1st. Sino-German Workshop "Impact of Plant Nutrition on Sustainable Agricultural Production. Kiel, 22. - 23.10.1998, 9 pages

Water-Use Efficiency as Influenced by Plant Mineral Nutrition

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Summary

Improved water use efficiency represents one major potential to increase productivity of plant production under conditions of limited water supply. Water-use efficiency depends mainly on atmospheric demand; CO_2 pathway and crop species, but can also be influenced by management practices (e.g. water conservation measures and plant mineral nutrition). Evapotranspirational water-use efficiency (WUE_{ET}) and transpirational water-use efficiency (WUE_T) can be increased by raising soil nutrient levels. Adequately fertilised soils promote rapid leaf area expansion, thus increasing transpiration, and more rapid ground cover, thus reducing evaporation and increasing WUE_{ET}. In contrast to drought, WUE_T at low and moderate salinity is not increased by salinity. Both stresses, however, show improved WUE_T as the availability of plant nutrients is increased. Raised soil nutrient levels seem to exert additive effects on WUE_T. Increased WUE_T due to higher nutrient levels can largely be ascribed to increased biomass production and to a much lesser degree to changes in transpiration. Increasing or optimising yields by adequate fertilisation will increase transpiration efficiency.

1. Introduction

On a global scale, water deficiency is the major factor limiting agricultural production. The increasing demand for food and water calls for a more efficient water use in agriculture. A better understanding of how water deficiency affects plant growth and yield production and of how water use and water-use efficiency in agriculture can be optimised is of great importance (Begg and Turner, 1976; Stanhill, 1986).
Water availability, water use and nutrient supply to the plants are closely interacting factors influencing plant growth and yield production (Viets, 1972). Limited soil moisture influences nutrient availability for plants (Olsen et al., 1961). Adequately fertilised plants may show higher drought tolerance (Lahiri, 1980). Water use of fertilised plants is known to be increased (Barraclough, 1989), but on the other hand water use efficiency is reported to be increased by adequate fertilization (e.g. Heitholt, 1989).
Improved water use efficiency represents one major potential to increase productivity of plant production under conditions of limited water supply. Water use efficiency is defined as the yield of plant product (grain, silage, forage, tuber, or other plant product of concern) produced per unit water used (Power, 1983). Water-use efficiency is expressed as:

$$WUE_{ET} = Y/ET \text{ or } WUE_T = Y/T$$

where Y is the quantity of the plant product (either biomass or marketable product) produced on a given surface area in a given time period, and ET and T are evapotranspiration and transpiration, respectively, from the same surface.

2. Evapotranspirational water-use efficiency

Evapotranspirational WUE (WUE_{ET}, grams total DM per kilogram evapotranspiration) can be increased by water conservation measures such as suppression of evaporation, control of weeds, irrigation scheduling, and breeding for increased leaf area (Unger and Stewart, 1983). WUE_{ET} has been shown to be increased by raising soil nutrient levels. Such increases have been mainly attributed to a larger ratio of transpiration to evapotranspiration as a result of greater leaf area (Tanner and Sinclair, 1983). Relative plant transpiration (T/ET) increased with leaf area index (Ritchie and Burnett, 1971) (Fig. 1).

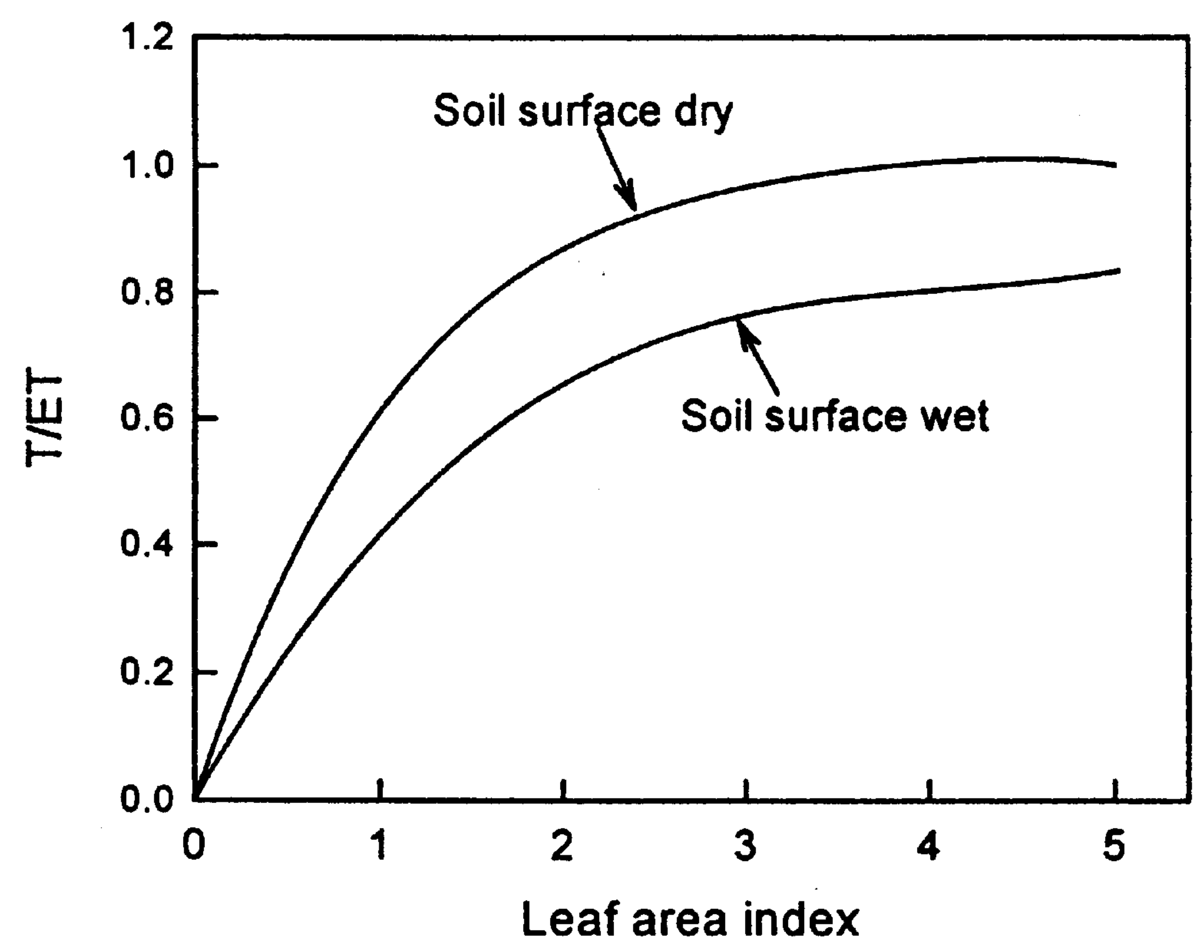

Figure 1: Relative plant transpiration as a function of leaf area index in cotton and grain sorghum. (Modified from Ritchie, 1983).

Nutrients influence leaf area duration, leaf growth rates and senescence and thus transpiration. Nitrogen and phosphorus deficiencies can reduce cell expansion which results in smaller leaves. Generally, adequately fertilised soils promote both rapid leaf area expansion, thus increasing transpiration, and more rapid ground cover, thus reducing evaporation. Application of N fertilisers e.g. can enhance new leaf growth (increased LAI) and delay plant senescence, resulting in increased transpiration.
In general, WUE_{ET} is improved with increasing plant nutrient availability as long as water availability is sufficient to provide reasonable growth rates. With limited water availability, however, maximum WUE_{ET} is often achieved with fertiliser rates somewhat lower than those required for maximum yield (e.g. Viets, 1962; Power, 1983).
Increasing the availability of plant nutrients increases yields as well as water use by the crop; however, the increase in water use is usually small - generally <25% (Power, 1983). A good example is provided by Carlson et al. (1959) who showed that maize yields were doubled primarily by N fertilisers whereas transpiration varied by less than 10 %. Therefore, the conclusion of Viets (1962) seems reasonable that, in most cases when water supply is fixed, any management factor that increases yield will increase WUE_{ET} efficiency because evapotranspiration will be little affected by the management (Ritchie, 1983).

3. Transpirational water-use efficiency

Transpirational water-use efficiency (WUE_T) is affected mostly by atmospheric demand, CO_2 pathway, and to a lesser extent crop species. Plants growing under conditions of drought and/or salinity stress may have a higher water use efficiency than unstressed plants (Winter, 1981; Studer et al., 1992). Nutrient availability to the plants may also affect their WUE_T. Several studies have demonstrated that plants growing under nutrient deficiency used water less efficiently than adequately fertilised plants (Viets, 1962; Goudriaan and van Keulen, 1979; Schmidhalter and Oertli, 1991; Andersen et al., 1992). However, there is no consensus on how nutrient deficiency affects WUE. Some researchers maintain that nutrient supply can substantially affect WUE_T (e.g. Ritchie, 1983), whereas others believe that nutrient deficiency decreases WUE_T only when severe. The effects of nutrient supply on plant growth and yield production under conditions of limited water availability are complex. Interactive effects of nutrient supply and water availability on WUE_T have little been studied.

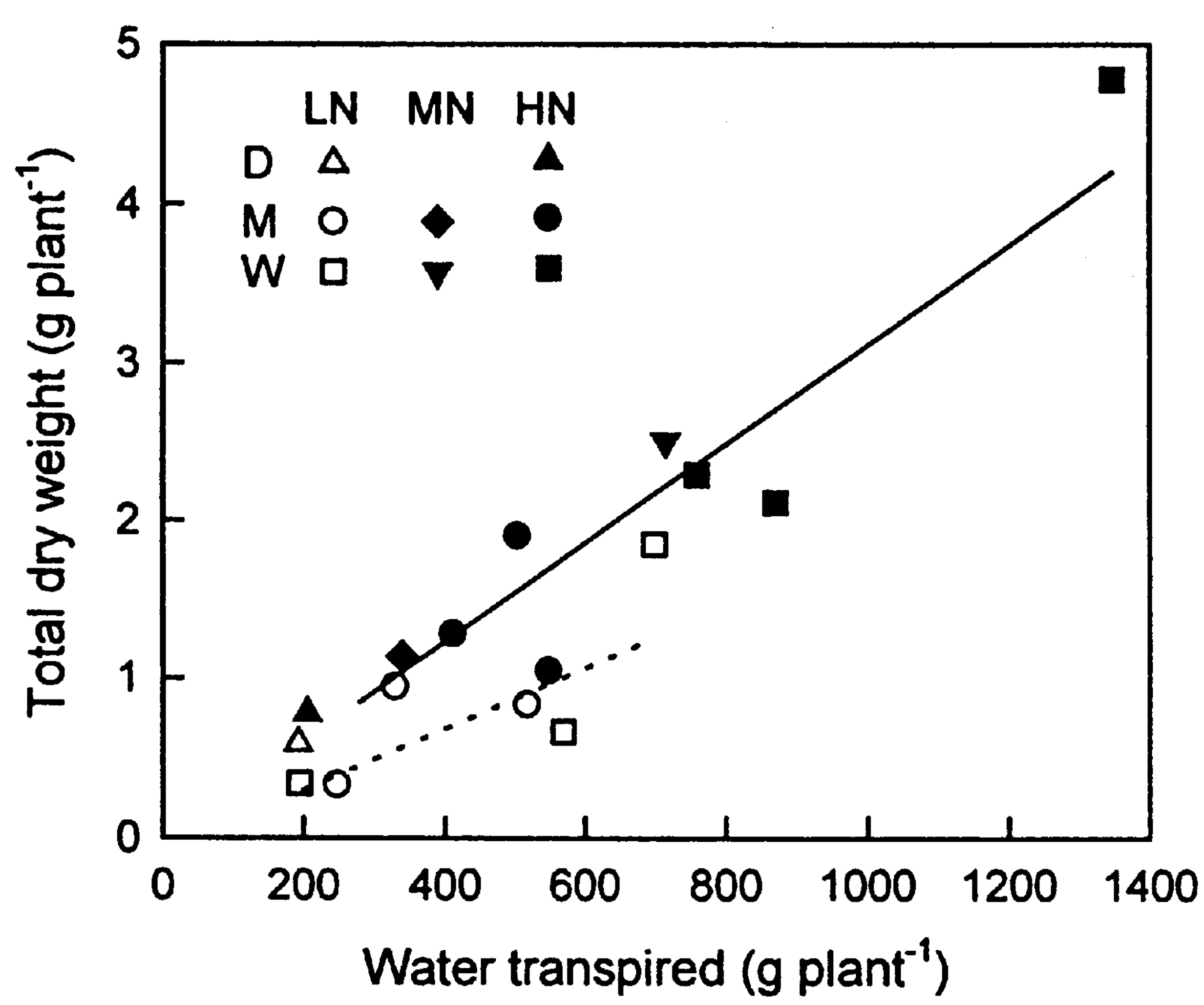

Figure 2: Transpirational water-use efficiency for wheat plants provided with low nitrogen (LN), medium nitrogen (MN) and high nitrogen (HN) under well-watered conditions (W), or subjected to moderate (M) or severe (D) drought. Dotted line = LN; full line = MN+HN. (Modified from Heitholt, 1989).

3.1 Influence of water availability and nutrient level on WUE_T

3.1.1 Nitrogen and WUE_T

Plant and soil N status play a role in WUE_T. In several studies, soil N level was positively related to WUE_{gas} (gas-exchange water-use efficiency (Campbell et al., 1977) and WUE_T (Parameswaran et al., 1981). This was confirmed with water- and N-stressed wheat plants. The results supported previous observations that optimal leaf N concentration promoted higher WUE (Heitholt, 1989). Mild water stress did not consistently affect WUE, but a more severe water stress consistently decreased WUE_T, especially under sub-optimal N supply (Fig. 2). Other studies showed that nitrogen fertilisation increased WUE of native mixed prairie, wheat, and sorghum (Carter, 1992). Yield reductions arising from N and drought were additive. For example, growth of smooth bromegrass was reduced 24% by N deficits, 32% by water deficits, and 54 % when both water and N were deficient (Power, 1983).

Heitholt (1989) observed that WUE_T and WUE_{gas} were well correlated as a function of N stress in *Triticum aestivum* L. Leaf gas exchange measurements could therefore offer a powerful tool for nearly instantaneous, in vivo assessment of plant nutrient status.

3.1.2 Phosphorus and WUE_T

Phosphorus fertiliser increased WUE_T of sorghum (Power et al., 1961). Pearl millet [Pennisetum glaucum (L.) R. Br.] production in the West African Sahel is constrained by low, erratic rainfall and low soil nutrient (particularly P) availability. Payne et al. (1992) tested in outdoor pot and growth chamber experiments the hypothesis that increasing soil P supply increases WUE_T. They demonstrate the positive effect of P on pearl millet production, photosynthetic rate, WUE_T (Fig. 3) and WUE_{gas} (gas-exchange

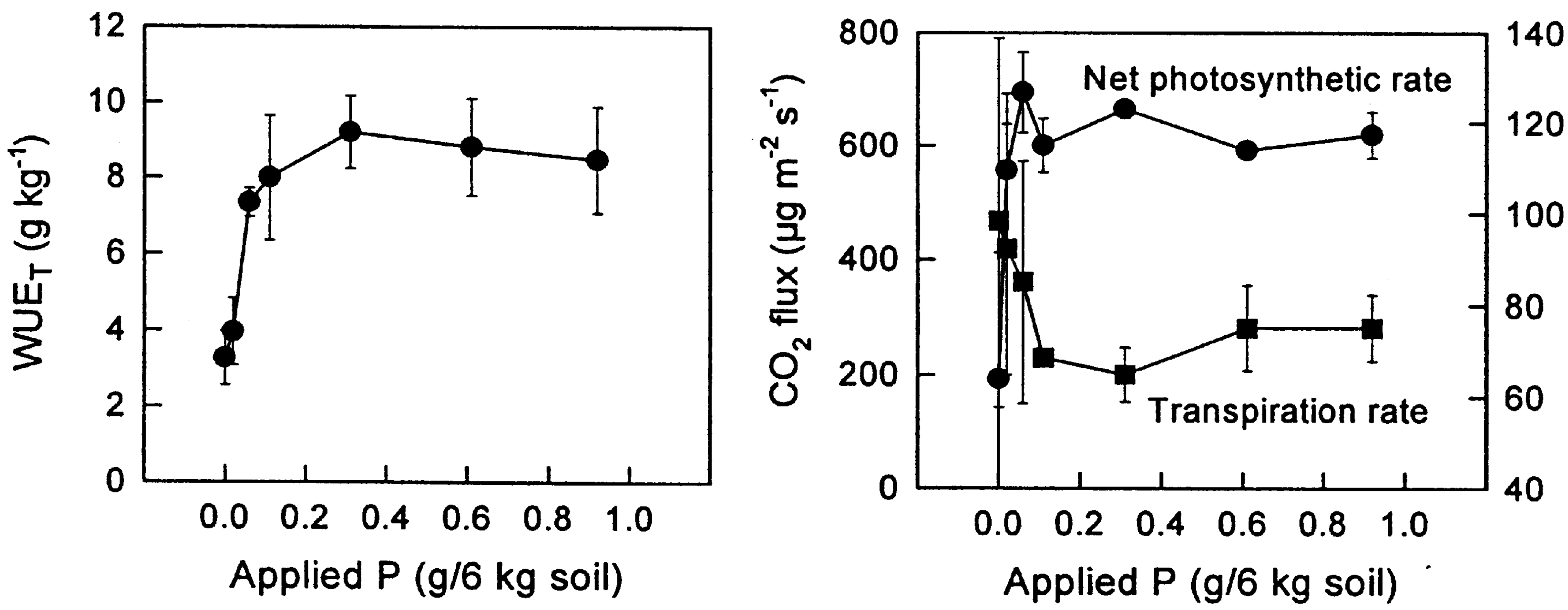

Figure 3: Transpirational water-use efficiency (WUE_T) (left figure) and CO_2 and H_2O fluxes of non-water-stressed pearl millet as affected by P availability (right figure) (Modified from Payne et al., 1992).

water-use efficiency) under well-watered and water-stressed conditions, supporting conclusions reached long ago by Briggs and Shantz (1913) on crop water requirement (the inverse of WUE_T): „Although the water requirement for a given crop varies widely according to season, soil, and fertiliser, the results show conclusively a marked reduction in the water requirement accompanying the use of phosphate as a fertiliser." In contrast to the growth chamber experiments WUE_T in outdoor experiments increased more steadily with raising levels of applied P. Whereas WUE_T of the whole plant biomass was higher under water-stress as compared to well-watered conditions the opposite was observed for grain production. Results of gas exchange measurements offered a partial physiological explanation for the observed differences in WUE_T. The increase in mean photosynthetic rate was stronger than the decrease in mean transpiration rate (Fig. 3).

3.1.3 Potassium and WUE_T

Sandy soils low in natural K content are widespread. Such soils are often exposed to intermittent periods of drought owing to the low water-holding capacity of the soil (Andersen et al., 1992). Water-use efficiency for total dry matter production was increased by K application; however, WUE for grain production was unaffected by the level of K application

(Andersen et al., 1992). Studer and Blanchet (1963) found that high additions of K increased yield and WUE of Italian ryegrass.

3.1.4 Interactive effects of nitrogen, phosphorus and potassium on WUE_T

There is hardly any study which compares the effects of different nutrient deficiencies and drought on WUE_T. Such a study was done with young seedlings of maize plants (Zea mays L. cv. Issa). Details are described by Studer (1993). Transpiration efficiency varied significantly with the age of the plants (data not shown) and was significantly affected by drought and by different nutrient regimes (Fig. 4). Drought increased WUE_T in all nutrient treatments. The effects of differential nutrition were more obvious in drought treatments than in well-watered treatments. However, in general the effects of different nutrient treatments were similar whether the plants were well-watered or drought-affected (no significant interaction between fertilization and water regime). This suggests additive effects of soil fertility on WUE_T.

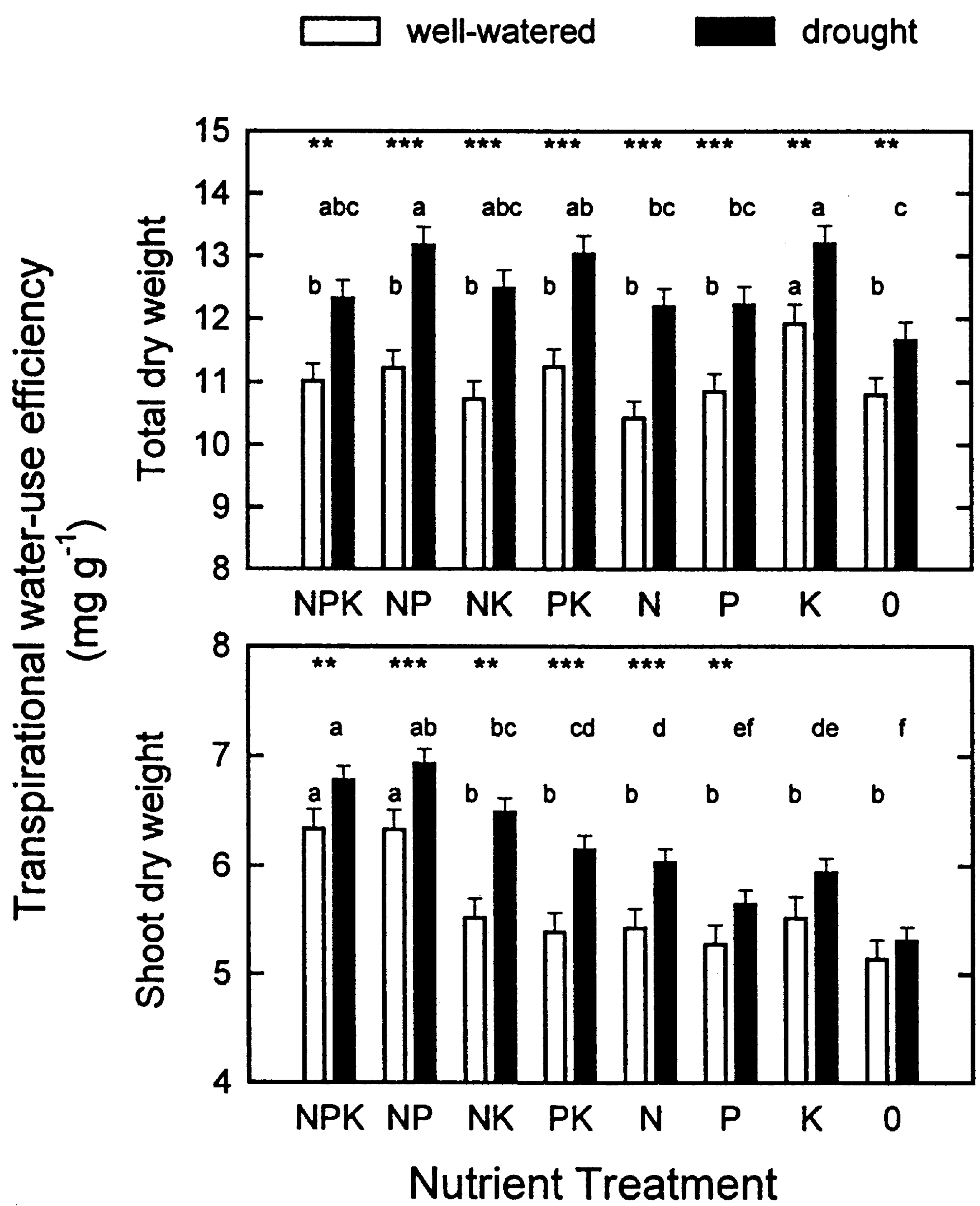

Figure 4: Transpirational water-use efficiency of well-watered and droughted maize seedlings as affected by different nutrient treatments. *, **, and *** indicate significance at $P \leq 0.1$, 0.05, and 0.01 respectively. Treatment means with the same letter are not significantly different.

Transpiration efficiency of the total dry weight was highest in the nutrient treatment with additional K and lowest in treatments with no nutrients added, N or P. However, the positive effect of K fertilization was only significant at the beginning of the experiment. Towards the end of the experiment, P-fertilization exerted a significant positive effect on WUE_T.

Transpiration efficiency of shoot dry mass was highest in treatments NPK and NK, and lowest in treatment P and the treatment with no nutrients added.

Transpiration efficiency and biomass yield
It is most desirable to combine a high transpiration efficiency with a good yield performance. Transpiration efficiency may be attractively high and general plant performance may be unsatisfactory. On the other hand, high WUE_T do not exclude acceptable yields (Fig. 5). Transpiration efficiency of total dry weight of the nutrient treatments K and PK were high under both well-watered conditions and drought. Total dry weight, however, was 13 to 42% below that of the best yielding nutrient treatments, which also had a high WUE_T. No relation was observed between WUE_T and total dry weight. However, a distinct positive correlation was observed between WUE_T and shoot dry weight (r=0.88 for well-watered treatments and r=0.79 for drought treatments). Both, high shoot dry weight and WUE_T, were achieved with treatments NPK and NP, whereas the results of WUE_T for total dry weight indicate that these parameters are not necessarily linked. Maximising WUE_T alone may not be a desirable strategy to achieve high plant productivity under non-optimal conditions.

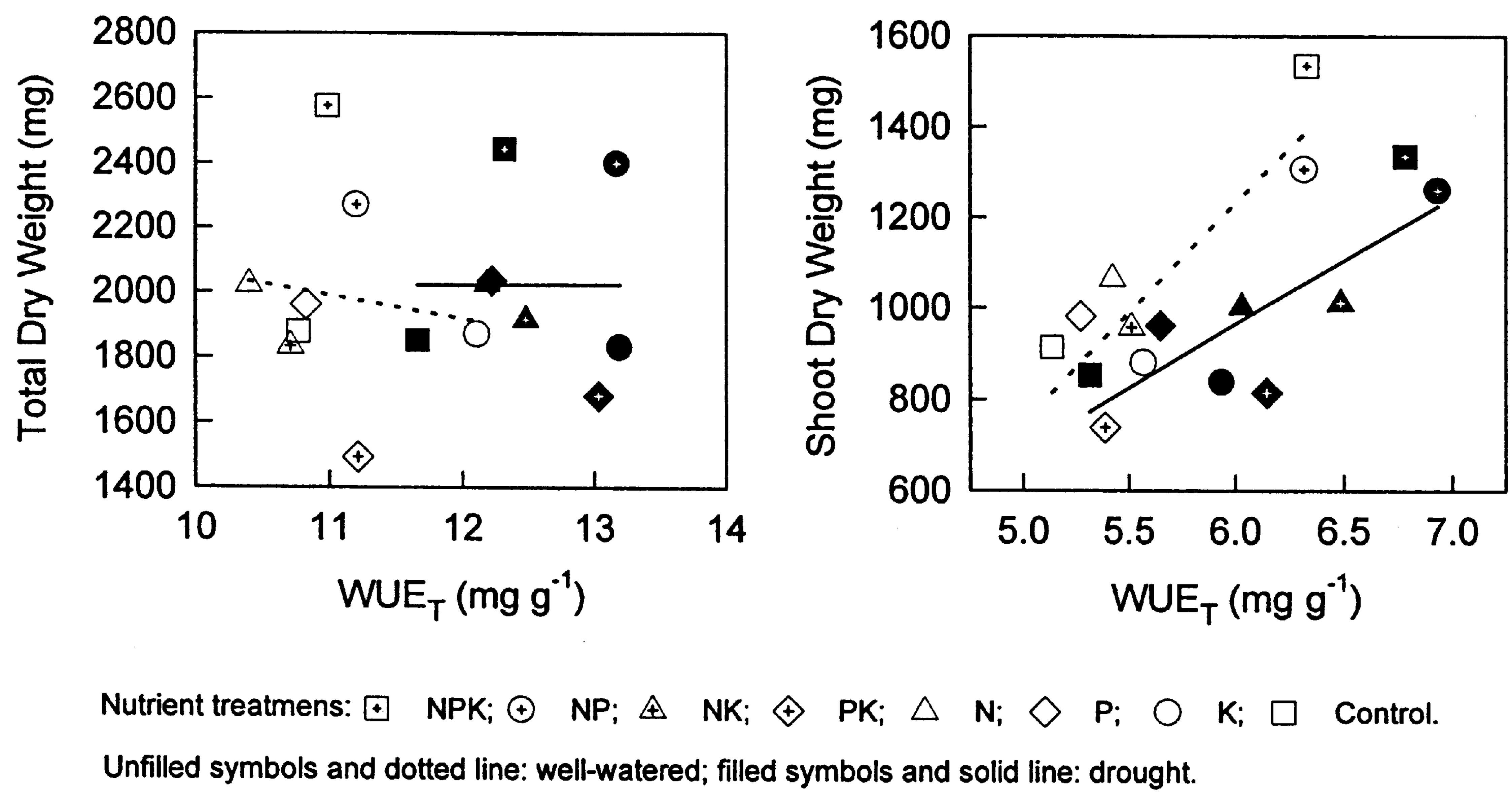

Figure 5: Relationship between yield and WUE_T for differently fertilised plants under well-watered conditions and drought. Regression lines were fitted separately through data from well-watered (dotted line) and drought (solid line) treatments.

3.2 Influence of salinity and nutrient level on WUE_T

Very few attempts have been made to investigate the relationship between soil nutrient status, salinity and WUE_T. For a given irrigation level, transpiration was lower under saline conditions, due to the lower soil water availability, whereas the relationship between yield and transpiration was similar regardless of different salinity levels (Stewart et al., 1977). More recently it was suggested that 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 (Schmidhalter and Oertli, 1991). This study included two treatments, treatment two had a more favourable nutrient supply and higher soil salinity as compared to the first treatment. Low nutrient levels significantly decreased WUE_T of storage root dry weight of carrots (marketable product) (Tab. 1). In the same study impeded aeration due to shallow groundwater did not affect WUE_T, whereas biomass production was clearly decreased. Non-optimal soil fertility decreased biomass much more strongly than transpiration. A similar conclusion, as reached by Viets (1962) for drought, applies for salinity 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, under salinity transpiration efficiency improves as the availability of plant nutrients increases.

Table 1: Biomass production and transpirational water-use efficiency (WUE_T) of differently fertilized 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)	WUE_T RDW (mg g^{-1})
Low nutrient level				
0.5	2.53	14.56	48.78	2.40
1.0	3.15	16.96	67.45	2.20
1.5	2.48	17.15	76.80	2.17
Medium nutrient level				
1.0 (a)[b]	8.20	43.72	124.75	3.31
1.0 (b)[b]	7.91	41.34	128.19	4.00
1.0 (c)[b]	7.01	41.66	121.75	3.35
$LSD_{0.05}$		5.55	26.86	1.03

[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 thickness, respectively

4. Conclusions

Evapotranspiration efficiency (WUE_{ET}) is increased in adequately fertilised soils mainly due to a higher leaf area index. A vigorous development of above ground biomass leads to a more rapid and dense ground cover and reduced penetration of radiant energy to the soil surface, thus reducing water evaporation from the soil.

Transpiration efficiency (WUE_T) is in general increased by drought whereas transpiration efficiency is not affected by salinity as long as neither toxic effects nor nutrient imbalances occur. In both cases, transpiration efficiency is normally improved as the availability of plant nutrients is increased. Increased transpiration efficiency due to higher nutrient levels results mainly from increased biomass production and to a much a lesser degree from changes in transpiration. Increasing or optimising yields by adequate fertilisation will increase transpiration efficiency.

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