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Comparative responses of seedlings of four arid zone tree species to salinity

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Abstract

The physiological and morphological responses of seedlings of four arid zone tree species to salinity were investigated under glasshouse conditions. The species used were *Acacia seyal*, *Acacia tumida*, *Acacia cyanophylla* and *Parkinsonia aculeata*. Seedlings were grown in transparent polythene tubes (volume 1571 cm3) filled with heavy clay soil and exposed to irrigation water with different salinity levels of 0, 1, 2, 5, 10 and 20 dS m^{-1} for three months. Effects of salinity on photosynthesis, stomatal conductance, transpiration rate, shoot growth, and dry matter accumulation and partitioning were evaluated. These parameters were adversely affected by the higher levels of salinity (> 5 dS m^{-1}) and no growth was observed at salinity level of 20 dS m^{-1}. However, the results revealed marked interspecific variations in the response of seedlings to salinity among the different species. *A. tumida* showed the greatest sensitivity of all the parameters to salinity, and failed to survive salt concentration as low as 2 dS m^{-1}, while both *A. cyanophylla* and *P. aculeata* proved to be the most tolerant, as they were able to survive at a high salinity level and displayed significantly higher photosynthetic rate, water use efficiency, stem length, total leaf area, and dry matter production at 10 dS m^{-1} compared with the other species. Photosynthesis was stimulated in *A. cyanophylla* and *A. seyal* by 2 dS m^{-1} and 5 dS m^{-1}, respectively. The results of this study paved the way to rank the studied species based on their tolerance to salinity into three categories, viz: intolerant (*A. tumida*), intermediate (*A. seyal*), and tolerant (*A. cyanophylla* and *P. aculeata*).

مقارنة استجابات بادرات أربعة أنواع من أشجار المناطق القاحلة للملوحة

أيوب خليل, محمد النور, الأمين عبدالماجد و عبدالله الحزورى

أجريت هذه الدراسة تحت ظروف الصوبة الزجاجية لمعرفة الاستجابات الفسيولوجية والظاهرية لبادارات أربعة أنواع من أشجار المناطق القاحلة . الأنواع التـى تمت دراستها هى الطلح (*Acacia seyal*) واكاسيا سيانوفيلا (*Acacia cyanophylla*) واكاسيا تومـيـدا (*Acacia tumida*) والسيـسـبان (*Parkinsonia aculeata*) . زرعت البادرات فى أكياس بالاستيكية شفافة (حجم ١٥٧١سم٣) مائت بتربة طينة ثقيلة . استخدمت خمسة تركـيـزات ملحيـة (١او ٢او ٥و ١٠او ٢٠ دسيسمن/م) لرى البادرات بالإضافة الى استخدام ماء الصنبور لرى مجموعة الشاهد وذلك لمدة ٣ شهور . تم تحليل اثر الملوحة علــى التمثيـل الضوئـى وحركة الثغور والنتح وطول الساق ومساحة الأوراق وتراكم وتوزيع الوزن الجاف . تأثرت الصفات المدروسة سلبا عند المستويات العليا للملوحة (اكثر مـن ٥ دسيسمن/م) ولم يلاحظ آي نمو عند التركيز ٢٠ دسيسمن/م آلا ان النتائج أظهرت تباينا نوعيا حادا فى استجابة البادرات للملوحة بين الأنواع المختلفة . فقد بــدا النوع توميدا اكثر حساسية للملوحة إذ فشل فى تحمل ملوحة اكثر من ٢ دسيسمن/م, بينما اثبت السيسبان والسيانوفيلا اكثر تحملا للملوحــــة إذ انــهما اظـهـرا معدلات أعلى معنويا للصفات المدروسة عند التركيز ١٠ دسيسمن/م مقارنة بالأنواع الأخرى لقد ارتفع معدل التمثيل الضوئي فى الطلح والسـيـانوفيلا بواسـطة التركيز ٥ دسيسمن/م و ٢ دسيسمن/م على التوالي . تمكن هذه الدراسة من تقسيم الأنواع التى تمت دراستها وفقا لتحملها للملوحة الى ثلاثـة مجموعــات هـى ضعيفة التحمل للملوحة مثل النوع توميدا ومتوسطة التحمل للملوحة كالطلح ومتحملة للملوحة مثل السيسبان واكاسيا سيانوفيلا.

Introduction

Soil salinity is one of the most important edaphic factors leading to a substantial long-term site degradation in arid and semi-arid zones of the world. The accumulation of high concentration of soluble salts in the soil limits the growth and development of most terrestrial plants more than any other inhibitory substances (Rush and Epstein, 1981). The ensuing losses in plant productivity are enormous, particularly in agricultural crops that are more sensitive to salinity than the woody plants. Thus, large scale

planting of multi-purpose salt-tolerant tree species may offer an attractive alternative for economic utilization of salt-affected areas in the arid and semiarid lands, to increase their productivity and to meet the increasing demands for fuelwood, timber and other indispensable forest products. However, the selection of genotypes with superior capacity to survive on salt-prone environments requires a thorough understanding of the biological basis of how trees avoid or tolerate the damaging impacts of salinity stress.

The terrestrial plants have evolved a number of adaptive mechanisms to cope with the presence of salt in their environment. The most significant of these mechanisms entails actual tolerance by plants of high levels of salt within their tissues (Allen et al.,1994). Salt-tolerance (i.e., the ability of a plant to grow and complete its life cycle on saline soils) depends on the ability for osmotic adaptation and acquisition of mineral elements needed for growth and functional metabolism (Jeschke, 1984). The salt-tolerance of forest tree species differs greatly (Allen et al., 1994) and there is ample scope for selection of species using physiological traits that are related to survival, growth and productivity (Hall et al., 1993). Generally, assessment of physiological response traits, such as photosynthesis, stomatal conductance, osmotic adjustment or changes in the appearance of certain morphological traits is the key factor in determining which species or geographic races of a species are suitable for an operational planting programme.

Salinity reduces plant growth by alterations in allocation of assimilates, nutritional balance, water status and other biochemical and physiological processes and conditions, or by a combination of such factors (Kajaji and Nalborezk, 1991, Ruiz et al., 1997). Salt stress has detrimental effects on photosynthesis, transpiration rate and stomatal response. The limitation imposed on photosynthesis may be due to reduced stomatal conductance and/or reduction of the chloroplast activity (Maas, 1993). Therefore, of the potential of a species to be

grown in salt-affected areas depends on its capacity to sustain the physiological processes and conditions under otherwise inhibitory levels of salinity. However, the effective utilization of this physiological information in the course of screening work necessitates the establishment of significant associations between tree growth and survival under stress and the various possible physiological components of salt-tolerance (Nobel and Rogers, 1992). Although some understanding of the salt-tolerance of a few tree species is available, rather little is known about the growth performance of many arid and semi-arid zone tree species on saline soils, or their potential for reclamation of salt affected areas.

The prime objective of this study was to evaluate the physiological and morphological performance of four deciduous tree species under elevated levels of soil salinity in order to screen for superior genotype with seedling characteristics acceptable for afforestation in salt-affected areas. The species used were A. seyal, A. cyanophylla, A. tumida and P. aculeata. Despite their potential economic values and their existence as major components of woodland, very little is known about the response of these species to salinity stress and their relative tolerance.

Materials and methods

This study was carried out to evaluate the impact of salinity on the physiological and morphological performance of seedlings of four arid-zone tree species, viz: A seyal, A. cyanophylla, A. tumida and P. aculeata. Seeds of the first species were obtained from the Forest Seed Centre at Soba, Sudan, while the seeds of the other species were collected from the Forest Seed Centre of Sana'a, - Republic of Yamen.

The seeds of the four species were pretreated with sulphuric acid to eliminate the seed coat dormancy. This was accomplished by immersion of the seeds into a solution of concentrated sulphuric acid (95%) for 2 minutes, quickly

washed with tap water, rinsed in distilled water and dried. Henceforth, the dry seeds were surface-sterilized with 5% sodium hypochlorite before sowing.

The experiment was carried out (between January 1996 to April 1996) in the glasshouse of the Faculty of Agriculture, Shambat, University of Khartoum, Sudan. Seeds were sown in transparent polythene tubes (20 cm x 10 cm), packed with heavy clay soil, after being sieved (5 mm mesh) and sterilized by heating at $140°C$ for 3 hours. The polythene tubes were perforated at their bases and lower portions to allow free drainage and aeration of the soil. They were then accommodated in plastic trays, with a total of twelve tubes per tray. Each tray represents an experimental unit, so that all tubes within it experienced similar treatments, as regards salt concentration and tree species. Five seeds of the same species were sown in each tube and irrigated to field capacity at three-day intervals with six levels of saline solution (i.e. 0, 1, 2, 5, 10, and 20 dS m^{-1}). The saline solutions were prepared by mixing NaCl and $CaCl_2$ at a fixed sodium adsorption ratio (5 mmol l^{-1}). The experiment was arranged in a split plot design, with three blocks, each block containing six levels of saline solution and four tree species. Twenty one days from sowing, seedlings were thinned to one plant per tube.

To estimate the impact of salinity stress on shoot development, data on stem elongation, and leaf area were collected at 72 days. Eighty days from the start of the experiment, gas exchange was measured at mid day. Net photosynthesis rate (μmol m^{-2} s^{-1}), (stomatal conductance, mol m^{-2} s^{-1}) and transpiration rate (mmol m^{-2} s^{-1}) were evaluated from CO_2 and water vapour fluxes in an open system after nine hours into the light period using a model LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). At the end of the measurement, data were recalculated to reflect the actual leaf surface area. Instantaneous water use efficiency (WUE = μmol of Co_2 gain

per mmol of water loss) was calculated for each seedling by dividing net assimilation rate by transpiration rate.

At ninety days, all the seedlings were destructively harvested, to estimate the influence of salinity on dry matter production and allocation among the different parts of the plant. Root and shoot fresh and dry weights were measured.

All the data obtained were subjected to analysis of variance by SAS programme. The Duncan multiple range test was applied to find whether there were significant differences between the means.

Results

Photosynthesis rate

In the absence of salinity, there were considerable differences among species in inherent photosynthetic rates, with *A. tumida* and *Parkinsonia aculeata* exhibiting significantly higher rates than those of *A. seyal* and *A. cyanophylla* (Fig. 1). The studied species reacted differently to elevated levels of salinity, with *A. tumida* being the most sensitive to salinity and *Parkinsonia aculeata* the least sensitive of all the species. Salinity concentration of 2 dS m^{-1} was critical for *A. tumida* while 10 dS m^{-1} concentration was the critical level for the other species.

Photosynthetic rate of *A. cyanophylla* was slightly stimulated with increase of salinity concentration of 2 dS m^{-1}, however, with the progressive increase in the salinity concentration to 10 dS m^{-1}, photosynthesis fell substantially (Fig. 1), relative to control seedlings. *A. seyal* showed considerable variations in photosynthesis rate at different levels of salinity. Initially, with 1 dS m^{-1} increase in salt concentration there was a slight increase in the photosynthetic rate, followed by a small reduction
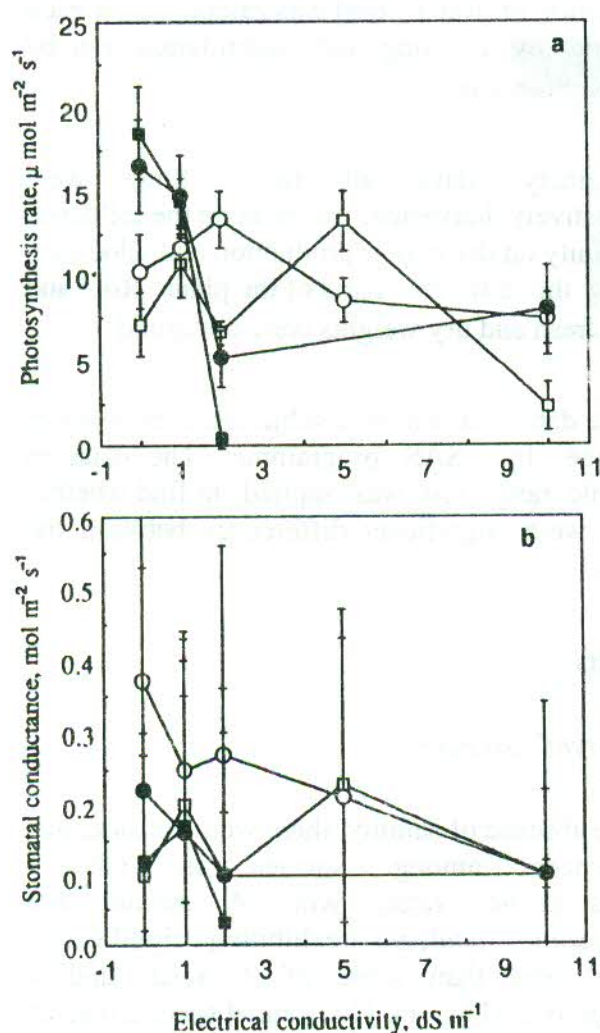
Figure 1: Effect of salinity on photosynthesis rate (a), and stomatal conductance (b) of *A. seyal* (□), *A. tumida* (■), *A. cyanophylla* (O) and *Parkinsonia aculeata* (●) seedlings. Points are means of three determinations ± standard error.

at 2 dS m^{-1}. However, with the progressive increase in salt concentration, photosynthetic rate was stimulated substantially at 5 dS m^{-1}, then fell significantly at 10 dS m^{-1}, relative to control seedlings. The photosynthetic rate of *P. aculeata*, responded sensitively to salinity stress, as there was a progressive reduction in the CO_2 uptake, reaching the lowest value at 5 dS m^{-1}, which was significantly lower than that of the control plants. However, with further increase in salt concentration, the photosynthetic rate in *P. aculeata* seedlings became less sensitive to salinity as there was a substantial increase in CO_2 uptake though the difference was still significant

relative to control. On the other hand, *A. tumida* showed a high sensitivity to salinity stress, as the photosynthesis fell linearly with the progressive increase in salt concentration, decreasing almost to zero at 2 dS m^{-1}.

As mentioned earlier, there was a considerable interspecific variation in the response of photosynthesis to salinity stress among the studied species (Fig. 1a). At salt concentration of 1 dS m^{-1}, there was no difference in photosynthetic rate among the four species. However, at salinity of 2 dS m^{-1} *A. cyanophylla* was able to display a significantly higher photosynthesis rate relative to the other species, while *A. tumida* exhibited a significantly lower photosynthetic rate than the other species. Moreover, at the salt concentration of 10 dS m^{-1} three species (viz: *A seyal, A. cyanophyalla* and *P. aculeata*) were able to survive this level of salinity stress. Here, both *A. cyanophylla* and *P. aculeata* seedlings displayed nearly similar level of photosynthesis, which was significantly higher than that of *A. seyal* seedlings.

Stomatal Conductance

In the absence of salinity in the root environment, there were considerable interspecific variations in the intrinsic stomatal conductance among the different species (Fig. 1b). In the non-saline treatment, *A cyanophylla* showed a significantly higher conductance value compared to that of *A tumida* and *A. seyal*, with *P. aculeata* being intermediate. Furthermore, as soil salinity increased to 1 dS m^{-1}, stomatal conductance of *A. cyanophylla* seedlings was inhibited substantially, though, it was still significantly higher compared with the corresponding values for the other species. Soil salinity of 2 dS m^{-1}, suppressed the stomatal conductances of *A. seyal, A. tumida* and *P. aculeata* more than that of *A. cyanophylla*, as they displayed significantly lower rates of stomatal conductance. However, with further increases in salt concentration, there was no apparent variation in stomatal conductance among those species, which were able to survive higher

levels of salinity stress. Generally, stomatal conductance of *A. tumida* appeared to be the most sensitive to salinity stress, while that of *A. cyanophylla* being the least sensitive.

Transpiration rate

The results (Fig. 2) displayed substantial interspecific variations in the intrinsic rate of transpiration and its response to salinity among the studied species. *A. seyal* seedlings grown at zero dS m^{-1} exhibited a significantly lower transpiration rate than those of *A. cyanophylla*, *A. tumida* and *P. aculeata* grown at the same level of salinity, while there was no significant difference in the transpiration rate among the later three species at zero dS m^{-1}. There was no difference in transpiration rate among the different species at 1 dS m^{-1}, however, the difference became most pronounced at 2 dS m^{-1}, with *A. tumida* showing a significantly lower transpiration rate relative to the other species. Among the species that survived salt concentration above 2 dS m^{-1} there was no difference in transpiration rate at 5 dS m^{-1}; however, with further increase in salinity level, *A. cyanophylla* was able to sustain a substantially higher rate of transpiration than those of *A. seyal* and *P. aculeata* seedlings.

A. cyanophylla seedlings grown at 1 dS m^{-1} displayed a significant reduction in transpiration rate relative to control seedlings, and further significant reductions occurred with the increase in salt concentrations reaching the lowest measurable value at 1 dS m^{-1}. Soil salinity of 1 dS m^{-1} had a significant positive impact (Fig. 2a) on the transpiration rate of *A. seyal* seedlings relative to control ones. However, as salt concentration increased transpiration rate fell ̄ubstantially, attaining the minimum rate at 10 dS m^{-1}. For *P. aculeata* seedlings, transpiration rate fell almost linearly over the range of salt concentration up to 5 dS m^{-1}; henceforth, there was little change up to the critical level of soil salinity. On the other hand, transpiration of *A. tumida* declined significantly relative to control seedlings, reaching the lowest value at 2 dS m^{-1}.
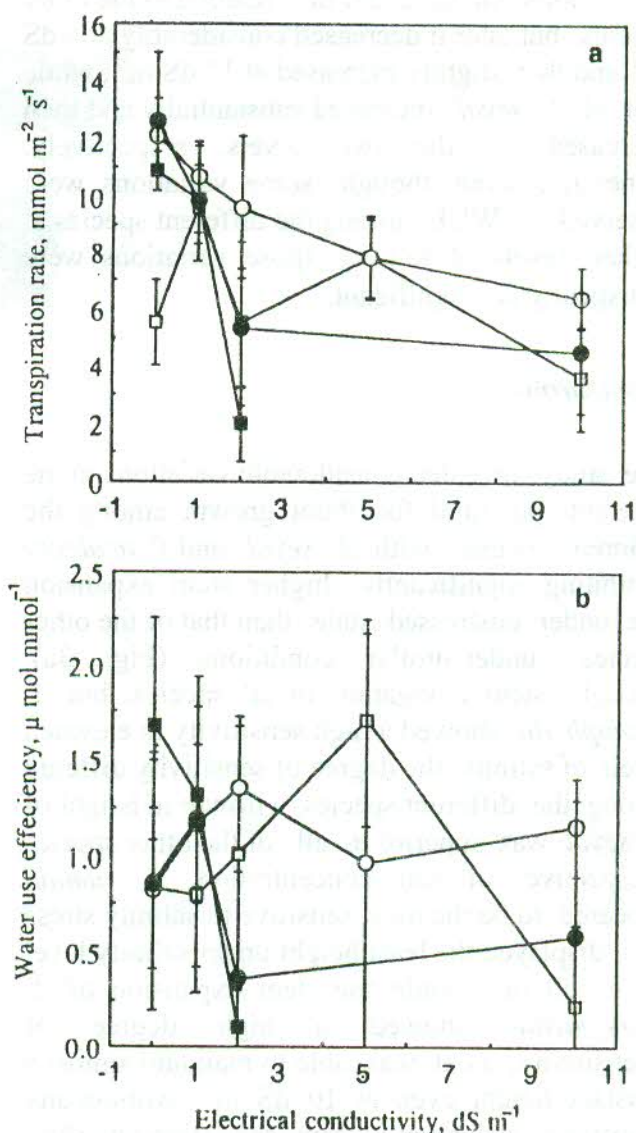

Figure 2: Effect of salinity on transpiration rate (a), and water use efficiency (b) of *A. seyal* (□), *A. tumida* (■), *A. cyanophylla* (O) and *Parkinsonia aculeata* (●) seedlings. Points are means of three determinations ± standard error

Water use efficiency (WUE)

Figure 2b, illustrates the impact of saline soil on the water use efficiency of seedlings of the different species. There were no appreciable interspecific variations in the water use efficiency among the different species under non-stress conditions. However, at higher levels of salinity, considerable differences in water use efficiency of the stressed seedlings were observed among the studied species. WUE increased significantly in

A. *cyanophylla* at 2 dS. m^{-1} relative to the other species, but later it decreased considerably at 5 dS m^{-1} and then slightly increased at 10 dS m^{-1}, while that of *A. seyal* increased substantially and then decreased at the two levels, respectively. Generally, even though some variations were observed in WUE among the different species at higher levels of salinity, those variations were statistically not significant.

Shoot Growth

The study revealed considerable variations in the inherent potential for shoot growth among the different species, with *A. seyal* and *P. aculeata* exhibiting significantly higher stem expansion rate under unstressed state than that of the other species under similar conditions (Fig. 3a): Though, stem elongation in all species, but *A. cyanophylla* showed a high sensitivity to elevated levels of salinity, the degree of sensitivity differed among the different species. Growth in height of *A. seyal* was superior to all of the other species irrespective of salt concentration. *A. tumida* appeared to be the most sensitive to salinity stress as it displayed the least height under salinity level of 5 dS m^{-1}, while the stem expansion of *A. cyanophylla* showed a high degree of insensitivity, as it was able to maintain almost a constant height even at 10 dS m^{-1} without any significant reduction in stem elongation rate (Fig. 3a). The heights of the other species were significantly affected at salinity of 10 dS m^{-1}, and no growth was observed at 20 dS m^{-1}.

The total leaf area per plant (Fig. 3b) showed comparatively lower sensitivity to salt stress than stem elongation rate. The leaf area of all the species was not significantly affected by salt concentration as high as 5 dS m^{-1} relative to control values, except *A. tumida* which produced significantly less leaf area at 5 dS m^{-1} than that of the controls. Soil salinity of 10 dS m^{-1}, induced no significant impact on the leaf area of *A. cyanophylla*, however, it imposed a significant reduction on the leaf area of the other species. Generally, leaf expansion of *A. cyanophylla*

appeared to be the least sensitive to salt stress, while that of *A.tumida* being the most sensitive.
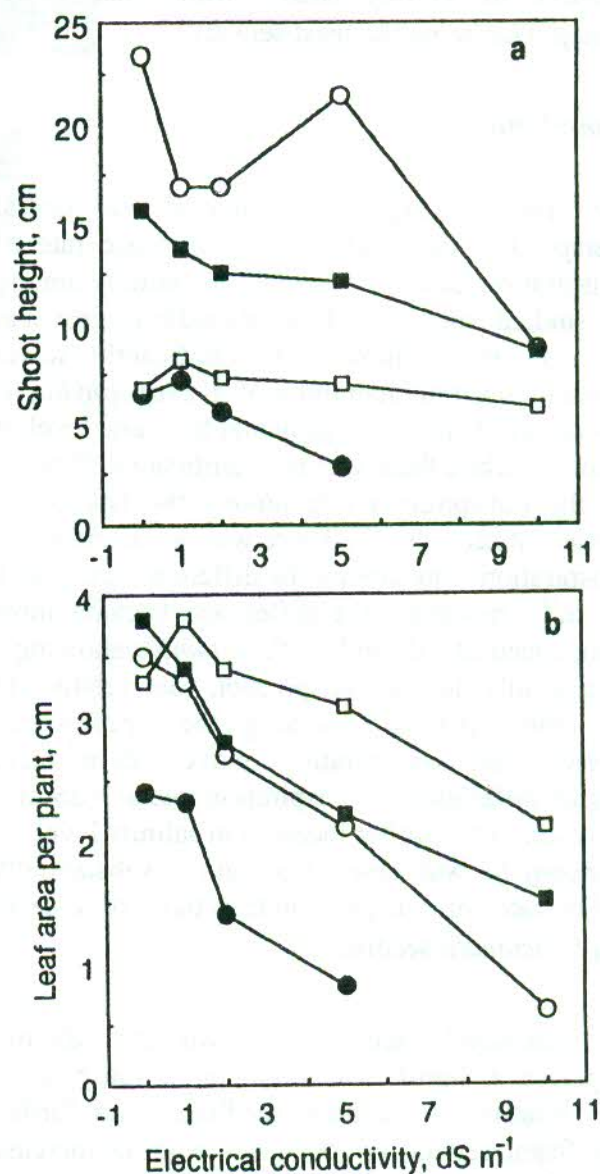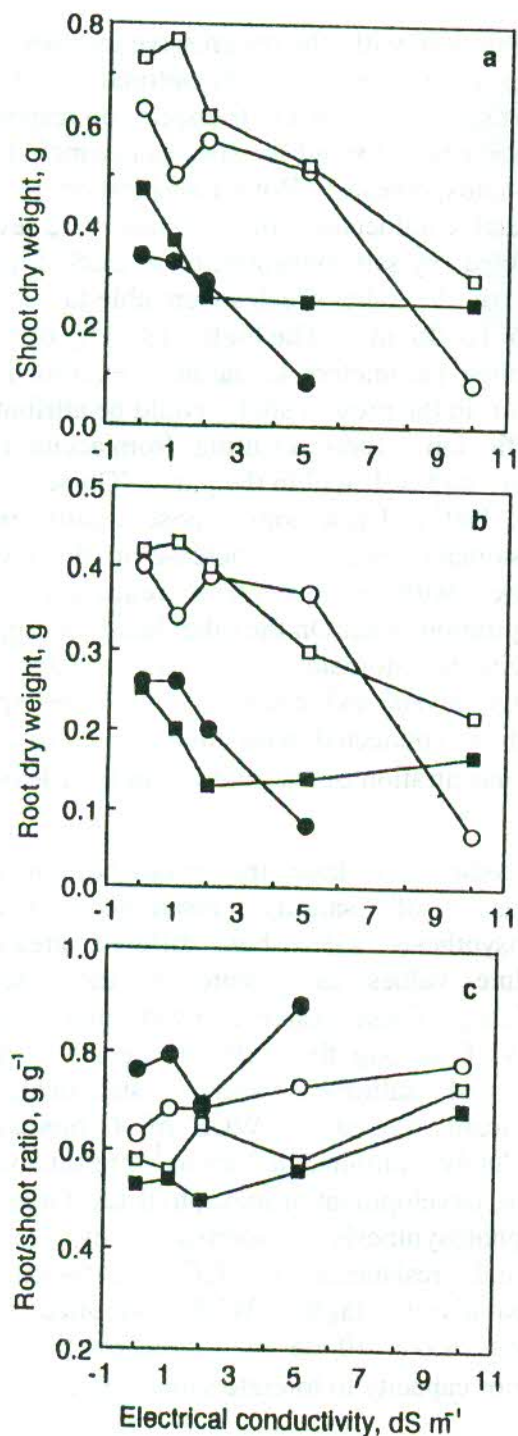

Figure 3: Effect of salinity on height growth (a), and leaf area (b) of *A. seyal* (O), *A. tumida* (●), *A. cyanophylla* (□) and *Parkinsonia aculeata* (■) seedlings after 72 days from sowing. Points are means of at least five replicates.

Dry matter production and partitioning

Soil salinity adversely affected the above and belowground biomass of the seedlings, nevertheless, substantial interspecific variations in response to salinity stress were observed among the studied species (Fig. 4). Although, with the

Figure 4: Effect of salinity on shoot dry matter (a), root dry weight (b) and root :shoot ratio (c) of *A. seyal* (O), *A. tumida* (●), *A. cyanophylla* (□) and *Parkinsonia aculeata* (■) seedlings after 90 days from sowing. Points are means of at least five replicates.

10 dS m^{-1} resulted in a significant reduction in dry matter production of all the species, but *P. aculeata* had maintained production of shoot and root dry matter at salinity levels up to 10 dS m^{-1} without any significant reduction relative to the control values (Fig. 4a and b). No dry matter was produced by *A. tumida* at 10 dS m^{-1} and the same was true for all the species at 20 dS m^{-1}. Generally, the results indicated that for all the species, salinity stress reduced shoot biomass more than root biomass, as attested by the substantial increases in root:shoot ratio (Fig.4c) with the progressive increase in soil salinity.

Discussion

The results displayed a remarkable interspecific variation in the intrinsic photosynthetic rate among the different species. Differences in photosynthetic capacity can be a reflection of differences in stomatal conductance, which control the gas exchange diffusion of CO_2 into the leaf, and/or difference in mesophyll characteristics of the plant, which include physiological and morphological properties of the cell wall, plasmalemma, cytoplasm, chloroplast, and the light and carboxylation reactions of photosynthesis (Von Caemmerer and Farquhar, 1981). In the unstressed state, stomatal limitations of photosynthesis appear to be the main factor responsible for the observed difference in photosynthetic capacity of *A. seyal* and *A. tumida*. However, the differences exhibited by the other species can be attributed to limitation of photosynthetic machinery as corroborated by the high stomatal conductance without correlated increases in the photosynthetic rate.

exception of *A. tumida*, no significant reduction in above and below ground biomass was observed up to salinity level of 5 dS m^{-1} in all the other species, further increases in salt concentration to

Though, salinity stress had a dramatic impact on the photosynthetic rate, the assimilatory apparatus of the studied species reacted differently to the elevated levels of salinity. *A. tumida* showed the greatest sensitivity of photosynthesis to salinity, with a consequent failure to survive salinity concentration as low as 2 dS m^{-1}. This detrimental impact of salinity on photosynthesis of *A. tumida* resulted, not only in a greater reduction in stem

elongation rate, but also in smaller leaf area, as well as lesser dry matter production compared to the other species. Apparently, the results indicate that *A. tumida* is a salt-intolerant species. On the other hand, *A. cyanophylla*, *P. aculeata* and *A. seyal* showed some tolerance to salinity as they were able to survive at a high salinity level and photosynthesized satisfactorily at 10 dS m^{-1}. This result suggests that these species could be used successfully in reclaiming soils of moderate salinity.

Of particular interest in this study is the significant stimulation of photosynthesis in both *A. cyanophylla* and *A. seyal* by 2 dS m^{-1} and 5 dS m^{-1}, respectively. These results are consistent with those reported for *Atriplex halimus* (Kaplan and Gale, 1972). Increases in yield were attained in sugar beet and *Aster trifolium* following treatments with 5 dS m^{-1} NaCl (Brownell and Crosland, 1968). The positive response of growth to salinity may be attributed to the relationship between salt uptake and turgor pressure leading to osmotic adjustment, with a consequent stimulation of photosynthetic capacity and the extension of growth. Osmotic adjustment can be achieved by accumulation of suitable amounts of Na^{+} and Cl^{-} leading to beneficial growth (Flowers *et al* ,.1977). The presence of NaCl in the soil solution in suitable amount has been shown to increase the chlorophyll a/b ratio (Ruiz *et al.*,1997). Moreover, it has been suggested that any growth stimulation by NaCl may be caused by a specific effect of Na^{+} in the plant species (Matschner, 1986). Thus, it is at least reasonable to suppose that the stimulation of photosynthetic machinery of *A. cyanophylla* and *A. seyal* at 2 dS m^{-1} and 5 dS m^{-1} observed in the present study can be considered as the optimal levels for growth of these species, and this further confirms that these species are suitable for afforestation in salt-affected areas.

Although stomatal conductance as well as transpiration rate revealed marked interspecific variations among the different species, there was a general reduction in conductance and transpiration with the progressive increase in salt concentration beyond the optimal level. The patterns of stomatal and transpiration response to salinity stress for all the species resembled those of photosynthesis. Both transpiration rate and stomatal conductance of *A. tumida* were severely restricted by salt concentration of 2 dS m^{-1}, while those of the other species were able to withstand up to 10 dS m^{-1}. The high sensitivity of the gas exchange parameters to salinity exhibited by *A. tumida* in the present study, could be attributed to specific ion effects resulting from accumulation of Na^{+} and Cl^{-} within the plants (Garacia-Legaz *et al*, 1993). These ions impose negative impact on stomata leading to increase in the level of closure, with a consequent reduction in the transpiration rate. On the other hand, the superior capacity for stomatal conductance under higher salinity levels exhibited by the other species might be connected with their ability to control the concentration of Na^{+} and Cl^{-} in their leaves.

The reduction of transpiration rate accompanying increase of salinity resembled that of photosynthesis rate, but differed greatly in absolute values, as indicated by the water use efficiency. These results showed some variations in WUE among the different species at higher levels of salinity, though, statistically not significant. Yet again, WUE of *A. tumida* was completely inhibited at 2 dS m^{-1}, presumably due to the development of mesophyll-level inhibition of photosynthesis exacerbated by increased stomatal resistance to CO$_2$ diffusion. The comparatively higher WUE exhibited by *A. cyanophylla* at 10 dS m^{-1}, indicates that it has superior capacity to tolerate salinity stress.

The morphological performance of the studied species further confirmed the existence of considerable inherent interspecific variations, as attested by the significantly longer shoots produced by both *A. seyal* and *P. aculeata* seedlings than that of the other species under non-saline conditions (Fig. 3). However, with the exception of *A. cyanophylla*, the growth in height was adversely affected by the elevated doses of

salt. The retardation of growth can be attributed to a reduction in photosynthesis as in many physiological studies on salinity (Munns, 1993). Moreover, the reduction in growth may also be connected with an increase in respiration. Salt stress may increase the whole plant respiration (Morabito *et al.*, 1994), in order to provide the energy necessary for maintenance of plant tissues that are dysfunctioned and/or impaired by salinity. Thus, high amounts of photosynthates are diverted from growth to increased expenditure of energy for maintenance, respiration or ion transport (Allen *et al*, 1994). Morabito *et al* (1994) reported that *Eucalyptus microtheca* shoots responded to the NaCl applications by a substantial accumulation of Na^+ and Cl^-, a decrease in K^+ and decrease in water potential, which collectively lead to growth inhibition. This might be the case with this study.

Height of *A. cyanophylla* was not only less affected by saline conditions than the other species, but it was also stimulated by salt concentration below 10 dS m^{-1}, though not significantly (Fig. 3). This superior capacity for salt tolerance may be associated with an enhanced ability to exclude high accumulation of Na^+ and Cl^- ions that inhibit uptake and accumulation of K^+ in shoots (Ruiz *et al.*, 1997), which plays an essential role in osmoregulation and many plant processes (Salisbury and Ross, 1992). An alternative plausible explanation for the higher growth rate of *A. cyanophylla* under elevated salinity might be attributed to its ability to tolerate accumulation of salt ions in tissues through compartmentation in vacuoles, with a consequent osmoregulation in cytoplasm (Allen *et al.*, 1994). Stimulated height growth in response to elevated salinity reported here is in agreement with previous observations on seedlings of several plants (Kaplan and Gale, 1972; Maas, 1993).

Leaf expansion in several woody plants has been found to respond negatively to the presence of salts in the soil, with a consequent inhibition in growth rates, either by osmotic effects, ion specific effects or toxic effects (Maas, 1993; Morabito *et al*, 1994; Ruiz *et al*, 1997). The studied species displayed strong interspecific variations in leaf expansion, with leaf area of *A. tumida* being depressed significantly at moderate salinity levels, which was reflected in a significantly lower below and above-ground biomass than the other species (Fig. 4). On the other hand, the greater capacity of the leaf area of both *A. cyanophylla* and *P. aculeata* to withstand salinity levels as high as 10 dS m^{-1} without any significant reduction, resulted in significantly higher shoot and root dry weights compared with the other species (Fig. 4). Although both shoot and root dry matter productions were adversely affected by higher levels of salinity, there were some indications that root biomass was favoured over shoot biomass (though not significantly), as indicated by the consistent increases in root:shoot ratio with progressive increase in salt concentration (Fig. 4c). The shift in biomass allocation pattern in favour of roots appears to be an adaptive mechanism characteristic of some woody plants in salt-affected regions.

The superior growth potential under long-term exposure to salinity displayed by *A. cyanophylla* and *P. aculeata* seedlings may be attributed to their capacity to tolerate maximum concentration of salt by fully expanded leaves, which is the most important factor affecting plant productivity under saline conditions (Sykes, 1992). As indicated earlier, these results further confirm that both *A. cyanophylla* and *P. aculeata* are reasonably suitable for combating secondary salinization and production of fuelwood, fodder and other indispensable forest products in salt-affected areas.

The results of this study provide insight into the factors governing productivity in salt-prone environments. The results of the measurements of seedling growth and gas exchange displayed substantial variations in reactions of the different species to salinity stress, paving the way to rank them into three groups: intolerant (*A. tumida*), intermediate (*A. seyal*) and tolerant (*A. cyanophylla* and *P. aculeata*). Investigations of

this type are essential for the determination of species with physiological and morphological characteristics acceptable for afforestation in salt-affected areas.

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