Characterizing Root Responses to Low Phosphorus in Pearl Millet
[*Pennisetum glaucum* (L.) R. Br.]

I. Faye, O. Diouf,* A. Guissé, M. Sène, and N. Diallo

ABSTRACT

Adaptation to low water and soil P availability has been related to root properties. Two experiments were conducted in a greenhouse. Under hydroponics conditions, plants of the Souna 3 cultivar were grown for 30 d with three levels of P (P0 = 0.0 mol L^{-1}, P1 = 0.073×10^{-3} mol L^{-1}, and P2 = 1.65×10^{-3} mol L^{-1}). In the pot experiment, two cultivars (Souna 3 and IBMV8402) were planted in pots filled with 19 kg of P-deficient and sandy soil and subjected to two watering regimes: well watered and water stressed at the vegetative phase from 23 d after sowing (DAS) to 30 DAS. Phosphorus treatment consisted of two levels: application of phosphate fertilizer (P_2O_5) at the rate of 649 mg per pot (34 mg P_2O_5 kg^{-1} soil), referred to as F1, and no phosphate application, referred to as F0. The results showed that under P deficiency, pearl millet [*Pennisetum glaucum* (L.) R. Br.] presented an alteration of root parameters, particularly root volume, by the formation of root hair. Under non-water-limited conditions as well as in high or low P, IBMV8402 showed a better root and shoot growth. However, under drought conditions, the leaf water potential (Ψ_f) of IBMV8402 ($\Psi_f = -5$ MPa) decreased more than that of Souna 3 ($\Psi_f = -3$ MPa). In spite of this, P supply improved the root and shoot growth of IBMV8402. Finally, except for the condition of water stress and without P supply, P utilization efficiency exhibited by IBMV8402 was 20 to 50% higher than that of Souna 3 on the basis of shoot biomass production.

P EARL MILLET is one of the most important cereals in drought-prone areas and is the staple grain for 150 million people in West Africa and India (FAO, 1997). However, its growth and productivity are limited by temporally and spatially erratic rainfall and poor soil fertility (Davis-Carter, 1989). Among soil fertility factors, P deficiency is one of the major or in some cases the main constraint to crop production. Many studies reported that N response is often not obtained without some basal P additions (Sedogo et al., 1991). Many Sahelian soils, including ferric lixisols and other degraded African savanna soils (FAO, 1997), are low in plant-available P (Timofeyev et al., 1988). In most of the soils that are planted to pearl millet, the percentage of clay (kaolinite) is very low (<0.055 kg kg^{-1} in Senegal) (Badiane, 1996).

Phosphate ions move through soils primarily through diffusion. As soil water content decreases, the radii of water-filled pores decrease and tortuosity increases; therefore, P mobility also decreases. Nye and Tinker (1977) stated that lower water availability causes a reduction in P availability and, therefore, in its absorption. The interaction of P and water supply has been reported on pearl millet growth and development under Sahel-like conditions (Payne et al., 1991a).

During the last 30 yr, many studies have been done to estimate P availability in cultivated soils of semiarid West Africa, P requirements of many crops, and the effectiveness of P fertilizers (Badiane, 1996; Bationo et al., 1999). Recently, many investigators have illustrated that plants display a wide array of adaptive responses to low P availability to enhance P mobility in the soil and increase its uptake. A well-known adaptive response is the alteration of root morphology and architecture to increase P acquisition from the soil at minimum metabolic cost (Neumann et al., 1999; Jonathan et Kathleen, 2001; Yong et al., 2003). In this regard, morphological and genotypic variations are well documented for many plants such as barley (*Hordeum vulgare* L.) (Gorny and Patyna, 1984), corn (*Zea mays* L.) (Aina and Fapohunda, 1986), and *Arabidopsis thaliana* (L.) Heynh. (Lynch and Bates, 2001). Brück et al. (2002) reported genotype differences in shoot and rooting parameters of pearl millet in fields with P deficiency, but little work has been done on the interaction with N uptake and water supply.

Hydroponic systems have been proven to be a rapid and valuable method for screening plant species and genotype adaptation to low-input conditions (e.g., water and mineral nutrients), including sorghum [*Sorghum bicolor* (L.) Moench] (Jordan et al., 1979) and rice (*Oryza sativa* L.) (Ekanayake et al., 1985; Price et al., 1997).

The objectives of our study were (i) to observe root modifications of pearl millet in response to P deficiency under hydroponic culture, including their effects on growth and nutrient (P and N) uptake and (ii) to analyze the response of two cultivars to different levels of P and water supply.

MATERIALS AND METHODS

In this study, two concurrent trials were conducted from September to November in the greenhouse at Regional Center for Studies on the Improvement of Plant Adaptation to Drought (CERAAS) near Thies, Senegal (14°81′ N, 16°28′ W). The first was conducted under hydroponic conditions and the second with soil under pot conditions. During the experiments, the temperature and the relative humidity in the greenhouse were recorded with a probe (type HOBO H08–

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Abbreviations: DAS, days after sowing; NbAR, number of adventitious roots; RB, root biomass; RV, root volume; SB, shoot biomass; SFI, structure function index; STR, water stressed; WW, well watered; $\varphi P0 = PHI(P0) = Fv/Fm$, maximum quantum yield of PSII photochemistry.
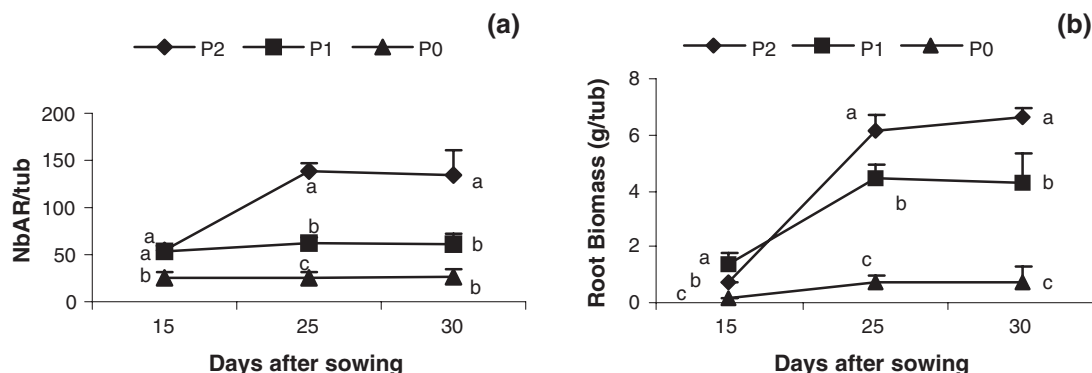
Fig. 1. Effect of P (a) on the number of adventitious roots (NbAR) and (b) on root biomass during the experiment in hydroponics. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.

032–08#538343, Prosensor, Amanvillers, France) every 30 min. The day/night mean temperature was 38/26°C, and relative humidity ranged from 41 to 90%. Two millet varieties (Souna 3 and IBMV8402) representing two of the main cultivars grown in Senegal were used for the study. These varieties were developed by ISRA (Senegal Agricultural Research Institute).

Hydroponic Culture

The objective of the trial on hydroponic culture was to assess the effects of P in root parameters of pearl millet that are important for the acquisition of nutrients and water under resource-limited conditions. Phosphorus treatments were 0 mol L^{-1} (P0); 0.073 10^{-3} mol L^{-1} (P1), and 1.65 10^{-3} mol L^{-1} (P2), and P was added as KH$_2$PO$_4$. The nutrient solution used was that described by Perez (1997). Macronutrients were added as 3.56 mmol NO$_3^-$ L^{-1}, 0.56 mmol SO$_4^{2-}$ L^{-1}, 4.5 mmol K$_2$O L^{-1}, 5.06 mmol CaO L^{-1}, and 1.69 mmol MgO L^{-1}, while the micronutrients were added as 0.449 mmol MnSO$_4$·H$_2$O L^{-1}, 7.028 10^{-5} mmol MoO4 [(NH$_4$)$_6$ Mo$_7$O$_2$ 4H$_2$O] L^{-1}, 0.033 mmol H$_3$BO$_3$ L^{-1}, 1.742 10^{-3} mmol ZnSO$_4$·7H$_2$O L^{-1}, and 5.01 10^{-4} mol CuSO4·5H$_2$O L^{-1}. The concentration of iron (Fe^{2+}) was increased with P concentration of the nutrient solution to avoid a very high P–Fe ratio, which often causes Fe chlorosis in many plants (Dobermann and Fairhurst, 2000). Iron was added as following P0 (1.82 10^{-4} mmol Na$_2$EDTA·2H$_2$O L^{-1} + 1.81 10^{-4} mmol FeCl$_3$ L^{-1}), P1 (2.417 10^{-4} mmol Na$_2$EDTA·2H$_2$O

L^{-1} + 1.81 10^{-4} mmol FeCl$_3$ L^{-1}), and P2 (5.364 10^{-4} mmol Na$_2$EDTA·2H$_2$O L^{-1} + 5.327 10^{-4} mmol FeCl$_3$ L^{-1}).

The hydroponic system consisted of nine tanks of 25-L capacity, each connected to four 4-L plastic tubs. Each tub contained four plants, which constituted a block. The experimental design consisted of three randomized complete blocks with each block corresponding to three tanks. Within a block, each tank corresponded to one of three P treatments. Nutrient solution was pumped into the tubs by multicellular pumps. The pumps were linked to an automatic timing system, which allowed the supply of solution in tides. At high tides of 8-min duration, the tubs were filled to capacity while at low tides of 5-min duration, the pumps stopped functioning as the nutrient solution slowly descended into the tanks. This allowed the roots to be reoxygenated. This system was earlier described by Ogbonnaya et al. (2003).

The experiment lasted for 4 wk. A packing material was placed on each tub to hold the plants at the root collar with the roots immersed in the culture solution. The seeds were germinated in pots before being transferred to the hydroponic system 3 d after emergence (i.e., after the expansion of the third leaf). The plants were grown in a 20% strength nutrient solution, and the pH was adjusted to 5.5 with HCl. Nutrient solution was replaced after 2 wk. The numbers of adventitious roots (NbAR) per tub at the collar of the plants were counted at each harvest. Root volume (RV) was also determined by measuring the volume of water displaced by the root system. Root biomass (RB) and shoot biomass (SB) were obtained after oven-drying fresh materials at 85°C to constant weight. Root–shoot ratio was obtained as the ratio of root dry weight to shoot dry weight. After each harvest, P content was analyzed by using the Olsen method (Olsen et al., 1945) as recommended by Morel and Fardeau (1987). Nitrogen content was determined in dried shoot and root tissue by using the Kjeldahl method. Total P and N concentrations were determined colorimetrically using a spectrophotometer. As samples were too small, the samples of each treatment were mixed for N and P analyses. The N and P concentrations shown are means of duplicate analyses.

Chlorophyll fluorescence analysis was measured on the third leaf with a fluorimeter [PEA (Plant Efficiency Analyzer), Hansatech Inst. Ltd, King's Lynn, England] at 15, 21, and 26 DAS. Among the chlorophyll fluorescence parameters, two were considered: the φP0 [PHI(P0) or Fv/Fm] and SFI (structure function index) (Gert et al., 2003; Stirbet et al., 1998; Strasser et al., 1999). The PHI(P0), or Fv/Fm, describes the maximal quantum yield of photochemistry in dark adapted state, and SFI, or vitality index, expresses the extent of nonphotochemical phenomena (fluorescence and heat dissi-
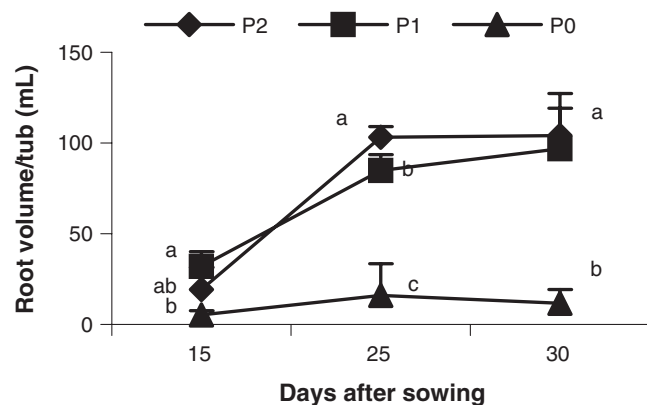

Fig. 2. Effect of P treatment on root volume during the experiment in hydroponics. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.
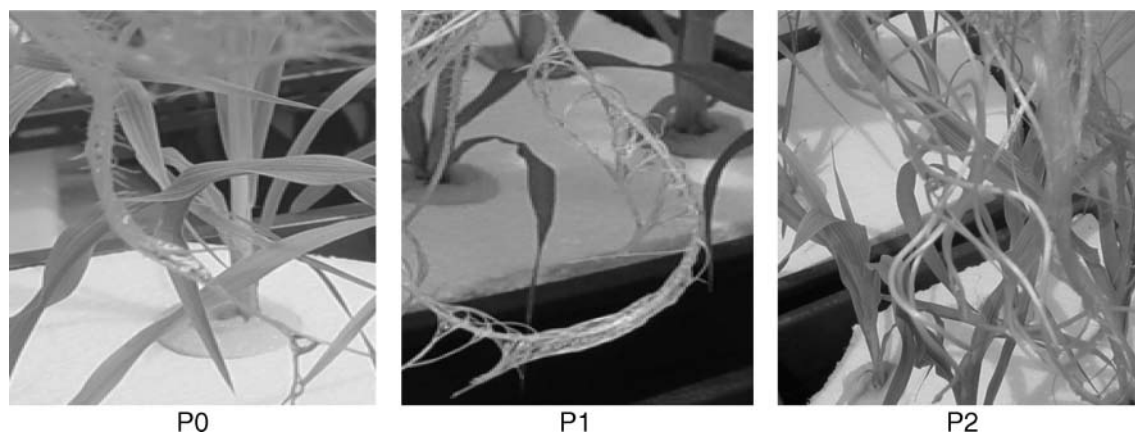
Fig. 3. Phosphorus deficiency (P1) induces the development of more root hairs compared with other treatments (hydroponic experiment). P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}.

pation) compared to photochemistry when the majority of the PSII reaction centers are open for maximal absorption (Strasser et al., 1999).

Pot Culture

This second experiment aimed to determine the effects of water deficit on the growth response of two Senegalese varieties cultivated under P deficiency. The experiment lasted 35 d. Seeds were sown in pots that had a diameter of 0.30 m and a height of 0.25 m with drainage holes at the bottom. Each pot was filled with 19 kg of an acid and P deficient sandy soil that was sieved before. The soil of the experiment has a sandy texture (910–940 10^{-3} kg kg^{-1}), a clay content less than 55 10^{-3} kg kg^{-1}, an organic matter of 2.7 10^{-3} to 3.4 10^{-3} kg kg^{-1}, a low C exchange capacity of 1.7 to 2.2 cmol kg^{-1}, a pH in water of 6.5, and an available P deficiency (22 10^{-6} kg kg^{-1}, Olsen method). Six pearl millet seeds were planted in each pot at a depth of approximately 4 cm. At 7 d after emergence, plants were thinned to one per pot. Insect attack, disease development, and weed proliferation were controlled using the appropriate chemicals [DECIS (deltamethrine) and SPINOX TBC (thirame, benomyl, and carbofuran)].

Treatments consisted of two varieties, two P levels and two water levels, with three blocks. Each replication of a treatment was made up of three pots. Thus, there were a total of 72 pots. The experimental design was a randomized complete block. Two pearl millet cultivars were used, Souna 3 and IBMV8402. The plants were subjected to two watering regimes: well watered (WW) and water stressed (STR) at the vegetative phase (23 DAS). Water stress was applied by suspending irrigation until 30 DAS. Two P treatments were considered: one referred to as F1 with phosphate fertilizer (P$_2$O$_5$) at the rate 649 mg per pot (34 mg P$_2$O$_5$ kg^{-1} soil) and another referred to as F0, without added phosphate. All pots also received N and K, respectively, at the rates of 1.895 g of urea per pot (0.100 g urea kg^{-1} soil) and 1.038 g of KCl (55 mg KCl kg^{-1} soil). While K and P were applied at seedling emergence, the N rate was applied two times as follows: one half at seedling emergence and the second half at 2 wk after sowing as urea.
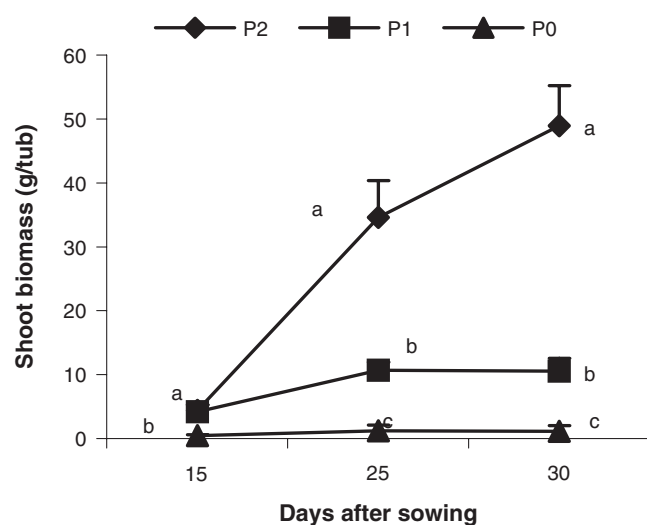

Fig. 4. Effect of P on shoot biomass during the experiment in hydroponics. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.

Fig. 5. Effect of P on the partitioning of biomass between root and shoot in the hydroponic experiment. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.
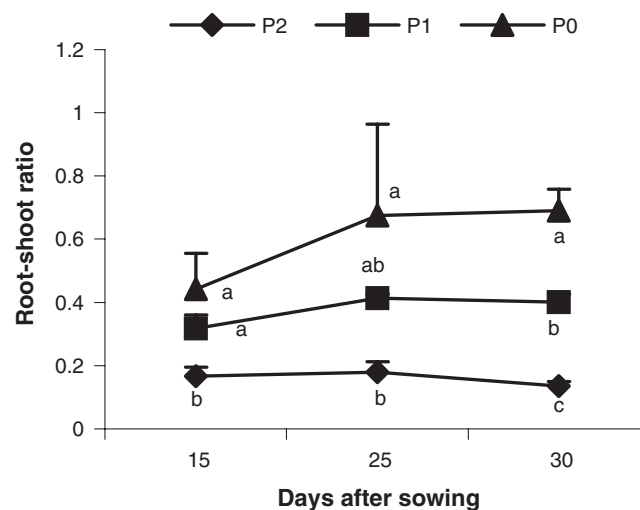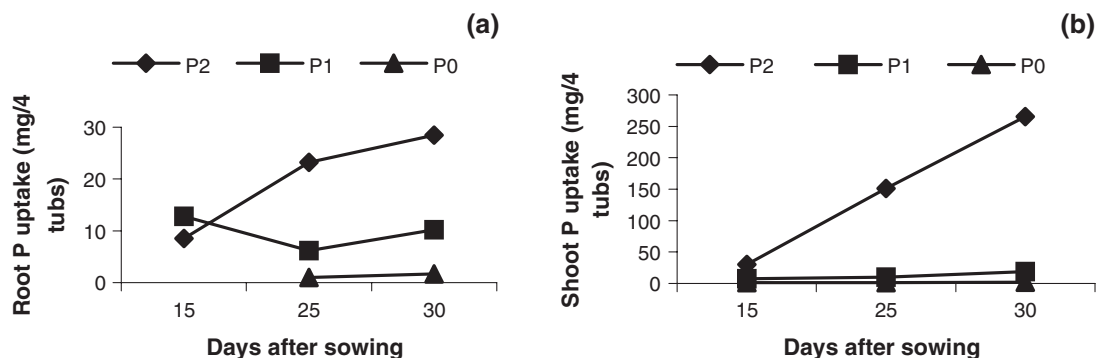
(a)

(b)

Fig. 6. Evolution of (a) root and (b) shoot P uptake under different P treatments in the hydroponic experiment. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}.

One week after the water stress, one pot for each replication was harvested. Then, plants were separated into root and shoot. Roots were thoroughly washed from soil before measuring NbAR, RB, and SB after oven-drying at 85°C. The same organs of the same treatment were mixed, giving a composite sample for the determination of the P and N contents as in the hydroponic study.

The water stress was applied at 23 to 30 DAS. During this period, the leaf water potential (ψ_f) was measured at three times. The measurements were performed on the third leaf from the top between 11 and 13 h with hydraulic press (Campbell J14, Campbell Scientific Inc., Logan, UT), which was earlier calibrated with psychrometers (C30, Wescor, Logan, UT). Two plants were measured per replication and per treatment, giving six measurements for each treatment.

Statistical Analysis

The data were subjected to a factorial analysis of variance (ANOVA) using SAS software package (SAS Stat. Inst., Cary, NC). The partitioning of the means was made with Newman Keul's Test at 5% probability level.

RESULTS AND DISCUSSION
Rooting Parameters and Shoot Growth

Significant variations due to P treatment were observed for both NbAR and RB (Fig. 1). At 15 DAS, P1 and P2 presented the same NbAR, which was higher than that in P0; however, after this date (15 DAS), when NbAR of P2 increased, that of P1 remained quite constant. At 15 DAS, RB of P1 was higher than that of P2 and P0. After this date, the RB increased more in P2 than P1. In both P treatments, NbAR and RB

showed a little increase beyond 25 DAS. In the P starvation treatment, nonsignificant increase has been observed for NbAR and RB parameters.

Root volume was higher in P1 after 2 wk of growth (Fig. 2). At 25 DAS, RV of P2 became significantly higher than that of P1. While RV of P2 remained constant after 30 DAS, that of P1 continued to increase until it was similar to the value of P2. In the P starvation solution, nonsignificant increase of RV was observed.

These results showed that the observed increase in RB in P1 couldn't be linked to the NbAR because this parameter remained constant. Also, the high RV expressed in P1 couldn't be explained only by increase in RB, which remained constant beyond 25 DAS while the RV increased continuously. However, if the high RV in P2 could be attributed to NbAR and RB, that of P1 was mainly due to the formation of root hairs (Fig. 3). In fact, P deficiency (P1) induced the formation of more root hairs than P starvation (P0) or optimal P treatments. The nonincrease in NbAR in P1 was compensated by an important formation of root hairs giving a high RV, which was associated with a wide root surface contact. This alteration of root morphology and architecture in response to low P availability was reported in other species (Neumann et al., 1999; Jonathan and Kathleen, 2001; Yong et al., 2003). Elsewhere, Bates and Lynch (2001) showed that root hairs confer a competitive advantage to plants in low-P environments by comparing wild-type and hairless plants. However, plants growing in P starvation solution (P0) developed less root hair than those in low-P solution but more root hair than those in high-P solution. This could suggest that a good expression of
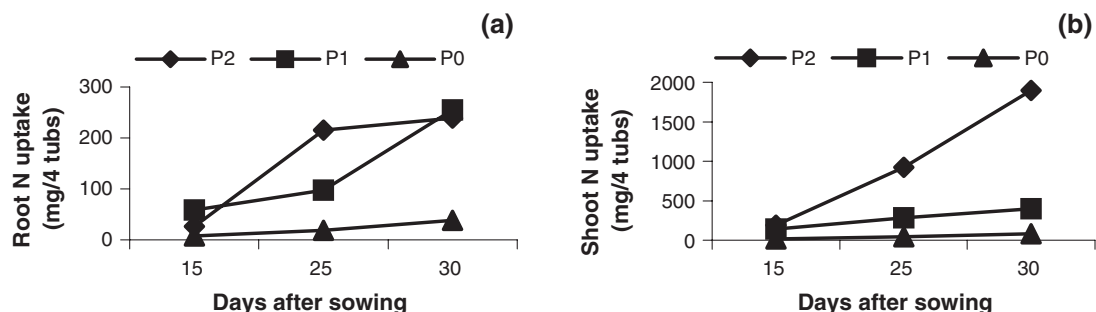
(a)

(b)

Fig. 7. Evolution of (a) root and (b) shoot N uptake under different P treatments in the hydroponic experiment. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}.
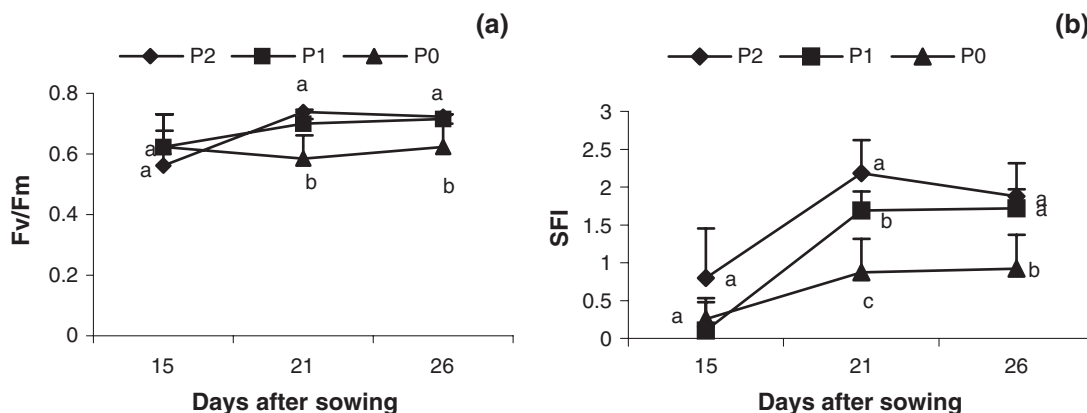
Fig. 8. Effect of P on chlorophyll fluorescence parameters {maximum quantum yield of PSII photochemistry (PHI(P0) = Fv/Fm) and vitality index (SFI)} in the hydroponic experiment. P0 = 0.0 mol L^{-1}, P1 = 0.073 10^{-3} mol L^{-1}, and P2 = 1.65 10^{-3} mol L^{-1}. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.

the mechanism for forming root hairs would need a minimum of P starter.

Shoot biomass had significant variations due to P. At 15 DAS, the aboveground biomass of P1 was similar to that of P2 (Fig. 4). But, beyond this date, little increase was observed for SB in P1 while that of P2 increased significantly. At 30 DAS, SB under P2 was fourfold greater than that under the P-deficient conditions of P1. A similar dynamic pattern was reported previously for wheat (*Triticum aestivum* L.) by Guitiérrez–Boem and Thomas (1998).

The proportion of biomass allocated to roots was enhanced when P concentration decreased in the nutrient solution (Fig. 5). Vetterlein and Marschner (1994) observed also in pearl millet of 6 wk old that shoot and root dry weight change with increasing levels of P fertilization. They argued that low amounts of fertilizer application generally enhance root growth while higher

Fig. 9. Changes in leaf water potential (Ψ$_f$) within the different treatments during the water deficit, F0 = 0.0, F1 = 649 10^{-6} kg P$_2$O$_5$ (34 10^{-6} kg P$_2$O$_5$ kg^{-1} soil); WW = well watered regime and STR = water-stressed regime. Each point is the mean of three replications (bars = ± standard error). For a given date of measurement, means followed by different letters are significantly different at $P < 0.05$ according to the Student Newman Keul's range test.

amounts have no effect on root growth or even inhibit it. This result agrees with the classical concept of a functional equilibrium between growth of shoot and root (Brouwer, 1983; Klepper, 1991). This suggests that C partitioning between shoot and root depends on the resource acquisition capacity of shoot and root components, which are controlled by their respective mass and activity.

P and N Uptake

At 15 DAS, root P uptake, contrary to shoot P uptake, was higher in P1 than P2 (Fig. 6). This response in low P (P1) integrating a higher RV allowed a sufficient P uptake, resulting in normal shoot growth. Beyond this period, the mobilized P in roots and shoot was insignificant in low-P treatments (Fig. 6), in spite of the importance of root responses. This was due to the rapid P depletion enhanced in severe P deficiency.

Smith et al. (1990) argued that P was rapidly absorbed from shoots to roots under low P, which maintained root growth but inhibited shoot growth. Furthermore, under extreme deprivation, P was remobilized from older parts of the root system as a source for continued growth of root meristems.

Similar to P, the N uptake in the roots was greater in low-P treatment (P1) than in high-P treatment (P2) up to 15 DAS (Fig. 7). However, at the end of the experiment (30 DAS), N uptake was the same between the plants in P1 and P2. In spite of the same concentration of N in all nutrient solutions, the shoot N uptake was more important in high-P treatment (P2) while it was very low in P-deficient treatment (P1). This showed an interaction between N and P uptake suggesting that N uptake depends also on P availability. N response is often not obtained without some basal P additions (Bationo et al., 1999; Timofeyev et al., 1988). These results demonstrated also that N partitioning, as between shoot and root, appears to be controlled to some extent by growth demand. In fact, Jescheke et al. (1996) demonstrated that the reduction of glutamine concentration in sap phloem of plants under P deficiency is a consequence of the limi-
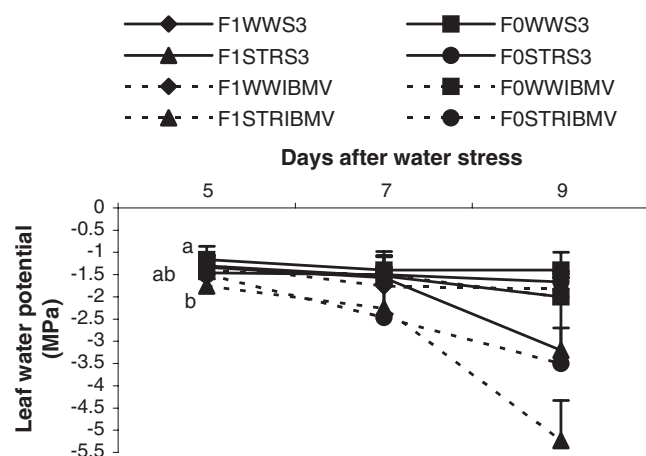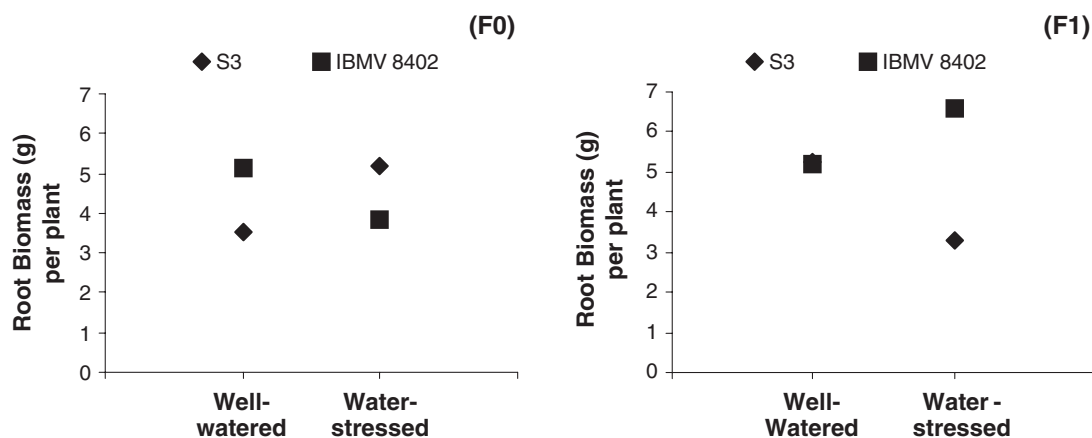
Fig. 10. Interaction between variety and water regime on root biomass for given P treatment; F0 = 0.0, F1 = 649 10^{-6} kg P_2O_5 (34 10^{-6} kg P_2O_5 kg^{-1} soil); each point represents the mean of three replications.

tation of the N uptake. This importance of P would be related to the energetic role of P in metabolic reactions when involved in ATP (adenosine triphosphate).

Photochemical Activity

P1 and P2 treatments exhibited high and similar values of maximum yield of photochemistry (Fv/Fm) and vitality index (SFI) during the experiment (Fig. 8) whereas these parameters of chlorophyll fluorescence were low in the P starvation condition. Thus, under this condition of low P (P1), these parameters didn't show a great inhibition of photochemical activity at this stage. Therefore, the important decrease of the shoot growth in this condition cannot be attributed to a limitation of photochemical activity but may be related to the alteration of root architecture. This root alteration results in an increased respiratory cost and enhances the transfer of assimilates from shoot to root, leading to a decrease in N demand for shoot growth in spite of the high availability of N in low-P solution (Fig. 7). As gas exchanges were not measured in our experiment, we have no evidence of whether this photochemical maintenance was associated with maintenance of net photosynthesis.

Elsewhere, this maintenance of a normal photosynthetic activity under P deficiency condition was observed in bean (*Phaseolus vulgaris* L.) by Kondracka and Rychter (1997) and could be explained by the increase of the specific leaf area and the leaf-specific chlorophyll content. In addition, the enhancement of inorganic phosphate recycling processes during photosynthesis could contribute to the maintenance of photosynthetic activity in low P deficiency (Kondracka and Rychter, 1997).

Effect of P and Water Deficit on the Responses of Two Varieties of Pearl Millet

From the fifth day after the water shortage, the leaf water potential (Ψ_f) decreased more rapidly in plants under high-P treatment with a lower leaf water potential for IBMV8402 compared with Souna 3 (Fig. 9). Toward the end of the water stress period, P fertilized and stressed plants of both varieties showed a great decrease in leaf water potential. But the decrease of Ψ_f observed in IBMV8402 was more important than that of Souna 3. In addition, under stress conditions and without P fertilizer, no decrease of Ψ_f was observed in Souna 3 contrary to IBMV8402. These results showed that
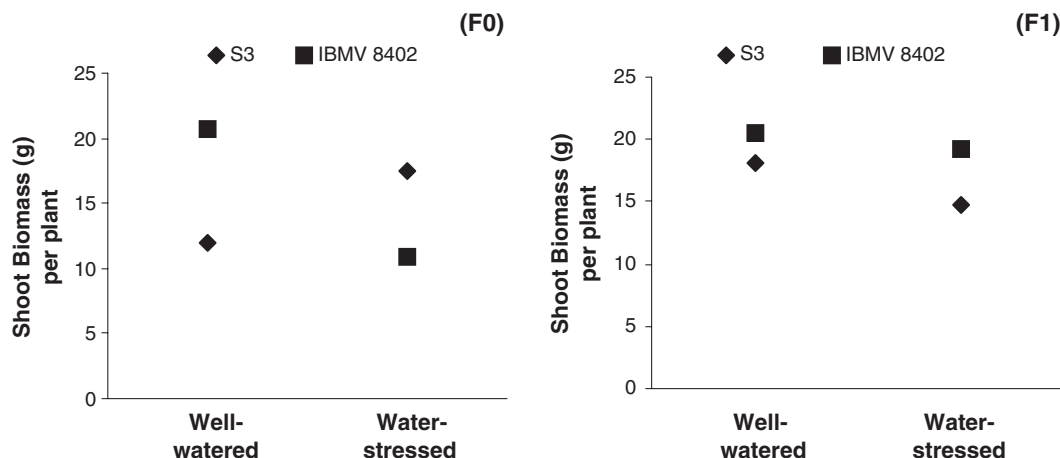

Fig. 11. Interaction between variety and water regime on shoot biomass for given P treatment; F0 = 0.0, F1 = 649 10^{-6} kg P_2O_5 (34 10^{-6} kg P_2O_5 kg^{-1} soil); each point represents the mean of three replications.

IBMV8402 was more affected by water stress than Souna 3, and P fertilizer enhanced the water stress effect.

Similarly for RB and SB, the interaction among water regime, variety, and P treatment was statistically significant (Fig. 10 and 11).

In P supply (F1), the RB and SB were similar between the varieties under WW conditions while under STR conditions, IBMV8402 presented the higher values of RB and SB.

Under conditions of no P supply (F0), the RB and SB of Souna 3 were higher than that of IBMV8402 under STR conditions while the contrary was observed under WW conditions.

In both P treatments, IBMV8402 showed a more important SB in WW conditions so that when water stress was applied, it lost its water more rapidly. This could explain the low water potential observed in IBMV8402 under water stress conditions as related by Payne et al. (1991b) with other varieties of millet. However, under water stress, P fertilizer improved SB response of IBMV8402 while the contrary was observed in Souna 3.

For both varieties, the P mobilized in shoot increased with P level (Fig. 12). For all treatments, the P mobilized in shoot tended to be more important for Souna 3 compared with IBMV8402 and particularly under water stress conditions. This suggested that root alteration was associated with some maintenance of P uptake under water deficit as shown by Diouf et al. (2004) for N with Souna 3 variety. With the exception of the STR plants, P0 plants of IBMV8402 exhibited higher P utilization efficiency of 20 to 50% compared with that of Souna 3 with regards to SB (Fig. 13).

Our data do not allow drawing conclusions about the relative importance of RV and P utilization efficiency on grain yield because the two experiments continued for only the 30 DAS. It remains to be determined whether such measurements can serve as a screen for grain yield under field conditions. Brück et al. (2002) concluded that, due to high variability for root traits, indirect selection for shoot parameters is more promising than direct selection for root length density or root length.
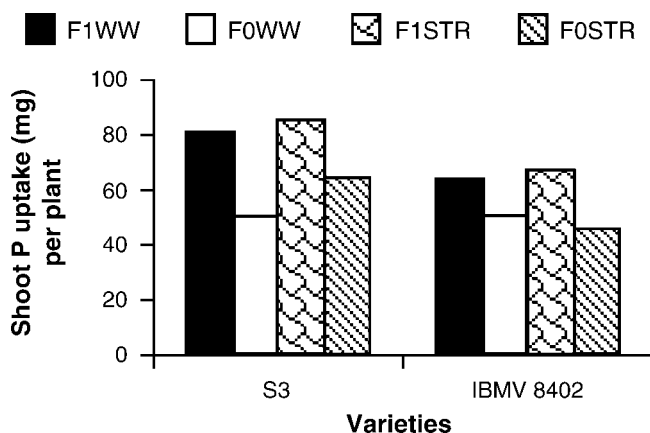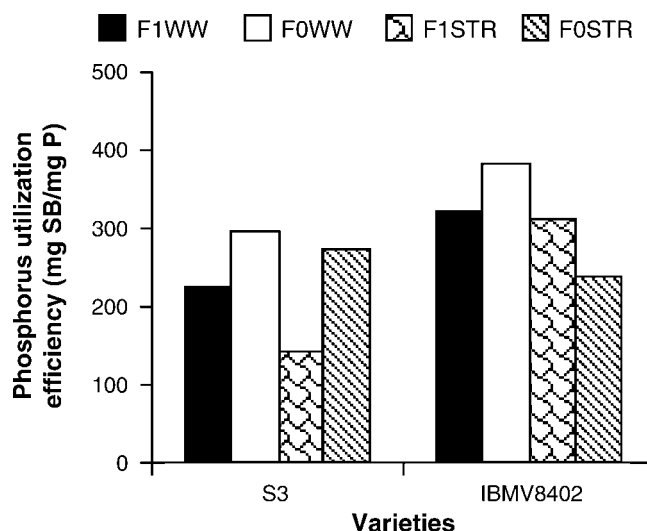

Fig. 13. Phosphorus utilization efficiency of the two varieties under different P and water treatments. F0 = 0.0, F1 = 649 10^{-6} kg P_2O_5 (34 10^{-6} kg P_2O_5 kg^{-1} soil); WW = well-watered regime and STR = water-stressed regime.

CONCLUSIONS

These results showed that pearl millet is a species that alters root morphology and architecture under P deficiency. Root volume (RV) can be considered a morphological parameter, which is altered in response to P deficiency. Therefore, it would be interesting to study the biochemical and molecular phenomenon involved in those responses. The hydroponic system used in this study appeared to be a rapid method for researching root trait response to P availability.

The two varieties exhibited different responses to water and P availability in terms of rooting parameters and shoot growth. On the basis of leaf water potential values, Souna 3 appears more drought tolerant than IBMV8402. However, P supply could improve the drought response of IBMV8402. In addition, the latter showed better growth behavior in WW conditions regardless soil P content. With the exception of the STR and P-treated plants, IBMV8402 raised higher P utilization efficiency in terms of SB production and probably for grains. This genetic variability should be used to improve the adaptation of pearl millet in low soil P generally found in Sahelian zones, in addition to soil P management.

Fig. 12. Shoot P uptake of the two varieties under different P and water treatments. F0 = 0.0, F1 = 649 10^{-6} kg P_2O_5 (34 10^{-6} kg P_2O_5 kg^{-1} soil); WW = well-watered regime and STR = water-stressed regime.

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