waterlogging treatments at EC_{iw} of 0 and 10 dS.m^{-1} , whereas, at EC : 20 dS.m^{-1} the soils after 8 weeks showed greater accumulation of salts.

Discussion

Various physiological processes operating in the plants are generally affected by salinity/waterlogging conditions. In the present studies, stomatal conductance, transpiration rate and quantum yield were affected by both salinity and waterlogging treatments in both soil types over a period of time. Since stomatal conductance and transpiration rate is a function of moisture influx from soil to aerial parts of the plant, the difference inside the plant to the outer atmosphere governs the opening/closing of the stomata and thus gas exchange. Stomatal conductance and transpiration rates have been shown to decline significantly both with salinity (0 and 400 mM NaCl) and waterlogging (14 days) in *A. amnicola* in glasshouse studies (Galloway & Davidson, 1993). Similar results have been reported in sugarbeet grown in 150 mM NaCl as compared to control (Terry & Waldron, 1984) and in cotton grown in soil with water potential

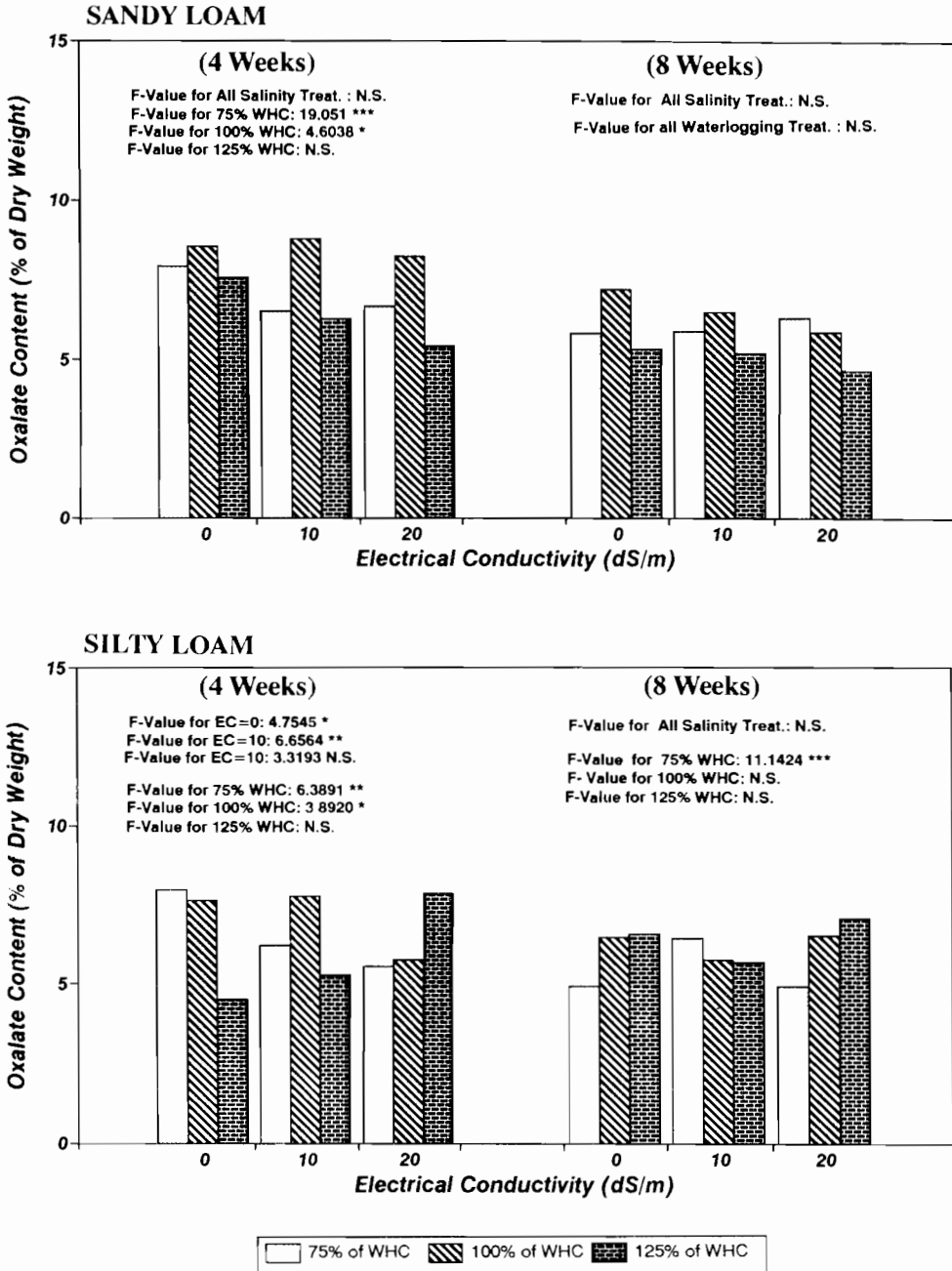


Fig.3. Oxalate content in leaves of *Atriplex amnicola* grown for different periods in two soils under different levels of salinity and waterlogging.

ranging from -0.2 to -1.2 MPa (Shalhavet & Hsiao, 1986). Usually lower rate of water movement is caused by reduction in osmotic potential (OP) which reduces the ability of plants to take up water (Suarez & Labron, 1993). Reduction in stomatal conductance may not be necessarily due to salt or water stress but due to partial closure of stomata or reduced size and number of stomata per unit area (Warne *et al.*, 1990). Transpiration rates are also known to be reduced in *Atriplex* species when grown in presence of sodium and chloride particularly when plants reach maturity (Waisel, 1972).

Halophytes are characterized in accumulating greater concentration of Na^+ and Cl^- for osmotic adjustments to low soil water potential (Lauchli & Epstein, 1984). Halophytic cells isolate these salts in the vacuole, as a result the salt concentration in the cytoplasm is low enough not to interfere with metabolic and enzymatic reactions. This is the most efficient mechanism operating in halophytes that enables them to grow on high salt concentration. However, presence of high salt content, even in the vacuole of a cell, makes the grazing material vulnerable for animals to be used as forage/fodder.

Atriplex amnicola plants grown under salinity and waterlogging conditions showed variations in Na^+ and Cl^- uptake by roots and their translocation to shoot. Plants grown in both sandy- and silty-loam soils exhibited maximum concentration in leaves followed by root and minimum in stem. This indicates that roots are primarily associated with ion absorption from the soil and hence show comparatively higher concentration of both Na^+ and Cl^- ions than in stem. These ions are then transported to stem from where they are readily transported to leaves through xylem conduction. The salts may then be accumulated in vacuoles or removed by salt bladders and glands as reported (Thomson, 1975). Greater concentration of sodium ions in leaves as compared to stem has been reported for *A. nummularia* and *A. barclayana* (Choukrallah, 1991), and that of chloride in five species of *Atriplex* including *A. amnicola* (Mafcolm *et al.*, 1988). High contents of Na^+ and Cl^- could also be attributed to the amount of salts present in the secretory structures alongwith the amount in vacuole. Harvey *et al.*, (1977) have reported in *Suaeda maritima*, that 63 % of total Na^+ and 73% of Cl^- ions are localized in the vacuole, followed by other cell parts. The salinity stress is first sensed in the roots, whereas, osmotic adjustment, growth inhibition and ion toxicity are most apparent in the shoot (Lauchli & Epstein, 1984). An increase in sodium and chloride ions with time appears to be highly significant. Although transpiration rate is reduced under saline conditions, yet it is still sufficient to increase the movement of ions into leaves. Such increase of Na^+ and Cl^- has been reported by Gorham (1993).

Ion content in roots on the other hand is reported to be greatly influenced by the contents of the soil solution (Pitman, 1976). The increase in both Na^+ and Cl^- with time in both soil types appears to be influenced by the total increase in soil salinity. Uptake of both these ions in more or less equal amount is very common in halophytes to balance the charges in the vacuole. Such high intake of both Na^+ and Cl^- in roots have been reported in *A. amnicola* under 400 mM NaCl salinity under hypoxic conditions. Though mobilization of ions from roots to shoot is a passive phenomena with water movement through xylem, yet roots are also reported to contain high amount of these ions to maintain a favourable K/Na ratio in the cytoplasm (Wallace *et al.*, 1973).

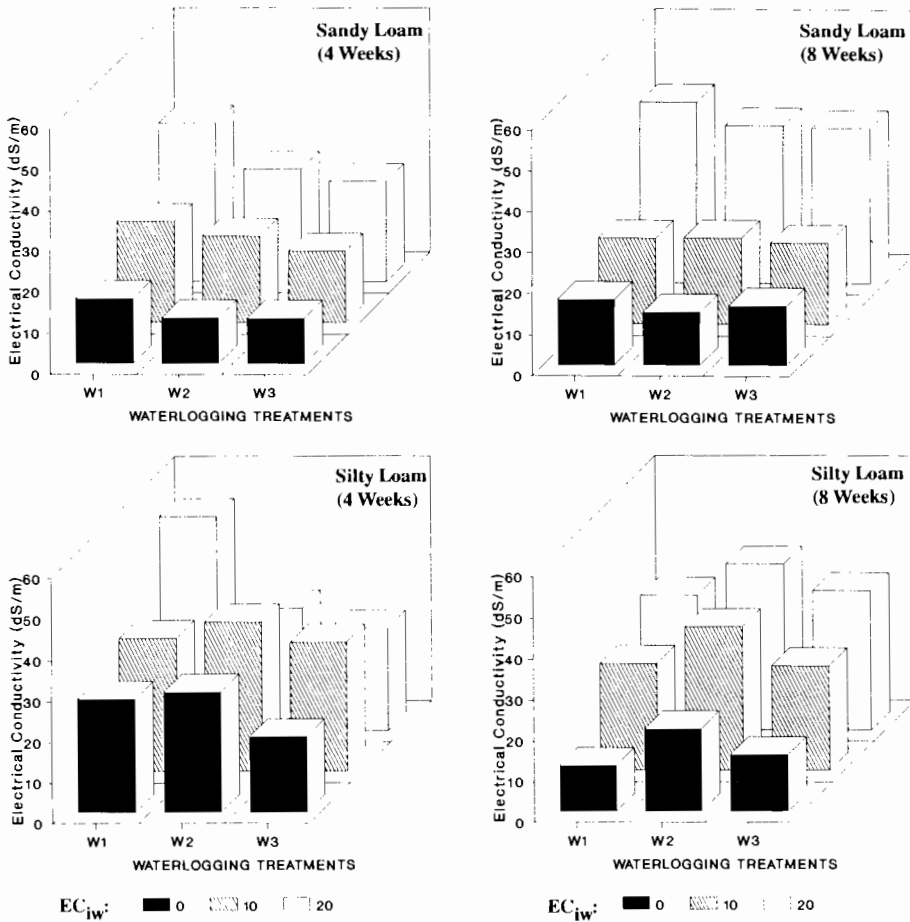


Fig.4. Salt accumulation in two soil types as affected by salt concentration in irrigation water and amount of water applied.

Many workers have reported a high nutritive value in *Atriplex* species with a high protein content, however, presence of oxalate affects the quality of the feed, since oxalate content has been reported to vary from 0.4% (Morcombe *et al.*, 1993) to 9.07% (Watson *et al.*, 1987; O'Leary *et al.*, 1985) in different *Atriplex* species. In the present study, salinity and waterlogging showed no significant effects on the oxalate content that ranged between 4-9% of dry weight.

Application of saline water at different moisture levels had great influence on the total salt accumulation in the soil. However, high rate of moisture in the soil ensures equal distribution in the soil profiles, whereas, low moisture levels tends to accumulate salts in the upper soil profile due to high evaporation rates.

The results of the present studies would suggest that forage quality of *Atriplex amnicola* varies with time and salinity/waterlogging conditions. Generally, sodium and chloride ions are higher in the foliage which could to be minimized by washing prior to feeding the animals. The oxalate content, however, remained unaffected due to salinity/waterlogging levels but still showed a reasonably higher quantity enough to cause health problems for feeding animals if supplied for prolonged periods.

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