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Adaptation Trials of *Atriplex* and *Maireana* Species and Their Response to Saline Waterlogged Conditions in Pakistan

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Abstract: Utilization of salt affected wasteland by growing forage shrubs has enormous economic and environmental implication for developing countries like Pakistan, where approximately 6.3 million ha of the land is salt affected. Considering the importance of *Atriplex* and *Maireana* species, research has been conducted using their different species on the salt affected soils of Faisalabad. Most of *Atriplex* and *Maireana* species survived under the environmental conditions of Faisalabad and gave the good yield in the form of forage. Some of these species are woody and can be used for fuel purposes. Sixteen genotypes of *Atriplex* and *Maireana* were tested for their tolerance to waterlogging in order to identify halophytic fodder shrubs suitable for growth on secondary salt-affected and waterlogged farmland. The physiological and morphological responses of the species tested were typical of species with a generally poor tolerance to waterlogging. Despite this, some species (eg *A. Amnicola*) were surprisingly resistant, surviving up to five months of waterlogging at moderate salinity and high evapotranspirational demand. The most resistant species, *A amnicola* maintained higher transpiration rates, leaf water potentials and shoot extension rates than most other species during five weeks of waterlogging, and a return to control levels more quickly than other species after plots were drained. Although little morphological adaptation to waterlogged conditions was detected, a shallow and extensive lateral root system and the formation of many short aerenchymatous adventitious roots from procumbent branches appeared to advantage *A. Amnicola* in an environment highly heterogeneous in salinity and low in oxygen concentration. Shallow fibrous rooted species were quickly killed by waterlogging, although the procumbent branches of some individuals survived as clones if they developed adventitious roots.

Key words: *Atriplex*, *Maireana*, saltbush, waterlog, saline

Introduction

Out of 700 x 10^6 ha salt affected areas of the world, 300 x 10^6 ha are saline sodic in nature (Barrett-Lennard *et al.*, 1986). Total annual losses of soils in the world due to salts are about 20 millions hectares (Dregne 1983), thus annually a sizeable hectarage is added to this category. Therefore, it appears essential to develop some suitable technology for bringing these salt affected soils under vegetation. Growing of *Atriplex* and *Maireana* species seems to be the most effective measure for this purpose. *Atriplex* a salt tolerant forage shrub belongs to a large and widely distributed genus of chenopodiaceae. Sheep, goats, camels and other animals utilize these shrubs for grazing. These shrubs provide also a valuable reserve feed for drought conditions. Mozafar *et al.* (1969), studied sodium and potassium interactions and uptake by *A. halimus*. They found that sodium absorption by *A. halimus* was not inhibited by high concentration of potassium and if sodium and potassium were present at equal concentrations, sodium uptake was twice as great as potassium. Aslam *et al.* (1986) studied the effect of different concentration of NaCl on the dry weight of *Atriplex amnicola*. Shoot dry weight was higher at 50 and 100 mol m^{-3} NaCl as compared to 10 mol m^{-3} NaC1. Ward (1989) found after conducting field experiment on *Atriplex* species that *Atriplex undulata* and *Atriplex paludosa* had the highest survival rate followed by *Atriplex cinerea* 524 and *Atriplex cinerea* 945 and he further found that *Atriplex amnicola* 573, 577 and 949 are not only palatable but also recovered most rapidly after grazing than the other *Atriplex* species included in the study.

In waterlogged soils, the principal effect of oxygen deficits on roots is to limit aerobic respiration and root metabolism, although an accumulation of toxic products of anaerobic metabolism (eg ethanol and acetaldehyde) and toxic ionic species(eg Mn^{2-}, Fe^{2-}, H_2S, NO^{2-}, organic acids) may also occur (Drew, 1983). Generally, species tolerant of waterlogging facilitate oxygen supply to their root systems by developing aerenchymatous adventitious roots and stem hypertrophy under the mediation of the plant hormone abscisic acid (Jackson *et al.*, 1978; 1981). There may also be some modification of the end products in the glycolytic pathway to limit the build up of ethanol (Joly and Crawford, 1982), although concentrations of ethanol seldom reach concentrations which damage plant tissue (Drew, 1983).

The response of aerial plant parts, not submerged by flooding, are a consequence of the perturbation of growth and metabolism in roots (Drew, 1983). Plant species tolerant to waterlogging may show transient water deficits, reduced stomatal conductance and transpiration, and reduced growth rates when roots suffer oxygen deficits immediately after waterlogging (Sena Gomes and Kozlowski, 1980a; 1980b). In contrast, species intolerant of waterlogging often show little morphological adaptation to the waterlogged environment and show little or no recovery of gas exchange and water relations during the period of waterlogging (e.g. Tang and Kozlowski, 1982). Previous studies of the waterlogging tolerance have investigated a wide range of glycoophytes (eg Senna Gomes and Kozlowski, 1980a; 1980b; Tang and Kozlowski, 1982) and aerenchymatous halophytes (eg. Clough *et al.*, 1982; Mendelssohn and McKee, 1988; Bertness *et al.*, 1992). However, nonaerenchymatous halophytes (e.g. *Atriplex* and *Maireana*) have received comparatively little attention despite the fact that much salt-affected land occupied by these halophytic communities is also prone to waterlogging.

No studies on the response of various *Atriplex* and *Maireana* species to saline sodic soil conditions have been reported. Similarly the physiological behavior of these species under the local natural environments is expected to vary from that reported for controlled conditions. The second aim of the study was to identify the morphological and physiological features that contributed to the superior waterlogging tolerance of some genotypes (eg *A. Amnicola*), using data from a wide range of genotypes of *Atriplex* and *Maireana* grown in trials in Pakistan. In this paper it is planned to focus attention on these objectives.

Materials and Methods

This adaptation experiment was carried out in the net house, post graduate Agricultural Research Station and in the laboratories of Soil Science Department, University of Agriculture, Faisalabad, Pakistan.

Nineteen species of *Atriplex* and *Maireana* were selected for this experiment (Table 1). Seeds of these species were sown in soil culture containing equal proportion of soil, sand and organic matter. Different species were sown in different tubs. The soil of the tubs was first irrigated and then seeds without brackets were spread over the wet surface of soil and covered (1-2 mm deep) with soil. After germination the young seedlings were shifted to polythene bags containing the same soil material, which was used in the tubs.These polythene bags containing the small seedlings were kept in the wire house for about two months and when the seedlings well established they were shifted to the naturally salt affected soil. Before shifting, a representative soil sample was taken for determining the physico-chemical characteristics of soil (Table 2). Temperature and humidity of experimental sites were recorded daily. Each treatment was replicated 20 times in a completely randomized block design for adaptation trial in Faisalabad. Following observations and analytical work were made before and after harvesting the bushes.

Volume and survival rate of bushes were taken after every month, up to 12 months. While weight of the bushes was taken when they were 12 months old (Table 3). Soil samples were analyzed for EC, pH, SAR, Na^+, K^+, Ca^{+3}, Mg^{+2}, HCO_3, CO_3 and N were determined by using the methods of US salinity laboratory staff (Richards, 1957) (Table 2). While $C1^-$ was determined by using Corning analysis 957 (Corning Limited Halstead, ESS, ES England) and texture by mechanical analysis (Moodie *et al.*, 1957) (Table 2). Provenance trials using 12 genotypes of *Atriplex* and four genotypes of *Maireana* were planted on three different soil types near Faisalabad, in the irrigated agricultural region of central Pakistan for studying the waterlogging response of these plant species. Two provenance trials were planted at Pindi Bhattian and the other at Sadhoke. These trials had the same design: eight replicate square randomised blocks of 16 genotypes; *A. amnicola* (accessions 573, 971 and 949), *A. Amnicola* x nummularia hybrid, *A. lentiformis* (accession 159), *A. cinerea*, *A. undulata*, *A. bunburyana* (accessions from Carnarvon and Leonora), *A. vesicaria*, *A. Sp pintheruka*), *A. stocksii*, *M. brevifolia*, *M. polypterigera*, *M. aphylla*, *M. appressa*.

At three monthly intervals, records were made of plant survival, height (h), maximum diameter (D_1) of the canopy and the diameter of the canopy (D_2) at right angles to D_1. The mean plant volume of surviving individuals was computed for each species using the formula for a hemisphere ($1/6\Pi \times D_1 \times D_2$). The duration of waterlogging was assessed from both shallow (50 cm) and deep (300 cm) piezometers placed at the centre of each of block in the provenance trials.

After 12 months growth one half of the Post Graduate Agricultural Research Station (PARS) Faisalabad, trials was artificially flooded to a depth of 15 cm for four weeks in an attempt to create waterlogged conditions. As the trial was planted on 15 cm high ridges so only the lowest of procumbent branches on prostrate plants were covered by the water. After four weeks of flooding, diurnal studies of the stomatal conductance (measured with a Licor 1600 porometer) and the water potential (measured with a pressure chamber) were made on three replicates of four

Table 1: *Atriplex* and *Maireana* species used in Faisalabad trials

Atriplex amnicola	573
Atriplex amnicola	949
Atriplex amnicola	971
Atriplex bunburyana (Kalgoorlie)	
Atriplex bunburyana	(Lot 227)
Atriplex lentiformis	(Lot 159)
Atriplex lentiformis	(Lot 178)
Atriplex sp. Pintharuka	951
Atriplex undulata	471
Atriplex vesicaria	
Atriplex halimus	
Commercial	
Maireana aphylla	
Maireana appressa	
Maireana brevifolia	
Maireana platycorpa	
Maireana polypterygia	
Maireana pyramidata	
Maireana tomentosa	

Table 2: Physico - Chemical characteristic of soil in Faisalabad trial

Properties	Unit	Values
Sand	%	22.8
Silt	%	50.4
Clay	%	26.8
Textural class	-	Silt loam
EC	dSm/m	26.65
Phe	-	8.5
SAR	mmole/1	67
Na	meg/1	219
K	meg/1	4.1
Ca + Mg	meg/1	11.82
HCO_3	meg/1	16.5
CO_3	meg/1	nil
C1	mmole/1	66
N	%	0.02

Table 3: Survival, volume and weight of the bushes in adaptation trial at Faisalabad. Data are represented as means ± S.E., n = 20 replications.

Species	Survival (%)	Volume (m^3)	Weight (kg)
Atriplex amnicola 573	75	06.50±2.44	23.34±10.16
Atriplex amnicola 949	90	05.00±0.91	20.50±04.35
Atriplex amnicola 971	90	12.38±3.88	36.40±05.46
Atriplex bunburyana(Kalgoorlie)	80	02.53±0.57	08.86±02.31
Atriplex bunburyana (Lot 227)	85	02.13±0.37	06.80±01.08
Atriplex lentiformis (Lot 159)	90	37.91±8.75	46.70±10.22
Atriplex lentiformis (Lot 178)	62	32.84±7.51	41.71±09.12
Atriplex sp. *Pintharuka* 951	90	03.12±0.81	09.31±01.73
Atriplex undulata 471	90	05.86±1.61	14.63±04.30
Atriplex vesicaria	80	02.18±0.30	09.93±02.22
Atriplex halimus	70	06.00±2.22	13.61±03.24
Commercial	55	02.86±1.30	08.61±04.18
Maireana aphylla	35	00.87±0.54	01.94±01.07
Maireana appressa	55	00.56±0.42	01.32±00.24
Maireana brevifolia	75	02.04±0.31	05.80±01.00
Maireana platycorpa	35	00.13±0.08	01.70±01.21
Maireana polypterygia	75	00.75±0.42	03.56±01.14
Maireana pyramidata	60	01.30±0.58	04.36±01.66
Maireana tomentosa	15	00.24±0.12	01.06±00.19

Atriplex species; A. lentiformis (178), *A. amnicola* (971), *A. bunburyana* (Carnarvon) and *A. halimus*, in both the flooded and the unflooded portions of the provenanc trial. At midday the sky was clear, the light intensity was high (PAR = 1840 uE $m^{-2}s^{-1}$), the temperature was high (T = 38.5°C) and the relative humidity moderate (RH = 52%). The extension growth of two tagged apical shoots on each experimental plant was measured after two weeks and four weeks of flooding. Water temperatures were measured and a soil profile was dug in the flooded segment of the trial to investigate the macroporocity of the soil. Soon after this experiment was completed heavy monsoonal rains fell. In late June, heavy monsoonal rains again fell at Faisalabad and six month old seedlings in the new plots at Pindi Bhattian and Sadhoke were waterlogged for 2 months and 5 months respectively.

In September, after the Sadhoke and Pindi Bhattian trials had grown for nine months, selected bushes were excavated, and the rooting pattern recorded and related to characteristics of the soil profile (depth, texture, sodicity and salinity of each horizon).

Results

Survival Rates: Twelve species of saltbush survived more than 70% at the end of 12 months of their growth while *A. amnicola* 949, *A. amnicola* 971, *A. lentiformis* 159, *A.* Sp. *pintharuka* 951, *A. undulata* 471, *A. bunburyana* (Kalgoorlie) and 227 *A. vesicaria, A. amnicola* 573, *M. ploypterygia* and *M. brevifolia* have 90, 90, 90, 90, 85, 80, 75, 75, and 75% survival rates, respectively (Table 3). *Maireana tomentosa*, *Maireana platycorpa* and *Maireana aphylla* have survival rate less than 40% because when these plants were transplanted to the field, the temperature of the Faisalabad district raised suddenly during May-June. Therefore, most of these plant species died due to high temperature (Table 3).

Volumes of Bushes: Weight of the bushes taken, when these were 12 months old (Table 3). *Atriplex lentiformis* 159 have maximum weight (46.70±16.22 kg) which is statistically non significant from the weight of *A. lentiformis* 178 and *A. amnicola* 971. *Atriplex amnicola* 573 and 949, *A. undulata* 471 and *A. halimus* have more or less same weight, while the weight, of rest of the species were statistically non significant (Table 3). Minimum weight was found in case of *M. tomentosa* (1.06±0.19 kg), which had also minimum survival rate. *Atriplex lentiformis* 159 and 178 have not only maximum volume and weight but they were also woody and could be used for fuel production. Root structures of various saltbush species are described in Fig.1. In all three-provenance trials conducted near Faisalabad in Pakistan, *A. lentiformis* (159 and 178) outperformed every other species (Fig. 2). The next most successful species was *A. amnicola*. (971 and 573). Other species were either far less productive (lower mean canopy volume) or exhibited low survival than *A. amnicola* and *A. lentiformis*.

Although the relative species of success in all three provenance trials were very similar, great differences in productivity and survival rate existed between trials at the end of the first years growth, and these reflected major differences in soil type and the duration of waterlogging at the trial sites (Fig. 2 and Fig. 3).

At the most successful trial, the Post Graduate Agricultural Research Station (PARS) all species survived and the most productive species, *A. lentiformis*, achieved canopy volumes of 20 m^3 in one year, which was more than twice the volume achieved by the next mostproductive species *A. aminicola* (Fig. 2). Two other *Atriplex* species achieved volumes greater than 2 m^3 in one year; *A. halimus* and *A. undulata*. The soil profile at PARS consisted of 90 cm of silty-clay-loam to sandy-loam over sand (Fig. 3) and was excellent for deep root penetration. Only the top 15 cm of the soil profile was highly saline (Ece-30 dS m^{-1}) and sodic (SAR=79). Surface soil characteristics were typical of high sodicity; powdery with a surface crust when dry, but slaking, dispersive and impermeable when wet. After rain or irrigation water ponded on the soil surface for extended periods. Attempts to waterlog the whole soil profile by flooding the trial to a depth of 15 cm for 4 weeks were unsuccessful because very low infiltration rates. Below 15 cm soils became coarser in texture and well structured with high degree of macroporocity and water quickly passed through towards the water-table (at about 6 m). Water was observed running out of macropores at 1.5 m depth in soil pits dug within the flooded portion of the provenance trial.

In late June, after half the PARS trials had been waterlogged for four weeks, midday measurements of water potential, transpiration rate and shoot extension made on four *Atriplex spp* indicated no serious symptoms of waterlogging stress existed in the flooded portion of the trial. Analysis of variance indicated species and treatment effects were non-significant. However, there was a significant interaction ($p \leq 0.05$) between species and waterlogging treatment for transpiration* and shoot extension data (Table 4). *Atriplex halimus* had higher transpiration rates, shoot extension rates and leaf water potentials than other species tested in the unwatered areas. The strong performance of *A. halimus* may well relate to its tropical North African origin. In contrasts, in the flooded portion of the same trial, *A. lentiformis* and *A. amnicola* exhibited higher transpiration rates and shoot extension rates than *A. halimus* and *A. amnicola* exhibited higher transpiration rates and shoot extension rates than *A. halimus* and *A. bunburyana*. The improved performance of *A. lentiformis* and *A. amnicola* in flooded conditions probably reflects the improved water supply to plants of large biomass (see Fig. 2) under conditions of high evapotranspirational demand. The poorer performance of *A. halimus* and *A. bunburyana* in the flooded region may indicate some suppression of growth of smaller plants (Fig. 2) with roots in the partially waterlogging upper part of the soil profile.

The most obvious effect of flooding was the death of partly submerged branches of the smaller prostrate species (eg *A. bunburyana* and *A. undulata*). These branches were probably damaged directly by hot water, which reached 62 °C.

At Pindi Bhattian all but two of the species grew well for the first 6 months. However, in late July, heavy monsoonal rains waterlogged the trial for approximately two months. Waterlogging eliminated nine species from the trial and of the remaining species, only *A. aminicola* and *A. lentifirmis* had more than four surviving replicates (see 12 month records, Fig. 2). It was apparent that only a few larger individuals of the hybrid *A. amnicola* x *nummularia*, *A. cinerea* and *A. undulata* had survived. Difference in the effect of flooding on plant survival at Pindi Bhattian in comparison to the artificially flooded portion of the PARS trial appeared to relate to soil characteristics (Fig. 3). The soil profile at Pindi Bhattian differed from that at PARS in three important respects. Firstly, the profile was highly sodic to a greater depth than

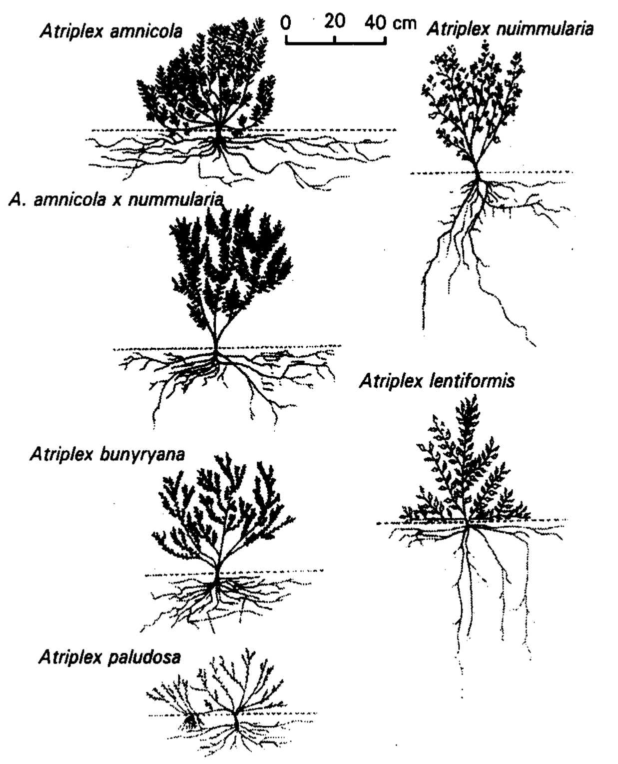
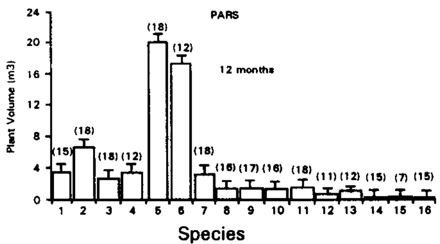
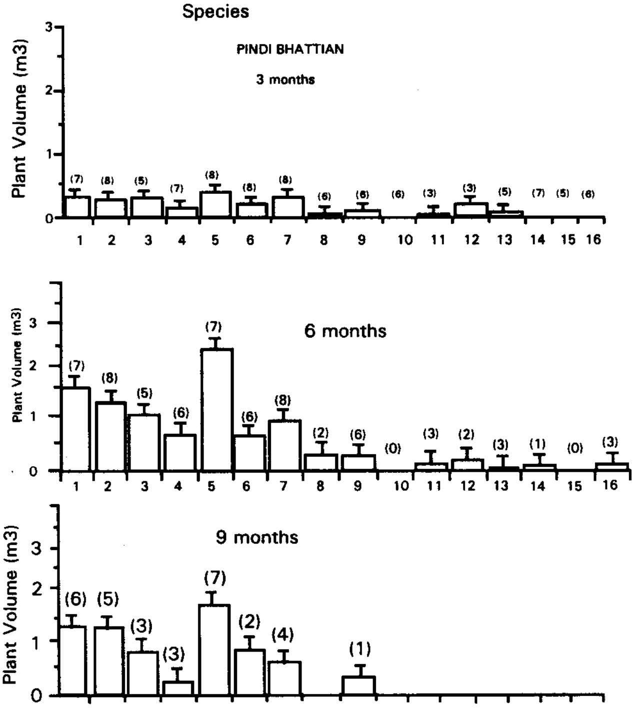
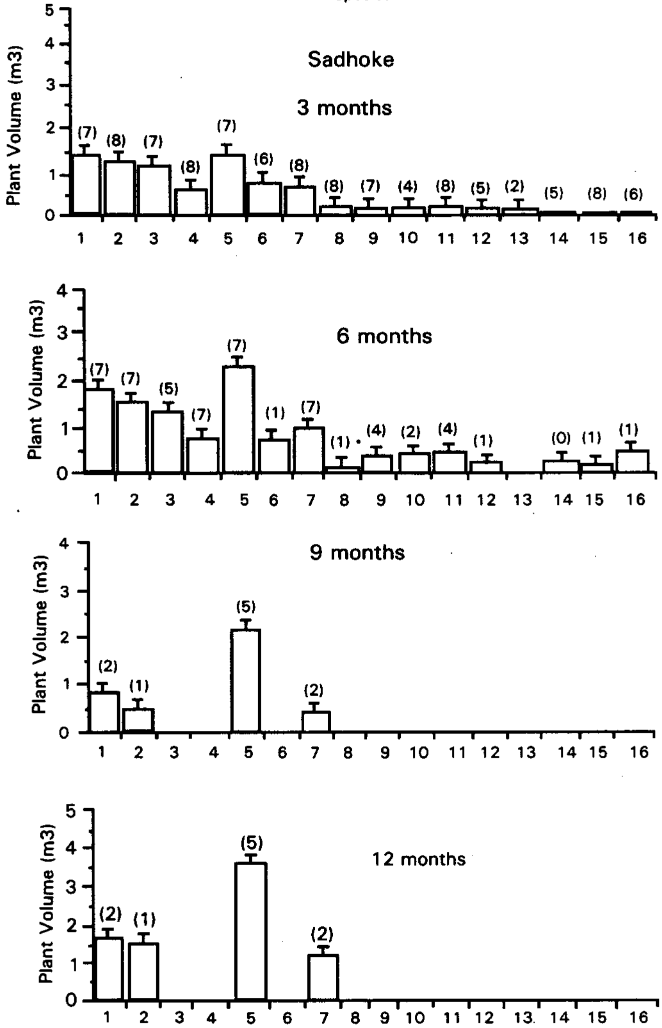


Fig. 1: Root structures of various Atriplex species in saline waterlogged soil.







Key

No.	species	No.	species
1.	Atriplex amnicola 573	2.	Atriplex amnicola 949
3.	Atriplex amnicola 971	4.	Atriplex bunburyana (Kalgoorlie)
4b.	Atriplex bunburyana (Lot 227)	5.	Atriplex lentiformis (Lot 159)
6.	Atriplex lentiformis (Lot 178)	6b.	Atriplex sp. Pintharuka 951
7.	Atriplex undulata 471	8.	Atriplex vesicaria
9.	Atriplex halimus	10.	Commercial
11.	Marieana aphylla	12.	Marieana appressa
12b.	Maireana brevifolia	13.	Maireana platycorpa
14.	Maireana polyterygia	15.	Marieana pyramidata
16.	Maireana tometosa		

b. The sult of species use in the three provinces trails differed slitely. Species marks "b" were used at the Post Graduate Agricultural Research Station (PARS) and replaced these of that number in other trails (10) number of surviving individual out of 20 plants in the (PARS) trail and out of 8 plants in other trails

Table 4: Midday (12-2 pm) leaf water potentials, transpiration rates, and shoot extension rates recorded at the Unversity of Agriculture Faisalabad, Post Graduate Agricultural Research Station in late July, for four selected *Atriplex* species in a trial exposed to two water regimes; unwatered and continuously flooded to a depth of 15 cm for four weeks. At midday the light intensity was high (PAR = 1840 uE $m^{-2}s^{-1}$), the temperature was high (T = 38.5°C) and the relative humidity moderate (RH = 52%).

Speciees	Treatment	Water Potential (Mpa)	Transpiration (uE m^{-2} s^{-1})	Shoot extension (cm)
A lentiformis	Unwatered	-3.48 ± 0.34	4.14 ± 0.82	25.5 ± 4.90
	Flooded	-3.45 ± 0.38	6.38 ± 2.00	71.0 ± 8.10
A. amnicola	Unwatered	-3.18 ± 0.28	5.53 ± 1.10	65.2 ± 11.4
	Flooded	-3.21 ± 0.14	7.36 ± 1.5	81.0 ± 10.0
A. halimus	Unwatered	-3.19 ± 0.31	6.67 ± 1.38	94.0 ± 8.0
B.	Flooded	-3.05 ± 0.10	5.37 ± 0.41	32.2 ± 14.1
A. bunburyana	Unwatered	-3.68 ± 0.08	3.73 ± 0.42	81.3 ± 10.6
	Flooded	-3.08 ± 0.12	3.11 ± 0.19	36.3 ± 7.4

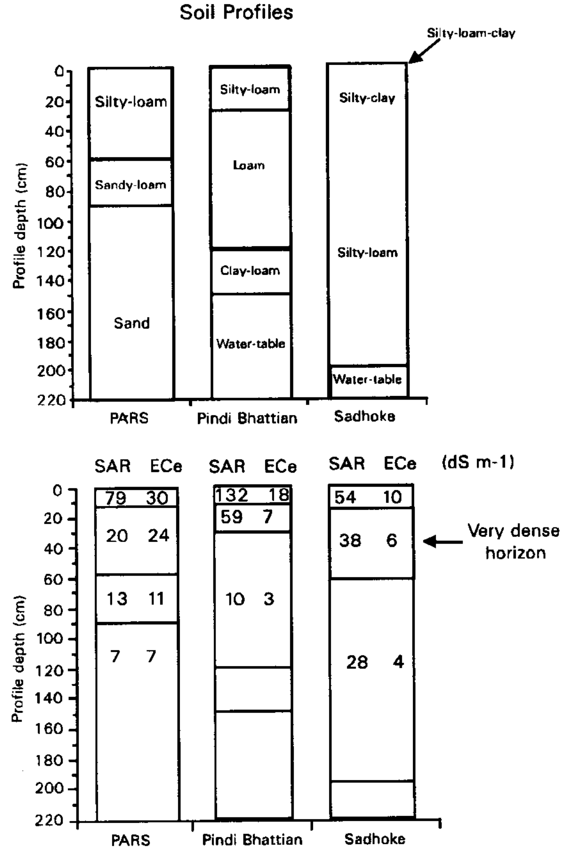


Fig. 3: Soil profiles of three sites (Faisalabad, Pindi Bhattian and Sadhoke) in Pakistan, where the trials of *Atriplex* and *Maireana* species were conducted.

PARS (Fig. 3). Secondly, the silty-loam horizon in the 15-30 cm depth interval was very dense and was only penetrated by roots of *A. lentiformis* (Fig. 3, evidence from plant excavations). Thirdly, there was a water-table at approximately 1.5m. The similarity between Pindi Bhattian and PARS was in the soil profile from 30cm to the water-table, which was well structured with a high degree of macroporocity. *Atriplex lentiformis* roots in this part of the soil profile were not subject to waterlogging, although some level of oxygen deficit may have existed as a result of isolation from the atmosphere (Drew, 1983). In contrast, other species were confined to surface horizons and had their entire root systems waterlogged after monsoon rains. Therefore, it appears *A. lentiformis* survived of waterlogging at Pindi Bhattian by avoidance, while A. amnicola survived by tolerance.

At Sadhoke, like Pindi Bhattian, most species grew well for the first six months, but in late July monsoonal rains waterlogged soils at Sadhoke. During the next five months occasional rains and exceptionally low infiltration rates maintained waterlogged conditions at the site, and by 12 months every replicate of all but three species; *A. lentiformis, A. amnicola* and *A. undulata* had been killed (Fig. 2). At 15 months all plants were dead. The soil profile at Sahoke was highly sodic to a greater depth and had higher clay content than at other sites (Fig. 3). All horizons in the soil profile had high bulk density and little macroporocity (from soil pits). Inter specific differences in root development were similar to those found at Pindi Bhattian, but at Sadhoke there was no part of the profile that did not become waterlogged and eventually during five months of almost continuous flooding even the deep roots of *A. lentiformis*. became waterlogged and the tolerance of *A. amnicola* was exceeded.

Discussion

From this experiment it may conclude that the growth of *Atriplex* and *Maireana* species was successful under the local conditions of Faisalabad (Table 3). Cost of their production was low and we grew them on highly saline and sodic soils, and got useful forage from wasted lands. Most of these species are drought tolerant and can be grown in areas where irrigation water is not available. Beside forage purposes they can be used for fuel purposes as well as for reducing the soil erosion and in this way *Atriplex* and *Maireana* species prevent the further degradation of salt affected soils.

The physiological responses of five *Atriplex* species exposed to five weeks of waterlogging in the field were similar to those previously described for species with poor tolerance to waterlogging (Tand and Kozlowski, 1982). Water deficits, depressed transpiration rates and much-reduced rates of shoot growth were maintained during the latter stages of the waterlogging trial. Morphological adaptations to waterlogging were weakly developed. Short aerenchymatous adventitious roots developed from the procumbent branches of some species. No recovery of physiological activity occurred during waterlogging and after the development of adventitious roots. Despite this, some species (eg *A. amnicola*) were surprisingly resistant, surviving up to five months of waterlogging at moderate salinity and high evapotranspirational demand. There were also significant inter specific differences in tolerance to waterlogging amongst the *Atriplex* species tested. Of the 16 species of *Atriplex* and *Maireana* investigated in field experiments in Pakistan, *A. amnicola* was the only species to consistently show high tolerance to waterlogging. In all the provenance trials in Pakistan *A. lentiformis* and *A. amnicola* were the most productive species in trials established in sites which varied form mildly to severely waterlogged.

Excavation of the root systems of six *Atriplex* species revealed major inter specific differences in rooting pattern and adventitious root development which were associated with tolerance or avoidance of waterlogging (Fig. 1). Two species, *A. bunburyana* and *A. paludosa*, had a highly branched shallow fibrous root system (Typed 5, Dodd *et al.*, 1984) similar to that previously described for *A. vesicaria* (Jones and Hodgkinson, 1970), and typical of a specialized xerophytic root system found in short lived perennials which experience marked seasonal variation in water relations (Dodd *et al.*, 1984). In the absence of any morphological adaptations to waterlogging (eg limited adventitious root development) these species were particularly susceptible to waterlogging damage. Two species, *A. nummularia* and *A. lentiformis* developed a deep taproot system plus laterals (Type 4, Dodd *et al.*, 1984), typical of species growing in environments where water stress is avoided by tapping a deep-seated water source (Dodd *et al.*, 1984). The root system of *A. nummularia* may penetrate to a depth of 10m or more even in the most intractable soils (Jones and Hodgkinson, 1970). Glasshouse waterlogging in trials showed that both *A. nummularia* and *A. lentiformis* exhibited poor tolerance where root systems were confined. However, in this trials *A. lentiformis* had deep root penetration even where very dense horizons existed within the soil profile, and when waterlogging occurred at least part of the root system avoided oxygen deficiencies in waterlogged compartments of the soil (Fig. 1). Therefore, the success of *A. lentiformis* in waterlogged soils in Pakistan was primarily a result of avoidance.

Atriplex amnicola had a very extensive lateral root system (Type 2, Dodd *et al.*, 1984). This characteristic was present but less well developed in the hybrid *A. amnicola x nummularia*. Lateral growth rates of 4.1 m have been measured for individual roots during the first six months growth of *A. amnicola* seedlings (Davidson *et al.*, unpublished). This is equivalent to a growth rate of 2.3 cm day^{-1} and occurred while the canopies grew to a mean diameter of 1.0 m (0.27 cm day^{-1}). The high tolerance of waterlogging conferred in part by this type of root system may be attributable to the effective exploration of a characteristically highly heterogeneous soil environment; heterogeneous in salinity, oxygen concentration, texture and water availability (Davidson *et al.*, 1993). This would maximise the chance *A. amnicola* might have to exploit favorable micro-sites in surface soils, particularly those with higher oxygen concentrations. Further, under waterlogged conditions, it may only be the surface few millimeters of soil that are oxygenated (Drew, 1983). Differences in relative rank order of *Atriplex* species in field trials may well reflect the confinement of roots in the glasshouse trials.

The second rooting characteristic which showed high inter specific variability in waterlogging trials was the development of adventitious roots from procumbent branches. Adventitious root development is common in *Atriplex* and in natural shrub lands of *Atriplex* in the rangelands it is typical for each bush to have a mound detritus collected at its base beneath the canopy (Jones and Hodgkinson, 1970). Adventitious roots exploit these mounds for nutrients and water, particularly after light rains (Jones and Hodgkinson, 1970). Anatomical studies of these roots in waterlogged environments have shown them to be aerenchymatous for *A. amnicola*. The absence of mounding beneath the crowns of most *Atriplex* species tested in the field may have contributed to the poor development of adventitious root in these trials and only procumbent species expressed this character.

At first glance, one of the surprising aspects of the current trials was the high degree of tolerance exhibited by some *Atriplex* species (eg *A. amnicola*) to extended periods of waterlogging (up to 5 months) under conditions of moderate salinity and high ev avpo-transpirational demand, and this despite a clear lack of the morphological adaptations known to be long term survival in waterlogged environments (Drew 1983). However, in their natural environments, many *Atriplex* species are exposed to occasional floods; for example, *A. amnicola* grows naturally on flood prone riverine planes in North Western Australia. It appears that the inherent salt tolerance *Atriplex* species (Greenway and Munns, 1980) and drought tolerance preadapts them to tolerate the water deficits caused by root damage and death under waterlogged conditions (Galloway and Davidson, 1993). Even after root tip death has occurred the primary root system of *A. amnicola* will regenerate from lateral roots high on the root crown (Galloway and Davidson, 1993). Alternatively there may be some biochemical adjustment associated with resistance to waterlogging in *Atriplex*, such as a modification in the end products of the glycolytic pathway to limit the build up of ethanol (Joly and Crawford, 1982). However, concentrations of ethanol seldom reach concentrations, which damage plant tissue (Drew, 1983).

Recent studies on root competition (Caldwell 1988; Reichenburger and Pyke 1990; Aerts *et al.*, 1991) suggest that root competition plays an important role in above ground production. To maximize the productivity from *Atriplex* forage crops on highly productive sites where competition is likely to occur it may be necessary to plant together species differing in rooting pattern, thus maximizing niche separation and minimizing inter specific competition for nutrient and water in the dry season and oxygen during periods of waterlogging. In natural mixed stands of *Atriplex* this relationship exists, for example in the rangeland *A. nummularia* (deep tap root system) and *A. vesicaria* (shallow fibrous root system) co-occur (Jones and Hodgkinson, 1970). It is probably no accident that, the commonly recommended seed mix for revegetating salt-affected farmland (Malcolm, 1989; 1990) consists of *A. amnicola* (extensive lateral root system) *A. lentiformis* (deep tap root system) and *A. undulata* (shallow fibrous root system).

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