Nitrogen and Phosphorus Uptake in Pearl Millet and Its Relation to Nutrient and Transpiration Efficiency

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ABSTRACT

Depending on soil and rainfall characteristics, pearl millet [*Pennisetum glaucum* (L.) R. Br.] production in the Sahel can be limited by inefficient use of nutrients, especially N and P, or by inefficient use of water. This study measured pearl millet N and P uptake and compared the efficiency with which N, P, and water are used for growth under varied soil P and water availability. Millet was grown outdoors in semiarid West Texas using rain-sheltered pots of low pH, P-deficient sandy soil. Treatments consisted of four P levels (0–56 g m^{-2}) and two water treatments (stressed and not). Plant P concentration decreased strongly with plant age; added P and water stress increased stem and leaf P concentration. Plant N concentration also decreased with age and increased with water stress, but decreased with added P. Because of the effects of age, water availability, and P level on organ nutrient concentration, P-use efficiency (PUE) increased with age, decreased with water stress, and decreased with added P. Nitrogen-use efficiency (NUE) also increased with age and decreased with water stress, but tended to increase with added P. Shoot transpiration efficiency (WUE_T) increased with water stress and added P, and so varied inversely with PUE throughout the growth cycle. Phosphate root uptake efficiency (PRE) was less sensitive than PUE to age, P availability, and water stress, because of the compensating effect of root growth; PRE was also positively correlated with WUE_T and yield. For crop improvement programs interested in increasing both P- and water-use efficiency, PRE is probably a better selection index than PUE.

PLANT GROWTH RATE is limited by the efficiency with which the most limiting growth factor is used to produce biomass. Because of a strong north–south rainfall gradient, pearl millet production in the West African Sahel is limited more often by water availability in the north, and by nutrient availability in the south (Penning de Vries and Djitèye, 1982; Payne et al., 1990). However, because of a large temporal and spatial variability of rainfall (Stroosnijder and van Heemst, 1982; Nicholson, 1983), the limiting factor to millet growth at any location during any year could be either water or nutrient availability.

Studies have been made of pearl millet growth and nutrient uptake under different fertility treatments (Smith and Clark, 1968; Munda et al., 1985), and of growth and transpiration under different water treatments (Gregory and Squire, 1979; Azam-Ali et al., 1984; Payne et al., 1992). Two papers summarized a field study that measured nutrient uptake and transpiration at two levels of irrigation (Gregory and Squire, 1979; Gregory, 1979). Another study reported nutrient concentration and evapotranspiration during wet and dry years (Bennett et al., 1964). None, however, have examined pearl millet growth, nutrient uptake, and transpiration under differing water and nutrient availabilities.

Our objectives were (i) to measure pearl millet P and N uptake, as a function of time, under varying levels of soil water and P availability and (ii) to analyze relations between nutrient-use efficiency and transpiration efficiency.

MATERIALS AND METHODS

This study was conducted outside in large pots at Lubbock, TX (Payne et al., 1991). Weather conditions approached those of millet growing regions of the Sahel in terms of air temperature, solar radiation, and humidity (Payne et al., 1991). The ICRISAT pearl millet cultivar ICTP 8203 (Rai et al., 1990) was grown in 75-L plastic-lined pots containing 85 kg of P-deficient Betis sand (sandy, siliceous, thermic Psammentic Paleudult) transported from Nacogdoches, TX. The Betis soil was selected because its chemical, physical, and mineralogical properties are similar to those of sandy millet fields in Niger, Senegal, and Mali (Payne, 1990). It has a pH in water of 5.5 and a Bray 1 available P level of 3 mg kg^{-1}. Soil area of the pots was 0.139 m^2.

Fixed effects were P level, water treatment, and time of harvest. A completely random design with five replicates was used. Phosphorus levels were 0, 8.3, 24.3, and 55.9 g of added P m^{-2}, as $CaH_4(PO_4)_2 \cdot H_2O$. Sufficient N (128.1 g NH_4NO_3 m^{-2}) and K (40.3 g K_2SO_4 m^{-2}) were added so as to be nonlimiting to plant growth. Fertilizer was thoroughly mixed into the upper 0.15 m of soil before planting.

Millet was planted on 25 June 1988 in 300 pots, and thinned to two plants per pot at 7 days after emergence (DAE). At 14 DAE, pot liners were sealed around the base of plants, so that water loss was through transpiration only. Rain shelters were used to cover plants during rain to prevent unmetered additions of water.

There were two water treatments, water-stressed and non-water-stressed. All pots were watered to ≈ 0.16 m^3 m^{-3} before planting. Average soil water content of each pot was determined two or three times weekly by weighing with a load cell balance. After weighing, pots with water-stressed plants were watered to an average soil water content of 0.07 m^3 m^{-3}, unless water content was already greater than this amount, in which case no water was added. 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 this amount. After each weighing, average daily transpiration (T) was calculated for each P level from a pot water balance equation (Payne et al., 1992). Sufficient water was then added at 1- or 2-d intervals to compensate for daily transpiration. At each subsequent weighing, a new rate was calculated. On isolated occasions when incipient water stress was evident in individual plants, several kilograms of water were immediately added.

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. This left 60 unharvested pots at the end of the experiment. Plants were separated into roots, living

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Abbreviations: DAE, days after emergence; DM, dry matter; NUE, nitrogen-use efficiency; PRE, phosphorus root uptake efficiency; PUE, phosphorus-use efficiency; WUE_T, transpirational water-use efficiency.

Table 1. ANOVA of the effects of harvest date, soil-added P, and water treatment on concentration of N and P in leaves and stems of pearl millet.

Source†	df	Mean squares	P
Leaf N concentration			
Harvest (H)	4	840	<0.001
P level (P)	3	870	<0.001
Water treatment (W)	1	2962	<0.001
H × P	12	53	0.051
H × W	4	228	<0.001
P × W	3	11	0.772
H × P × W	12	57	0.034
Error	75	28	–
Leaf P concentration			
Harvest (H)	4	19.3	<0.001
P level (P)	3	9.0	<0.001
Water treatment (W)	1	1.6	0.001
H × P	12	0.7	<0.001
H × W	4	0.7	0.002
P × W	3	1.4	<0.001
H × P × W	12	0.5	<0.001
Error	76	0.1	–
Stem N concentration			
Harvest (H)	4	793	<0.001
P level (P)	3	1043	<0.001
Water treatment (W)	1	4590	<0.001
H × P	12	22	0.323
H × W	4	341	<0.001
P × W	3	48	0.066
H × P × W	12	42	0.021
Error	75	19	–
Stem P concentration			
Harvest (H)	4	32.5	<0.001
P level (P)	3	2.8	<0.001
Water treatment (W)	1	0.3	0.236
H × P	12	0.7	<0.001
H × W	4	1.8	<0.001
P × W	3	1.2	<0.001
H × P × W	12	0.4	0.018
Error	74	0.2	–

† Model R^2 values: leaf N concentration, 0.84 ; leaf P concentration, 0.92; stem N concentration, 0.90; stem P concentration, 0.92.

leaves, dead leaves, stems, and panicles. These were weighed after drying to obtain total dry weight (DM) in each pot.

All panicles from a given P level, water treatment, and harvest were combined and threshed together to increase threshing efficiency. Additional experimental details, including daily weather data, were presented by Payne et al. (1991).

Stems and dead and live leaves of three replicates from each P level and water treatment were randomly selected from Harvests 2 to 6 for nutrient analyses. Only three of five replicates were used, to save time and expense and because nutrient concentration tends to be less variable than biomass (Chapin and Van Cleve, 1989). Root samples were not analyzed for nutrients.

Stem, leaf, grain, and chaff samples were ground to pass through a 1-mm sieve and were thoroughly mixed. Samples ($\approx$ 1 g) were digested using the wet oxidation procedure (Nelson and Sommers, 1980). Digests were analyzed simultaneously for N and P using a Technicon autoanalyzer (Technicon Industrial Systems, Tarrytown, NY).[1] Concentration of P was determined using the molybdate blue procedure, and N concentration was determined using the salicylate-hypochlorite-nitroprusside colorimetric procedure (Technicon, 1976).

Plant nutrient accumulation was determined by multiplying nutrient concentration by partition mass, then summing over partitions. Nutrient concentration of grain was obtained by multiplying panicle weights by the mean threshing percentage and grain nutrient concentration. Nutrient content of the rest of the panicle was obtained by multiplying one minus the mean threshing percentage by the nutrient concentration of the chaff.

For the second through sixth harvests, shoot transpiration efficiency (WUE_T, kg DM kg^{-1} transpiration) was calculated from shoot DM/T_{cum}, where T_{cum} is cumulative transpiration and DM is aboveground biomass. We used WUE_T data only from the three replicates for which nutrient analyses were made. Phosphorus-use efficiency (PUE, g dry matter mg^{-1} P uptake)

[1] Mention of trade names does not constitute an endorsement.

Table 2. Nitrogen content of pearl millet partitions at different harvests as affected by soil-added P, water supply, and ontogeny.

		N content									
		28 DAE†		42 DAE		56 DAE		70 DAE		80 DAE	
Plant part	Added P	NWS‡	WS	NWS	WS	NWS	WS	NWS	WS	NWS	WS
	g m^{-2}	g kg^{-1}									
Leaves	0	44	50	35	49	31	43	36	42	34	43
(SE = 3)	8	45	41	29	34	28	42	24	39	21	37
	24	44	39	23	25	23	38	17	32	9	38
	56	39	45	21	29	28	38	17	43	12	29
Stems	0	41	50	29	46	27	39	24	41	19	38
(SE = 3)	8	42	36	20	31	23	28	20	36	14	35
	24	32	35	19	20	23	36	14	28	6	35
	56	30	31	13	26	14	32	10	31	5	27
Dead leaves	0	–§	–	–	–	–	–	5	–	27	30
	8	–	–	–	–	21	–	10	–	16	32
	24	–	–	–	–	11	–	9	12	12	25
	56	–	–	–	–	12	22	9	27	10	19
Chaff¶	0	–	–	–	–	–	–	29	–	26	30
	8	–	–	–	–	30	–	39	–	23	37
	24	–	–	–	–	41	–	27	43	18	31
	56	–	–	–	–	33	43	20	36	13	34
Grain¶	0	–	–	–	–	–	–	–	–	30	–
	8	–	–	–	–	–	–	–	–	25	37
	24	–	–	–	–	–	–	27	–	25	26
	56	–	–	–	–	–	–	29	29	21	31

† DAE, days after emergence.
‡ NWS, non-water-stressed; WS, water-stressed.
§ Blanks indicate negligible dry matter production.
¶ No SE: panicles of a given treatment were threshed together.

Table 3. Phosphorus content of pearl millet partitions at different harvests as affected by soil-added P, water supply, and ontogeny.

		P content									
		28 DAE†		42 DAE		56 DAE		70 DAE		80 DAE	
Plant part	Added P	NWS‡	WS	NWS	WS	NWS	WS	NWS	WS	NWS	WS
	g m^{-2}	g kg^{-1}									
Leaves	0	2.0	2.1	0.7	1.0	0.5	0.6	0.5	0.3	1.0	0.8
(SE = 0.2)	8	3.0	1.8	0.8	0.8	0.3	0.9	0.3	0.5	0.3	0.5
	24	3.7	2.2	1.5	1.3	0.6	1.2	0.3	1.1	0.3	1.0
	56	3.6	4.9	1.9	2.6	1.6	2.2	0.6	1.9	0.5	1.1
Stems	0	2.1	2.1	0.9	1.2	0.4	0.8	0.4	0.4	0.3	0.3
(SE = 0.3)	8	4.3	2.2	0.8	1.0	0.3	0.4	0.1	0.3	0.2	0.3
	24	4.2	2.3	1.5	1.3	0.2	1.0	0.1	0.6	0.1	0.4
	56	3.9	4.2	1.6	2.3	0.5	1.3	0.2	1.1	0.1	0.5
Dead leaves	0	—§	–	–	–	–	–	0.1	–	0.4	0.1
	8	–	–	–	–	0.2	–	0.2	–	0.2	0.3
	24	–	–	–	–	0.2	–	0.5	0.6	0.1	1.0
	56	–	–	–	–	0.5	0.9	0.2	2.0	0.4	0.7
Chaff¶	0	–	–	–	–	–	–	2.0	–	2.2	2.4
	8	–	–	–	–	2.2	–	4.2	–	1.6	3.3
	24	–	–	–	–	5.1	–	1.9	5.1	0.9	1.7
	56	–	–	–	–	4.0	5.3	3.9	3.9	0.7	3.1
Grain¶	0	–	–	–	–	–	–	–	–	2.3	–
	8	–	–	–	–	–	–	–	–	1.9	–
	24	–	–	–	–	–	–	2.2	–	1.8	2.1
	56	–	–	–	–	–	–	3.8	3.8	1.9	3.1

† DAE, days after emergence.
‡ NWS, non-water-stressed; WS, water-stressed.
§ Blanks indicate negligible dry matter production.
¶ No SE: panicles of a given treatment were threshed together.

and N-use efficiency (NUE, g dry matter mg^{-1} N uptake) were calculated from the ratio of shoot DM to total P and N accumulation. Phosphorus root uptake efficiency (PRE, mg shoot P g^{-1} root DM) was calculated from shoot P accumulation divided by root DM.

Least squares ANOVA for stem and live leaf N and P concentrations, and for shoot WUE_T, were made using SYSTAT's MGLH module (SYSTAT, Evanston, IL; Wilkinson, 1990), using P level, water treatment, and harvest as main factors. Occasionally there were missing values due to lost samples or insufficient amount of sample for chemical analyses; these are reflected in degrees of freedom given for ANOVA results. Means for nutrient concentrations of dead leaves, grain, and chaff are reported for individual harvests, since these were not present at all harvests.

RESULTS AND DISCUSSION

ANOVA results (Table 1) indicate that both stem and leaf nutrient concentrations were influenced by interactive effects between plant age (i.e., harvest), P level, and water treatment (Table 1). The decrease of N and P concentrations (Tables 2 and 3) with ontogeny is similar to values reported separately by Gregory (1979) and Munda et al. (1985) for pearl millet grown in India. Although there were large relative increases in leaf and stem P concentration with increasing P level at all harvests (Table 3), because of the ontological decrease in P concentration, absolute differences were small at final harvest, especially for stems. This same trend was evident in the study by Munda et al. (1985).

Increased P level was associated with decreased stem and leaf N concentration at all harvests (Table 2). Adding P tended to decrease mean N concentration in chaff and grain, but there was no obvious effect on P concentration. Nutrient concentration in chaff was very similar to grain nutrient concentration. Even though no statistical inference can be made from these data, they do have practical significance for nutrient cycling in Sahelian agricultural systems, since chaff is generally discarded (Powell and Fussell, 1993).

Water stress increased nutrient concentration in stems, live leaves, and dead leaves (Tables 2 and 3). Water stress seemed to increase chaff and grain nutrient content, but again no statistical inference can be made. Gregory (1979) found that nutrient concentration decreased in water-stressed pearl millet, whereas Bennett et al. (1964) found that water stress increased nutrient concentration. Richards and Wadleigh (1952), summarizing existing data on soil

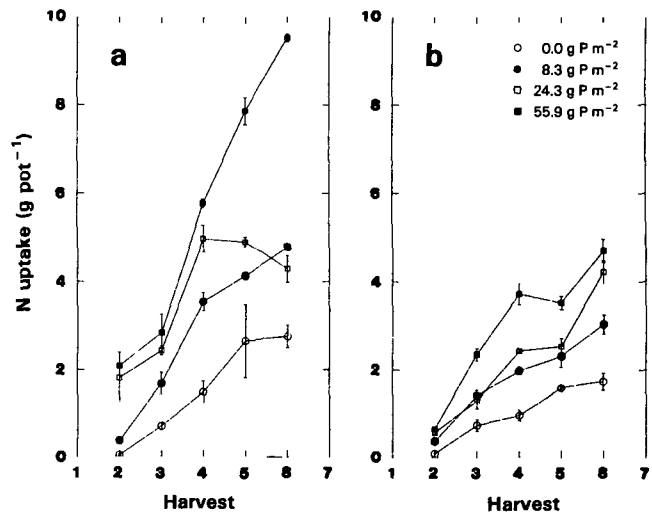

Fig. 1. Nitrogen uptake of pearl millet shoots at sequential harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Points are means of three replicates; bars represent ±1 SE.

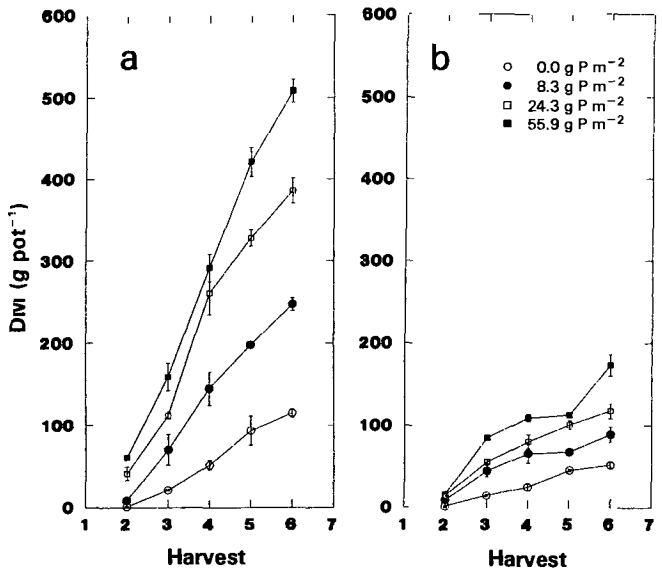

Fig. 2. Shoot dry matter (DM) evolution of pearl millet as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Points are means of five replicates; bars represent ±1 SE.

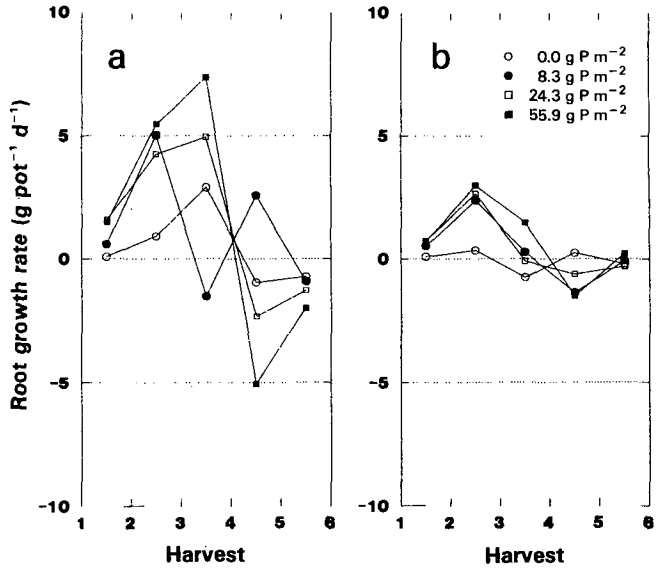

Fig. 4. Root growth rates of pearl millet as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Points are means of five replicates; bars represent ±1 SE.

nutrient availability as a function of soil water availability, concluded that decreasing water supply produced a definite increase in plant N concentration, and variable effects on P concentration. Viets (1972), however, pointed out that plant nutrient concentration can decline under water stress when most nutrients are in a dry, upper soil layer while most of the water is being extracted from lower, nutrient-poor depths. Such was probably the case in the irrigation study of Gregory (1979).

Shoot N uptake increased with added P, but decreased with water stress (Fig. 1). Curves of N uptake with time, as affected by P and water availability, were similar in form to DM accumulation (Fig. 2), with the unexplained exception of the non-water-stressed plants at 24.3 g P m^{-2}. The data show that water stress reduced the ability of plants to take up N; i.e., N availability was reduced (Viets, 1972).

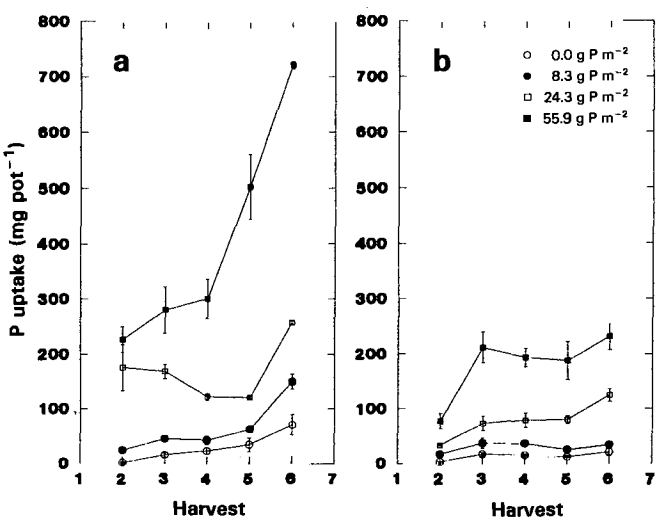

Fig. 3. Phosphorus uptake of pearl millet shoots at sequential harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Points are means of three replicates; bars represent ±1 SE.

Shoot P accumulation (Fig. 3) was more difficult to interpret than N uptake, but there seem to be the following general trends. First, P uptake after the first 4 wk of growth (i.e., at Harvest 2) increased with soil-added P, but less so for water-stressed plants than non-water-stressed plants. Second, between the second and third harvests, the only large additional accumulation of P was observed in the highest P level of water-stressed plants; additional accumulation was small or nonexistent for other treatments. Third, generally, from the third to fifth harvests additional P accumulation was very small, the only exception being the highest P level of the non-water-stressed treatment. As with N uptake, there was an apparent decline in P uptake between Harvests 3 and 5 of the non-water-stressed plants at the 24.3 g P m^{-2} level, for which we have no explanation. Finally, from the fifth to sixth harvest, shoot P accumulation increased in non-water-stressed plants, but remained fairly constant in water-stressed plants.

One interpretation consistent with these trends is a rapid initial uptake of any available P in the soil during the first 4 wk of plant growth, during which time roots explored the soil volume. Thereafter, total shoot P uptake remained constant until and unless root senescence caused translocation from roots to shoots. Most non-water-stressed plants had pronounced negative root growth rates between the fourth and sixth harvests (Fig. 4), whereas water-stressed plants had smaller growth rates. (See Payne et al., 1991, for more detailed growth analysis data.) The most negative root growth rates were observed between fourth and sixth harvests for the non-water-stressed plants at the highest P level; these plants also had the greatest shoot P uptake during this period (Fig. 3). Root DM was poorly correlated with shoot P uptake (data not shown).

Nitrogen uptake was linearly related to plant transpiration (Fig. 5). However, slopes of linear models indicate that about twice as much N was taken up per kilogram

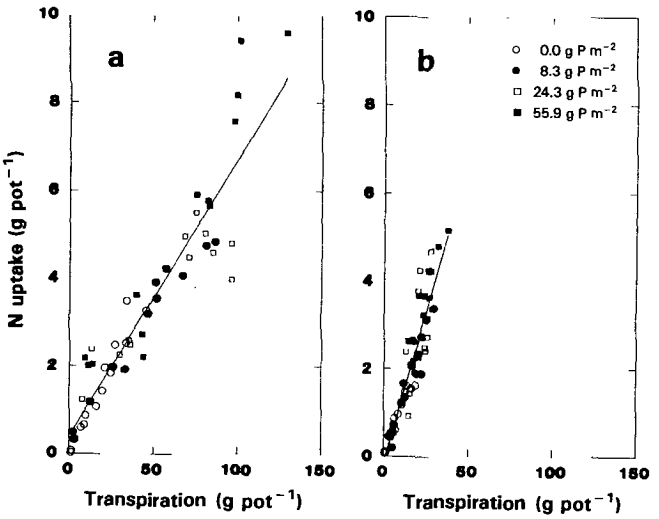

Fig. 5. Nitrogen uptake of pearl millet shoots as a function of transpiration, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Linear equations fitted to data are $Y = 0.063X + 0.40$ ($R^2 = 0.88$) for non-water-stressed plants and $Y = 0.138X - 0.16$ ($R^2 = 0.85$) for water-stressed plants.

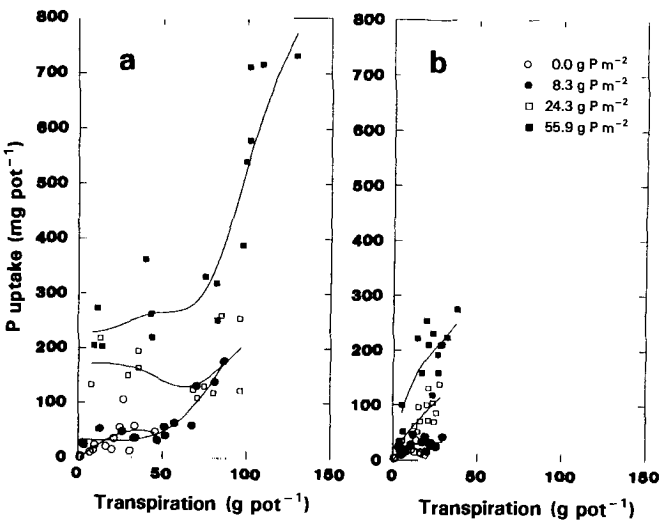

Fig. 6. Phosphorus uptake of pearl millet shoots as a function of transpiration, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed.

of transpiration in water-stressed plants than in non-water-stressed plants. Since soil water content for water-stressed treatments was roughly half that of non-water-stressed treatments, this implies roughly twice the N concentration in the soil solution and therefore also in the transpiration stream. The linear relation between N uptake and transpiration, and the steeper slope for water-stressed plants, is consistent with N transport through the plant by mass flow. An alternative hypothesis might be that solute concentrations were below that required for maximum flux across the root surface and therefore uptake per unit root area was proportional to N concentration in the soil solution.

The linearity shown in Fig. 5 is probably due to the relatively large amount of fertilizer N added in plant-available form. N uptake is not always this well correlated with transpiration (Barber, 1962). In soils of low fertility, N uptake is probably much more related to diffusion than mass flow (Clarkson and Hanson, 1980), and N availability would vary with many environmental parameters.

There was no clear relation between P uptake and transpiration, particularly for non-water-stressed plants (Fig. 6). This was also observed in maize (*Zea mays* L.) by Barber (1962). Non-water-stressed plants accumulated P rapidly during the first 10 kg of transpiration, but P accumulation remained more or less constant between 20 and 60 kg of transpiration. Thereafter, shoot P uptake increased, which we suggest was due to translocation from roots. Initial root growth rates increased with added P supply in non-water-stressed plants (Fig. 4), suggesting that the increased initial P accumulation was due to a combination of rapid root exploration through increased surface area, and increased soil solution concentration.

Lesser P uptake within water-stressed plants was due to lower root growth rate (Fig. 4) and, presumably, lower P diffusion caused by greater soil tortuosity. However, slopes of P uptake as a function of transpiration (Fig. 6) suggest that greater P concentration in the soil solution can increase P uptake even under water stress. No further P was taken up after the first 10 kg of water was transpired by water-stressed plants in the lower two P levels; however, those receiving 24.3 and 55.9 g P m^{-2} continued taking up P until final harvest, at which point they had transpired ≈ 35 kg. The amount of P accumulated by water-stressed plants was, at final harvest, more or less the same as those taken up by non-water-stressed plants of the same P level between 20 and 60 kg of transpiration. We speculate that differences thereafter were attributable to P translocation from roots.

Shoot NUE generally increased with added P (Fig. 7), but for Harvests 5 and 6 it decreased between P levels of 24.3 and 55.9 g P m^{-2}. Greater NUE was due to lesser N concentrations associated with higher P levels (Table 2). Water stress generally reduced shoot NUE (Fig. 7), because it increased N concentration (Table 2). Shoot NUE slightly increased with ontogeny, due to the associated reduction in N concentration (Table 2).

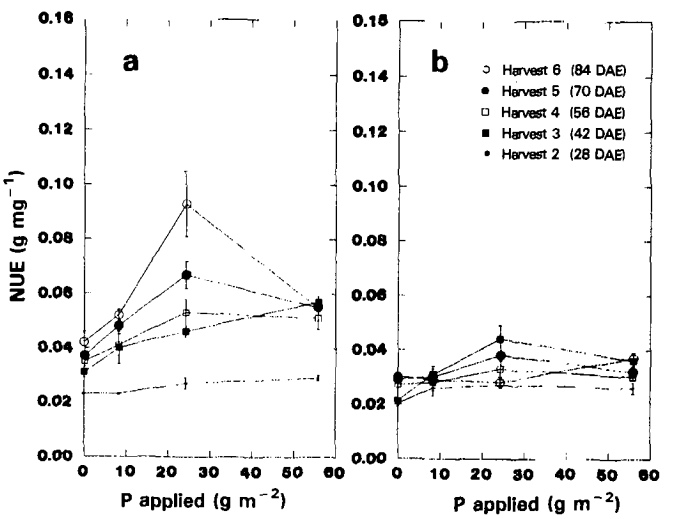

Fig. 7. Nitrogen-use efficiency (NUE) of pearl millet at different harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. DAE, days after emergence.

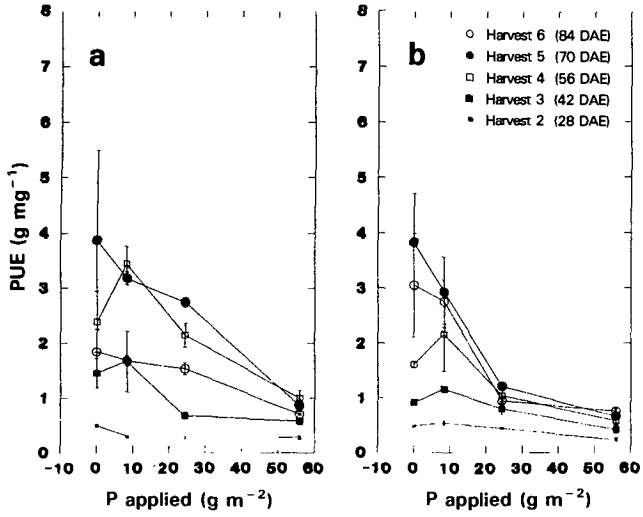

Fig. 8. Phosphorus-use efficiency (PUE) of pearl millet at different harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. DAE, days after emergence.

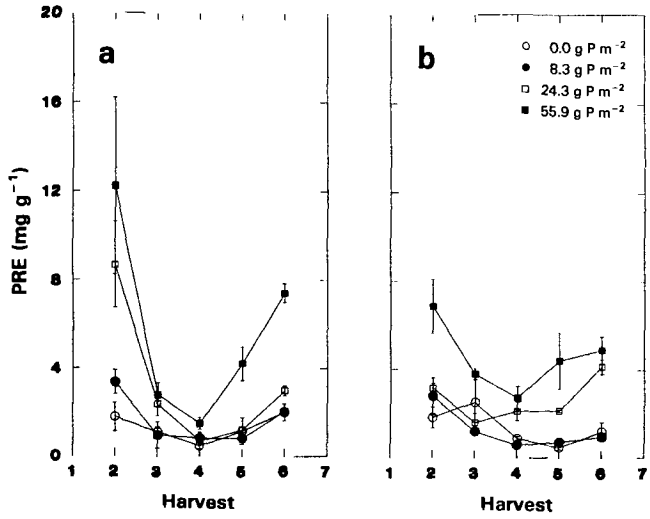

Fig. 10. Phosphorus root uptake efficiency (PRE) of pearl millet at sequential harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. Points are means of three replicates; bars represent ±1 SE.

Shoot PUE increased greatly with time (Fig. 8) due to the associated decrease in P concentration (Table 3). Shoot PUE decreased with added P due to higher P concentration in stems and leaves, and to higher partitioning to panicles, which had high P concentration (Table 3).

As with whole-plant WUE_T data (Payne et al., 1992), shoot WUE_T increased with added P and water stress, and changed with harvests (Fig. 9). Shoot WUE_T generally increased with NUE, with exceptions between 24.3 and 55.9 g P m^{-2} for some harvests. Throughout the life cycle, however, and irrespective of water availability, PUE decreased as WUE_T increased, and vice versa.

Phosphorus root uptake efficiency did not increase so strongly with ontogeny as PUE because of the compensating effect of root growth (Fig. 10). Aside from the PRE values of the two greater P levels in the non-water-stressed treatment at Harvest 2, which had very high standard errors, the range of PRE values was relatively conservative, and less affected by water stress and P level than was PUE. Phosphate root uptake efficiency generally declined between Harvests 2 and 4 due to rapidly growing roots (Fig. 4) and low P uptake (Fig. 3). From Harvests 4 to 6, PRE increased due to continued shoot P uptake and decreased root growth. Variation in root growth rates and shoot uptake was less for water-stressed plants than for non-water-stressed plants, so their PRE was less variable as well. Phosphorus-use efficiency rapidly decreased as PRE increased from 0 to 5 mg g^{-1} (Fig. 11), but shoot WUE_T increased over this same range of PRE values (Fig. 12). At higher PRE values, PUE and WUE_T were more or less constant.

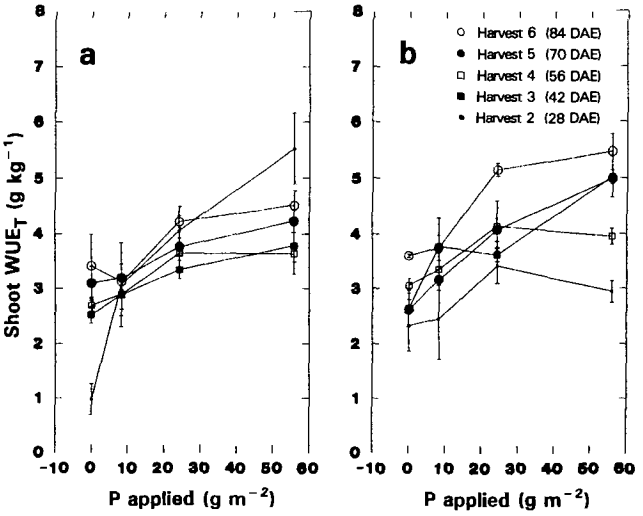

Fig. 9. Shoot transpirational water-use efficiency (WUE_T) of pearl millet at different harvests, as affected by soil-added P and water supply: (a) non-water-stressed; (b) water-stressed. DAE, days after emergence.

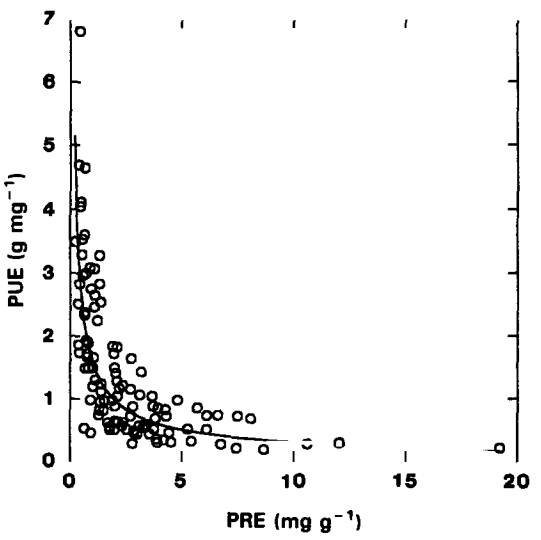

Fig. 11. Relation between mean P-use efficiency (PUE) and mean P root uptake efficiency (PRE) in pearl millet. Points are mean values taken from the data of Fig. 8 and 10.

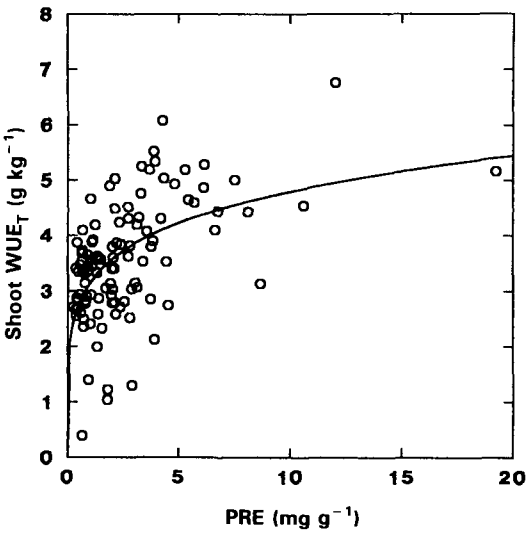

Fig. 12. Relation between shoot transpirational water-use efficiency (WUE_T) and P root uptake efficiency (PRE) in pearl millet. Points are mean values taken from the data of Fig. 9 and 10.

At final harvest, PRE could be empirically related to grain yield (G) for water-stressed plants by $G = (10.9\ PRE) - 10.4$ ($R^2 = 0.83$), and for non-water-stressed plants by $G = (87.6\ PRE) - 120.5$ ($R^2 = 0.94$). Shoot dry matter at final harvest could be empirically related to PRE using the nonlinear models $S = (67.3\ PRE)^{0.51}$ ($R^2 = 0.95$) for water-stressed plants, where S is shoot dry matter (g), and for non-water-stressed plants using the equation $S = (140\ PRE)^{0.60}$ ($R^2 = 0.95$). The larger regression coefficients for non-water-stressed plants result from the larger growth response to P in the presence of greater water supply. These empirical models illustrate that PRE was positively correlated with yield, and with WUE_T up to a limiting value lying between 5 and 6 g kg^{-1}.

Based on our results, one would generally expect pearl millet to have higher WUE_T at the expense of PUE during dry years, and higher PUE at the expense of WUE_T in wetter years. Among other things, this complicates comparison of pearl millet genotypes' efficient use of phosphate due to year-to-year or site-to-site variations in soil P and water status. Furthermore, increased PUE was associated with reduced growth rate, reduced grain yield, and smaller WUE_T. Because PRE offers an indication of root activity, which is important to both nutrient and water acquisition in the Sahel and similar agroecosystems, it seems to be a better criterion for evaluating efficient use of phosphate and water in pearl millet.

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