

Germination and seedling growth of carrots under salinity and moisture stress

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Abstract

Poor crop stand is a common problem in saline areas. Germination and seedling emergence may be depressed as a result of impeded aeration, saline or dry conditions. In this study, we examined the effects of salinity and moisture stress and their interactions on seed germination and seedling growth of carrots. Variable soil matric and osmotic potentials were either obtained by equilibrating soil salinized to different degrees on a 0.5 MPa ceramic plate soil moisture extractor or by adding different amounts of salt solutions to the same mass of air-dried soil, based on a previously determined soil moisture release curve, and allowing to equilibrate for 1 week.

Germination decreased significantly in the investigated silty soil (Aquic Ustifluent) at soil moisture potentials higher than -0.01 MPa, whereas osmotic potentials as low as -0.5 MPa did not influence germination. Matric potentials of -0.3 and -0.4 MPa, respectively, resulted in a strong decrease (35–95%) of germination and delayed germination by 2 to 5 days in the silty soil to which different amounts (18 and 36%, respectively) and sizes (0.8–1.2 mm and 1.5–2.2 mm, respectively) of sand particles had been added. No effect of sand and grain diameter was detected. Germination was not affected by comparable osmotic potentials.

Seedling growth showed a much higher sensitivity than germination to decreasing matric potentials, but was not affected by osmotic potentials ranging from -0.05 to -0.5 MPa. Optimum shoot growth occurred at matric potentials between -0.025 and -0.1 MPa. Shoot and root growth decreased markedly at matric potentials higher than -0.01 MPa. Fresh weight of shoots decreased gradually at matric potentials lower than -0.2 MPa. Root growth was significantly increased at matric potentials of -0.1 to -0.3 MPa, whereas comparable osmotic potentials did not have equivalent effects.

It is concluded that germination and seedling growth are differently affected by comparable matric and osmotic stresses and that water stress exerts a more negative effect than salt stress.

Introduction

A common problem which occurs with vegetable production in saline areas is poor crop stand. Seedling emergence is usually influenced by soil water potential and other environmental factors such as temperature or soil aeration. The soil microenvironment, in which a seed germinates and becomes established as a seedling, is likely

to have a higher salt concentration and lower moisture content than the remainder of the soil because of the evaporation and capillary rise of saline water (Pasternak *et al.*, 1979). Soluble salts accumulate at the top of the seed bed where seeds are planted. The investigated area in the southwestern part of Switzerland (Rhône valley), on which this report is based, is characterized by silty soils of alluvial origin which are

influenced by saline groundwater. High groundwater tables increase the risk of salinization and frequently result in impeded soil aeration. The latter problem may be aggravated by heavy rainfall or large amounts of irrigation water leading to surface sealing.

In this study, we examined the effects of salinity and moisture stress on seed germination and seedling growth of carrots to identify the processes leading to poor crop stand. Carrot (*Daucus carota* L., var Nandor) was chosen as the experimental crop because it is one of the major crops cultivated in the investigated area. In general, the rate at which plants absorb water from a drying or salinized soil decreases as the soil water potential decreases. Matric and osmotic potentials may affect plant growth to varying degrees and by differing mechanisms (Sepas-khah and Boersma, 1979).

Whereas many investigations regarding the effects of either matric or osmotic potentials on plant growth have been made, relatively few studies exist which compare matric and osmotic effects and their interactions. Only very few studies have been conducted with soil systems. Therefore, this investigation was made to compare the effects of soil matric and osmotic potentials, and their interactions, on germination and seedling growth.

Materials and methods

Germination and seedling growth of carrots (*Daucus carota* L. var. Nandor) were investigated in a silty soil (Aquic Ustifluent). The soil consisted of 31% sand, 60% silt and 9% clay. Before the beginning of the experiment, the strongly salinized soil was leached with tap water to an EC_{se} (electrical conductivity of the saturation extract) of 0.5 mS cm^{-1} and the leachate was collected. The composition of the leachate was as follows: Ca 18, K 1.1, Mg 94.7, Na 42.4, Cl 37.9, NO_3 16.5, SO_4 54.5 meq L^{-1} , and its electrical conductivity 12 mS cm^{-1} . Various matric and osmotic potentials in soil were created by saturating air-dried desalted soil with different dilutions of this leachate solution and equilibrating on a 0.5 MPa ceramic plate soil moisture extractor. The osmolalities of the diluted salt

solutions were measured with an osmometer (Advanced Micro-Osmometer, Advanced Instruments, Inc.) and converted in osmotic potentials. The contribution of the salts, originally contained in the soil, to the soil osmotic soil potential was less than -0.035 MPa at a soil matric potential of -0.5 MPa and was taken in account in creating desired soil osmotic potentials. Thereafter, the soil was sieved to 3 mm and filled into cylindrical soil containers (8.5 cm in diameter, 2.5 cm high) to a density of 1 g cm^{-3} . In each container 50 seeds were sown and incubated in tightly sealed transparent boxes (9 cm diameter, 5 cm high). These boxes were placed in germinators kept at a constant temperature of 25°C . The experiment ran for 25 days. Fluorescent lighting was provided for 12 hours daily at a photon flux density of $95 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Seeds were considered germinated when the length of the coleoptiles exceeded 2 mm. The seedlings were harvested 25 days after seeding and shoot fresh and dry weights determined. The roots were carefully excavated from the soil by gently rinsing with water. Root dry weights were determined after drying for 48 hours at 65°C . The gravimetric water contents were measured at the end of the experiment and converted in soil matric potentials based on a previously determined water retention curve. Soil osmotic potentials at the end of the experiment were calculated assuming linear decreases of the initially established osmotic potentials at decreasing soil moisture.

In a second experiment, the influence of numerically equivalent soil osmotic and matric potentials on germination and seedling growth was investigated with three different treatments: (i) at an initial osmotic potential of -0.05 MPa and matric potentials ranging from -0.05 to -0.5 MPa , (ii) *vice versa* and (iii) at equal matric and osmotic potentials corresponding to the same total soil water potentials as in (i) and (ii). The silty soil was mixed with 18% or 36% by weight of white silica sand (0.8–1.2 mm and 1.5–2.2 mm in diameter, respectively). The soil mixtures will be referred to as E18, E36, F18 and F36 (E and F denote particle sizes of 0.8–1.2 mm and 1.5–2.2 mm, respectively, and the numbers indicate percent of sand). Soil water release curves were determined for all soil mixtures in

Table 1. Soil matric and osmotic potentials (MPa) at the beginning of the experiment (BE) and after 25 days (EE). F18 and F36 refer to the soil mixtures as described in the text

| F18/F36 BE | | F18 EE | | F36 EE | |
|---------------|----------|-----------|----------|-----------|----------|
| ψ_m | ψ_0 | ψ_m | ψ_0 | ψ_m | ψ_0 |
| -0.05 | -0.05 | -0.075 | -0.060 | -0.080 | -0.070 |
| -0.10 | -0.05 | -0.195 | -0.075 | -0.325 | -0.115 |
| -0.20 | -0.05 | -0.475 | -0.097 | -0.325 | -0.096 |
| -0.30 | -0.05 | -0.930 | -0.109 | -1.050 | -0.167 |
| -0.40 | -0.05 | -1.700 | -0.156 | -1.500 | -0.169 |
| -0.50 | -0.05 | -1.425 | -0.129 | -1.650 | -0.163 |
| -0.05 | -0.05 | -0.075 | -0.061 | -0.075 | -0.065 |
| -0.05 | -0.10 | -0.080 | -0.126 | -0.073 | -0.128 |
| -0.05 | -0.20 | -0.085 | -0.260 | -0.073 | -0.256 |
| -0.05 | -0.30 | -0.075 | -0.366 | -0.073 | -0.389 |
| -0.05 | -0.40 | -0.074 | -0.488 | -0.077 | -0.528 |
| -0.05 | -0.50 | -0.073 | -0.600 | -0.070 | -0.610 |
| -0.075 | -0.075 | -0.150 | -0.104 | -0.210 | -0.117 |
| -0.125 | -0.125 | -0.210 | -0.180 | -0.262 | -0.217 |
| -0.175 | -0.175 | -0.325 | -0.343 | -0.260 | -0.297 |
| -0.225 | -0.225 | -0.640 | -0.441 | -0.475 | -0.450 |
| -0.275 | -0.275 | -0.850 | -0.555 | -0.750 | -0.594 |

the range of -0.05 to -2.0 MPa. Different amounts and dilutions of a Hoagland nutrient solution (3/4 strength) containing 27.06 g CaCl_2 and 20.435 g NaCl were added to the same mass of air-dried desalted soil to create various osmotic and matric potentials in soil (Table 1) based on previously determined soil moisture release curves and calculated osmotic potentials. Desired soil osmotic potentials (ψ_0) were obtained by using the following experimentally determined relationship: ψ_0 (-MPa) = $-0.0078 - a * 0.000533$, where a (dimensionless) represents the percentage of stock solution to be added. The soil was thoroughly mixed and kept in tightly closed plastic boxes for one week to facilitate equilibration. Thereafter, the soil was sieved and seeded as described above. The same experimental conditions as outlined for the first experiment were adopted.

Every treatment in both experiments was repeated four times and subjected to analysis of variance. The results presented are the means of four boxes each planted with 50 seeds.

Results

At soil moisture potentials higher than -0.01 MPa germination decreased significantly

in the silty soil (Fig. 1). The air-filled pore volume was smaller than 7% at this soil matric potential. Lower matric potentials in the investigated range did not influence germination percentage. The same results were observed irrespective of the osmotic stress (-0.1 to -0.5 MPa) at all investigated potentials.

Seedling growth showed a much higher sensitivity to changes in matric potential, but was not affected by osmotic potentials ranging from -0.1 MPa to -0.5 MPa (Fig. 2). Optimum shoot growth was at matric potentials between -0.025 and -0.1 MPa. A marked decrease in shoot growth occurred at matric potentials higher than -0.01 MPa and a gradual decrease in shoot fresh weight was observed at potentials lower than -0.2 MPa. Decreases in shoot dry weight were only observed at matric potentials higher than -0.01 MPa. Root growth responded most sensitively to moisture stress. High matric potentials severely inhibited root growth, whereas lower matric potentials caused a marked increase in root growth (Fig. 2).

Comparable results were obtained with the silty soil to which different amounts and sizes of sand particles had been added. The analysis of variance for germination and seedling growth parameters showed statistically significant differences between the investigated soil mixtures,

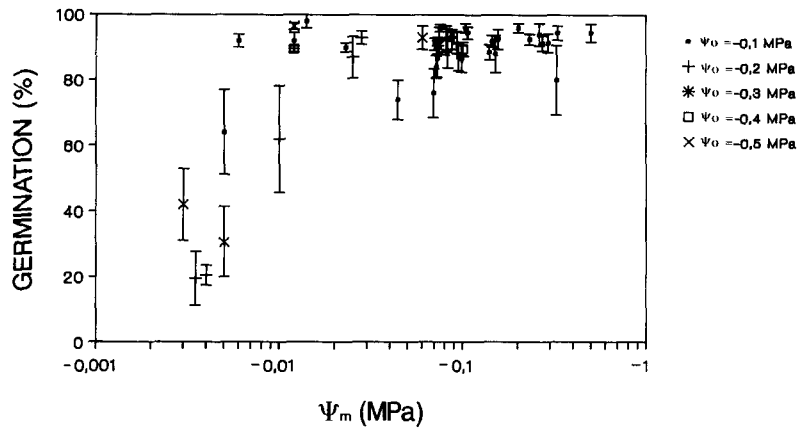


Fig. 1. Germination of carrots in a silty soil as influenced by soil matric and osmotic potentials. The bars represent \pm SE of the mean.

treatments and levels of initial soil water potentials (Table 2). At an initial matric potential of -0.05 MPa, osmotic potentials between -0.1 MPa and -0.5 MPa did not influence germination percentage, whereas matric potentials of -0.3 MPa (treatments containing 36% added sand) and -0.4 MPa (treatments containing 18% added sand), at an initial osmotic potential of

-0.05 MPa, strongly decreased germination percentage and delayed germination rate (Fig. 3). Soils which contained 36% added sand delayed and reduced germination more than soils containing 18% added sand. No effect of sand grain diameter was detected, therefore results are only presented for one size (1.5–2.2 mm diameter) (Fig. 3). Osmotic potentials of -0.4 and

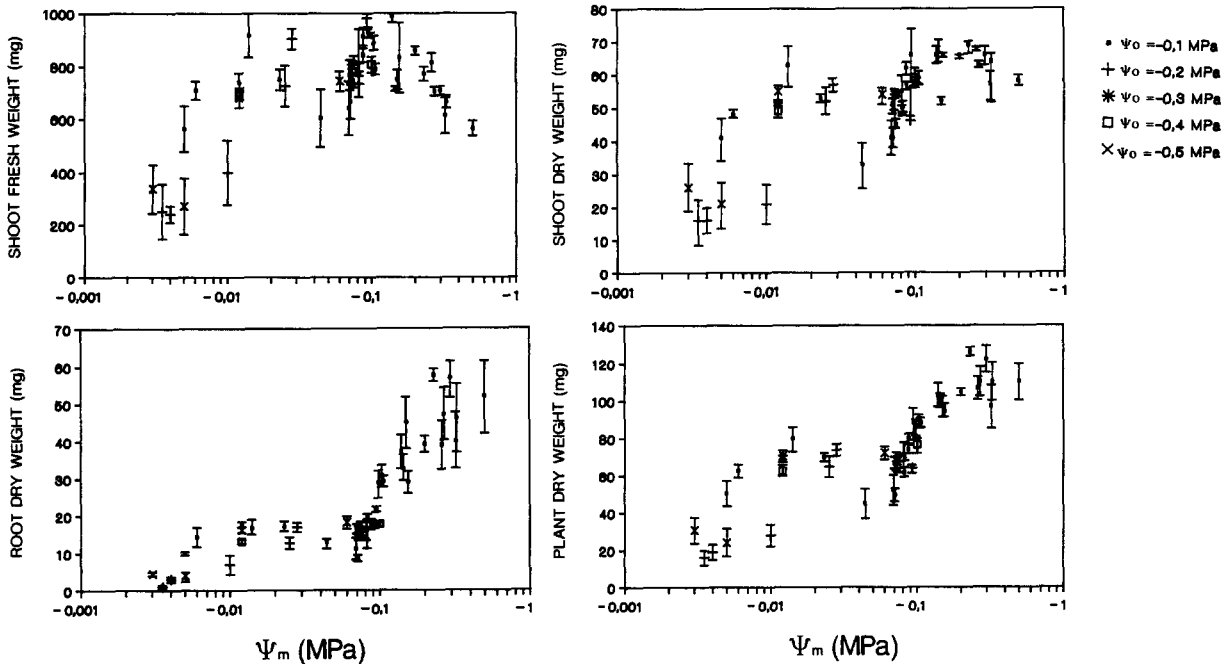


Fig. 2. Biomass production of carrots in a silty soil as influenced by soil matric and osmotic potentials. The bars represent \pm SE of the mean.

Table 2. Analysis of variance for germination and seedling biomass production of carrots under the following conditions: Four soil mixtures (S), three treatments (T) and five levels of soil water potential (L)

| Source of variation | F values | | | | | |
|---------------------|----------|-----------------|-------------------------|-----------------------|----------------------|-----------------------|
| | df | Germination (%) | Shoot fresh weight (mg) | Shoot dry weight (mg) | Root dry weight (mg) | Plant dry weight (mg) |
| Soil mixture (S) | 3 | 7.0** | 15.8** | 12.6** | 14.3** | 17.6** |
| Treatment (T) | 2 | 75.8** | 422.9** | 43.7** | 96.0** | 37.4** |
| Levels (L) | 4 | 44.3** | 108.7** | 31.3** | 6.5** | 14.7** |
| S × T | 6 | 7.2** | 3.5** | 3.4** | 12.3** | 11.1** |
| S × L | 12 | 1.7 NS | 1.8** | 1.2** | 2.3** | 1.7 NS |
| P × L | 8 | 18.1** | 40.7** | 14.2** | 5.5** | 10.3** |
| S × T × L | 24 | 2.5** | 1.7** | 1.1** | 3.1** | 2.7** |

** Significant at the 0.01 level.

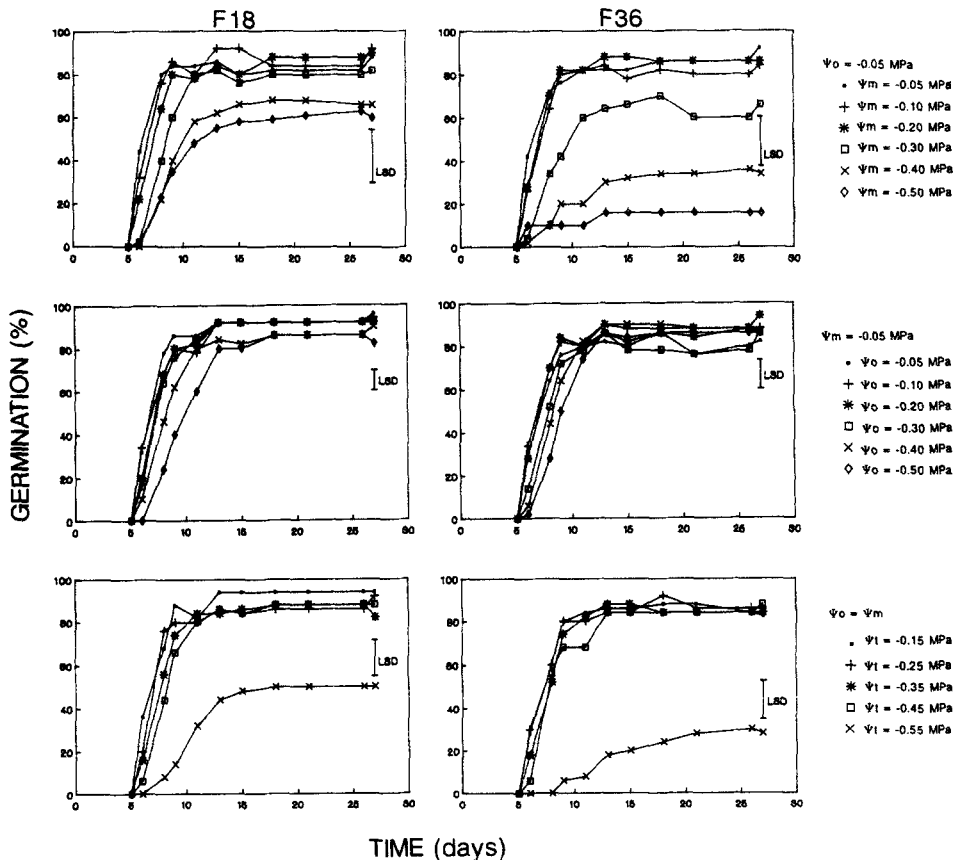


Fig. 3. Influence of soil osmotic (ψ_0) and matric (ψ_m) potential components on germination of carrots in a silty soil to which 18% (F18) or 36% (F36) sand has been added. ψ_T indicates the total soil water potential. The vertical scale bars show the LSD at the 0.05 probability level.

-0.5 MPa delayed germination by two to three days. In the treatments with numerically equivalent matric and osmotic potentials germination decreased only at the lowest investigated soil water potential of -0.55 MPa. The negative effect was due primarily to the matric component. Osmotic potentials as low as -0.5 MPa did not affect seedling growth (Fig. 4). Shoot fresh weight was more negatively affected than shoot dry weight by decreasing matric potentials in the range of -0.1 to -0.4 MPa. Shoot fresh weight was highest at matric potentials of -0.05 (treatments E36, F18, F36) and -0.1 MPa (treatment E18), respectively, whereas lower matric potentials caused marked reductions.

A moderate water stress (-0.1 to -0.3 MPa) significantly increased root growth in all treatments (Fig. 4). Matric potentials for maximum

root growth depended on the particle size of the medium, and were at -0.1 (treatment E36), -0.2 (treatment E18), and -0.3 MPa (treatments F18 and F36), respectively. Root growth decreased at lower matric potentials, except in treatment F18. Comparable osmotic potentials did not have equivalent effects on root growth.

Soil water potentials consisting of numerically equivalent matric and osmotic potentials either had intermediate effects on seedling growth as compared to equivalent water potentials consisting mainly of either matric or osmotic components or had effects comparable to those of the treated simulating osmotic stress (Fig. 4). Evidence for an additive effect of soil matric and osmotic potential components on shoot fresh and dry weight was only observed with the lowest investigated numerically equivalent matric and

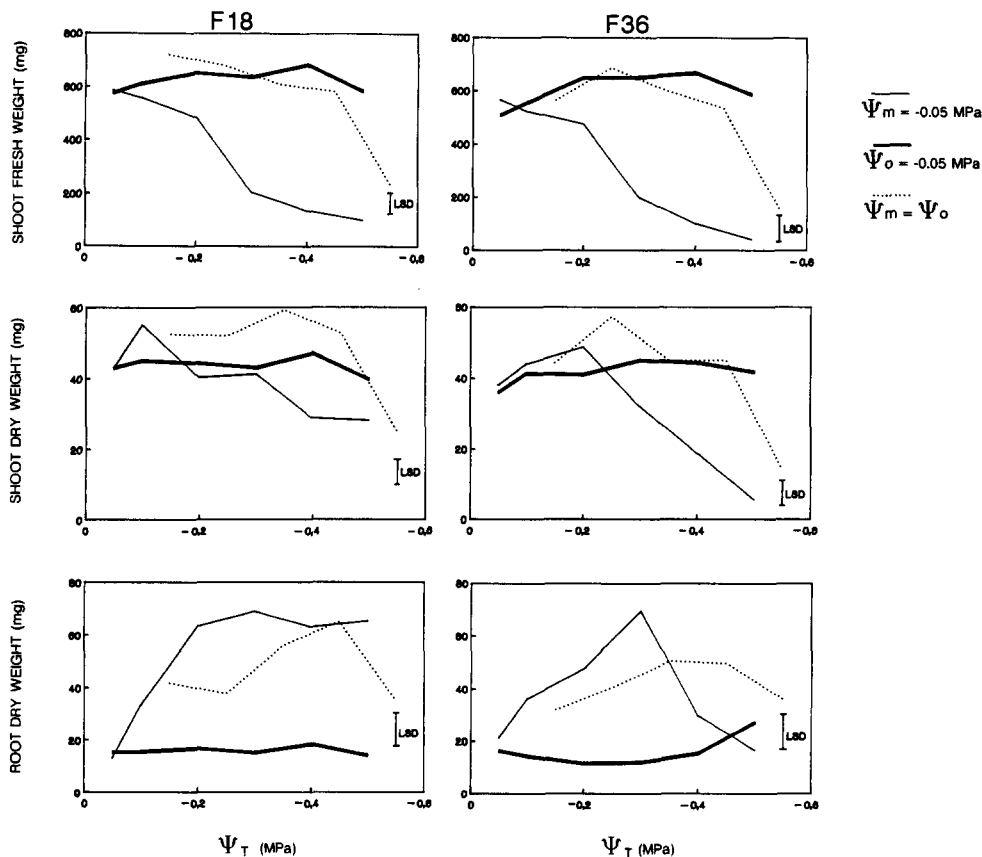


Fig. 4. Influence of soil osmotic (ψ_o) and matric (ψ_m) potential components on biomass production of carrot seedlings in a silty soil to which 18% (F18) or 36% (F36) sand had been added. ψ_T indicates total soil water potential. The treatment denoted as $\psi_m = \psi_o$ in the legend had numerically equivalent soil matric and osmotic potential components. The vertical scale bars show the LSD at the 0.05 probability level.

osmotic soil water potential of -0.275 MPa in treatments F18 and F36.

In comparative investigations on the effects of soil matric and osmotic potential components on plant growth, it is necessary to consider the changes in soil water content and soil solution composition which occur as a consequence of water uptake by the plants. Soil matric and osmotic potentials may be changed differently. Comparisons are valid only if growth parameters refer to the actual water potential or the water potential integrated over time and depth. By growing seedlings in a closed system and thus creating conditions of high relative humidity, evapotranspirational losses could be minimized. Table 1 shows initial and final soil matric and osmotic potentials. Whereas the shoot fresh weight was e.g. depressed in the treatment F36 with initial soil matric and osmotic potentials of -0.2 and -0.05 MPa, respectively, no growth reduction was observed in the treatment F18 with initial soil osmotic and matric potentials of -0.5 and -0.05 MPa, respectively. The corresponding total soil water potentials at the end of the experiment were -0.42 and -0.68 MPa, respectively. It is concluded that shoot growth was more negatively affected by water stress than salt stress.

Discussion

Adequate crop stands resulting from vigorous seedling emergence are important for optimum crop production. Germination and seedling emergence may be depressed as a result of impeded aeration, saline or dry conditions. These factors interact frequently with each other. The results obtained in this study reveal that seedling growth is a more sensitive indicator of adverse soil conditions than is germination. A qualitative correlation between these two stages was found at high matric potentials, whereas seedling growth under drier conditions (≤ -0.1 MPa) was more strongly inhibited than germination. Impeded aeration, as a consequence of a low air-filled pore volume at high matric potentials, is probably one of the main factors leading to poor emergence in the investigated soil. Root growth was more negatively affected than shoot growth

under extremely wet soil conditions. Kennedy *et al.* (1980) found too that root growth was greatly restricted under impeded aeration.

Different sand grain sizes did not affect germination and seedling growth. This agrees with the results of Schneider and Gupta (1985). Large amounts of sand and correspondingly lower water contents, at comparable water potentials, delayed and reduced germination more than soils containing smaller amounts of sand.

The effects of the total soil water potential on germination and seedling growth can be reduced to those of matric and osmotic potential components in a non-swelling soil, because differences in gravitational and pressure potentials are negligible in the vicinity of an organism (McWilliam and Phillips, 1971). From a thermodynamic point of view, the two potentials would be expected to be equivalent and therefore to be additive in their effects on the availability of water to plants, provided that the plants behave as perfect osmometers.

The results obtained suggest that seeds and seedlings responded differently to induced matric and osmotic potential components. However, it can be argued that the calculated water potentials represent a gross spatial averaging of the matric and osmotic potentials and do not take into account the increase in suction and salt concentration in the soil at the immediate periphery of the absorbing roots. Gardner (1960) and Cowan (1965) estimated the gradients of soil matric potential in the rhizosphere. According to their calculations, when the soil is no drier than -0.2 or -0.3 MPa, quite small gradients occur, but as the soil dries further, the gradients required to maintain the same rate of flow become large. The uptake rate of water per centimeter root was most likely quite small due to the dense root system and the low transpirational demand. Therefore, only small gradients of water potentials were necessary to obtain the water in the required amounts, even under quite dry soil conditions. Passioura and Frere (1967) found that appreciable accumulations of salts near the root only occur at extremely high rates of water uptake.

Therefore, it can be concluded that a reduction of the water potential by adding a matrix or osmoticum did not exert equivalent effects on

plant growth. This is in contrast to the suggestions of Wadleigh and Ayers (1945). They postulated that yield is related to the total soil water potential, regardless of which component or combination of components contributes to the total potential. Additive effects were assumed by Richards and Wadleigh (1952), and since then by many other authors (Bresler *et al.*, 1982; Childs and Hanks, 1975; Hillel, 1980; Sharma, 1976).

This study showed that germination and seedling growth were differently affected by comparable osmotic and matric potentials. The matric potential delayed and reduced seed germination and seedling shoot growth more effectively than did the numerically equivalent osmotic potential. This result is supported by findings of Collis-George and Hector, 1962; McWilliam and Phillips, 1971; Roundy *et al.*, 1985; Sharma, 1976; Sepaskhah and Boersma, 1979).

The non-equivalence of matric and osmotic potential effects on plant growth may be explained by the following factors: Plants differ greatly in their ability to adjust to matric and osmotic stresses. Osmotic adjustment in a saline medium is generally favoured by the presence of solutes, whereas in the case of matric stress the plant is much more dependent on internally generated osmotica which is probably associated with a higher metabolic energy requirement. Sepaskhah and Boersma (1979) found that salt stress was more effective in reducing the osmotic potential of the cell sap in wheat (*Triticum aestivum* L.) and resulted in stronger osmoregulation than the stress induced by water deficit. Comparative investigations to determine the effects of salt and water stress on barley (*Hordeum vulgare* L.) and maize (*Zea mays* L.) plants showed that the shoots had a more efficient osmoregulation under salt stress conditions as compared with water stress conditions, whereas roots did not differ to any great extent (Schmidhalter and Evéquoz, unpublished data). On the other hand, this suggests that roots osmoregulate more efficiently under water stress than do shoots, which is further supported by the enhanced root growth of carrots as compared with shoot growth under water stress. Root growth was generally favored over shoot growth under water stress. Stress enhanced root growth, not only relative to shoot growth but absolutely as

compared to initially well watered plants. Sharp and Davies (1979) and Taylor *et al.* (1982) reported a more efficient osmotic adjustment in roots of maize and tomato (*Lycopersicon esculentum* Mill) seedlings than in shoots. A greater capacity for osmotic adjustment under moderate water stress in roots of maize and barley seedlings than in shoots was also found by Schmidhalter *et al.* (1988). Under mild water stress, biomass production was not affected. This is reflected not only by increased root growth but also by an increase in plant dry weight. Promotion of root growth and translocation of carbohydrates for the maintenance of root growth is regarded as an important short-term adaptive mechanism (Sharp and Davies, 1979). This enables the roots to explore more soil volume for available water. On a long-term basis, biomass production will decrease due to a reduced photosynthetically active leaf surface area. Hence, although plant dry weight production was increased under moderately dry conditions as compared to salt stress, matric potentials are expected to result in a stronger reduction in plant production.

Osmotic potentials may cause equivalent or even more negative effects on plant growth than matric potentials due to toxic effects of ions taken up in large amounts or due to ionic imbalances despite full turgor maintenance. Interactive effects of matric and osmotic potentials could intensify the effects on plant growth. We expect that differences between matric and osmotic potentials are mainly found under mild to moderate stress conditions, whereas under severe stress conditions, the behavior of plants to these stress components could show more similar effects. Ionic imbalances causing toxicities or nutrient imbalances might impair the growth of plants under these conditions more than the negative effects of decreasing water potentials. A generalized relationship of relative plant yield to decreasing potentials and possible interactive effects of matric and osmotic potentials was suggested by Schmidhalter and Oertli (1986). Optimal management strategies and prognosis of potential yield require a better knowledge of the functional relationship of soil water availability to plant yield than is presently available. Therefore, further detailed studies comparing the ef-

fects of osmotic and matric stresses on plant growth are urgently needed.

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