Title
Phosphorus Uptake Kinetics, Root-Shoot Relations and P-Influx of Groundnut and Maize Grown in Solution Culture

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Introduction

Different plant species and cultivars differ greatly in their response to low soil P-content. Some species can grow well at low P-supply, because they are able to take up enough P for optimum growth. The reason for the high uptake efficiency could either be a high influx, for example spinach, rape and groundnut, or a large root-shoot ratio, for example, rye grass, wheat and vegetable crops (Föhse et al., 1988; Bhadoria et al., 2001; Schenk, 2006). The present study was based on the results of a field experiment on a low P-supplying Alfisol with wheat, groundnut and maize (Bhadoria et al., 2001). The results showed that at early growth stages groundnut was very P-efficient mainly because of a high P-influx, which declined later. On the other hand, maize had poor growth at the beginning of the season, however, in the middle of the season its growth increased by 6-fold. The differed P-influx between species as well as with plant age within a species was responsible for the differences in P-uptake efficiency.

The relation between a nutrient influx into the root and concentration of that nutrient in the external solution at the root surface can be described in terms of a modified Michaelis-Menten kinetics function (Nielsen, 1972). Differences in influx at the same concentration are related to the uptake kinetic parameters (I_{max}, K_m and C_{Lmin}), which result from plants adaptation to low nutrient concentrations. The objective of this study was to investigate P-uptake efficiency of groundnut and maize in nutrient solution as related to root-shoot relations, P-influx and uptake parameters. In this study a flowing solution culture system was used which allows for maintaining a constant P-concentration even at low values.

Materials and methods

Plant growth and P-uptake of groundnut (*Arachis hypogea* L.) and maize (*Zea mays* L.) at different P-levels were studied in a flowing nutrient solution culture in a controlled growth chamber. A light/dark regime of 18/6 hours at 25/20°C, relative humidity of 60/80% and light intensity of 250 $\mu E\ m^2\ s^{-1}$ were utilized for the study. One week old pre-germinated seedlings were transplanted into modified Hoagland nutrient solution in 1.5L plastic pots. According to the treatments, the solutions contained 0.2, 1 or 100 μM P as $NaH_2PO_4.2H_2O$. Number of plants per pot was 10, 3, 1 and 1 for the first, second, third and fourth harvests, respectively. The nutrient solution units were 400 L capacity tanks in which 1.5 L pots with plants were placed. The solution in the plant pots is renewed every 1 to 2 minutes. P-concentrations were maintained at the planned levels by daily analysis of the solution and addition of P with a peristaltic pump by continuous injection at a rate aimed to balance the uptake rate of the plants. In order to study the plant growth and calculate the net P-influx, 4 harvests were conducted. The first, second, third and fourth harvests for maize were made at 0, 10, 24 and 34 days after transplanting, for groundnut the respective times were 0, 10, 28 and 35. At each harvest, shoot dry weight and P-concentration were determined. Root length was measured using the line intersection method of Tennant (1975). Assuming that the roots of young plants have exponential growth, the average influx was calculated as per Williams (1948).

The methodology described by Claassen and Barber (1974) was used to quantify P-uptake kinetics. The method is based on the rate of depletion of a nutrient from solution over a range of concentrations. The plants grown in the flowing solution culture were taken from the nutrient solution and allowed to stand in the solution with the least P-concentration, i.e. 0.2μM for 12 hours. Thereafter, the P-concentrations were adjusted to about 50μM to allow for a P-uptake rate close to I_{max}, and also to enable the plants to deplete P in the solution to a minimum value within about 12 hours. As the plants absorb P, samples of 5ml were continuously withdrawn using a pipette in every 10-20 minutes and their P-concentrations measured. This enabled measuring the P-depletion in relation to time of uptake. Sampling of the solution was continued till C_{Lmin} was reached, i.e. no further P-uptake was recorded.

Results and Discussion

At all the harvests both species were assumed to reach maximum dry matter yield at 100 µM. At 0.2µM P-concentration, both groundnut and maize were P-deficient producing between 10-30% of their maximum yield at the third and fourth harvests (Fig. 1). At 1µM P-concentration maize was highly P-efficient producing up to 90% of its maximum yield, whereas groundnut produced only 35 and 21% at the third and fourth harvest, respectively indicating a decrease in P-efficiency with plant age. After 28 days groundnut showed almost no growth at 0.2 and 1 µM P, while maize grew maximum at the later concentration. This result contrasts with the findings of Bhadoria et al. (2001) where under field conditions groundnut in early growth stages grew with no limitations on a low P soil, while maize only yielded 15 to 35% of its maximum yield.

Figure 2 shows the total P-uptake of groundnut and maize only at 0.2 and 1.0µM P, because the comparison is interesting at low P-supply. Notice the 10 times difference in scale on the Y-axis. It can be seen that in groundnut at 0.2µM P concentration, after a small increment in shoot P-content decreased again and at 34 days no net P-uptake was found. Even at 1µM P, groundnut showed no P-uptake. In contrast, in maize, at 0.2µM P, increased its P-uptake from 0.01-0.20 mmol plant^{-1} and at lµM P the increase was up to 1.3 mmol plant^{-1}. The higher P-efficiency of maize was due to the higher P-uptake efficiency of the root system. At all P-concentrations in solution, maize had between 2-15 times higher P-uptake than groundnut. The uptake efficiency comprises both the root system size and the uptake rate per unit root length and time, i.e. the influx.

The root system of maize was almost 10-times larger than that of groundnut, but because the size of plants is different, the root length-shoot weight ratio, which gives the amount of roots available to feed the shoot, is a better parameter for characterizing the uptake efficiency. Both the species responded to decreasing P-concentration by increasing their root-shoot ratio (Fig. 3). At 100µM P, the root-shoot ratio of both crops was similar, but at low P concentration, maize increased the root-shoot ratio by a factor of 9 while in groundnut the increase was only by a factor of around 3. This shows that maize root system has a much higher flexibility to respond to varying P-supply than groundnut. These results are in agreement with several others, which reported larger root-shoot ratios under macro and micro nutrient deficiency (Steingrobe and Schenk, 1991; Machado and Furlani, 2004; Schenk, 2006).

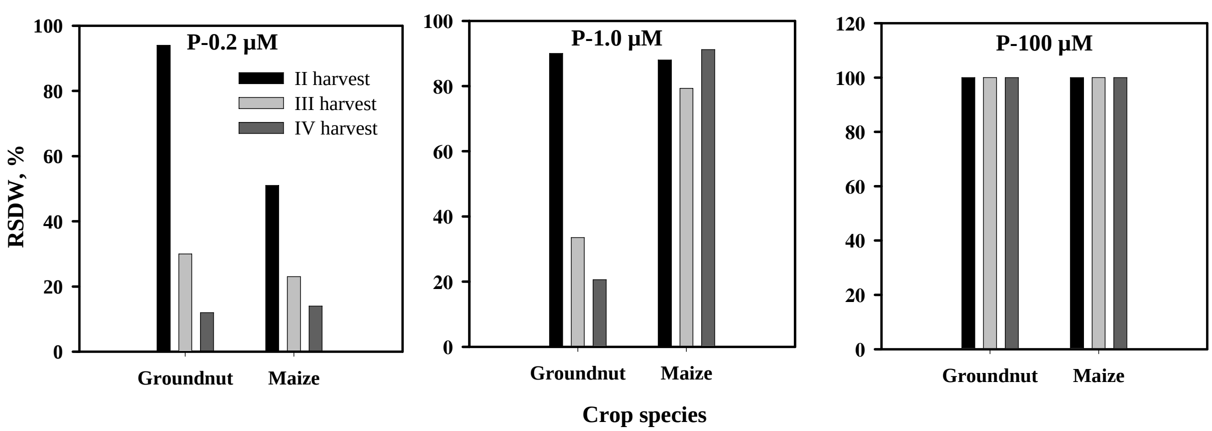

Figure 1: Relative shoot dry weight (RSDW) of groundnut and maize at different time of growth

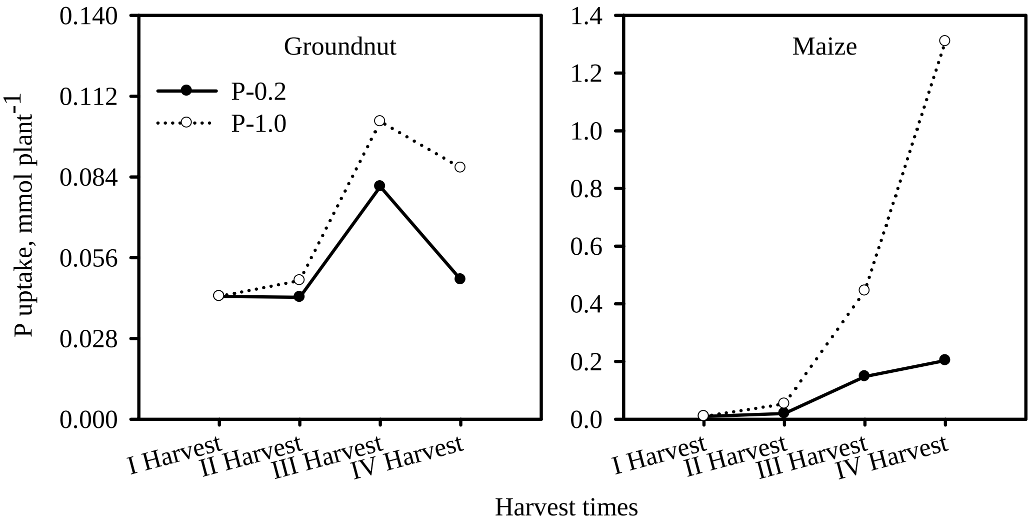

Figure 2: P-uptake by groundnut and maize at different time of growth

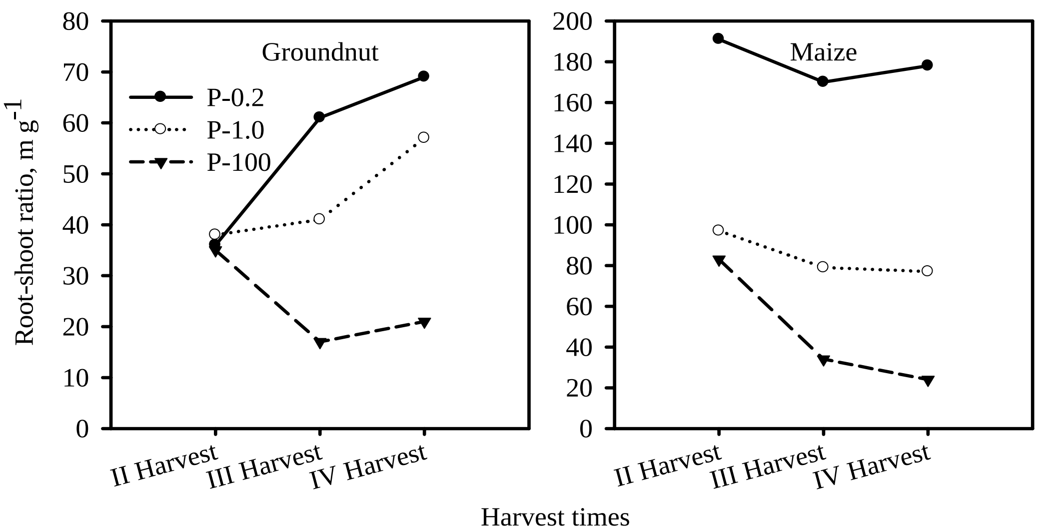

Figure 3: Root-shoot ratio of groundnut and maize at different time of growth

In this paper, the average influx was calculated from changes in P-content of the shoots. Figure 4 shows the average P-influx for the low P-concentrations only. The average influx decreased with plant age for both species at 0.2 and 1µM P-concentration. At 0.2µM it was almost nil for groundnut, but clearly positive for maize. At 1 µM P in solution, the average P-influx of groundnut was about 1 x 10^{-14} mol cm^{-1} s^{-1} in the first growth period and declined later being even negative between third and fourth harvest. Maize started with a three times higher average influx, which also declined, but even in the last phase it was close to 1 x 10^{-14} mol cm^{-1} s^{-1}. This shows that maize roots are much more efficient than groundnut roots in absorbing P from low P concentrations. A reason for the high P-uptake of maize was its higher P-influx where maize had 3-times higher average influx than groundnut at 1µM P-concentration and even the least influx realized by maize between the third and fourth harvests was comparable to the highest influx of groundnut at the early growth stages (Fig. 4). The low P-influx of groundnut in nutrient solution culture was the reason behind the different behavior of groundnut in the field, since the high P-efficiency of groundnut in the field was because at low-P concentrations in soil solution, it had high P-influx (6.8 x 10^{-14} and 10.3 x 10^{-14} mol cm^{-1} s^{-1}) at early and middle growth stages, respectively (Bhadoria et al., 2001). Since groundnut was incapable of obtaining a high P-influx in nutrient solution at low-P concentration, this would indicate that groundnut adopted other mechanisms for increasing the influx under field conditions, for example, chemical mobilization of P bound to the soil solid phase by root exudates (Ae et al., 1990; Ishikawa et al., 2002) or cell wall components (Ae et al., 2001) or contribution of AM (Marschner, 1995).

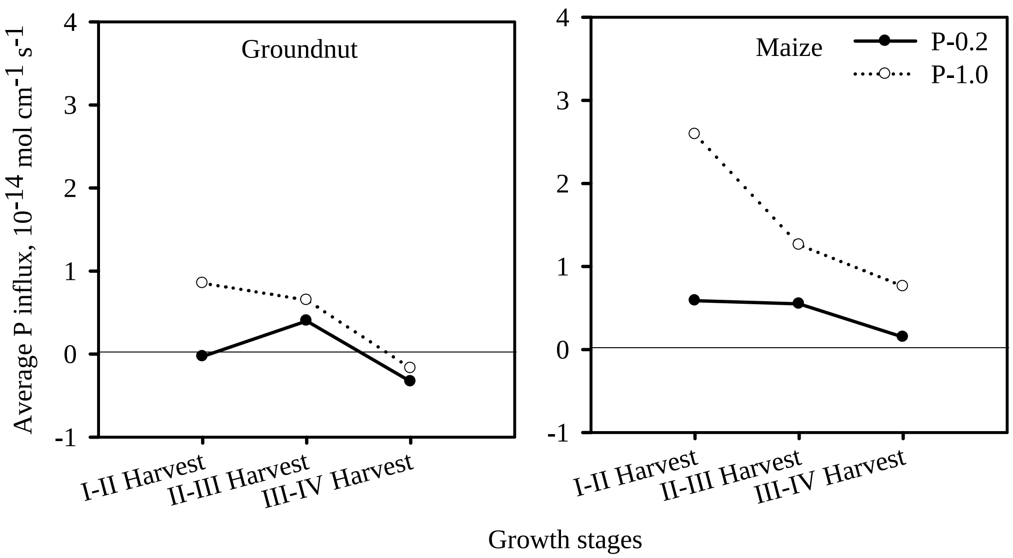

Figure 4: Average P-influx of groundnut and maize at different time of growth

The results obtained by the depletion techniques shows that when groundnut and maize grown at pretreatment P-concentrations of 1 and 100µM, the rate of depletion was almost constant at the beginning, but below 20µM it decreased for maize. The minimum concentration was below 1µM for maize grown at low P-concentration (Table 1). For maize grown at high P-concentration, the rate of depletion was much slower and the decrease was only down to 4µM, but C_{Lmin} was not reached. The depletion pattern for groundnut was similar to maize when grown at low P-concentration, but in contrast to maize when grown at 100µM, the plants were not able to take up P at a concentration of about 40µM. The P-influx was derived from the rate of P-depletion in nutrient solution and plotted as a function of P-concentration in solution. From these influxes, the values of I_{max} and K_m were obtained from the Hanes plot: $(C_L - C_{L\min})/I_n = [K_m/I_{\max} + (C_L - C_{L\min})/I_{\max}]$. The fitted regression line gave a reasonable approximation to the data. From this plot, I_{max} could be obtained from the slope of the line and K_m from the intercept on the X-axis. C_{Lmin} was directly read from the depletion curves.

Table 1: P-uptake parameters of groundnut and maize at different P-concentration in solution

Solution P-concentration μM	I_{max} 10^{-14} mol cm^{-1} s^{-1}	K_m μM	C_{Lmin} μM
Groundnut			
0.2	5.4	10	0.2
1	4.8	9	0.6
100	*	*	*
Maize			
0.2	24.7	14	0.1
1	34.2	22	0.1
100	18.9	18	4.0

* Shows no P-uptake at a P solution concentration of 40 μM

Table 1 shows the uptake parameters of groundnut and maize plants previously grown at different P-levels. I_{max} was larger by a factor of 1.7 when comparing maize of low and high P status even though shoot yield was about the same. Further decrease in P-status to 0.2μM, which caused a stronger reduction in yield, did not cause further increase of I_{max}. Groundnut had 6-times smaller values of I_{max} than that of maize. For maize, K_m values were ranged from 14-22 μM and for groundnut ranged from 9-10 μM. The minimum concentration, C_{Lmin} to which the plants reduced the concentration in solution can be seen from Table 1. Maize previously grown at low P-concentrations decreased the concentration to 0.1μM while groundnut decreased it to only 0.2 and 0.6 μM. Maize grown at 100μM depleted P only to 4μM, but groundnut was not able to absorb P even at 40μM.

The differences in P-influx of groundnut and maize in nutrient solution culture can be explained by differences in their uptake kinetics. The data showed that for the plants grown at low P-concentrations, maize even though its K_m values were 2-times higher than those of groundnut (Table 1), but the 6-times larger I_{max} explains the higher influx of maize as compared to groundnut (Fig. 4). Another factor contributing to P-inefficiency of groundnut is that at low P-concentration it had a high C_{Lmin} value (Table 1) which might have been even one of the reasons for the negative P-influx (Fig. 4). Plant adaptation to low P-supply by changing the uptake parameters was not evident from our data where it can be seen that I_{max} was not much different between 0.2 and 100μM P (Table 1). Also K_m was not much decreased with decreasing P-concentration from 100μM, similar unchanged K_m values between plants of different P-status were found by Drew et al. (1984). In the field experiment, Bhadoria et al. (2001) showed that P-influx of maize roots at low P-supply increased with plant age making it P-efficient. This adaptation to low P-supply was not observed in our solution experiment, on the contrary, the P-influx even decreased strongly with plant age. The adaptation of older maize plants to low P-supply in the field is not because of improved uptake kinetics, but probably more because of changes in root exudation pattern or AM infection, as was suggested above for groundnut. The results of this study show that differences in P-efficiency between maize and groundnut in solution culture are largely due to differences in uptake kinetics and to a lesser extent the size of the root system. The differences in P-efficiency observed in the field were opposite to those observed in solution culture and are, therefore, probably based on factors other than the uptake kinetics.

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