Plant and Soil **135**: 125–132, 1991.

PLSO 8345

Transpiration/biomass ratio for carrots as affected by salinity, nutrient supply and soil aeration

U. SCHMIDHALTER and J.J. OERTLI
Institute of Plant Sciences, ETH Zürich, Eschikon 33, CH-8315 Lindau, Switzerland

Received 5 September 1989. Revised February 1991

Key words: *Daucus carota* L, soil aeration, soil nutrient level, soil salinity, transpiration/biomass ratio, transpiration coefficient

Abstract

The influence of salinity, nutrient level and soil aeration on the transpiration coefficient, defined as amount of water transpired/unit biomass produced (transpiration/biomass ratio) of carrots was investigated under non-limiting conditions with respect to water supply.

Under optimum conditions and favorable nutrient supply, the transpiration coefficient amounted to 280–310 g H_2O g^{-1} storage root dry weight (RDW). The transpiration coefficient did not change significantly up to salt concentration of 16 mS cm^{-1} in the soil solution under otherwise optimum conditions. Higher salt concentrations or low nutrient levels increased the transpiration coefficient to values of 390–540 g H_2O g^{-1} RDW. It is suggested that the transpiration coefficient is not affected by salinity as long as toxic effects and nutrient imbalances do not occur. The transpiration coefficient was not increased by impeded soil aeration. Biomass production was more negatively influenced by adverse soil conditions (salinity, low nutrient level, impeded soil aeration) than was the transpiration coefficient.

Introduction

Planning irrigation requires a knowledge of the plant's demand for water which in turn depends on its stage of growth and the meteorological conditions. Most water-requirement studies have concentrated on the climatic factors that influence water use for crop production (Hanks, 1983). The water requirement of a plant is influenced frequently by additional factors such as nutrient supply, salinity and impeded aeration. Relatively little is known about the influence of these factors on the transpiration coefficient, which is defined as the amount of water transpired per unit biomass produced (transpiration/biomass ratio).

Transpiration coefficients are usually evaluated on the basis of the plant's reaction to water supplies which vary temporarily and quantitatively. A different approach was chosen for our experiments. The ability of the experimental soil to transport water was sufficiently high so as to create non-limiting conditions for supplying water to the plants. Therefore, the influence of salinity, nutrient level and soil aeration on the transpiration coefficient could be studied independently of water supply. The data of these experiments were also analyzed according to de Wit (de Wit, 1958) who concluded that for dry, high radiation climates an equation relating yield to water use is

$$Y = mT/E_0 ,$$

where Y is dry matter yield, T is transpiration, m is a crop factor dependent only on variety and species and at first approximation independent of soil nutrition and water availability, and E_0 is free water evaporation.

Two growth chamber experiments were performed. 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 the southwestern part of Switzerland, where secondary salinization, due to capillary rise from the saline groundwater, poses a serious problem. The experimental conditions were created by salinizing or desalinizing soil and by supplying different amounts of nutrients. Differences in soil aeration resulted from different groundwater levels.

Materials and methods

PVC-tubes, with a diameter of 0.25 m, were homogeneously packed with a silty soil to a bulk density of 1.32 g cm^{-3}. Groundwater tables were established at 0.5, 1.0, 1.5 m. The electrical conductivity of the groundwater was 2.6 mS cm^{-1} and its composition in meq L^{-1}: Ca, 12; Mg, 16; Na, 5; K, 0.35; SO_4, 21; Cl, 5; HCO_3, 7.35. All treatments were replicated three times. The investigated soil consisted of 9.1% clay, 59.5% silt, 31.4% sand and 0.85% organic matter. Cation exchange capacity was 4.8 cmol kg^{-1} and the pH (H_2O) 8.2. Non-saline conditions were obtained by leaching the soil with tap water and desired salinity levels by percolating the soil with salt solutions.

Differences in soil aeration, resulting from different groundwater depths, were not directly measured but were related to air-filled pore volumes which were derived from the soil water retention curve (data not shown) and soil water suctions measured at various depths.

The experimental design is depicted in Fig. 1. Soil water suction was measured by means of tensiometers and salt concentrations were determined with salinity sensors. The soil solution was extracted by applying suction to soil water samplers. Tensiometers and salinity sensors were inserted horizontally at 5, 10, 20, 40, 80 and 120 cm depth, and soil water samplers every ten centimeters and at depths of 2 and 5 cm. Readings from the tensiometers, salinity sensors and extraction of soil solution were made twice a week. Cation and anion composition and electrical conductivity of the soil solution were determined.

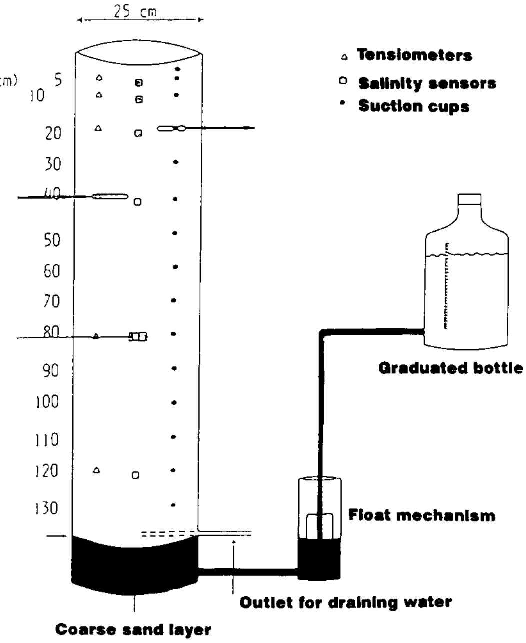

Fig. 1. Experimental design. Carrots were grown on soil columns which had groundwater tables at different depths. Tensiometers, salinity sensors and soil water samplers were inserted at the depths as indicated by the symbols.

A constant groundwater level was maintained by using a float (Fig. 1). Water was supplied from graduated bottles which allowed the daily determination of water consumption. The plants depended entirely on water supply from the groundwater by means of capillary rise. Because the soil water matric potential measured at the bottom of the root zone never decreased to values lower than −0.036 MPa, the investigated soil could supply extraordinarily high quantities of water from groundwater levels as low as 1.5 m. The following relationship for the unsaturated hydraulic conductivity $k(h) = 1209/(228 + h^{1.355})$ was determined with the instantaneous profile method (Watson, 1966) on the field site (Charrat, Switzerland), where the experimental soil had been collected. Due to the soil's high water transmitting capacity no significant changes in soil moisture content occurred in any of the experiments. Therefore daily evapotranspiration rates corresponded to the amount of water supplied from the graduated bottles.

Fifty seeds were planted in each soil column. Twenty days later the plants were thinned to ten plants per column. Germination and seedling growth were recorded twice a week. Shoot fresh and dry weights, storage root dry weight (RDW) and storage root length were measured at the end of the experiments. Results of fresh and dry weight production are indicated as gram per soil column. Biomass production was related to soil solution salt concentration averaged over 0–30 cm depth and the experimental time.

Long term average temperatures and relative humidities from the weather station next to the field site (Sion, Switzerland) were simulated in the growth chamber. The duration of the simulated meteorological conditions varied for the different experiments: 31, 33, 30, 27 days (first growth chamber experiment), and 23, 36, 30 and 23 days (second growth chamber experiment) for the months of April, May, June and July, respectively. The average daily mean temperatures were 11.0, 15.2, 18.2 and 18.2°C for the same months. The daily relative humidities and photon flux densities did not differ between months and their values were 64% and 579 μmol m^{-2} s^{-1}, respectively. Evaporation measured from the free water surface of a same PVC-tube as used for the experiments was 0.49, 0.60, 0.78, and 0.78 cm day^{-1}, respectively, for the months of April, May, June and July. The same experimental setup and conditions as used for the first growth chamber experiment were used to determine evaporation from bare soil columns. Evaporation averaged about the whole experimental period amounted to 0.187, 0.166 and 0.130 cm day^{-1}, respectively, for the treatments with groundwater in 50, 100, and 150 cm depth, respectively. Transpiration coefficients, defined as amount of water transpired per unit biomass produced, were calculated for all treatments. Transpiration rates were obtained as difference between evapotranspiration and evaporation. Further details about the methods used in this study will be given with the descriptions of the individual experiments.

Results

Transpiration-biomass relationship at low and moderate soil salinity as influenced by soil nutrient level and soil aeration

This experiment consisted of two treatments. In the first treatment, the soil was extensively leached with tap water for three months. Desalting not only decreased soil solution salinity from 6.3 mS cm^{-1} to less than 2 mS cm^{-1} but also leached out nutrients. This was only partially compensated by fertilizing with 35 kg P, 84 kg K and 40 kg N per ha in the form of superphosphate, potassium chloride (60%) and ammonium nitrate (26%), respectively. The soil solution concentration averaged 1.6 meq L^{-1} for K and was between 0.8 and 2.5 meq L^{-1} for NO_3 (Fig. 2) in 0–30 cm depth. The corresponding concentrations in the subsoil (≥30 cm depth) were 0.8 meq L^{-1} K and ≤1.0 meq L^{-1} NO_3. Groundwater tables were established at depths of 50, 100 and 150 cm.

Since the seeds and seedlings are initially restricted to a small soil volume, success or failure in establishing crops in saline soils depends essentially on the existence of non-saline conditions in the root zone. Therefore, in the second treatment, the influence of salt free topsoils (EC_s of soil solution 1 mS cm^{-1}) of 20, 30 and 40 cm thickness and homogeneously salinized subsoils (EC_s 5.75 mS cm^{-1}) with a constant groundwater depth of 100 cm was investigated. The composition of the salt solution used to percolate the soil columns was: Na 16.3, K 0.75, Ca 32.2, Mg 53.8, Cl 18.2, NO_3 7.4 and SO_4 80.7 meq L^{-1}. Additionally, the same amounts of fertilizers as in the first treatment were applied. These soils were therefore better supplied with nutrients as compared to the first treatment.

Soil suction did not change during the experiments and closely approximated hydrostatic equilibrium conditions. Increasing plant dry weight (PDW) and storage root dry weight (RDW) were observed at increasing transpiration (T). The combined regression equations (values in parentheses are standard errors of coefficients) of both treatments were: PDW = −17.9 (48.8) + 2.06 (0.73) T (cm) ($R^2 = 0.40^{**}$) and RDW = −8.0 (35.8) + 1.49 (0.53) T (cm) ($R^2 = 0.39^{*}$). A higher biomass production and lower transpiration coefficients were found with higher salt concentrations (Table 1).

No differences were observed in initial growth stages or with the final biomass production (Table 1) in the moderately salinized treatments (second treatment). A salt free horizon of 20 cm depth rendered a safe emergence and establishment of carrot plants in the investigated soil.

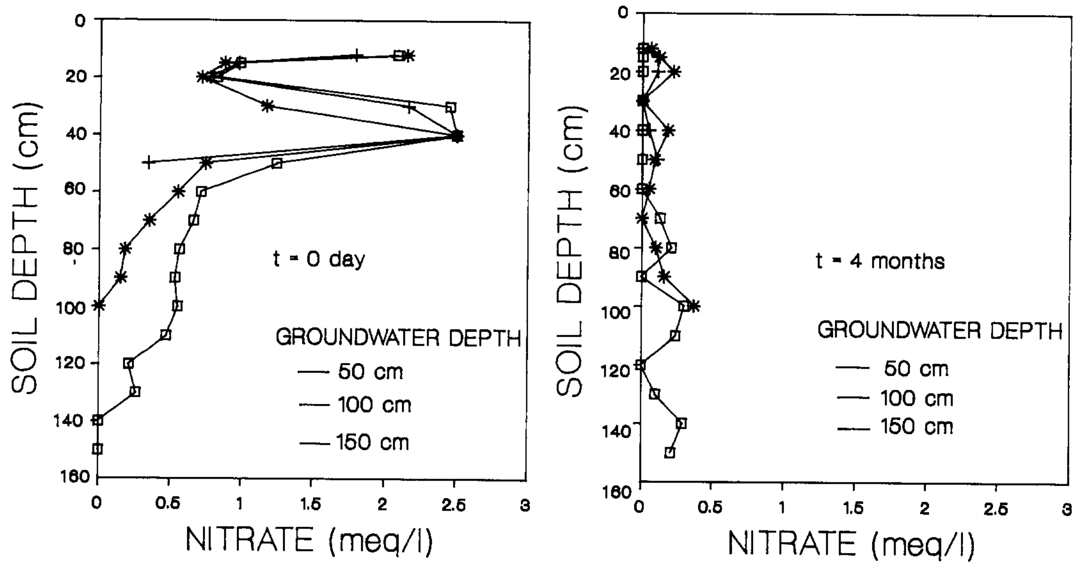

Fig. 2. Initial (t = 0 days) and final (t = 4 months) nitrate concentrations measured in the soil solution of soil columns having groundwater tables at three different depths. The soil columns were planted with carrots which depended entirely on water supply from the groundwater by means of capillary rise.

Table 1. Biomass production and water-use relations of carrots as influenced by groundwater depth and soil salinity

Groundwater depth (m)	Average root zone salinity[a] ($mS\ cm^{-1}$)	Shoot dry weight (g)	Storage root dry weight (RDW) (g)	Storage root length (cm)	Transpiration coefficient of RDW ($g\ g^{-1}$)	$m = Y_T E_0/T$ ($kg\ ha^{-1}\ d^{-1}$)	$m = Y_R E_0/T$ ($kg\ ha^{-1}\ d^{-1}$)
Treatment 1							
0.5	2.53	14.56	48.78	10.6	417	206.6	159.5
1.0	3.15	16.96	67.45	13.7	454	185.9	148.5
1.5	2.48	17.15	76.80	16.7	459	175.2	143.2
Treatment 2							
1.0 (a)[b]	8.20	43.72	124.75	16.3	302	312.4	232.9
1.0 (b)[b]	7.91	41.34	128.19	15.7	250	347.3	263.0
1.0 (c)[b]	7.01	41.66	121.75	16.1	298	299.2	222.8
LSD 5%		5.55	26.86	5.9	137	85.8	76.7

[a] Soil solution salinity averaged over the duration of the experiment and 0–25 cm depth.
[b] Letters a, b, c indicate nonsaline topsoils at the beginning of the experiment of 20, 30, and 40 cm thicknesses, respectively.
Y_T = Dry matter production of shoot and storage root.
Y_R = Dry matter production of storage root.

In the second treatment, with a more favorable nutrient supply and higher soil salinity as compared to the first treatment, the transpiration coeffficient averaged 283 g H_2O g^{-1} storage root dry weight (Table 1). This value increased to 443 g H_2O g^{-1} storage root dry weight in the first treatment. The values of m found were clearly higher in the second treatment (Table 1). Different groundwater depths did not affect the m value. There was no appreciable change in the K concentration during the course of the experiment in any of the treatments. Whereas NO_3 was almost completely depleted in the first treatment (Fig. 2), initial and final NO_3 concentrations did not differ much in the second treatment. Therefore, the higher biomass production and more efficient water use, as demonstrated by plants growing in the second treatment, are probably due to the higher nitrate uptake as compared to the first treatment.

By restricting the regression analysis to the first treatment a closer relationship between transpiration and biomass production than for the two treatments combined was found: PDW = 28.1 (15.8) + 0.86 (0.26) T (cm) (R^2 = 0.65*) and RDW = 16.3 (14.3) + 0.79 (0.23) T (cm) (R^2 = 0.65*). Biomass production and transpiration increased considerably by lowering the groundwater depth (GD) from 50 to 150 cm: PDW = 49.4 (9.4) + 0.31 (0.09) GD (cm) (R^2 = 0.66*) and T = 28.0 (6.2) + 0.33 (0.06) GD (cm) (R^2 = 0.83**). Transpiration coefficients and soil salt concentration were not correlated with groundwater depth. The remaining air-filled pore volumes at 5 cm depth were 2.5, 4.5 and 5.9% for the treatments with groundwater depths at 50, 100 and 150 cm, respectively. The differences in biomass production and transpiration were, therefore, probably due to impeded aeration which increased with lower groundwater depths and negatively influenced biomass production and/or transpiration.

Transpiration-biomass relationship at increasing salinity with optimum nutrient supply

The influence of increasing salinity levels on water use was investigated in soils well supplied with nutrients. Salinity levels of 4, 8, 12, 16, 20 and 24 mS cm^{-1} were obtained by leaching the subsoil (30–100 cm depth) with a one strength Hoagland nutrient solution containing appropriate amounts of NaCl. Prior to this treatment, the top thirty centimeters of the soil were removed and percolated with the same nutrient solution and thereafter refilled in the soil columns to a density of 1 g cm^{-3}. Due to the initially favorable conditions prevailing in the rooting horizon, germination and seedling establishment were not affected by the salts contained in the subsoils.

Increases in storage root dry weight and plant dry weight production were closely correlated with increasing transpiration (Fig. 3). Biomass production decreased with increasing salt con-

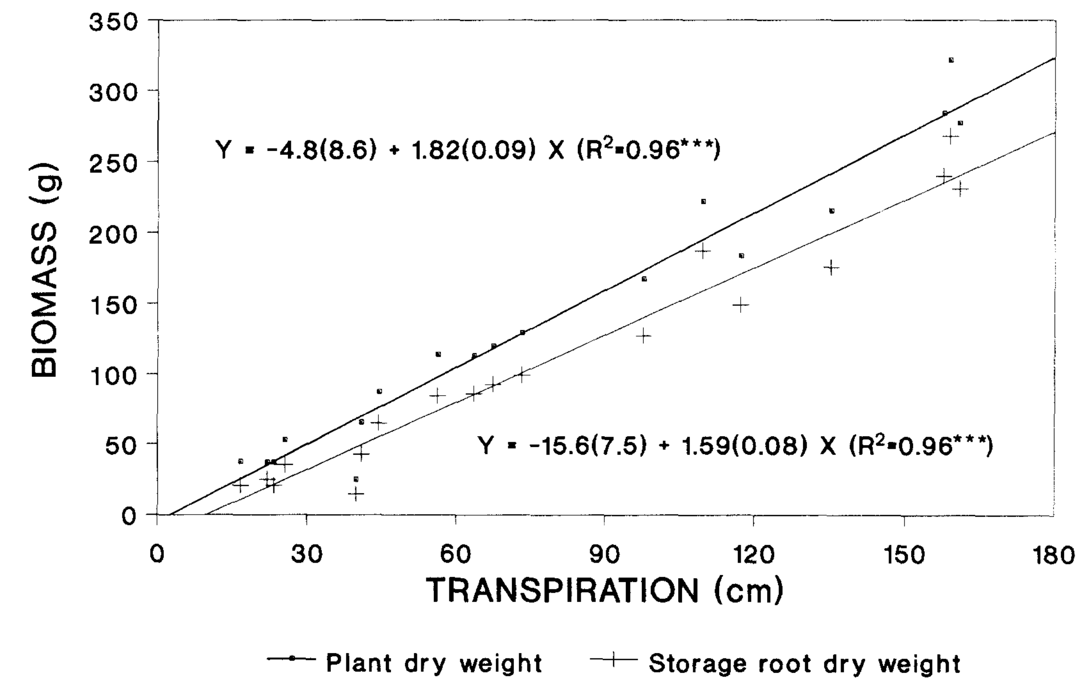

Fig. 3. Biomass-transpiration relationship of carrots well supplied with nutrients. Increasing biomass and transpiration, respectively, resulted from decreasing soil salinity. Values in parentheses are standard errors of coefficients.

centration: PDW = 317.3 (15.1) − 12.8 (0.9) EC (mS cm^{-1}) ($R^2 = 0.92^{**}$). Although the biomass-transpiration relationship and the biomass-salt concentration relationship deviate from linearity at low transpiration rates and high salinity, respectively, they can fairly well be approximated by linear regression equations.

Transpiration coefficients were not affected by salt concentrations as low as 16 mS cm^{-1} (Table 2). At higher salt concentrations, the transpiration coefficients increased from 304–351 to 394–540 g H_2O g^{-1} storage root dry weight and the m values calculated for storage root dry weight decreased from 203 to 162 kg ha^{-1} d^{-1}. However, the transpiration coefficients and m values calculated for plant dry weight were not differently influenced by soil solution salinities ranging from 4 to 24 mS cm^{-1}. The ventilation used for temperature control continuously removed the transpiration water and thus created a high gradient in vapour pressure and reduced the laminary boundary resistance. Extremely high transpiration rates as compared to field conditions were observed under the investigated growth chamber conditions. The highest measured value was 3 cm d^{-1}. At this transpiration rate, soil suction only increased to 360 cm at a depth of 20 cm. This shows that, with regard to water supply, non-limiting conditions existed in the investigated soil.

The decrease in dry matter production with increasing salt concentration was due to lowered water potentials which reduced the water availability. Salt concentrations up to 16 mS cm^{-1} did not significantly affect the transpiration efficiency. This suggests a primarily osmotic effect of the increased salinity. At higher values, toxic and/or nutrient imbalances probably affected plant growth and development.

Discussion

Under optimum conditions and favorable nutrient supply, transpiration coefficients amounted to 280–310 g H_2O g^{-1} storage root dry weight (RDW). At optimum nutrient supply, yields decreased linearly with increasing soil salinity, whereas the transpiration coefficients were affected only at the highest salt concentrations. The transpiration coefficients were not significantly different up to salt concentrations of 16 mS cm^{-1} in the soil solution. At higher salt concentrations, the transpiration coefficients increased to 390–540 g H_2O g^{-1} RDW, but did not increase per unit plant dry weight produced. Stewart et al. (1977) found that, for a given irrigation level, transpiration was lower under saline conditions, due to a lower soil water availability, whereas the relationship between transpiration and yield was similar regardless of different salinity levels. We suggest that the transpiration efficiency is not affected by salinity as long as water uptake is reduced by a decreased osmotic potential and as long as neither toxic effects nor nutrient imbalances occur.

Low nutrient levels increased the transpiration coefficients to values of 440 g H_2O g^{-1} RDW.

Table 2. Biomass production and water-use relations of carrots as influenced by increasing soil salinity levels

Average root zone salinity[a] (mS cm^{-1})	Storage root dry weight (RDW) (g)	Transpiration coefficient of plant dry weight (g g^{-1})	Transpiration coefficient of RDW (g g^{-1})	$m = Y_T E_0/T$	$m = Y_R E_0/T$
				kg ha^{-1} d^{-1}	
4	246.3	254.8	304.1	260.2	218.0
8	170.5	274.9	334.6	243.5	200.7
12	104.1	268.4	350.8	246.0	188.2
16	80.8	245.2	324.4	270.0	203.8
20	30.9	260.1	393.7	258.0	170.9
24	22.1	261.3	539.8	258.8	153.2
LSD 5%	30.6	51.9	85.7	58.6	40.8

[a] Soil solution salinity averaged between the days 20 to 112 of the experiment and 0–30 cm depth.
Y_T = Dry matter production of shoot and storage root.
Y_R = Dry matter production of storage root.

Transpiration coefficients as compared to biomass production were not decreased at low air-filled pore volumes at shallow groundwater depths.

Viets (1962) concluded that, in most cases where water supply is fixed, any management factor that increases yield will increase transpiration efficiency because transpiration is only slightly affected by management practices. In general, transpiration efficiency improves as the availability of plant nutrients increases.

Lowering the water table from 50 to 150 cm increased transpiration from 42.8 cm to 74.9 cm and RDW from 48.9 to 76.8 g, respectively, but did not decrease the transpiration coefficient for RDW. At 100 cm groundwater depth an adequate nutrient supply as compared to a low nutrient level increased transpiration from 64 to 74 cm in the first growth chamber experiment whereas the transpiration coefficient decreased from 454 to 283 g H_2O g^{-1} RDW. Management practices such as fertilization or lowering the groundwater table to improve the aeration in the soil therefore affected yields and transpiration efficiency differently in the investigated soil. The data of Carlson et al. (1959) showed that maize yields were doubled primarily by N fertilizers whereas transpiration varied by less than 10%. Likewise, Power (1983) showed that yield responses due to increased water supplies increased greatly with increasing rates of N fertilizers. Since most transpiration occurs from leaf surfaces, water use is markedly affected by soil fertility status (Campbell et al., 1977; Power and Alessi, 1978) which greatly influences leaf area and leaf area duration. De Wit (1958), Tanner and Sinclair (1983) and Ritchie (1983) state that reduced transpiration due to a lower leaf area index is the main mechanism in reducing transpiration efficiency in plants having an inadequate supply of nutrients. As pointed out by Viets (1962) and Tanner and Sinclair (1983), transpiration efficiency is essentially constant at high yield levels. This is confirmed by the results obtained in this study.

Fischer and Turner (1978) predicted an m factor of 110–140 kg ha^{-1} d^{-1} for wheat and many other C_3 species, and about 210 kg ha^{-1} d^{-1} for C_4 species, if root production was included in the total dry matter production. De Wit (1958) showed that m values found in container experiments generally applied to the field with an adjustment of about 10%. The m values for carrots agree more with values as found for C_4 species. De Wit (1958) showed that m was independent of soil nutrition and water availability unless seriously nutrition-limited or unless soil water content was too high. Whereas in this study the biomass production was clearly depressed at high groundwater levels – probably due to impeded aeration – and by a low nutrient level, decreases of m were only observed at low nutrient levels. Reductions in the water availability as a consequence of lowered water potentials at increasing salinity, did not affect the m factor up to soil solution salinities of 16 mS cm^{-1}. Similar m values regardless of water shortage have been reported by de Wit (1958).

References

Campbell C A, Cameron D R, Nicholiachuk W and Davidson H R 1977 Effects of fertilizer N and soil moisture on growth, N content, and moisture use by spring wheat. Can. J. Soil Sci. 58, 39–51.

Carlson C W, Alessi J and Mickelson R H 1959 Evaporation and yield of corn as influenced by moisture level, nitrogen fertilization, and plant density. Soil Sci. Soc. Am. Proc. 23, 242–245.

De Wit C T 1958 Transpiration and crop yields. Versl. Landbouwk. Onderz. 64.6, Inst. of Biol. and Chem. Res. on Field Crops and Herbage, Wageningen, The Netherlands.

Fischer R A and Turner N C 1978 Plant productivity in the arid and semi-arid zones. Annu. Rev. Plant Physiol. 29, 277–317.

Hanks R J 1983 Yield and water-use relationships: An overview. *In* Limitations to Efficient Water Use in Crop Production. Eds. H M Taylor et al. pp 393–411. Am. Soc. Agron., Madison, WI.

Power J F 1983 Soil management for efficient water use: Soil fertility. *In* Limitations to Efficient Water Use in Crop Production. Eds. H M Taylor et al. pp 461–470. Am. Soc. Agron., Madison, WI.

Power J F and Alessi J 1978 Tiller development and yield of standard and semidwarf spring wheat varieties as affected by nitrogen fertilization. J. Agric. Sci., Camb. 90, 97–108.

Ritchie J T 1983 Efficient water use in crop production: Discussion on the generality of relations between biomass production and evapotranspiration. *In* Limitations to Efficient Water Use in Crop Production. Eds. H M Taylor et al. pp 29–44. Am. Soc. Agron., Madison, WI.

Stewart J I, Danielson R E, Hanks R J, Jackson E B, Hagan R M, Pruitt W O, Franklin W T and Riley J P 1977 Optimizing crop production through control of water and salinity levels in the soil. Utah Water Lab. Pub. no. PRWG 151–1, Logan. 191 p.

Tanner C B and Sinclair T R 1983 Efficient water use in crop production: Research or Re-search? *In* Limitations to Efficient Water Use in Crop Production. Eds. H M Taylor et al. pp 1–27. Am. Soc. Agron., Madison, WI.

Viets F G Jr 1962 Fertilizers and the efficient use of water. Adv. Agron. 14, 223–264.

Watson K K 1966 An instantaneous profile method for determining the hydraulic conductivity of unsaturated porous materials. Water Resources Res. 2, 709–715.