Soil Phosphorus Availability and Pearl Millet Water-Use Efficiency

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ABSTRACT

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. Outdoor pot and growth chamber experiments tested the hypothesis that increasing soil P supply increases transpirational water-use efficiency (WUE_T), under water-stressed and non-water-stressed conditions. Pearl millet was grown outdoors under semiarid conditions in covered pots containing 85 kg of acid, P-deficient Betis sand (sandy, siliceous, thermic Psammentic Paleustalf). Plants were treated with four P levels and two water treatments, and harvested at 14-d intervals. Significant main and interactive effects on WUE_T due to P level, water treatment, and time of harvest were found. The slope of the curve relating DM to cumulative transpiration (T_{cum}) increased with P level and water stress when data from all harvests were pooled. In the growth chamber, WUE_T of non-water-stressed plants ranged with increasing P level from 3.22 to 9.12 g kg^{-1} at 29 days after sowing (DAS) in pots containing 6 kg soil, and from 0.84 to 9.24 g kg^{-1} at 49 DAS in pots containing 18 kg soil. The ratio of leaf net photosynthetic rate to transpiration (WUE_{gas}) at 500 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD) ranged from 1.88 $\mu g\ mg^{-1}$ for plants receiving no P to 10.25 $\mu g\ mg^{-1}$ for those receiving 0.310 g P 6 kg^{-1} soil. Between PPFD levels of 500 and 2000 $\mu mol\ m^{-2}\ s^{-1}$, plants receiving no P increased WUE_{gas} to only 3.60 $\mu g\ mg^{-1}$, whereas those receiving higher levels of P increased WUE_{gas} to as much as 18.2 $\mu g\ mg^{-1}$. Our finding that increasing soil P availability increases WUE_T under water-stressed and non-water-stressed conditions reinforces previous conclusions that water supply in the Sahel and similar semiarid environments cannot be effectively managed for improved crop production without addressing soil fertility constraints.

Evapotranspirational water-use efficiency (grams total DM per kilogram evapotranspiration) can be increased by water conservation measures such as suppression of evaporation, control of weeds, prudent irrigation scheduling, and breeding for increased leaf area (Unger and Stewart, 1983). Raising soil nutrient levels has been shown to increase WUE_{ET} in pearl millet (Lahiri, 1980), sorghum [*Sorghum bicolor* (L.) Moench] (Onken and Wendt, 1989), and other crops (Viets, 1962; Power, 1983), but such increases have been attributed to a larger ratio of transpiration to evapotranspiration as a result of greater leaf area (Tanner and Sinclair, 1983). Many authors (e.g., De Wit, 1958; Fischer and Turner, 1978; Tanner and Sinclair, 1983; Gregory, 1989) have concluded that WUE_T (grams total DM per kilogram transpiration) is affected mostly by atmospheric evaporative demand, CO_2 pathway (i.e., whether the crop is a C_4 or C_3 plant), and to a lesser extent crop species, while nutrient deficiency decreases WUE_T only when severe. Others (e.g., Ritchie, 1983) have maintained that nutrient supply can have a substantial effect on WUE_T.

Onken and Wendt (1989) obtained significant increases in WUE_T of sorghum due to variety, N level, and water stress. Similarly, Parameswaran et al. (1981, 1984) observed increases in wheat (*Triticum aestivum* L.) WUE_T due to water stress and increased N level. However, we know of no detailed reports on the effects of P nutrition on WUE_T of crops in general or pearl millet in particular. Pearl millet is the staple cereal of semiarid Sahelian Africa. The low levels of soil P in pearl millet fields of the Sahel have been well documented (Vidal, 1963; Jones and Wild, 1975; Scott-Wendt et al., 1988; Bationo et al., 1989; Davis-Carter, 1989). We investigated the effects of P nutrition on pearl millet WUE_T under soil and climatic conditions similar to the West African Sahel. The purpose was to test the hypothesis that increasing soil P availability increases pearl millet WUE_T under water-stressed and non-water-stressed conditions.

MATERIALS AND METHODS

Experiments were made in the summer of 1988 in outdoor pots at Lubbock, TX, as part of a growth analysis experiment (Payne, 1990; Payne et al., 1991a) and in the summer of 1989 under controlled conditions in a growth chamber at College Station, TX. In both experiments, soil and weather conditions approached those of the Sahel.

Outdoor Pot Experiment

Treatments in the outdoor pot experiment consisted of P level, water treatment, and time of harvest, all considered fixed effects. A completely random design with five replications was used. The pearl millet cultivar ICTP 8203 (Rai et al., 1990) was planted in 300 plastic-lined 75-L pots containing 85 kg of acid, P-deficient Betis sand. This soil was selected because its chemical, physical, and mineralogical properties are similar to those of sandy millet fields of Niger, Senegal, and Mali (Payne et al., 1991a). Pots were treated with four levels of added P (0, 1.15, 3.38, and 7.77 g P m^{-2} in pots of 0.139 m^2 area) and sufficient amounts of N (128.1 g $NH_4NO_3\ m^{-2}$) and K (40.3 g $K_2SO_4\ m^{-2}$) to allow the assumption that these nutrients were non-limiting to plant growth. The levels correspond roughly to field rates of 0, 10, 30, and 70 kg P ha^{-1}. Fertilizer was applied in powder form and thoroughly mixed into the upper 0.15 m of soil before planting. For each P level, there were two water treatments: water-stressed and non-water-stressed. Phosphorus levels and water treatments were randomly assigned to pots.

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Abbreviations: DAE, days after emergence; DAS, days after sowing; DM, dry matter; ET, evapotranspiration; PPFD, photosynthetic photon flux density; *T*, transpiration; T_{cum}, cumulative transpiration; WUE_{ET}, evapotranspirational water-use efficiency; WUE_{gas}, gas-exchange water-use efficiency; WUE_T, transpirational water-use efficiency.

Plants were thinned to two plants per pot at 7 DAE; at 14 DAE, pot liners were sealed around the base of plants so that water loss was by transpiration only. Pots contained two holes through which watering portals were inserted. The liners were covered with a layer of Betis soil to keep surface albedo more representative of field conditions. Rainfall shelters were used to cover plants during rain to prevent unmetered additions of water.

Plants were watered as follows. All pots were watered to field capacity, or ≈ 0.16 m^3 m^{-3}, before planting. Average soil water content was determined two or three times weekly by weighing pots with a load-cell balance, accurate to 0.05 kg. For water-stressed plants, if average soil water content of pots was ≥ 0.07 m^3 m^{-3} at weighing, no water was added; otherwise, pots were watered to an average soil water content of 0.07 m^3 m^{-3}. When plants of the water-stressed treatment appeared to be severely wilted between weighings, 0.5 kg of water was added. For non-water-stressed plants, if average soil water content at weighing was ≤ 0.16 m^3 m^{-3}, sufficient water was added to bring water content to 0.16 m^3 m^{-3}. The average daily rate of transpiration was then calculated for each P level from

$$T = I - dS$$

where I is the amount of water added to pots, and dS is the change in pot mass between weighings. Sufficient water was then added at 1- or 2-d intervals to compensate for the daily transpiration rate until the next weighing, at which point a new rate was calculated. On isolated occasions when incipient water stress was evident in individual plants, several kilograms of water were given immediately.

Two 75-L pots were prepared similar to the others except not sown with millet. Their water loss during the entire growth period was below the limit of detection of the load-cell balance, from which we concluded that water loss other than that due to transpiration was negligible. Additional experimental details, including daily weather data, were presented by Payne et al. (1991a).

Five pots from each water treatment of each P level were randomly selected for harvest at 2-wk intervals after emergence, for a total of six harvests. For each pot, both plants were separated into leaves, stems, dead material, grain, and roots as described by Payne et al. (1991a), and each partition weighed after drying to obtain total plant DM.

Statistical analyses were made using the MGLH module of SYSTAT[1] (Evanston, IL; Wilkinson, 1987). For the second through sixth harvests, WUE_T was calculated from DM/T_{cum}, where T_{cum} is cumulative transpiration. The ratio of grain dry matter to T_{cum} was calculated at final harvest to obtain an expression of WUE_T in terms of grain yield only. Analysis of variance was made using P level, water treatment, and time of harvest as factors. To obtain an average WUE_T for each P level of each water treatment, DM was regressed on T_{cum} for all harvests using the model statement

$$DM = wT_{cum} + \epsilon,$$

where w represents the slope of DM vs. T_{cum}, and ϵ is the error term. The coefficient **w** represents an average WUE_T for the entire experiment.

Growth Chamber Experiment

The pearl millet cultivar ICTP 8203 was sown under a fluorescent light bank in pots of 0.0346 m^2 area, containing 6.000 kg Betis sand. The experimental design was completely random with fixed effects due to P level with four replicates for each P level. Pots were watered to an average soil water content of 0.17 m^3 m^{-3} and treated with 0, 0.023, 0.062, 0.116, 0.310, 0.621, and 0.931 g P per pot, added as $Ca(H_2PO_4)_2 \cdot H_2O$. Additionally, pots received 1.76 g K_2SO_4 and a total of 5.92 g NH_4NO_3. A second set of larger pots containing 18.00 kg of Betis sand was planted the same day and received 0.00 or 1.78 g P (three replicates each). These received additionally 3.30 g K_2 SO_4 and a total of 12.65 g NH_4NO_3.

At 6 DAS, all pots were thinned to one plant per pot, fitted with a plastic collar to restrict water loss to transpiration, and transferred to a closed growth chamber equipped with fluorescent lights. Conditions in the growth chamber were 500 μmol m^{-2} s^{-1} PPFD, 32/21 °C day/night temperature (14 h day/10 h night), $\approx$40% relative humidity, and $\approx$0.5 m s^{-1} windspeed.

Transpiration was calculated from change in pot mass, which was determined gravimetrically every 2 or 3 d. After each weighing, pots were repositioned randomly in the growth chamber. Water content was maintained near 0.17 m^3 m^{-3} by watering to compensate for daily transpiration, as with non-water-stressed plants in the outdoor pot experiment. There were no water-stressed plants in the growth chamber experiment.

At 28 DAS, photosynthesis and transpiration were measured on the youngest fully expanded leaf of each plant in the small pots. Leaf gas exchange was measured using an ADC infrared gas analyzer (Analytical Development Co., Hoddesdon, Herts, England) equipped with a 50- by 56-mm leaf cuvette. The ADC, which operates as an open system, was calibrated using known CO_2 concentrations. At 29 DAS, photosynthesis and transpiration rates were measured in the same manner at PPFD of 1000, 1500, and 2000 μmol m^{-2} s^{-1}, using a rheostat-controlled light apparatus. A circulating water bath was kept between the light source and leaf to absorb infrared radiation and to maintain constant leaf temperature. Measurements were taken at higher PPFD after plants had reached a new steady-state gas exchange rate, which required 20 to 30 min. Only two replicates of each treatment were used for photosynthesis measurement at higher PPFD. No measurements were obtained for the 0.310 g P treatment at 2000 μmol m^{-2} s^{-1}, due to instrument failure.

At 29 DAS, plants in small pots were harvested and their roots were washed. Roots and shoots were oven-dried to obtain whole-plant DM. Plants in large pots were harvested at 49 DAS. For both large and small pots, WUE_T was calculated as previously described for the outdoor pot experiment. From gas exchange measurements, the mean ratio of CO_2 flux density to H_2O flux density (WUE_{gas}) was calculated as an instantaneous index of leaf WUE. A nonlinear regression model was fitted, using SYSTAT's NONLIN module, to data on plant WUE_{gas} response to PPFD for each P level. The model statement was

$$WUE_{gas} = B/(1 + e^{-0.002PPFD})$$

where B is a statistical coefficient determined for each P level, and PPFD is photosynthetic photon flux density. It follows from the model statement that a statistical increase in the value of B at a given PPFD level will result in a larger WUE_{gas} at that irradiance.

RESULTS AND DISCUSSION

Outdoor Pot Experiment

Non-water-stressed plants clearly increased T_{cum} with increased P level (Fig. 1). Water-stressed plants receiving no P transpired least. At final harvest, there was no statistically significant difference in T_{cum} among the upper three P levels of water-stressed plants. Whole-plant DM (Fig. 2) increased with added P for water-stressed and non-water-stressed plants, with differ-

[1]Mention of trademarks does not constitute an endorsement.

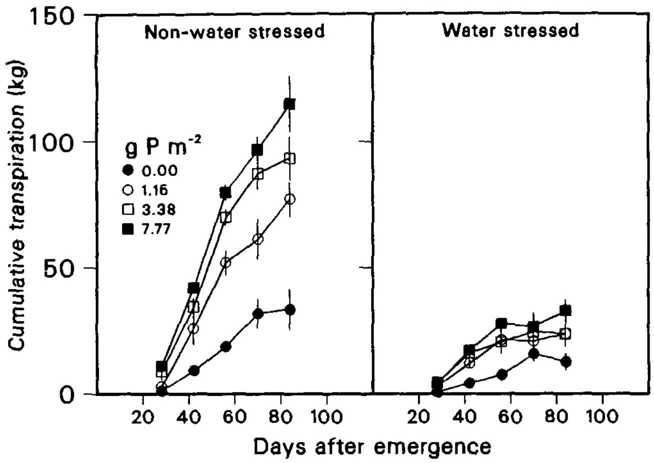

Fig. 1. Cumulative transpiration (T_{cum}) of pearl millet as affected by P and water supply, in an outdoor pot experiment at Lubbock, TX (1988). Bars represent ± 1 SD.

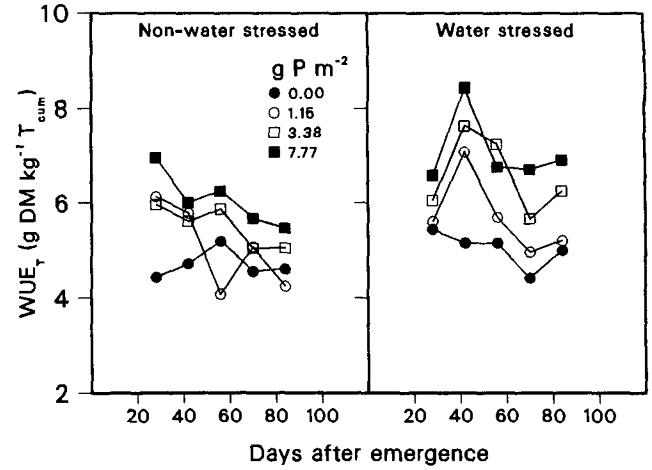

Fig. 3. Mean transpirational water-use efficiency (WUE_T) at 14-d intervals of pearl millet grown in an outdoor pot experiment at Lubbock, TX (1988), as affected by P and water supply. DM = dry matter.

ences becoming most pronounced during the exponential growth phase. As data in Fig. 3 show, WUE_T increased with P level for both water-stressed and non-water-stressed plants. Furthermore, WUE_T increased with water stress, and was not constant with time (Fig. 3). An interaction between time of harvest, water treatment, and P level was found (Table 1). Fluctuations in WUE_T with time may be due to changes in weather, such as atmospheric vapor pressure deficit (Tanner and Sinclair, 1983) or changes in conversion efficiency of photosynthate (Penning de Vries et al., 1974) associated with developmental stage. An increase in WUE_T due to water stress could be due to a number of factors, including increased conversion efficiency from increased starch production (McCree et al., 1990) and the differential effect of partial stomatal closure on CO_2 flux relative to H_2O flux (Nobel, 1983). There is a dearth of data on the mechanisms by which P stress affects WUE_T.

Results of regression of DM on T_{cum} for each P level and water treatment and the resultant interaction between these factors are illustrated in Fig. 4. Slope R^2 values ranged from 0.97 to 0.99. The data show a clear increase in slope with applied P and with increased water stress. Furthermore, WUE_T continued to increase beyond severe nutrient stress in both water treatments. When calculated in terms of g grain produced per kg water transpired, WUE_T increased with P level (Fig. 4), as did whole-plant WUE_T. However, grain WUE_T decreased with water stress, unlike whole plant WUE_T.

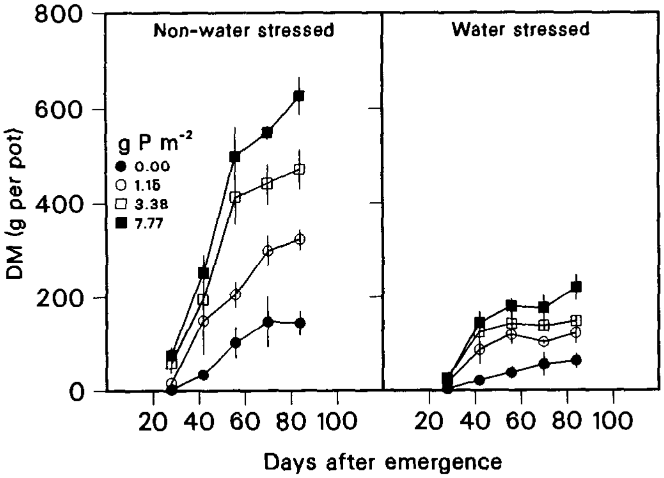

Fig. 2. Whole-plant dry matter (DM) of pearl millet grown in an outdoor pot experiment at Lubbock, TX (1988), as affected by P and water supply. Bars represent ± 1 SD.

Growth Chamber Experiment

For small pots, DM and T_{cum} increased with applied P up to ≈0.3 g P pot^{-1} (Fig. 5). Not surprisingly, T_{cum} is approximately parallel to DM. However, the ratio DM/T_{cum} (i.e., WUE_T) is not at all constant (Fig. 6). For large pots harvested at 49 DAS, the 1.78 g P level produced 193.83 ± 14.56 g (± 1 SD) of DM, transpired a total of 20.98 ± 0.41 kg of water, and had a WUE_T of 9.24 ± 0.70 g kg^{-1}. The 0.00 g P level, on the other hand, produced only 1.22 ± 0.52 g of DM, transpired a total of 1.42 ± 0.47 kg, and had a WUE_T of 0.86 ± 0.11 g kg^{-1}, or less than one-tenth the value for the 1.78 g P level. Thus, the positive effect of P on WUE_T for pearl millet in this soil system seems to be a general phenomenon, demonstrable both outdoors and in the growth chamber.

Table 1. Analysis of variance and probability levels for pearl millet transpirational water-use efficiency. Fixed effects were time to harvest (H), P level (P), and water treatment (W). Plants were grown outside at Lubbock, TX (1988), in covered pots containing 85 kg of acid, P-deficient Betis sand, and harvested at 14-d intervals.

Source	df	Mean square	*P*
Harvest (H)	4	3.20	0.031
Phosphorus (P)	3	38.85	0.000
Water (W)	1	28.52	0.000
H × P	12	2.71	0.010
H × W	4	0.84	0.580
P × W	3	0.90	0.509
H × P × W	12	2.95	0.005
Error	140	1.17	

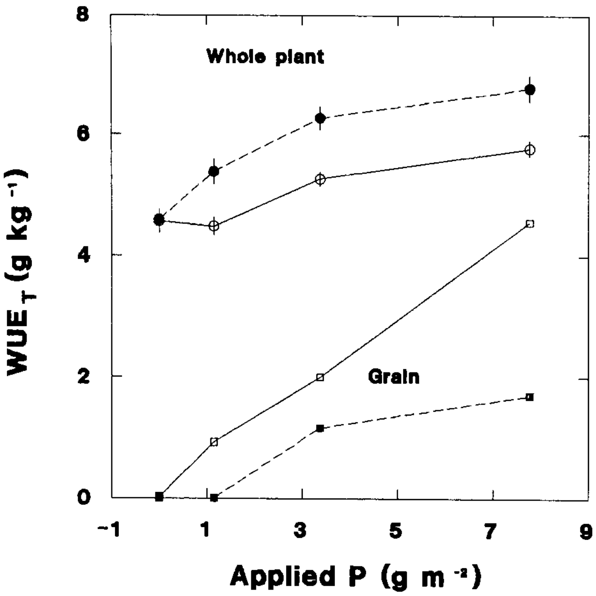

Fig. 4. Average pearl millet transpirational water-use efficiency (WUE_T) for outdoor pot experiment as a function of P level for water-stressed (solid symbols) and non-water-stressed (open symbols) treatments. For whole-plant data, points represent slopes calculated using dry matter (DM) and cumulative transpiration (T_{cum}) from Harvests 2 through 6. Bars represent ± 1 SD of slopes. Grain WUE_T was calculated from grain yield and T_{cum} at harvest 6 only. Standard deviation cannot be calculated because all heads from the same water treatment and P level were threshed together.

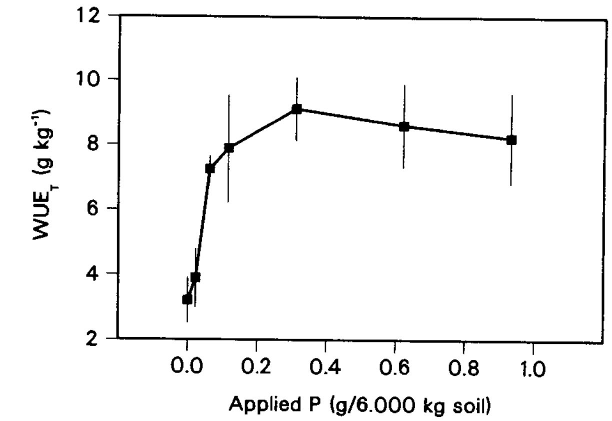

Fig. 6. Transpirational water-use efficiency (WUE_T), as affected by P availability for non-water-stressed pearl millet grown in a growth chamber.

Results of gas exchange measurements for plants in small pots (Fig. 7) offer at least a partial physiological explanation for observed differences in WUE_T. Mean photosynthetic rate was <200 μg CO_2 m^{-2} s^{-1} for plants receiving no P and increased to ≈600 μg m^{-2} s^{-1} for plants receiving higher levels of P. Concurrently, mean transpiration rate decreased from ≈100 mg m^{-2} s^{-1} to ≈70 mg m^{-2} s^{-1}. As a result, WUE_{gas} increased from ≈2 μg mg^{-1} in plants receiving no P to ≈10 μg mg^{-1} in plants receiving higher levels of P, implying an approximate fivefold increase due to added P (Fig. 8).

Results of the nonlinear model fitted to data on WUE_{gas} response to PPFD (Table 2) show that the coefficient B significantly increased with applied P up to ≈0.2 g P, after which B was approximately constant. It follows from the model statement that for a given PPFD irradiance, WUE_{gas} increased with added P (Fig. 9). Data in Fig. 9 also suggest that WUE_{gas} of plants receiving low levels of P became light saturated as PPFD increased. For example, between PPFD of 500 and 2000 μmol m^{-2} s^{-1}, the WUE_{gas} of plants receiving 0 g pot^{-1} increased from 1.84 to 3.60 μg CO_2 mg^{-1} H_2O, while those receiving 0.932 g P pot^{-1} increased WUE_{gas} from 8.22 to 18.23 μg CO_2 mg^{-1} H_2O.

There is a striking similarity between the P response of WUE_T shown in Fig. 6, which was obtained after a growing period of 29 d, and WUE_{gas} (Fig. 8), which was obtained within a few minutes at 29 DAS. Heitholt (1989) observed that WUE_T and WUE_{gas} were well correlated as a function of N stress in *Triticum aestivum* L. If the similarity between WUE_T and WUE_{gas} as a function of nutrient stress represents a general phenomenon in other species, then leaf gas exchange measurements could offer a powerful tool for nearly

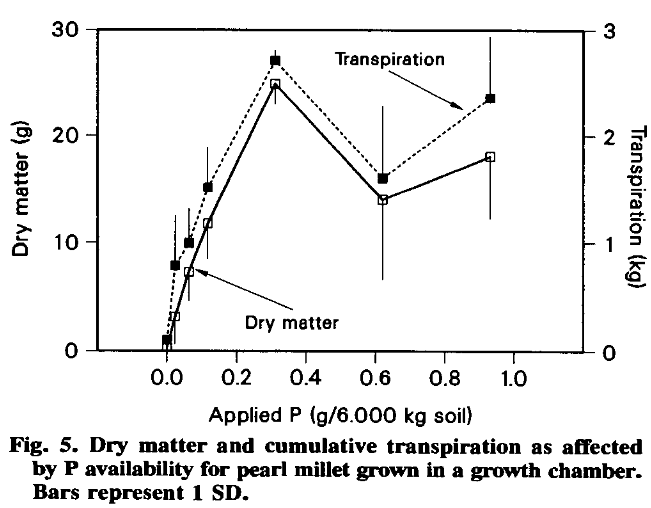

Fig. 5. Dry matter and cumulative transpiration as affected by P availability for pearl millet grown in a growth chamber. Bars represent 1 SD.

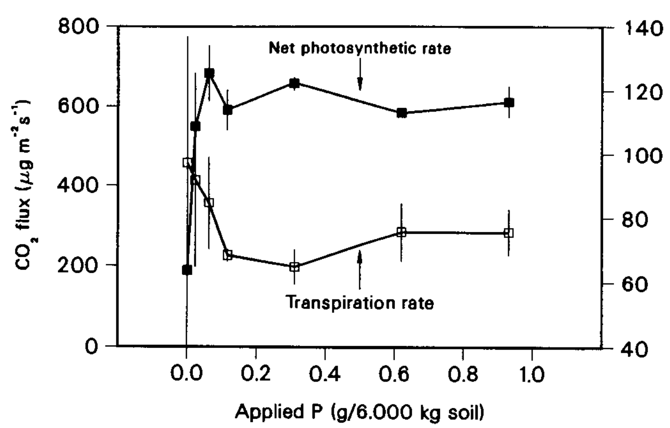

Fig. 7. The CO_2 and H_2O fluxes of the youngest fully expanded leaves of non-water-stressed pearl millet, as affected by P availability, at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1}. Points represent means of four leaf measurements; bars represent ± 1 SD.

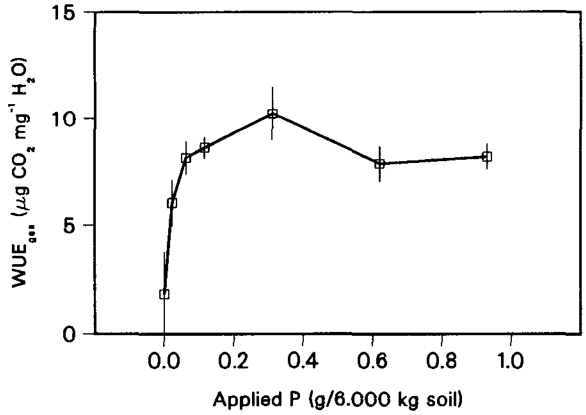

Fig. 8.The ratio of CO_2 to H_2O flux (WUE_{gas}) of the youngest fully expanded leaves of non-water-stressed pearl millet, as affected by P availability, at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1}. Points represent means of four leaf measurements; bars represent ± 1 SD.

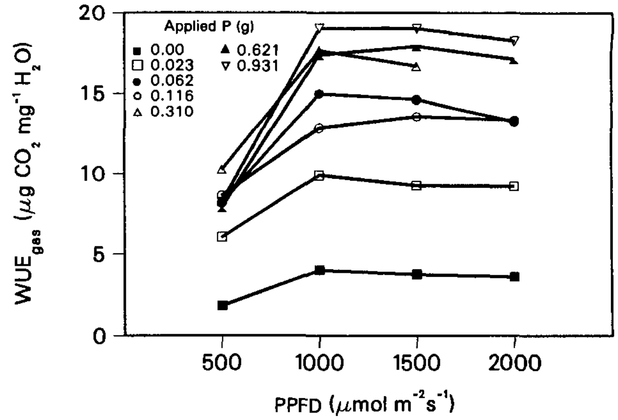

Fig. 9. Response of ratio of CO_2 to H_2O flux (WUE_{gas}) of pearl millet leaves to P availability at different photosynthetic photon flux densities (PPFD). Points represent the means of two leaf measurement. No measurements were obtained for the 0.310-g P treatment at 2000 μmol m^{-2} s^{-1} due to instrument failure.

instantaneous, in vivo assessment of plant nutrient status.

There have been several reports on the inhibitory effect of P deficiency on photosynthetic rate (e.g., for *Hordeum vulgare* L., Pham Thi Nhu Nghia et al., 1981; *T. aestivum* L., Machler et al., 1984; and *Glycine max* L., Lauer et al., 1989). However, a decrease in net photosynthetic rate does not imply a decrease in WUE_{gas} when accompanied by a compensatory decrease in stomatal conductance. For example, Wong et al. (1985) observed that nutrient deficiencies in *Gossypium hirsutum* L. and *Zea mays* L. decreased net photsynthetic rate, but the ratio of CO_2 assimilation to stomatal conductance remained constant at various levels of nitrate, phosphate, and PPFD. However, these plants were grown in 5 L of "sterilized garden soil," which probably was higher in available P than the Betis sand used in this experiment. The ratio of assimilation to conductance might not be constant at lower nutrient levels. Ackerson (1985), for example, observed that photosynthesis of *G. hirsutum* L. increased with added P, but stomatal conductance decreased, thus increasing WUE_{gas}. Similarly, Morgan (1984) and Heitholt (1989) observed a positive effect of N level on WUE_{gas} in *T. aestivum*, and Penning de Vries and Van Keulen (1982) state that certain annual grasses in Israel cannot control their stomates (i.e., stomates continue to transpire freely), when photosynthesis is inhibited by N deficiency. It seems, then, that the mechanisms by which nutrient stress affects stomatal control of CO_2 fixation and the ratio of assimilation to conductance remain unclear. In other studies we are addressing this topic within the context of P stress and pearl millet water use.

Table 2. Summary statistics for the nonlinear model $WUE_{gas} = B/(1 + e^{-0.002PPFD})$, fitted to millet WUE_{gas} data obtained at different levels of soil P and photosynthetic photon flux density (PPFD). The coefficient *B* was determined for each P level.†

P level	Model R^2	*B* estimate	95% confidence interval	
			Lower	Upper
g 6.000 kg^{-1}				
0.000	0.76	3.47	2.10	4.84
0.023	0.97	9.50	8.17	10.83
0.062	0.97	14.05	12.08	16.01
0.116	0.97	13.56	11.71	15.42
0.310	0.97	17.36	14.59	20.13
0.621	0.95	16.35	13.57	19.14
0.931	0.95	16.84	13.90	19.78

† WUE_{gas} = leaf net photosynthetic rate/transpiration rate.

SUMMARY AND CONCLUSIONS

Data presented in this study demonstrate the positive effect of P on pearl millet DM production, photsynthetic rate, WUE_T, and WUE_{gas}, supporting conclusions reached long ago by Briggs and Shantz (1913, p. 51) on crop water requirement (the inverse of WUE_T): "Although the water requirement for a given crop varies widely according to season, soil, and fertilizer, the results show conclusively a marked reduction in the water requirement accompanying the use of phosphate as a fertilizer."

It is important to emphasize that the low levels of P used in this study are comparable to those often found in low-input millet fields of the Sahel. From a practical point of view, therefore, results of this study further reinforce our previous conclusions (Payne et al., 1990, 1991a, 1991b) and those of Penning de Vries and Djiteye (1982) that water supply in the Sahel and similar semiarid environments cannot be effectively managed for production without addressing soil fertility constraints.

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