

# Pearl Millet Growth as Affected by Phosphorus and Water

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## ABSTRACT

The interaction of soil water and P supply is of paramount importance to pearl millet [*Pennisetum glaucum* (L.) R. Br.] growth in Sahelian Africa due to unreliable rainfall and low soil P availability. This study was conducted to quantify the growth response of pearl millet to water supply and P under conditions analogous to the Sahel in terms of climate and soil. Millet was grown for 84 d in pots containing 85 kg of Betis sand (sandy, silicious, thermic Psammentic Paleustalf) at a semiarid location near Lubbock, TX, and harvested at regular intervals. Pots were treated with four levels of applied P (0.00, 1.15, 3.38, and 7.77 g P m<sup>-2</sup>) and two water levels (water stressed and non-water stressed). Whole plant biomass at final harvest increased within the non-water stressed treatment from 145 g per pot in the 0.00 g P m<sup>-2</sup> level to 626 g per pot in the 7.77 g P m<sup>-2</sup> level, and from 64 to 220 g per pot within the water stressed treatments. Analysis of variance showed highly significant statistical interaction between water and P level during most of the experiment. Maximum whole plant production rates for non-water stressed plants occurred between 42 and 58 days after emergence (DAE), increasing from 5.0 g d<sup>-1</sup> in the 0.00 g P m<sup>-2</sup> level to 18.5 g d<sup>-1</sup> in the 7.77 g P m<sup>-2</sup> level, and between 28 and 42 DAE for water stressed plants, increasing from 1.3 g d<sup>-1</sup> to 8.5 g d<sup>-1</sup>. Growth rates of plant organs also increased with P level irrespective of water level. Our study quantifies the strong influence and interaction of P and water supply on pearl millet growth and development in Sahel-like environments, and demonstrates that water supply under such conditions cannot be effectively managed for pearl millet production without addressing soil fertility constraints.

SOIL WATER AND NUTRIENT SUPPLY and their interaction are of particular importance in the African Sahel because the staple cereal, pearl millet, is grown under dryland conditions characterized by low and erratic rainfall (Sivakumar, 1989), high potential evapotranspiration (Cochemé and Franquin, 1967), and impoverished soils (Jones and Wild, 1975) of low water holding capacity (Payne et al., 1990, 1991a). The sandy soils upon which pearl millet is typically cultivated have been shown to be so deficient in available soil P (Jones and Wild, 1975; Scott-Wendt et al., 1988; Davis-Carter, 1989) that N-response are often not obtained without some basal P additions (Vidal, 1963; Bationo et al., 1985; Timofeyev et al., 1988).

Growth analysis is a standard method of estimating net photosynthetic production of plants, and serves as a link between merely recording plant production and analyzing it by means of physiological methods (Kvet et al. 1971). There are very few growth analysis studies of pearl millet (Gregory and Squire, 1979) despite its importance as a major cereal in drought- and famine-prone areas of the world. Studies have been conducted (i) under optimal conditions for forage production in

Katherine, Australia (Begg, 1963), (ii) under irrigated and unirrigated conditions during the post-monsoon season at Hyderabad, India (Gregory and Squire, 1979), (iii) as a function of row spacing, using only profile-stored water in a sandy soil at Niamey, Niger (Azam-Ali et al., 1984), (iv) under rain-fed and irrigated conditions at Niono, Mali (Jansen and Gosseye, 1986), and (v) using a 150 d variety of pearl millet during a relatively dry (448 mm) year at Bambey, Senegal (Vidal, 1963). The last author demonstrated that grain yields in excess of 2000 kg ha<sup>-1</sup> were obtainable by applying relatively high rates of fertilizer. Local subsistence farmers generally obtain much lower yields on this amount of rainfall (Dancette, 1983).

Because the response of pearl millet growth to soil water and P supply has not been systematically investigated, a growth analysis experiment was made in an environment resembling the Sahel in terms of plant, climate, and soil. Our objective was to measure and analyze the growth response of an African variety of pearl millet to P and water supply in a sandy, acid, and P deficient soil under semiarid conditions.

## MATERIALS AND METHODS

The study was made at the Texas Agricultural Experiment Station near Lubbock, which has a semiarid climate. The pearl millet cultivar ICTP 8203, developed from African landraces by ICRISAT scientists (Rai et al., 1990), was grown in large pots containing an acid, P deficient, Betis sand (sandy, silicious, thermic Psammentic Paleustalf), and harvested at regular intervals. The experiment consisted of a completely random design with fixed effects (P and water level) and five replications.

The Betis soil had a pH in water of 5.5, an available P (Bray 1) of 3 mg kg<sup>-1</sup>, an organic C content of 2 g kg<sup>-1</sup>, and a CEC of 5.0 cmol kg<sup>-1</sup>. Physically, it had a bulk density of 1.64 Mg m<sup>-3</sup>, a sand content of 920 g kg<sup>-1</sup>, and a clay content of 60 g kg<sup>-1</sup>. Chemically, physically, and mineralogically, the Betis soil is similar to soils typically sown to millet in Niger, Mali, and Senegal (e.g., Charreau and Nicou, 1971).

### Site Preparation

Approximately 38 m<sup>3</sup> of the Betis soil were excavated from below a depth of 1 m near Nacogdoches, Texas, fumigated with methyl bromide to prevent transfer of fire ants (*Solenopsis invicta* Buren), and transported to Lubbock, where the soil was dried, mixed, and sieved through a 6.4-mm screen.

Eighty-five kg of soil were poured into each of 300 numbered, 75-L pots (0.21-m radius, approximately 0.75-m depth) which were fitted with two plastic liners. Pots were placed into two 11 × 16 × 1.5-m deep pits, and arranged originally in two columned, north-south rows, with approximately 2 m between columns. Columns were sufficiently far from pit walls that morning and evening shadow effects were negligible. Within columns, pots were separated by about 5 cm. Pits were required to allow rain shelters to cover maturing millet plants without damaging stalks; rain shelters were used to eliminate uncontrolled additions of water to

**Abbreviations:** B, biomass; DAE, days after emergence; D, dead mass; CPR, crop production rate; GR, growth rate; NAR, net assimilation rate; PAR, photosynthetically active radiation; RGR, relative growth rate; and SR, senescence rate.

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pots during rain and on a few occasions to elevate temperature during cool nights. The two pits were approximately 20 m apart, and oriented in the same direction in relation to the sun. Hygrothermographs installed in each pit verified that temperature and humidity in the two pits were identical.

### Planting and Harvesting

Ten to 20 pearl millet seeds were planted 25 June 1988 in each pot at a depth of approximately 5 cm. At 7 DAE, pots were thinned to two plants per pot. At 14-d intervals after emergence, plants from five pots were harvested from both watering treatments of four P levels (described below), for a total of six harvests. Pots were selected for harvest by random number generation irrespective of the pit in which they were located. After each harvest, remaining pots were rearranged to minimize shading. As will be later discussed, all treatments did not reach maturity.

### Phosphorus

Treatments consisted of four relatively low additions of P (0.00, 0.16, 0.47, and 1.08 g P per container), added as  $\text{CaH}_4(\text{PO}_4)_2 \cdot \text{H}_2\text{O}$  and thoroughly mixed into the top 0.15 m of soil. On a per area basis, this equals 0.00, 1.15, 3.38, and 7.77 g P  $\text{m}^{-2}$ , and corresponds roughly to 0, 10, 30, and 70 kg P  $\text{ha}^{-1}$ . Each container also received before planting 18.1 g K  $\text{m}^{-2}$  and 44.8 g N  $\text{m}^{-2}$ . Additionally, 11.2 g N  $\text{m}^{-2}$  was added to each pot in liquid form on 6 Aug. 1988, and 22.3 g N  $\text{m}^{-2}$  on 12 Aug. 1988. Relatively high rates of K and N were applied so that these could be assumed to be non-limiting to plant growth.

### Water

For each level of P there were two watering treatments, "non-water stressed" and "water stressed." Watering regimes and P treatments were randomly assigned to pots before planting.

At 14 DAE, soil evaporation was prevented by sealing the exposed portion of pot liners around a plastic "collar" at the base of the plants. Two watering portals were inserted into the liners, and pea gravel (approx. 3-mm radius) placed at their bottom to prevent soil dispersion during irrigation. Portals were sealed to prevent evaporation when pots were not being watered. A layer of Betis sand was placed over the sealed liners in an effort to maintain a surface albedo more representative of field conditions. Whenever portals, gravel, sand, etc., were added to a pot, their mass was first determined so as not to confound watering, which is described below.

All pots were watered to field capacity, or about 0.16  $\text{m}^3 \text{m}^{-3}$ , before planting. Average soil water content was determined two or three times weekly by weighing pots with a load cell balance, which was accurate to within 0.050 kg.

For water stressed treatments, if average soil water content at weighing was  $\geq 0.07 \text{ m}^3 \text{m}^{-3}$ , no water was added; otherwise, pots were watered to 0.07  $\text{m}^3 \text{m}^{-3}$ . If plants appeared visually to severely wilt between weighings, 0.5 L of water was added. Once plants were stressed, average soil water content within water stressed treatments ranged from approximately 0.03 to 0.07  $\text{m}^3 \text{m}^{-3}$ , corresponding in soils of this texture from about -200 to -30 kPa pressure potential (Payne et al., 1990; 1991a).

For non-water stressed treatments, if average soil water content was  $\leq 0.16 \text{ m}^3 \text{m}^{-3}$ , pots were watered to this amount. The average daily rate of transpiration ( $T$ ) was then calculated for each P level of the non-water stressed treatment from

$$T = I - dS,$$

where  $dS$  represents change in container mass between

weighings, and  $I$  is the amount of water added between weighings. Sufficient water was added at 1- or 2-d intervals to compensate for the daily  $T$  rate until the next weighing, at which point a new rate was calculated. If beginning signs of water stress were evident in individual plants, several liters of water were immediately given.

Two 75-L containers were used as controls, i.e., they were prepared as were the other containers, but were not sown with millet. Water loss from these containers was below the limit of detection of the load cell balance. We therefore concluded that pot water loss other than transpiration was negligible.

### Growth Analysis

At each harvest, plants were separated into roots, stems, green leaves, dead material, and heads, and oven dried at 70 °C. Roots were washed from soil on a grate of 6.4-mm mesh. For growth analysis, measurements at harvest were biomass ( $B$ ), defined as dry mass of live portions of the whole plant or its components, and dead mass ( $D$ ), defined as dry mass of dead portions of the plant. Neither  $D$  nor head  $B$  were appreciable until the fourth harvest. Heads from each treatment for a given harvest were combined for threshing to increase threshing efficiency, and separated into threshings and grain. The term "threshable" grain is used because some heads, particularly those under P and water stress, contained grain too small to be separated by the thresher. Since heads were combined, standard deviation could not be calculated for grain.

For each harvest, ANOVA was used to evaluate the statistical significance of treatment (P and water level) main and interactive effects on  $B$  and  $D$  using SYSTAT (Wilkinson, 1987). Derived parameters were mean Crop Production Rate (CPR), mean organ Growth Rate (GR), mean Senescence Rate (SR), mean Relative Growth Rate (RGR), and Net Assimilation Rate (NAR). These were expressed in terms of  $B$ ,  $D$ , LA, and  $t$ , where  $t$  is time (d), and LA is leaf area ( $\text{cm}^2$ ). Definitions were:

$$\begin{aligned} \text{CPR} &= [(B_2 + D_2) - (B_1 + D_1)] / (t_2 - t_1), \\ \text{GR} &= (B_2 - B_1) / (t_2 - t_1), \\ \text{SR} &= (D_2 - D_1) / (t_2 - t_1), \\ \text{RGR} &= \text{CPR} / (B + D), \\ &\text{and} \\ \text{NAR} &= \text{CPR} / \text{LA}. \end{aligned}$$

For NAR, LA was calculated from green leaf dry mass (LM) using the equation (Payne et al., 1991b):

$$\text{LA} = 133.6 \times \text{LM} + 22.69.$$

Growth between harvests was assumed to be linear, so all growth analysis parameters are presented as means between harvests.

### Weather

In one of the two pits, hourly observations of relative humidity, photosynthetically active radiation (PAR), total incoming radiation, and air temperature were taken from sensors mounted on a vane of adjustable height. Sensor height was maintained at approximately 0.10 m above the tallest millet plants. Daily means of these parameters are presented in Fig. 1 to characterize the growing environment.

## RESULTS AND DISCUSSION

### Biomass and Dead Mass

For all harvests, whole plant and individual plant components'  $B$  increased with applied P and water supply (Fig. 2). During the entire experimental period,

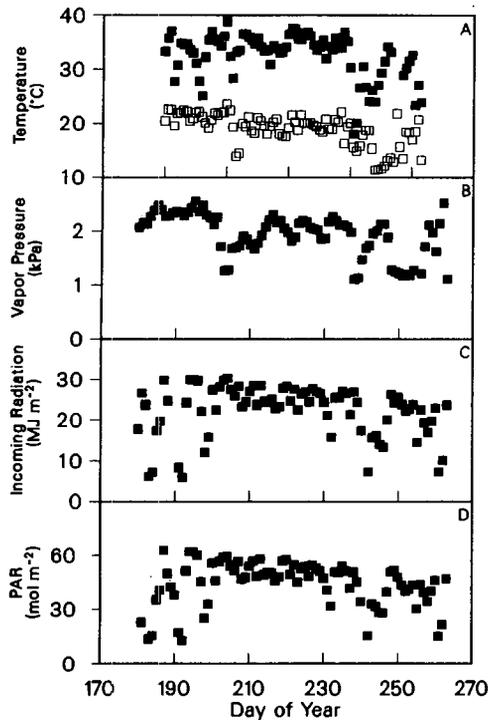


Fig. 1. Characterization of growing season weather in Lubbock, 1988; A) maximum and minimum daily air temperature; B) average daily atmospheric water vapor pressure; C) daily incoming radiation; and D) daily incoming photosynthetically active radiation.

whole plant  $B$  increased with water and P supply, with differences becoming most pronounced during the exponential growth phase. At first harvest (14 DAE), growth was influenced more by P than water supply (Table 1). However, this cannot be generalized to every field situation because pots were watered to field capacity at planting, and therefore plants were not water stressed at emergence. Furthermore, plants of higher P levels within the water stressed treatment tended to grow and transpire more rapidly than those of lower P levels, thereby exhausting available water supply more quickly and becoming water stressed earlier.

Plants of all P levels in the water-stressed treatment showed visible signs of water stress by 21 DAE. At 28 DAE and thereafter (Harvests 2 through 6), P and water additions significantly increased whole plant and plant component  $B$  (Table 1). During this same time, positive interactive effects of P and water level were statistically significant or highly significant for all components except roots at the third harvest. The orderly nature of this interaction at 70 DAE is illustrated in Fig. 3.

In non-water stressed plants, LM was generally greatest between 58 and 72 DAE, whereas in water stressed plants LM increased little if at all after 42 DAE (Fig. 2B). Since pearl millet LM can be related linearly to LA (Payne et al., 1991b), a plot of LA vs. time would duplicate curves shown in Fig. 2B. Increased LA due to P level has many implications for field water and energy balance, water use, and water use efficiency (Tanner and Sinclair, 1983; Lascano et al., 1987).

Root  $B$  was initially increased by P and water addition (Fig. 2C). However, root  $B$  peaked in non-water

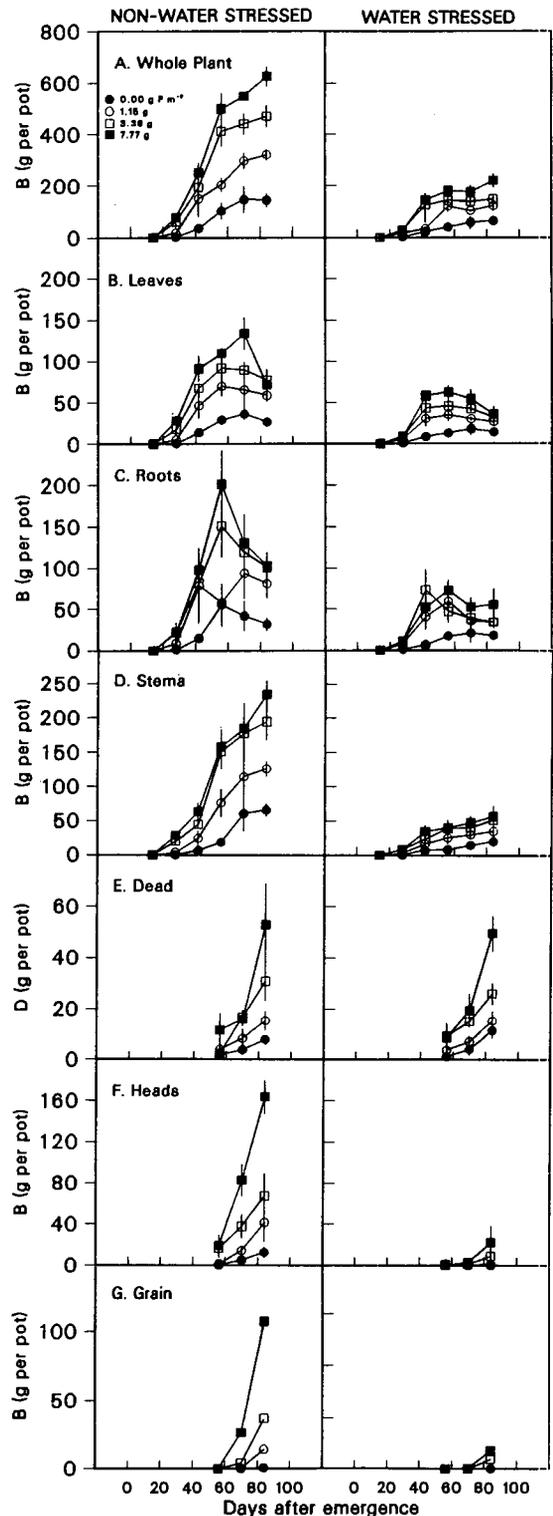


Fig. 2. Dry mass of A) whole millet plants, B) leaves, C) roots, D) stems, E) dead material, F) heads, and G) threshable grain. Points represent means of plants from five 75-L pots. Vertical bars, which are not shown in G), represent one standard deviation

stressed plants at 58 DAE, except for the 1.15 g P m<sup>-2</sup> treatment. Root  $B$  of water stressed plants did not substantially increase after 42 DAE, similar to LM. Furthermore, root  $B$  of water stressed plants increased slightly as P application increased from 0.00 to 1.15 g

Table 1. Degrees of freedom, mean square values, and level of significance from ANOVA for pearl millet dry mass partitions grown near Lubbock, TX, in 1988. Head and dead dry mass was negligible for the first three harvests.

Harvest	Source	df	g per pot						Total
			Roots	Stems	Leaves	Heads	Dead		
1	Water (W)	1	0.014*	0.000	0.001	NA	NA	0.007	
	Phosphorus (P)	3	0.018**	0.013**	0.054**	NA	NA	0.224**	
	W × P	3	0.002	0.000	0.001	NA	NA	0.003	
	Error	31	0.003	0.001	0.001	NA	NA	0.006	
2	W	1	313**	585**	402**	NA	NA	3634**	
	P	3	417**	605**	490**	NA	NA	4350**	
	W × P	3	85.6*	235**	214**	NA	NA	1417**	
	Error	27	26.2	12.4	14.4	NA	NA	108.2	
3	W	1	5539**	1749**	3399**	NA	NA	34314**	
	P	3	8506**	2954**	6339**	NA	NA	47080**	
	W × P	3	841.7	374.4**	308.7*	NA	NA	3358.5*	
	Error	27	535.1	61.07	112.8	NA	NA	1244.2	
4	W	1	40594**	46794**	11376**	670**	5.48	302983**	
	P	3	17954**	14537**	6660.2**	220**	114**	126767**	
	W × P	3	7882.2**	5796.1**	440.57*	230**	44.8	37126.5*	
	Error	28	605.98	264.92	119.75	29.8	15.6	1467.9	
5	W	1	35420**	101527**	20190**	11366**	0.378	572291**	
	P	3	65249**	13092.3**	7907.9**	3228.5**	426.3**	124033**	
	W × P	3	17923**	4896.3**	1675.4**	2767.4**	14.36	37343.8*	
	Error	28	390.91	550.79	149.90	49.823	11.66	857.205	
6	W	1	1819**	126356**	9619**	38550**	19.90	618977**	
	P	3	5432**	20626.8**	2524**	14242**	3102**	180885**	
	W × P	3	1177**	8391.54**	474.3**	7657.4**	111.7	50212.9*	
	Error	31	183.8	213.807	67.44	180.93	60.68	765.500	

\*,\*\* Significant at 0.05 and 0.01 probability levels, respectively.

P m<sup>-2</sup>, but no further increase was observed with higher amounts of P. This suggests root *B* was limited more by water than P supply. A decline in root mass as plants matured was observed in all treatments except the lowest P rate of the water stressed treatment. This may be due to roots dying off, i.e., "shedding" (Taylor, 1983), or translocation to shoots. The fact that neither root nor leaf *B* peaked in the 0.00 g P m<sup>-2</sup>, water stressed treatment suggests that these plants were maturing at a greatly reduced rate.

Unlike leaves and roots, stem *B* (Fig. 2D) continued to increase throughout the growth cycle. Response was similar to those of whole plants (Fig. 2A), but stem *B* was more inhibited by water stress than was whole plant *B*. Despite the low stem *B* in water stressed plants, a highly significant positive response to P, as well as an interactive effect between water and P, are evident (Table 1 and Fig. 3).

Data in Table 1 (see Harvests 4, 5, and 6) and Fig. 2E demonstrate that accumulation of *D*, which consisted almost entirely of leaves, was strikingly similar for equal levels of P irrespective of watering level. If such can be shown to be a general phenomenon, it would greatly ease modeling of leaf senescence in pearl millet. Since whole plant *B* and LM were reduced by water stress, the proportion of total dry matter and leaf mass comprised by *D* was higher in water-stressed plants.

Data for storage organ (heads) and threshable grain are shown in Figs. 2F and 2G, respectively. The influence of water and P supply on time to maturity are clearly indicated by the early appearance of heads in the higher P rates of non-water stressed plants. Water stressed plants of the lower two P treatments exhibited crop failure in terms of grain production. Data show an approximate linear response of grain *B* with time from the fourth to sixth harvests, but the slope was increased by both water and P supply.

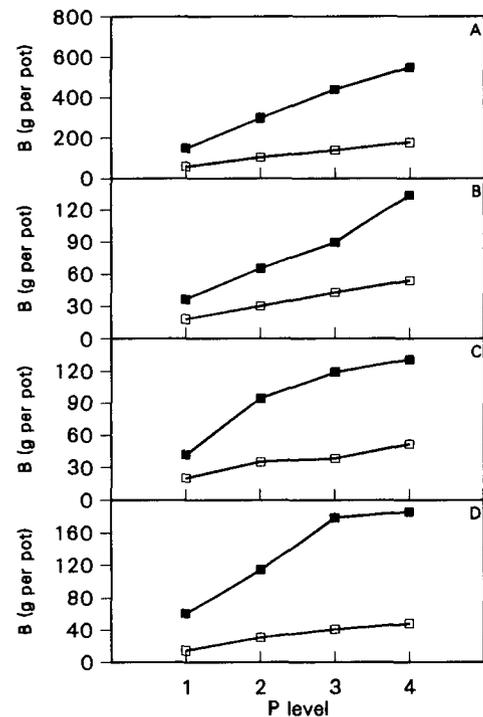


Fig. 3. Mean biomass (*B*) response at 70 days after emergence of A) whole millet plants, B) leaves, C) roots, and D) stems, as a function of water treatment and P level. See also Table 1.

#### Crop Production Rate, Organ Growth Rate, and Senescence Rate

Applying greater amounts of P increased maximum GR and CPR irrespective of water supply (Fig. 4). Maximum CPR occurred from 42 to 58 DAE in non-water stressed plants, and from 28 to 42 DAE in water stressed plants. From 56 to 70 DAE, CPR of the upper three P rates of water stressed plants was zero to slight-

ly negative, suggesting either dying off and/or C transport to growing storage organs (Jacquinot, 1970). The water stressed, 0.00 g P m<sup>-2</sup> plants, which produced no heads (Fig. 2F), showed no depression of CPR. This

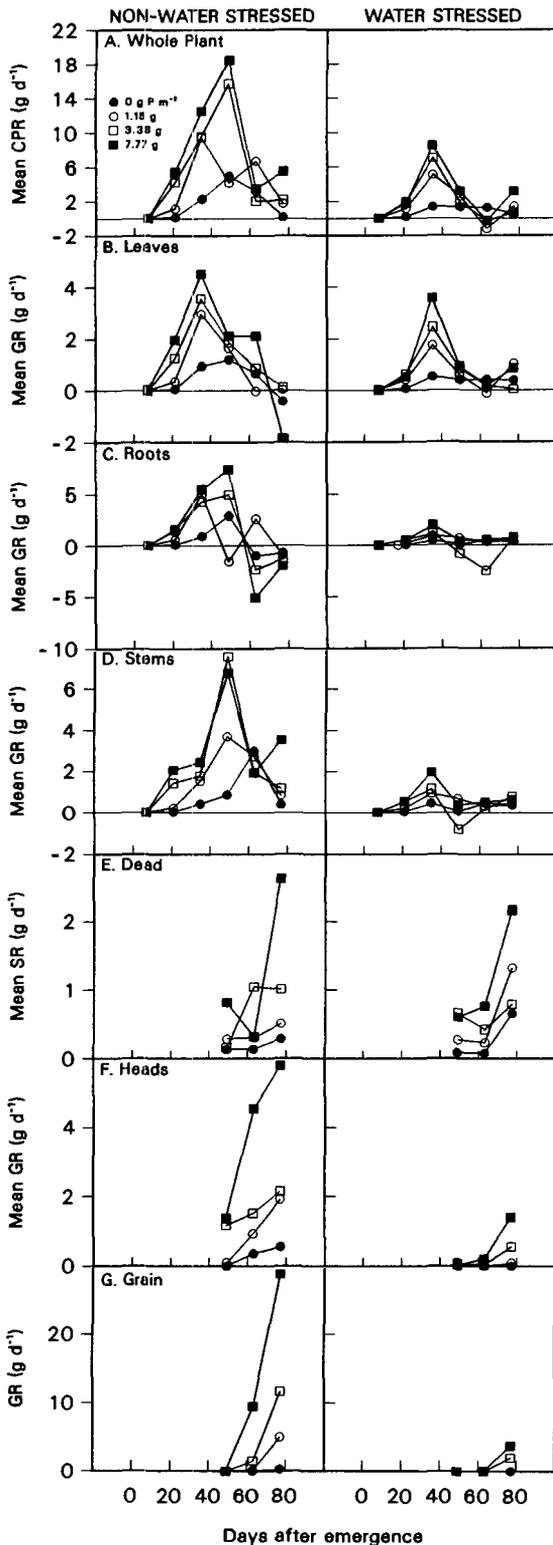


Fig. 4. Crop production rate (CPR), organ growth rates (GR), or senescence rate (SR); A) whole millet plants, B) leaves, C) roots, D) stems, E) dead material, F) heads, and G) threshable grain. Points represent means of plants from five 75-L pots, and were calculated from data shown in Fig. 2.

may reflect in part a higher metabolic cost during flowering and the initial stages of head formation. The CPR values of head producing, water stressed plants rose slightly from 70 to 84 DAE.

For both water treatments, mean leaf GR was maximal between 28 and 42 DAE (Fig. 4B). Before and after this period, leaf GR of water stressed plants was near zero. For non-water stressed plants, leaf GR was lowest during the last 2 wk of the growth cycle; conversely, for water stressed plants, leaf GR was lowest during head formation (56–70 DAE). During the last two weeks (70–84 DAE), leaf GR of some water stressed treatments increased slightly. The most negative leaf GR was observed in the non-water stressed, highest P rate (7.77 g P m<sup>-2</sup>) during the last 2 wk of the growth cycle, indicating rapid leaf senescence.

Root GR (Fig. 4C) was calculated from data shown in Fig. 2C, where error bars indicate high variability. Nonetheless, data serve to point out interesting trends from the standpoint of fertility/water supply interaction. Generally, non-water stressed plants achieved maximum root GR between 42 and 56 DAE. Thereafter, increasing P was associated with a more negative GR. Again, this may indicate root senescence, translocation from roots to shoots, or both. In water stressed plants, roots achieved highest GR between 28 and 42 DAE, when GR increased with applied P. Thereafter, root GR was generally near zero irrespective of P supply. This observation is consistent with root growth (and possibly export) being more limited by water stress than P shortage.

As with leaf and root GR and CPR, stem GR was maximal from 42 to 58 DAE for non-water stressed plants, and from 28 to 42 DAE for water stressed plants. While a large increase due to P was evident in non-water stressed plants, under water stressed conditions added P increased stem GR only from 28 to 42 DAE. Before and after this period, stem GR in water stressed plants appeared to be more strongly limited by water supply irrespective of P level.

Calculated SR (Fig. 4E) again indicates leaf senescence was more associated with P level than water supply. Head (Fig. 4F) and grain GR (Fig. 4G) show another example of how P and water supply can interact. In both water stressed and non-water stressed treatments, increased P was associated with increased GR. Water stress delayed head production, and was associated with a further decrease in the slope of GR vs. time. Head and grain GR remained low until sometime between the fifth and last harvest in water stressed plants, resulting in much less total grain yield. Non-water stressed plants receiving no P formed heads with very few grains. In the water stressed, lower two P treatments, head and grain production rates were essentially zero.

### Relative Growth Rate

In both non-water stressed and water stressed treatments, there was a general decline in RGR with time. Among non-water stressed plants, no clear differences emerged among P levels. Among water stressed plants, the three highest P levels had negative RGRs (Fig. 5) from 56 to 70 DAE. The water stressed, 0.00 g P m<sup>-2</sup> plants maintained a slightly higher RGR than did

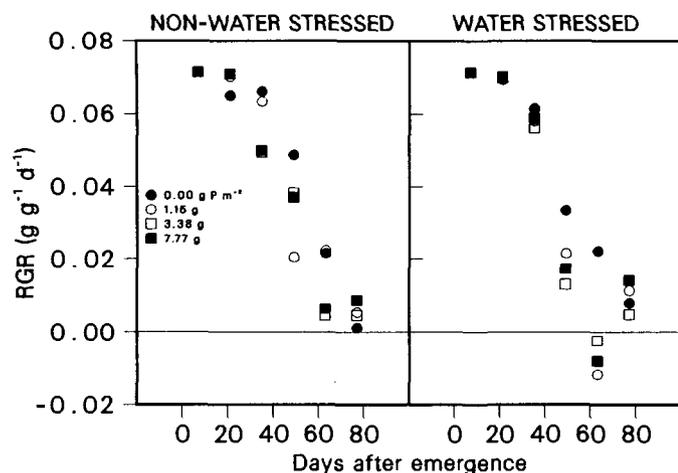


Fig. 5. Relative growth rate (RGR) of pearl millet. Points represent means of plants from five 75-L pots.

other water-stressed plants, which again may be due to the fact that they formed no storage organs. Non-water stressed plants' RGR continued to decrease to nearly zero with time.

#### Net Assimilation Rate

The NAR is an expression of the rate of dry mass increase on a leaf area basis, with leaf area representing a size estimate of the plant's "assimilatory apparatus" (Kvet et al., 1971). Therefore, senesced leaf portions were not used in calculation of NAR. There was an ontogenetic decrease of NAR with age (Fig. 6), which is typically attributed to mutual shading of leaves. As with CPR (Fig. 4A) and RGR (Fig. 5), most water stressed plants had a NAR of approximately 0 between 56 and 70 DAE, after which NAR increased. Also, 0.00 g P m<sup>-2</sup> plants in both water treatments had high NAR between 0 and 14 DAE. Otherwise, NAR values were similar among treatments.

Although Vaclavik (1967, 1969) observed a decrease in NAR due to water stress in maize (*Zea mays* L.), Stoy (1965) detected no change in wheat (*Triticum aestivum* L.) NAR due to water and N supply, and therefore concluded NAR was simply a function of phase of development. Kvet et al. (1971), however, stated that NAR depends more on intercepted radiation than any other environmental factor. This in turn may be expected to be strongly related to leaf specific chlorophyll content, since this pigment harvests incoming photosynthetically active radiation. Payne (1990) measured an increase in leaf specific chlorophyll content in P stressed pearl millet under conditions of non-limiting water and N supply. The high NAR observed between 0 and 14 DAE in both watering regimes of P stressed plants may therefore be due to a combination of lower mutual leaf shading due to lower shoot:root ratio, reduced rate of maturity and higher leaf specific chlorophyll content.

#### CONCLUSIONS

Phosphorus availability and water supply interact to increase the GR and development in pearl millet. Although RGR and NAR are in general only slightly

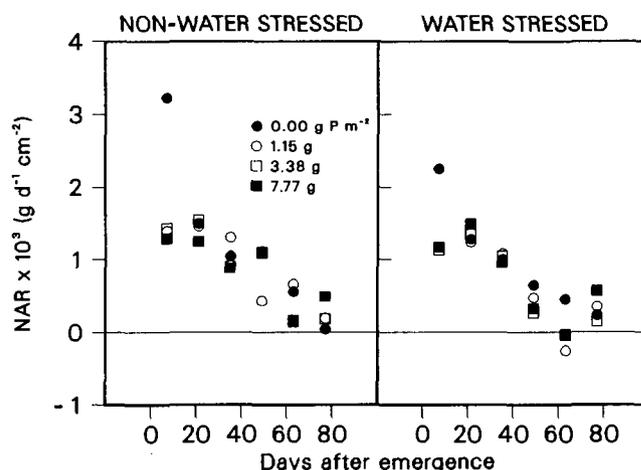


Fig. 6. Net assimilation rate (NAR) of pearl millet. Points represent means of plants from five 75-L pots.

affected, CPR and GR data demonstrate that the efficiency of pearl millet dry matter production is decreased under both wet and dry conditions when soil-P supply is inadequate. This implies that water supply cannot be effectively managed for increased grain and dry matter production under Sahel-like conditions without addressing soil fertility constraints.

#### ACKNOWLEDGMENTS

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