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Phosphorus Use Efficiency of Safflower (*Carthamus tinctorius* L.) and Sunflower (*Helianthus annuus* L.) Studied in Nutrient Solution

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Abstract: Safflower represents an important oil crop internationally and may have a production potential under low input conditions, but its putatively high phosphorous use efficiency is not sustained. This study aims to directly compare safflower with sunflower in terms of phosphorus use efficiency in nutrient solution under controlled conditions. Growth of both species responded strongly to increasing P supply. Safflower recovers less proportion of added P than sunflower. External P requirement ((g P supply (100 g dry matter (DM) produced)$^{-1}$) was higher in safflower than sunflower. The efficiency of the crops for DM production based on accumulated P (mg P pot^{-1}, efficiency ratio), and P concentration in DM ((mg P (g DM)$^{-1}$), utilization index) were interpreted using Michaelis-Menten kinetics as growth response curves. Accordingly, K_m constant was lower in sunflower compared to safflower in terms of utilization index, but both were similar in terms of efficiency ratio. High K_m constant in safflower in terms of utilization index indicates the high P concentration in tissues to produce 50% of potential maximum DM, consequently less efficient crop. Utilization efficiency contributed more than uptake efficiency in overall PUE in the efficient cultivar and could be the cause of its superiority in PUE. It can be concluded that safflower has a high requirement for P with respect to growth, sunflower is more efficient in terms of uptake and utilization of P at optimal and sub-optimal P supplies indicating that safflower can not be considered a low nutrient input crop compared to sunflower with respect to phosphorus.

Key words: Phosphorous, nutrient utilization efficiency, yield response curve, *Carthamus tinctorius*, *Helianthus annuus*.

1. Introduction

Although many soils have large reserves of total P, only a small fraction is immediately available making many agricultural areas P deficient [1]. The application of fertiliser P represents an important measure to correct nutrient deficiencies and to replace elements that have been removed in the products harvested [2]. In developing countries, where the proportion of less fertile soils is particularly high, it may be difficult to fulfil the nutritional requirements of high-yielding crops [3, 4]. However, due to chemical immobilization in the soil [5], recovery of fertiliser P is very low [6, 7], causing serious ecological and economical consequences of contaminating the environment [8-10]. It is thus desirable to aim for efficient use of P, both in view of resource limitations and environmental constraints, through the identification of crops species or cultivars with greater tolerance to suboptimal P availability to increase the production potential on marginal lands [11, 12].

The ability of cultivars to tolerate low P may be due to either high P absorption ability at low P concentrations and/or more efficient use of P for more yield production [13-15]. Efficient cultivars are of great importance to enable farmers to achieve reasonable yields with minimum input of P. However,

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cultivating P-efficient species or cultivars to improve yields or developing genotypes that are more P-efficient may be possible if phosphorus efficiency mechanisms are elucidated [16, 17]. Overall nutrient use efficiency (NUE) in plants is a function of capacity of soils to supply adequate levels of nutrients, and the ability of plant to acquire nutrients, transport them in roots and shoot and to remobilise them to other parts of the plant. Therefore, NUE involves various soil and plant mechanisms and processes that contribute to genetic variability in efficiency of uptake and utilization of nutrients [18].

Safflower (*Carthamus tinctorius* L.) and sunflower (*Helianthus annuus* L.), both belonging to the *Asteraceae*, are important oil crops in tropical areas. Safflower is highly branched, herbaceous, thistle-like annual, 30-150 cm tall with globular flower heads (capitula), characterised by a strong taproot, which enable it to thrive in dry climates and can access and utilize nutrients below the root zone of cereal crops [19]. The oil crop sunflower, however, is much taller, usually un-branched, lacks a taproot, and is considered more demanding in terms of nutrients and water [20].

Although both crops thrive in similar environments, direct comparisons of their response to increasing P availability with respect to P use efficiencies are not available, and since a two-year pot experiment using soil mixture [15, 21] shows the high P requirement and low P UE of safflower compared to sunflower. Therefore, the aim of this study is to directly compare the P use efficiency of safflower as compared to sunflower in nutrient solution under controlled conditions.

2. Material and Methods

2.1 Experimental Conditions

An experiment using safflower (*Carthamus tinctorius* L., variety "Sabina") and sunflower (*Helianthus annuus* L., variety "Salut R.M.") was carried out in the period from May to August 2006 in a greenhouse in which the day and night temperature was adjusted to 28 °C, and 15 °C, respectively, with additional lighting (intensity at canopy level equals to 260 μmol m^{-2} s^{-1}). Young plants of safflower and sunflower were grown in aerated nutrient solution with increasing phosphorus supply and randomised completely. Five phosphorus levels (in KH_2PO_4 form) were used for both species (0.05, 0.1, 0.2, 0.4, 0.8 mM) in 5 L plastic pots in eight replicates (pots) for each treatment. Other nutrients added were 5.0, 4.0, 1.0, 0.7, 0.5 mM N, K, Ca, Mg, and Fe, respectively in the following chemical forms: K_2SO_4, KCl, KNO_3, $Ca(NO_3)_2{\cdot}4H_2O$, NH_4NO_3, $MgSO_4{\cdot}7H_2O$, Fe-Na-EDTA. Micronutrients were added in adequate amounts (μM): 2.97 $MnCl_2{\cdot}4H_2O$, 1.24 $ZnCl_2$, 0.66 $CuCl_2{\cdot}2H_2O$, 24.75 H_3BO_3, 0.083 $(NH_4)_6Mo_7O_{24}{\cdot}4H_2O$ and 0.0413 $NiCl_2$.

Achenes were germinated between moist paper tissues and the roots of three-days-old, germinated achenes were passed through wholes of Styrofoam plates floating on aerated 0.2 mM $CaSO_4$ solution. Either two sunflowers or three safflowers of seven-days-old uniform-sized seedlings were transferred to each 5 L pot provided with lids, containing half the concentrations of nutrients solution for each P treatment. Nutrient solutions were constantly aerated, and the initial solution pH was 5.8, which was monitored during the first two weeks of the experiment every other day. Abundance of nutrients in pots was checked every other day using nitrate strips (nitrate as indicator range from 10 to 500 mg/L NO_3^- from Merck KGaA, Darmstadt, Germany) to ensure that the nutrients are not depleted by the growing plants. When the nitrate in the highest P level treatments is less than 10 mg/L (the two cultivars were checked separately), new nutrient solutions substituted the old ones in all pots for the same species. The volume of remaining nutrient solution each time before changing to new one and after harvest was measured. A sample from each pot was taken to be analysed for P at each time the nutrient solution was changed and after harvest. After 50% flowering, the plants received nutrient solution contain all nutrients

without P (P-free nutrient solution), and new nutrient solutions (P) were added when nitrate was depleted after nitrate test for each cultivar independent of the other species. The total P supply (mg P pot^{-1}) for each treatment was calculated from the number of times where new nutrient solution was added and the P content (mg) of the added nutrient solution for each pot individually. The remaining P in the nutrient solution after renewing the nutrient solutions was calculated by multiplying the volume of the remained nutrient solution by the P concentration in the sample taken from that solution for each pot individually. Aphids were controlled with regular pesticide applications of Metasystox® (S-[2-Ethylsulfinyl) ethyl] O, O-dimethyl phosphorothionate), and infestations with *Perenospora* sp. were controlled by application of Amistar® (azoxystrobin) according to manufacturers recommendation.

2.2 Harvesting and Analytical Procedures

Growth parameters were monitored along the growing period. A young mature blade (YMB) of each plant was taken for leaf area measurement using leaf area scanner. Plants were harvested in two growth stages (anthesis and maturity), four replicates of each P treatment for each species were harvested at 50% flowering stage (end of June), and the other four replicates were let to mature (end of July). Each pot was harvested individually when it reached the stage of maturity. Plants were separated into capitula, leaves, stems and roots. Leaves and stems were separated to upper and lower parts by cutting the stem into two equal parts in length in both harvest stages, achenes were also separated from the mature plants. All plant parts were dried (except achenes that were dried at room temperature in a well-aerated area) at 70 °C until constant weight in a drying oven, grinded to pass a 1.5 mm sieve, of which, after thorough mixing, a sub-sample of 5 g was ball-milled to a fine powder. The samples were prepared for P analysis using dry ashing method [22], in which 50 mg of dried sample was ashed in a crucible at 450 °C in a muffle furnace overnight. Then 1 mL of 0.35 M HNO_3 solution was added, and after swirling left for at least 10 minutes. After addition of 9 mL of purified water (18.2 MΩ cm^{-1}), the sample is filtered through ashless filter paper (blue ribbon, Whatman®, Schleicher und Schüll, Whatman International Ltd, England) into polypropylene tubes. Total P of the plant material was measured using colorimetric method (Ammonium-Vanadate-Molybdate) according to Gericke and Kurmies [23], and in the remaining nutrient solutions using the colorimetric method according to Schüller [24].

2.3 Statistics and Yield Component Analysis

All statistical analysis was carried out using SAS (SAS Institute Inc., Cary, USA, Release 8.02, 2001). Comparisons of means with respect to the influence of P supply were carried out using the GLM procedure considering a fully randomised design. Where appropriate, data were transformed to maintain homogeneity of variance. The Bonferoni procedure was employed with multiple *T*-tests in order to maintain an experiment wise α of 5%.

Response curves were derived from the relationship between each parameter tested (e.g., g DM pot^{-1}) on the y-axis and the amount of P accumulated in the plants, P supply, or P concentration in DM (e.g., for P accumulated in plants; mg P total $plant^{-1}$ pot^{-1}) using the following Michaelis-Menten-type equation:

$$\text{Yield parameter} = (A_{max} \times (\text{mg } P)/(c + (\text{mg } P))$$

with "A_{max}" as an estimate of maximum yield, and "c" as the P accumulation or P concentration in DM required for half maximum yield production, corresponding to the K_m in Michaelis-Menten kinetics. The Michaelis-Menten equation proved superior to the Mitscherlich curve and has been widely used to describe nutrient efficiency [12, 25]. Curve fitting was carried out using the procedure NLIN in SAS, employing the Gauss-Newton algorithm. The Michaelis-Menten equation was applied to compare

both species in terms of accumulation efficiency (mg P accumulated pot^{-1}), and DM response curves based on accumulated P and P concentration in DM [26-29].

Linear regression was used to compare the linear relations between P supply and some parameters (external P requirement, P recovery, P concentration in DM) using the procedure "mixed" in SAS program. Significant difference was based on the 95% confidence limit for the "*a*"; slope and "*b*"; the Y-intercept of the linear equations of the two species.

NUE may be broken down into its components and expressed in a multiplicative fashion as: Nutrient use efficiency [g DM $(g\ P\ supply)^{-1}$] = P uptake efficiency ((mg P accumulated $(g\ P\ supply)^{-1}$) × P utilization efficiency $((g\ DM\ produced\ (mg\ P\ accumulated)^{-1})$. In order to quantify the impact of individual NUE components (uptake and utilization efficiencies) multiple regression analysis is biased as the mathematical product, rather than a statistical relationship, of "Uptake efficiency" and "Utilization efficiency" result in NUE. Hence, a component analysis according to Piepho [30] was employed, allowing the contribution of individual components of NUE to be quantified [15, 29]. This approach assumes that the SD of log-transformed yield is close to the coefficient of variance of the yield, uses the log-transformed component data and interprets values of $C_i = Cov$ [log (NUE), log $(component_i)$] as an aggregate measure of the ith component's contribution to the variability in yield.

3. Results

3.1 Growth Parameters

Both crops responded strongly to increasing P supply with respect to growth. Growth and achene yield of safflower increased up to 186 mg P per pot (0.2 mM [P])♣, and sunflower's optimal growth (DM production) was achieved at 533 mg P pot^{-1} (0.2 mM [P]). Sunflower achene yield was not consistent according to pollination problems, consequently the presence of high percent of hollow achenes. Leaf area and stem diameter increased as solution [P] increased (Table 1). Plant height of both species reduced in deficient solution [P] but was more pronounced in sunflower. As safflower a branching plant, the total number of branches was highly affected in deficient solution [P], accordingly, the secondary branches of safflower were totally inhibited under severe deficit solution [P], and also the number of primary branches was decreased under inadequate solution [P]. The number of capitula per plant in safflower was reduced with decreasing external solution [P]. Deficient solution [P] reduced the number of leaves in both species as a result of reducing new leaf formation in the upper half of the plant while the number of leaves in the lower half was not affected in both species (Table 2).

Total dry matter of both species in both harvesting times was improved with increasing external solution [P] (Tables 3, 4, and 5). The dry matters of both upper and lower leaves of both plants were improved, taking in consideration that the number of leaves of the upper half in both species (measured at anthesis) was increased with increasing solution [P] which can be the cause for the improved total dry matter of this part of the plants, but this parameter (number of leaves) was not affected by increasing solution [P] in the lower part of both plants. The dry matter of both upper and lower parts of stems of both species were positively influenced in the same manner, as external solution [P] increased resulting in an increment in the dry matter of stem of both plants. Dry matter of safflower capitula was increased with increasing solution [P] but that of sunflower was not affected. Root dry matter of both species was not affected with different P supplies in the solution.

3.2 Effect of P Supply on Some P Uptake Efficiency Indicators

3.2.1 Effect of P Supply on C_{min}

The minimum concentration of P which still remain in the nutrient solution, although the plant suffering from P deficiency (C_{min}) does not differ significantly

♣ [P] indicates P concentration in the nutrient solution.

Table 1 Effect of P supply on growth parameters of safflower and sunflower[a].

P supply (mM)	P supply (mg pot^{-1})	Leaf area (cm^2)	Number of leaves plant^{-1}			Plant height (cm)	Stem diameter (mm)
			Upper	Lower	Total		
Safflower							
0.05	46.5	20.8±3.4 B	26.8±2.6 C	13.0±0.8 A	39.8±2.2 C	73.0±5.0 B	5.5±0.4 C
0.1	92.9	32.3±4.2 A	67.0±7.1 B	13.0±0.8 A	79.5±6.9 B	83.8±3.9 A	7.4±0.2 B
0.2	185.8	38.4±2.0 A	87.5±9.9 A	11.0±1.6 A	98.5±11.2 A	86.0±3.6 A	8.3±0.4 A
0.4	371.6	37.4±4.8 A	78.0±5.9 BA	10.8±1.0 A	88.5±6.8 BA	87.8±2.1 A	8.1±0.2 A
0.8	743.3	36.9±2.3 A	84.8±3.2 A	12.0±1.4 A	96.8±3.9 A	86.0±3.7 A	8.7±0.3 A
Sunflower							
0.05	133.2	110.9±8.1 D	16.0±0.8 B	12.0±0.8 A	27.8±1.3 C	163.8±10.3 C	15.2±0.7 C
0.1	266.3	167.0±13.9 C	17.3±1.0 B	13.0±1.4 A	30.0±1.6 BC	188.8±8.5 B	18.9±1.1 B
0.2	532.7	264.5±5.0 A	19.8±1.0 A	11.5±1.0 A	31.0±0.8 BA	218.8±8.5 A	20.8±0.8 BA
0.4	1065.4	231.5±14.3 B	22.0±0.8 A	11.8±1.2 A	33.8±1.0 BA	212.5±2.9 A	22.4±1.8 A
0.8	2130.7	209.6±5.9 B	20.3±1.3 A	11.8±1.7 A	32.0±1.4 A	208.8±2.5 A	23.1±0.9 A

[a] Figures within each column followed by the same letter are not significantly different ($P < 0.05$, n = 4), values are means ± SD.

Table 2 Effect of P supply on number of branches and capitula of safflower[a].

P supply (mM)	Number of branches plant^{-1}			Capitula plant^{-1}
	Primary	Secondary	Total	
0.05	5.7±0.3 C	0.3±0.5 C	5.9±0.3 C	6.8±0.5 C
0.1	6.5±0.4 BC	6.5±1.2 B	13.0±0.9 B	14.8±1.0 B
0.2	7.5±0.6 BA	6.6±1.0 B	14.1±1.1 B	15.0±0.8 BA
0.4	7.5±0.2 BA	6.4±0.9 B	13.9±0.9 B	14.0±0.8 BA
0.8	7.8±0.6 A	9.3±0.7 A	17.1±1.1 A	16.3±0.5 A

[a] Figures within each column followed by the same letter are not significantly different ($P < 0.05$, n = 4), values are means ± SD.

Table 3 Effect of P supply on growth parameters of safflower and sunflower at anthesis[a].

P (mM)	Leaf DM (g pot^{-1})			Stem DM (g pot^{-1})			Capitula DM (g pot^{-1})	Root DM (g pot^{-1})	TDM (g pot^{-1})
	Upper	Lower	Total	Upper	Lower	Total			
Safflower									
0.05	1.3±0.2 C	2.8±0.4 C	4.1±0.4 C	2.0±0.3 C	5.3±0.9 B	7.2±1.0 C	6.5±0.5 C	4.4±0.6 C	22.2±1.3 C
0.1	3.0±0.4 B	4.3±0.2 BA	7.4±0.4 B	5.1±0.7 B	9.5±0.5 A	14.6±1.2 B	11.7±1.5 B	6.6±0.8 BA	40.2±3.5 B
0.2	4.3±0.5 A	4.5±0.5 BA	8.8±0.9 BA	6.4±0.2 A	9.2±1.6 A	15.6±1.7 BA	12.7±2.8 B	5.4±0.6 BC	42.4±5. B7
0.4	3.8±0.4 BA	3.9±0.3 B	7.7±0.7 BA	6.3±0.4 A	8.8±1.0 A	15.1±0.8 BA	12.3±0.7 B	5.8±0.4 BC	40.9±1.9 B
0.8	4.1±0.2 A	5.0±0.8 A	9.1±0.9 A	6.7±0.1 A	11.2±1.6 A	17.9±1.7 A	17.1±1.9 A	7.7±0.3 A	51.7±4.6 A
Sunflower									
0.05	18.9±1.4 C	11.7±1.2 C	30.6±2.0 C	16.3±0.8 B	32.0±3.7 B	48.3±3.9 B	12.3±1.6 A	18.7±2.7 A	109.8±8.8 B
0.1	28.4±2.7 B	15.4±1.3 BC	43.7±3.5 B	26.0±3.3 A	50.0±2.5 A	76.0±4.8 A	13.6±1.9 A	16.3±3.5 A	149.7±12.1 A
0.2	31.2±3.0 B	17.1±2.2 B	48.3±4.0 B	22.5±3.2 A	57.5±5.0 A	80.0±6.8 A	11.0±1.2 A	16.3±4.1 A	155.6±13.6 A
0.4	42.3±1.1 A	19.5±2.2 BA	61.7±2.9 A	26.6±4.2 A	61.4±6.4 A	88.0±10.3 A	9.8±2.1 A	20.6±1.7 A	180.1±15.8 A
0.8	39.2±4.5 A	23.3±2.0 A	62.5±5.7 A	24.2±1.8 A	62.4±9.9 A	86.6±11.4 A	12.0±3.6 A	20.0±3.6 A	181.2±20.6 A

[a]Figures within each column followed by the same letter are not significantly different ($P < 0.05$, $n = 4$), values are means ± SD.

Table 4 Effect of P supply on leaves and stem DM of safflower and sunflower at maturity[a].

P (mM)	Leaf DM (g pot^{-1})			Stem DM (g pot^{-1})		
	Upper	Lower	Total	Upper	Lower	Total
Safflower						
0.05	1.1±0.4 C	2.1±0.4 B	3.2±0.7 C	1.9±0.3 C	3.8±0.8 B	5.7±1.1 C
0.1	2.8±0.3 B	3.4±0.4 A	6.1±0.5 B	5.4±1.1 B	6.4±0.9 A	11.7±1.8 B
0.2	3.1±0.6 B	3.8±0.6 A	6.9±1.2 B	6.4±0.4 BA	7.7±0.7 A	14.1±1.0 BA
0.4	3.2±0.3 B	3.4±0.3 A	6.6±0.5 BA	5.4±0.5 B	6.8±0.5 A	12.2±1.0 B
0.8	4.7±0.6 A	4.1±0.7 A	8.8±1.1 A	7.7±0.5 A	7.6±0.7 A	15.3±1.1 A
Sunflower						
0.05	16.5±2.4 C	12.4±1.7 B	28.9±1.3 C	13.5±2.4 B	29.3±1.9 C	42.8±3.8 C
0.1	26.8±3.1 B	17.1±0.4 A	43.9±3.4 B	22.1±2.2 A	51.2±4.4 B	73.3±5.8 B
0.2	40.2±5.1 A	17.4±2.5 A	57.6±3.5 A	27.9±6.1 A	62.5±6.7 BA	90.4±9.5 BA
0.4	38.2±3.7 A	15.9±0.5 BA	54.0±3.9 A	26.3±2.9 A	61.5±3.3 BA	87.7±2.6 BA
0.8	39.9±3.1 A	19.0±2.7 A	58.9±1.9 A	28.3±3.2 A	71.0±9.6 A	99.3±11.5 A

[a]Figures within each column followed by the same letter are not significantly different ($P < 0.05$, $n = 4$), values are means ± SD.

Table 5 Effect of P supply on the dry matter (g pot^{-1}) of capitula, roots, achenes, and total plant of safflower and sunflower at maturity[a].

P (mM)	Capitula DM	Roots DM	Achene yield	TDM
Safflower				
0.05	5.8±0.8 C	3.7±0.7 C	9.9±1.6 C	28.2±4.0 D
0.1	12.7±1.7 B	4.7±0.5 CB	18.7±1.3 B	54.0±3.7 C
0.2	15.1±0.7 BA	5.0±0.4 B	24.5±2.4 A	65.6±4.4 B
0.4	12.8±1.1 B	5.3±0.3 B	23.0±0.5 A	59.9±2.5 BC
0.8	17.2±1.6 A	7.0±0.2 A	25.6±0.9 A	73.7±4.8 A
Sunflower				
0.05	17.2±2.0 B	15.2±1.3 B	28.2±3.4 A	132.3±8.0 C
0.1	23.3±3.9 BA	19.5±2.6 BA	20.9±3.6 A	180.8±6.9 B
0.2	22.2±4.1 BA	24.4±4.3 A	25.2±23.5 A	219.9±17.4 A
0.4	28.6±4.9 A	14.0±2.1 B	40.3±18.5 A	224.7±23.1 A
0.8	21.8±3.3 BA	18.9±2.7 BA	24.1±15.5 A	217.0±17.3 BA

[a]Figures within each column followed by the same letter are not significantly different ($P < 0.05$, $n = 4$), values are means ± SD.

Table 6 Phosphorus C_{min} (mg P L^{-1}) values at two P deficient supplies in safflower compared to sunflower at anthesis and maturity[a].

P supply	Anthesis		Maturity	
	Safflower	Sunflower	Safflower	Sunflower
0.05	0.24 ± 0.14 A [n.s]	0.23 ± 0.06 A	0.43 ± 0.29 A [n.s]	0.37 ± 0.06 A
0.1	0.41 ± 0.21 A [n.s]	0.61 ± 0.32 A	0.36 ± 0.01 A [n.s]	0.39 ± 0.01 A

[a] Figures within each column followed by the same letter are not significantly different, n.s represents not significant between two species at the same P level and the same experiment (anthesis or maturity) ($P < 0.05$, $n = 4$), values are means ± SD.

between both species at two deficient P levels (0.05, and 0.1 mM P), was measured at both anthesis and maturity (Table 6). Also there was no significant difference in C_{min} in the same plant at both mentioned P deficient levels.

3.2.2 Effect of P Supply on P Accumulation

As the total P supplies (mg P pot^{-1}) at equivalent [P] (mM P) are not the same for the two crops (Table 1),

the comparison of means is not helpful. Therefore, the P accumulation of both species related to P supply was the best fitted using Michaelis-Menten-type equations (Fig. 1). Although this type of equation is applied, less explanation can be given from the differences of the

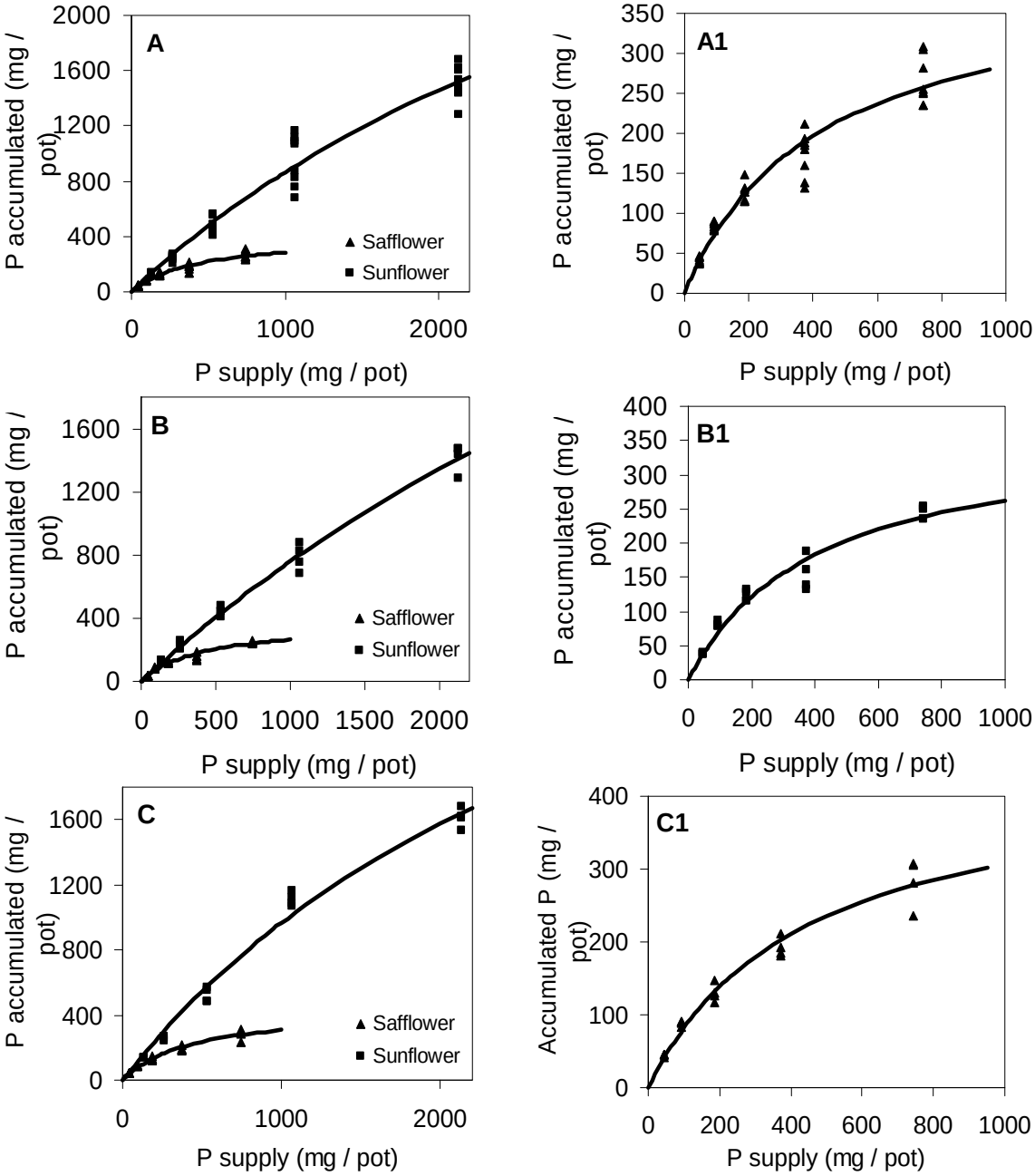

Fig. 1 P accumulation response curves for safflower and sunflower based on the P supply per pot; sub-figures A, B, and C represent both crops in the same scale and sub-figures A1, B1, and C1 represent safflower only in a smaller scale to make it more clear; Michaelis-Menten-type equations are given as: Accumulated P = (A_{max} × (mg *P* supplied))/(*c* + (mg *P* supplied)), with "P" representing the P supplied per pot, "*c*" the K_m, "*A*" the maximum P accumulation potential. (A) accumulated $P_{sunflower\ (anthesis\ and\ maturity)}$ = (4638.6* × *P*)/(4359*+ *P*); (A1) accumulated $P_{safflower\ (anthesis\ and\ maturity)}$ = (404.6 × P)/(421.0 + P), (B) accumulated $P_{sunflower\ (maturity)}$ = (5767.4* × P) / (6582.3*+ P), [B], (B1) Accumulated $P_{safflower\ (maturity)}$ = (368.3 × P) / (405.0 + P), (C) accumulated $P_{sunflower\ (anthesis)}$ = (4262.5* × P) / (3410*+ P), (C1) accumulated $P_{safflower\ (maturity)}$ = (440.1 × P) / (434.4 + P); * indicates significant difference between the two species in the same constant (*P* < 0.05).

equation constant between the two plants as will be shown in the yield response curves later. Both species accumulated increasing P amounts in their shoots as P supply increased. A_{max} and K_m were significantly higher in sunflower compared to safflower at anthesis, maturity, and when both data are pooled.

3.2.3 Effect of P Supply on P Recovery

The linear response curves relating P recovery in the plants to P supply for both species (Fig. 2) at each harvesting stage and when the data were pooled showed that the two species are significantly different from each other in terms of the slope according to the 95% confidence limits. The linear curves of sunflower lay over that of safflower. The P recovery decreases with increasing P supply in both species, but the slope of this decrease is significantly less in sunflower than in safflower, which indicates that sunflower has advantage over safflower to recover added P. The y-intercept was not significantly different between species and reveals that at the levels of P supply near zero, both species could recover the same percentage of external P supply. At anthesis, both species removed almost all added external solution P at low external [P] and this percentage is sharply decreased in safflower with increasing P level to reach less than 40% at the highest P supply, while sunflower still removed all added P at deficient and optimal P supply, then decreased to nearly 80%, at the highest external [P].

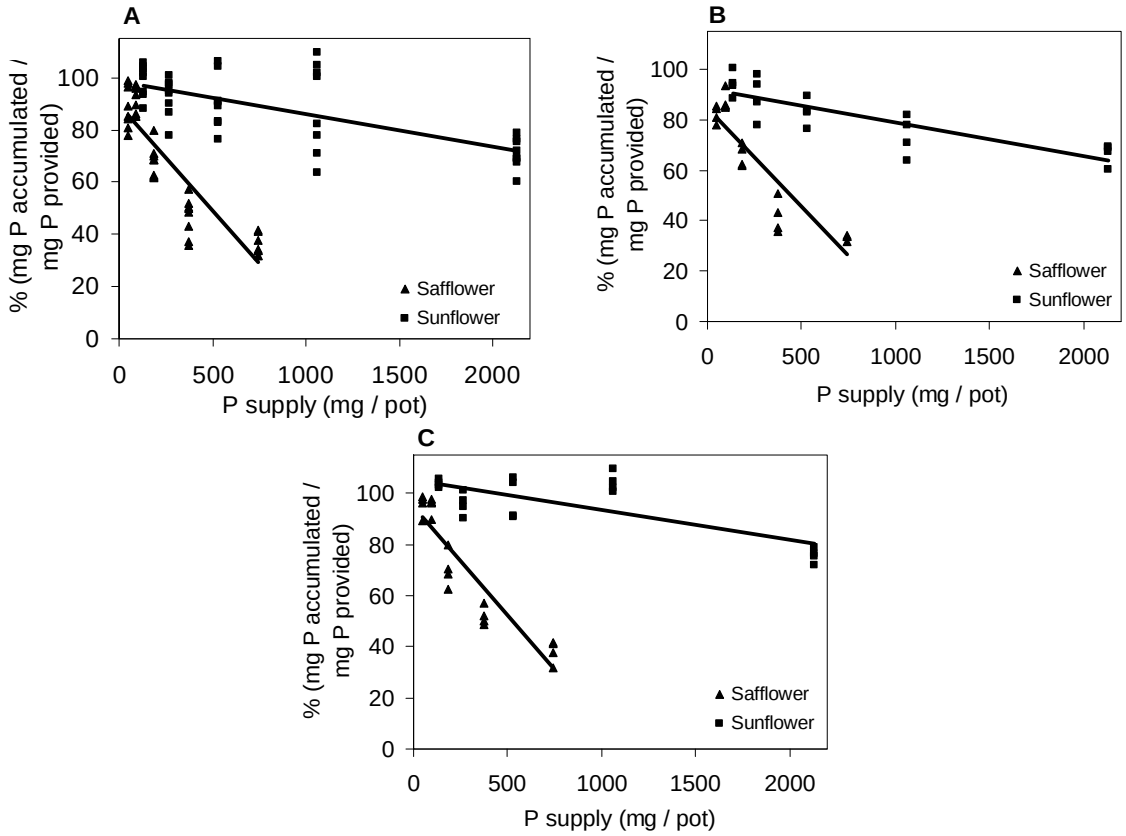

Fig. 2 P recovery response curves for safflower and sunflower based on the P supply per pot. Linear regressions are given. (A) Recovered P (%) $_{\text{sunflower (anthesis and maturity)}}$ = -0.0124* × P supply (mg pot $^{-1}$) + 98.587$^{n.s}$ (r^2 = 0.45*), Required P (g pot $^{-1}$) $_{\text{safflower (anthesis and maturity)}}$ = -0.0811 × P supply (mg pot $^{-1}$) + 89.412 (r^2 = 0.80***), (B) Recovered P (%) $_{\text{sunflower (maturity)}}$ = -0.0132* × P supply (mg pot $^{-1}$) + 92.175$^{n.s}$ (r^2 = 0.70***), Required P (g pot $^{-1}$) $_{\text{safflower (maturity)}}$ = -0.0777 × P supply (mg pot^{-1}) + 84.435 (r^2 = 0.82***); (C) Recovered P (%) $_{\text{sunflower (anthesis)}}$ = -0.0115* × P supply (mg pot $^{-1}$) + 105$^{n.s}$ (r^2 = 0.56***), Required P (g pot $^{-1}$) $_{\text{safflower (anthesis)}}$ = -0.0844 × P supply (mg pot $^{-1}$) + 94.39 (r^2 = 0.85***). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively, n.s indicates not significant.**

3.3 Effect of P Supply on P Utilization Efficiency Indicators

3.3.1 Yield Response Curves

DM response curves relating the accumulated P in DM with the DM produced (Fig. 3) are homologous to the efficiency ratios (will be discussed later). The functional relationship between nutrient supply and yield parameters may be described in several ways. Polynomial functions are easily applied, but do not allow interpreting their coefficients in a straightforward fashion. The classical Mitscherlich equation has often been used to describe yield responses, but in order to characterize nutrient efficiency, the Michaelis-Menten equation has been more frequently employed [12, 25]. In analogy to enzyme kinetics, the P accumulation required to produce 50% of the predicted maximum yield (term "*c*") corresponds to the K_m in Michaelis-Menten kinetics and essentially describes the curvature of the graph. It is thus a good indicator of the sensitivity of a crop to reduced nutrient supply, hence its nutrient efficiency. However, this approach requires a well-defined response curve from which the yield maximum can be deduced. The data of DM for both crops was applied from both harvesting stages of the experiment (anthesis and maturity) and when all data were pooled. Characterizing nutrient efficiency according to this approach reveals that K_m of both species is not significantly different, which indicates that both species have the same efficiency to use accumulated P for DM production at 50% maximal DM yield, because the term "*c*" is always the same for sunflower and safflower (Fig. 3).

3.3.2 Agronomic P Efficiency (External P Requirement)

The term "external nutrient requirement" refers to the amount of nutrient in the media required to produce a given percentage of maximum yield [31, 32]. Accordingly, we adopted a calculation that defines the required external P quantity (in g) to produce 100 g of DM. Comparing the linear response curves of both species (Fig. 4), it obviously shows the higher requirement of safflower for external P than sunflower at both harvesting times (anthesis and maturity) and when data were pooled. This can be proved by the significantly large slope of the linear relationship between P supply and P requirement of safflower compared to that of sunflower. The y-intercept indicates the requirement of external P at near zero P supply, was higher in safflower than sunflower but the difference was significant at maturity only.

3.3.3 Utilization Index

According to the comparison of the linear curves of both species at both harvesting stages (Fig. 5), it was observed that the linear curves of both species are significantly differing from each other in both slope and y-intercept at maturity and in only y-intercept at anthesis. The sunflower response curves lay significantly higher than that of safflower, indicating the higher utilization index values in the former compared to the later. At the very low P supplies (y-intercept), sunflower can produce much higher DM per unit of P concentration than safflower. In both species, at the higher P levels, P use efficiency decreased, implying the "law of diminishing returns" in P use for production of dry matter.

The DM response curve based on the P concentration in DM is homologous to the term utilization index. It was applied to the Michaelis-Menten equation and represents more clear response (Fig. 6) than the calculated UI based on the P supply. The response curves showed higher A_{max} and lower K_m values for sunflower compared to safflower indicating clearly the higher utilization efficiency of the former compared to the later in term of this efficiency indicator. Consequently, sunflower required less P concentration in DM to produce 50% of the maximum yield (K_m) than safflower, in addition, the former had a significantly higher DM production potential (A_{max}) than the later.

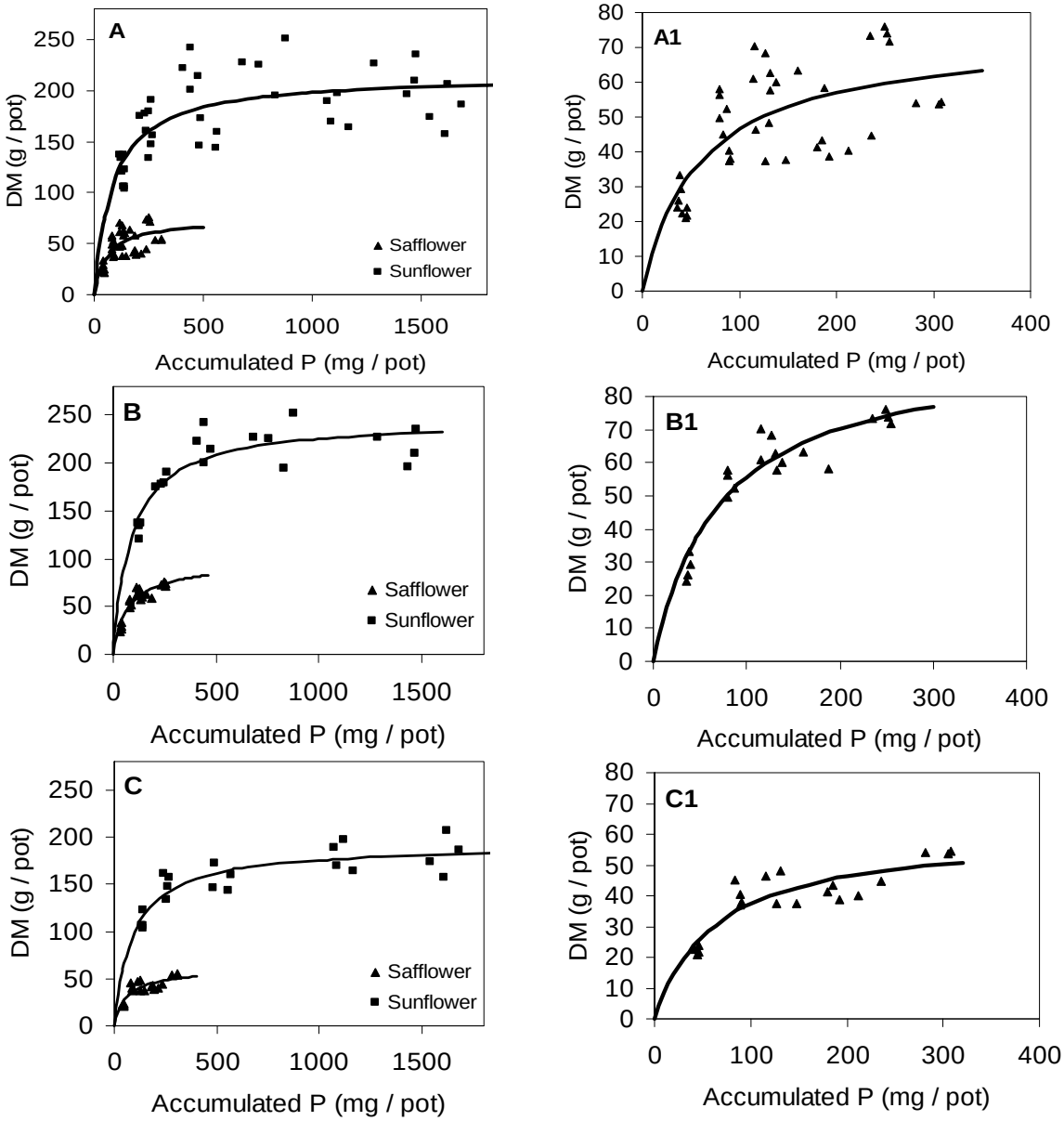

Fig. 3 DM response curves for safflower and sunflower based on the total P accumulated in above-ground biomass per pot. Sub-figures A, B, and C represent both crops in the same scale and sub-figures A1, B1, and C1 represent safflower only in a smaller scale to make it more clear. Michaelis-Menten-type equations are given as: DM = (A_{max} × (mg *P*))/(*c* + (mg *P*)), with "mg *P*" representing the P accumulated in biomass per pot, "*c*" the K_m, "*A*" the maximum yield potential. (A) TDM sunflower (anthesis and maturity) = (215* × (mg *P*))/(85.04n.s + mg *P*); [A1] TDM safflower (anthesis and maturity) = (73.7 × (mg *P*))/(58.10 + mg *P*); (B) TDM sunflower (maturity) = (246.0* × (mg *P*))/(90.8^{ns} + mg *P*), (B1) TDM safflower (maturity) = (95.5 × (mg *P*))/(72.2 + mg *P*); (C) TDM sunflower (anthesis) = (192.3* × (mg *P*))/(94.0^{ns} + mg *P*), [C1] TDM safflower (anthesis) = (60.7 × (mg *P*))/(62.8 + mg *P*). * indicates significant difference between the two species in the same constant (*P* < 0.05).

The shoot P concentration at 50% of the maximum yield (K_m) of sunflower was less than that of safflower. However, sunflower required a low level of external P to produce fixed amount of yield compared to safflower. The use of agronomic use efficiency and to less extent ER and UI as efficiency indicators involve the uptake of the nutrient and its utilization to produce final yield and does not indicate the mechanism

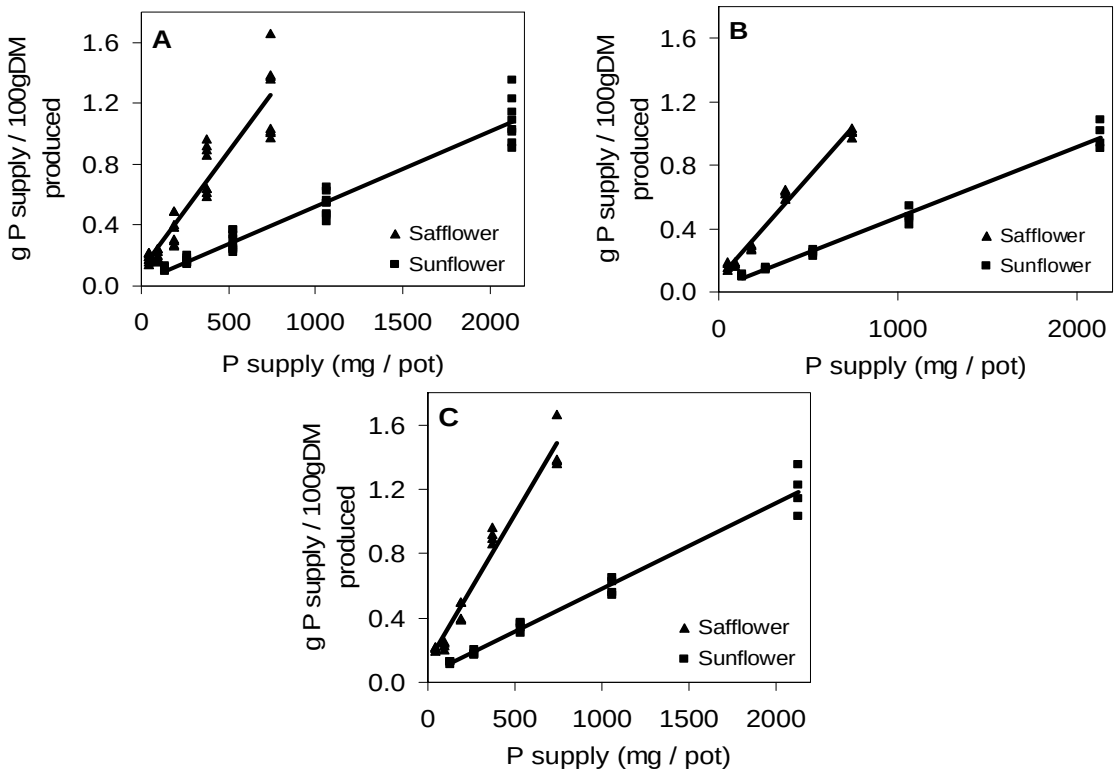

Fig. 4 P requirement (for production of 100 g DM) response curves for safflower and sunflower based on the P supply per pot. Linear regressions are given. (A) Required P (g pot^{-1}) $_{\text{sunflower (anthesis and maturity)}}$ = 0.0005* × P supply (mg pot^{-1}) + 0.0339$^{n.s}$ (r^2 = 0.96*), Required P (g pot^{-1}) $_{\text{safflower (anthesis and maturity)}}$ = 0.0016 × P supply (mg pot^{-1}) + 0.1008 (r^2 = 0.89***); (B) Required P (g pot^{-1})$_{\text{sunflower (maturity)}}$ = 0.0004* × P supply (mg pot^{-1}) + 0.0226* (r^2 = 0.98***), Required P (g pot^{-1}) $_{\text{safflower (maturity)}}$ = 0.0013 × P supply (mg pot^{-1}) + 0.0849 (r^2 = 0.98***); (C) Required P (g pot^{-1}) $_{\text{sunflower (anthesis)}}$ = 0.0005* × P supply (mg pot^{-1}) + 0.0452$^{n.s}$ (r^2 = 0.98***), Required P (g pot^{-1}) $_{\text{safflower (anthesis)}}$ = 0.0018 × P supply (mg pot^{-1}) + 0.1166 (r^2 = 0.97***). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively. n.s indicates not significant.**

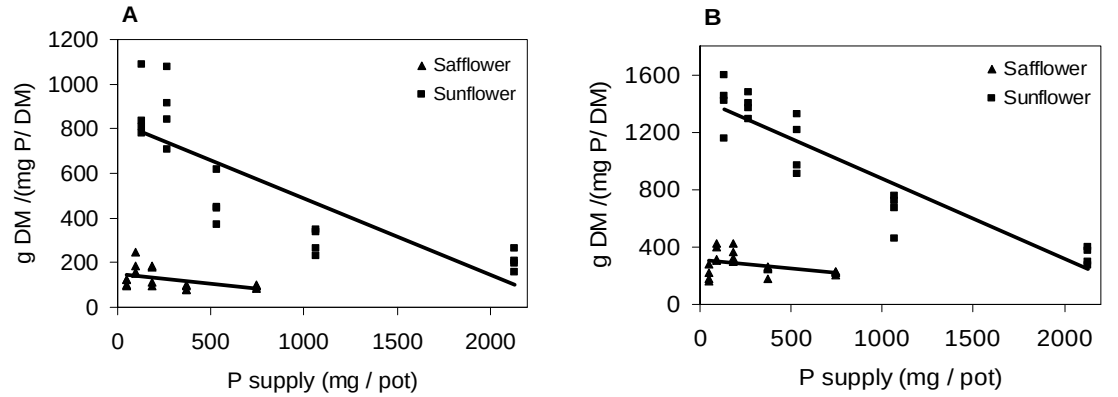

Fig. 5 P utilization index (PUI) (g DM/(g P (g DM)$^{-1}$)) response curves for safflower and sunflower in term of DM production based on the P supply per pot. Linear regressions are given. (A) PUI $_{\text{sunflower (anthesis)}}$ = -0.3414$^{n.s}$ × P supply (mg pot^{-1}) + 828.35* (r^2 = 0.68*), PUI $_{\text{safflower (anthesis)}}$ = -0.0848 × P supply (mg pot^{-1}) + 148.69 (r^2 = 0.24$^{n.s}$); (B) PUI $_{\text{sunflower (maturity)}}$ = -0.5583* × P supply (mg pot^{-1}) + 1436.6* (r^2 = 0.86***), PUI $_{\text{safflower (maturity)}}$ = -0.1179 × P supply (mg pot^{-1}) + 310.53 (r^2 = 0.15$^{n.s}$). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively. n.s indicates not significant.**

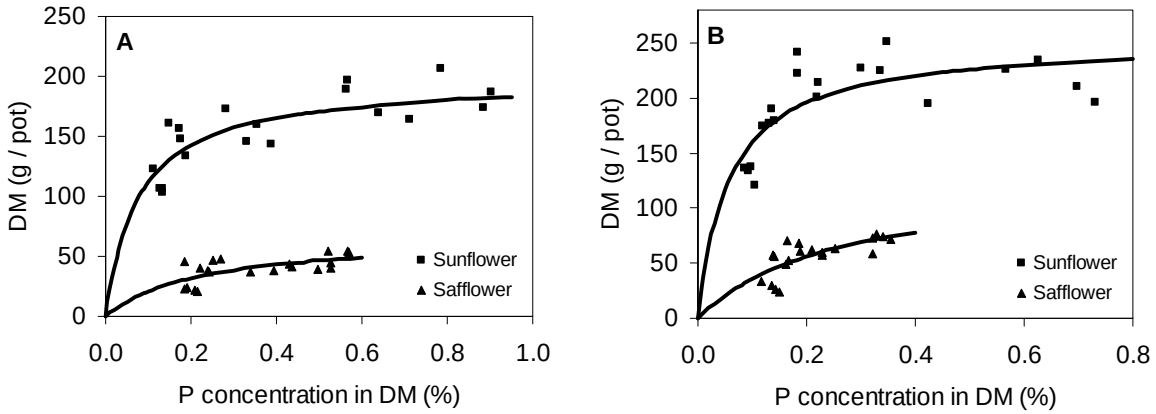

Fig. 6 Dry matter (DM) response curves for safflower and sunflower based on the P concentration in above-ground biomass per pot. Michaelis-Menten-type equations are given as: DM = (A_{max} × (P concentration))/(c + (P concentration)), with "*Pconc*" representing the P concentration in above-ground biomass per pot, "*c*" the K_m, "*A*" the maximum DM yield potential. [A] DM sunflower (anthesis) = (197.3* × (*Pconc.*))/(0.0765* + *Pconc.*), TDM safflower (anthesis) = (66.8 × (*Pconc.*))/(0.2196 + *Pconc.*), [B] DM sunflower (maturity) = (252.7* × (*Pconc.*))/(0.0581* + *Pconc.*), DM safflower (maturity) = (128 × (*Pconc.*))/(0.257 + *Pconc.*). * indicates significant difference between the two species in the same constant ($P < 0.05$).

through which the efficient cultivar interprets its efficiency. This difference between the two species implied that the superior P efficiency of sunflower compared to that of safflower is associated with P utilization efficiency, and P uptake efficiency (P recovery), but the contribution of both efficiency components to overall NUE still not clear. For this reason, the contribution of uptake efficiency and utilization efficiency to the overall P use efficiency can be evaluated, according to Piepho [30] (Table 7).

3.3.4 Contribution of Uptake Efficiency and Utilization Efficiency to Phosphorus Use Efficiency

According to Moll et al. [33], the nutrient use efficiency is defined as the yield per unit of nutrient available in the soil (supplied), and has two primary components: uptake efficiency (accumulated nutrient/supplied), and utilization efficiency (yield/accumulated nutrient), in which all parameters are expressed in the same units (e.g., g/plant). The c_i coefficients, based on the variance of log-transformed uptake and utilization efficiency (components of PUE), were calculated to quantify the contribution of each component to final PUE variability, and the yield component analysis according to Piepho [30] was adapted for these calculations (Table 7) [15, 29]. It was found that in both harvest stages, and when data are pooled, both uptake and utilization efficiency are important to the final PUE in safflower, but in sunflower the utilization efficiency is influencing the final PUE much more than the uptake efficiency.

3.3.5 Phosphorus Translocation

Because achene yield in sunflower was not consistent along the P supply, the real translocation efficiency was not possible to be calculated for this plant. The ability of a cultivar to reduce the nutrient concentration of its lower parts or the supporting plant part as stem can indicate its efficiency in translocation [18]. Accordingly, the concentration of P in lower leaves of safflower was significantly higher than that of sunflower at anthesis and maturity with increasing P supplies (Fig. 7). Also safflower's higher leaves still contain higher concentration of P compared to that of sunflower, but sunflower maintains the same slope of the curve with increasing P supply in both upper and lower leaves when compared at anthesis and maturity, separately, while the slope of the curve in safflower's lower leaves is much higher than that of its upper leaves. On the other hand, the P concentration in both species are statistically not different in lower and upper stem parts, and safflower contained less P concentration in both lower and upper stem parts compared to those of sunflower at maturity (Fig. 8).

Table 7 Estimation of variation coefficients (VC) of phosphorus use efficiency PUE, SD and variation of log-PUE, and c_i coefficients for phosphorus uptake efficiency, and phosphorus utilization efficiency as components of PUE of safflower and sunflower[a].

Species	VC of PUE (%)	SD log-PUE (×100)	Variance log-PUE (×100)	C_i for efficiency components	
				Uptake (×100)	Utilization (×100)
	Anthesis				
Safflower	64.98	77.74	60.44 (100%)	28.24 (46.72%)	32.20 (53.28%)
Sunflower	72.73	84.15	70.82 (100%)	6.88 (09.73%)	63.93 (90.27%)
	Maturity				
Safflower	60.42	73.64	54.24 (100%)	28.68 (54.20%)	25.57 (47.14%)
Sunflower	69.48	84.09	70.71 (100%)	10.95 (15.49%)	59.75 (84.50%)
	Pooled				
Safflower	63.94	76.73	58.88 (100%)	26.59 (45.16%)	32.29 (54.84%)
Sunflower	71.10	83.82	70.25 (100%)	07.74 (11.02%)	62.51 (88.98%)

[a]Calculations according to Piepho [30] (n = 20 for each harvesting stage, n = 40 when pooled).

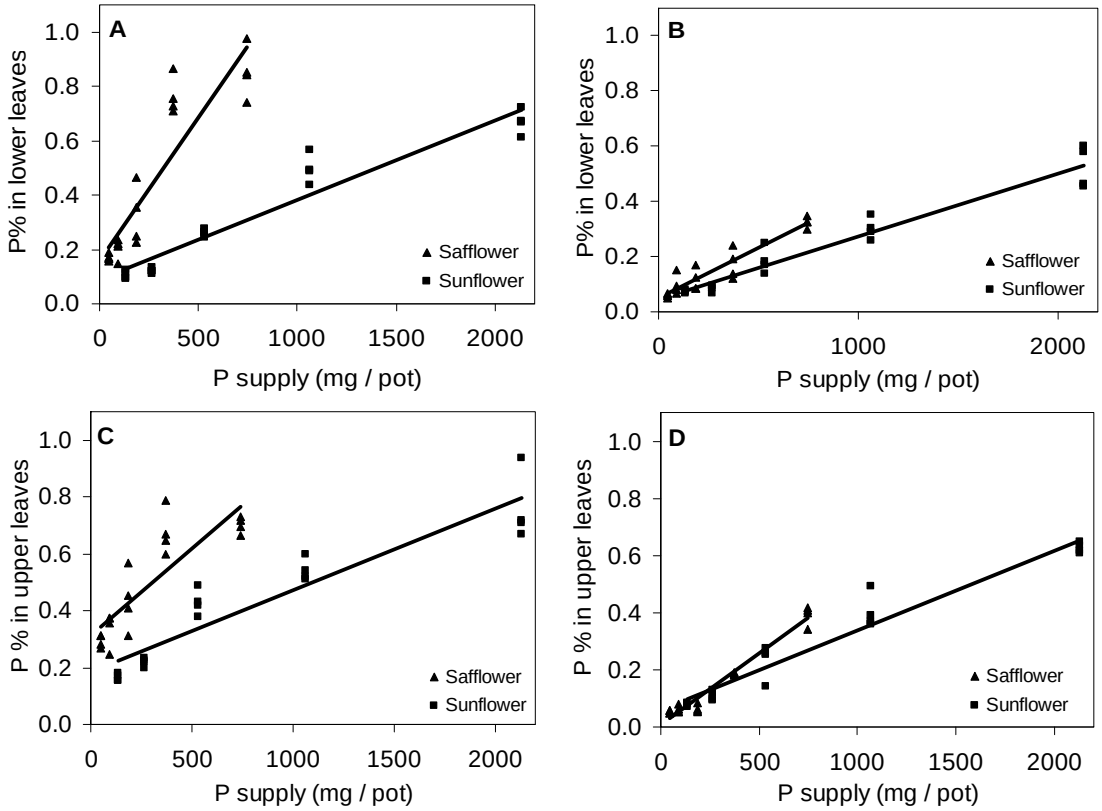

Fig. 7 P concentration response curves for safflower and sunflower leaves based on the P supply per pot. Linear regressions are given. (A) P concentration (%) $_{\text{sunflower lower leaves (anthesis)}}$ = 0.000294* × P supply (mg pot $^{-1}$) + 0.0882$^{n.s}$ (r^2 = 0.93*), P concentration (%) $_{\text{safflower lower leaves (anthesis)}}$ = 0.0011 × P supply (mg pot $^{-1}$) + 0.1589 (r^2 = 0.82***); (B) P concentration (%) $_{\text{sunflower lower leaves (maturity)}}$ = 0.00023* × P supply (mg pot $^{-1}$) + 0.0447$^{n.s}$ (r^2 = 0.94***), P concentration (%) $_{\text{safflower lower leaves (maturity)}}$ = 0.000365 × P supply (mg pot $^{-1}$) + 0.0486 (r^2 = 0.89***); (C) P concentration (%) $_{\text{sunflower upper leaves (anthesis)}}$ = 0.000287* × P supply (mg pot $^{-1}$) + 0.1851* (r^2 = 0.87***), P concentration (%) $_{\text{safflower upper leaves (anthesis)}}$ = 0.00061 × P supply (mg pot $^{-1}$) + 0.3142 (r^2 = 0.73***); (D) P concentration (%) $_{\text{sunflower upper leaves (maturity)}}$ = 0.00028* × P supply (mg pot $^{-1}$) + 0.0606* (r^2 = 0.95***), P concentration (%) $_{\text{safflower upper leaves (maturity)}}$ = 0.00051 × P supply (mg pot $^{-1}$) + 0.0055 (r^2 = 0.96***). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively. n.s indicates not significant.**

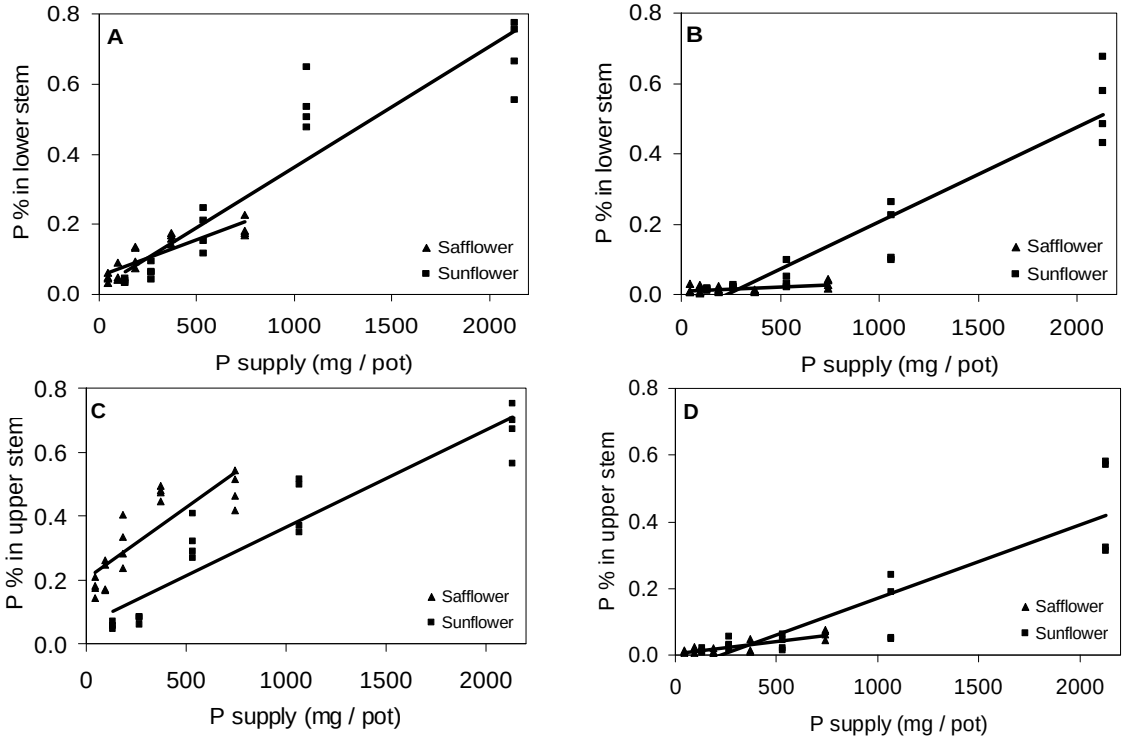

Fig. 8 P concentration response curves for safflower and sunflower stems based on the P supply per pot. Linear regressions are given. (A) P concentration (%) $_{\text{sunflower lower stem (anthesis)}}$ = 0.0003$^{n.s}$ × P supply (mg pot $^{-1}$) + 0.018$^{n.s}$ (r^2 = 0.87*), P concentration (%) $_{\text{safflower lower stem (anthesis)}}$ = 0.00021 × P supply (mg pot $^{-1}$) + 0.0533 (r^2 = 0.77**); (B) P concentration (%) $_{\text{sunflower lower stem (maturity)}}$ = 0.00027* × P supply (mg pot $^{-1}$) - 0.0634* (r^2 = 0.90***), P concentration (%) $_{\text{safflower lower stem (maturity)}}$ = 3E-05 × P supply (mg pot $^{-1}$) + 0.0087 (r^2 = 0.35$^{n.s}$); (C) P concentration (%) $_{\text{sunflower upper stem (anthesis)}}$ = 0.0003$^{n.s}$ × P supply (mg pot $^{-1}$) + 0.0599* (r^2 = 0.88***), P concentration (%) $_{\text{safflower upper stem (anthesis)}}$ = 0.00045 × P supply (mg pot $^{-1}$) + 0.2023 (r^2 = 0.71***); (D) P concentration (%) $_{\text{sunflower upper stem (maturity)}}$ = 0.00022* × P supply (mg pot $^{-1}$) – 0.049$^{n.s}$ (r^2 = 0.81***), P concentration (%) $_{\text{safflower upper stem (maturity)}}$ = 7E-05 × P supply (mg pot^{-1}) + 0.0031 (r^2 = 0.71$^{n.s}$). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively. n.s indicates not significant.**

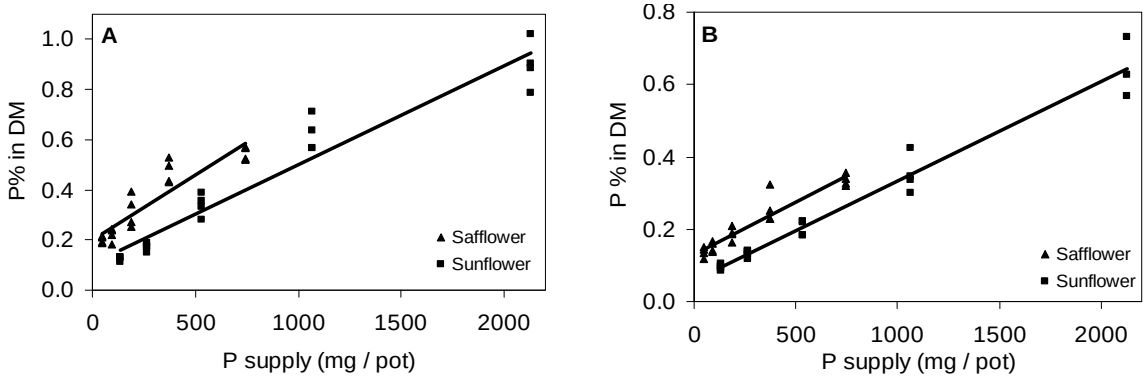

Fig. 9 P concentration response curves for safflower and sunflower DM based on the P supply per pot. Linear regressions are given. (A) P concentration (%) $_{\text{sunflower (anthesis)}}$ = 0.000393* × P supply (mg pot $^{-1}$) + 0.1061* (r^2 = 0.94*), P concentration (%) $_{\text{safflower (anthesis)}}$ = 0.000512 × P supply (mg pot $^{-1}$) + 0.2032 (r^2 = 0.84***); (B) P concentration (%) $_{\text{sunflower (maturity)}}$ = 0.000281$^{n.s}$ × P supply (mg pot $^{-1}$) + 0.05498* (r^2 = 0.96***), P concentration (%) $_{\text{safflower (maturity)}}$ = 0.00029 × P supply (mg pot $^{-1}$) + 0.1304 (r^2 = 0.91***). * in linear equation constants indicates significant difference between the same constants in both species (P < 0.05). *, **, *** for r^2 indicate significant correlation within each plant at P < 0.05, 0.01, and 0.001, respectively. n.s indicates not significant.**

Comparing the two species in terms of P concentration of total DM (Fig. 9) reveals that safflower contains significantly higher values than sunflower at anthesis, but the difference was not significant at maturity.

4. Discussion

4.1 Growth and Morphology

The effect of P supply on growth and yield of safflower and sunflower was previously studied in soil by the investigators of this study [15, 21]. In agreement with results obtained from soil experiments, and this experiment, P deficiency limits shoot growth of safflower [21, 34, 35], and sunflower [21, 36, 37]. In this investigation, the reduction in leaf area could be the cause for the reduction of dry matter of lower leaves of both species in P deficient levels [21, 38]. The reduced number of leaves in the upper part of both plants [38] as well as the reduction of leaf area contributes to the dry matter reduction of leaves and consequently the total dry matter in both species under P deficiency. The contribution of the stem in reducing dry matter as affected by sub-optimal external solution [P] may be caused by the reduction of stem diameter and the height of the plants. As found in this work, the effect of P supply on increasing the number of branches per plant in safflower was reported [21, 39-41]. Secondary branches of safflower were extremely reduced with decreasing P supply, and they were totally inhibited under extreme deficient P supply.

4.2 Phosphorus Use Efficiency

Evaluation of the nutrient use efficiency (NUE) is useful to differentiate plant species for their ability to absorb and utilize nutrients for maximum yields and can be interpreted according to many definitions [14, 18]. The NUE in terms of yield per unit of nutrient supplied results in its dependence on two interrelated groups of plant factors: 1) properties related to uptake efficiency, which is nutrient uptake relative to its supply, and 2) factors related to utilization efficiency representing plant yield relative to nutrient accumulated in the plant [14, 27, 28]. The characterization of nutrient supply under field conditions has to face several uncertainties related to the loss of nutrients and the dependence of their availability on soils and climatic conditions as well as on water supply. However, screening for crops efficient in uptake requires a simpler rooting substrate; solution cultures are less adequate due to the lack of physical root-soil interaction [3].

4.2.1 C_{min}, P Accumulation and P Recovery

As uptake efficiency depends on soil parameters and root physiology parameters [42], the soil parameters could not be studded in nutrient solution experiments using small volume pots in which the nutrient is all the time available to the root system. Under ample nutrient supply conditions, the capacity of the uptake mechanism (A_{max}) rather than its affinity (K_m) will be of primary significance in the case of mobile nutrients such as nitrate, but in the case of less mobile nutrients such as P, under low nutrient solution concentration, the affinity of the uptake mechanism (K_m) and the minimum concentration for uptake (C_{min}) are of significance [3].

As the total P supply (mg P pot^{-1}) differed among the two species at equivalent external [P] (mM), response curves rather than comparing means were applied to differentiate the response of both species. Response curves for each crop were derived either using Michaelis-Menten equations or linear regressions and both regression models were tested for invariance to determine whether the two response curves were significantly different ($P < 0.05$). The measures related to the P uptake used in this study to assess differences between the two species were: C_{min} (solution P concentration at which net uptake is zero), P accumulation (mg P accumulated pot^{-1}) and P recovery (% (mg P accumulated/mg P provided)) [43, 44]. Unfortunately, the small-volume nutrient solution culture techniques are of limited effectiveness in

screening for root morphological factors critical in the acquisition of P from the soil. One reason is that in solution culture, nutrients are continually brought to root surfaces by agitation. Also, during most of the growth period, P concentration in the nutrient solution is much higher than in the soil solution. As a result, several adaptive features induced by low P, such as root hair growth, may not be detected [45].

The minimal P concentration in the nutrient solution where P influx in roots is zero (C_{min}) is an uptake mechanism factor obtained in this nutrient solution experiment and related to genetic difference between plant species. C_{min} was not different between the two species under investigation (Table 6).

In this investigation, the higher A_{max} in sunflower compared to safflower in terms of P accumulation based on P supply (Fig. 1) indicates the higher accumulation potential of the former compared to the later. But because sunflower produces more biomass and accumulates more nutrients (including K and N), it also received more P, thus, A_{max} can not be interpreted as higher accumulation efficiency. The K_m in this case can be misleading which indicates the P supply at which half maximum P accumulation could be reached, therefore, sunflower accumulates much external P compared to safflower as its half maximum accumulation is higher than that of safflower. The difference in P recovery between the two species (Fig. 2) is possibly according to the higher absorption affinity of available P by roots of sunflower compared to safflower; ranking sunflower is more efficient than safflower in this trait.

Generally, the difference in P uptake efficiency between plants indicates mechanisms differentiating the two species in terms of P uptake efficiency including soil factors and plant factors [18]. It was reported that the most important parameters controlling nutrient uptake are the average dissolved nutrient concentration (soil parameter) and the maximal rate of nutrient uptake (root physiological parameter), and the next most important parameter is the effective diffusion coefficient (soil parameter) [42]. Availability of nutrients at root surfaces in soil is controlled by movement in the soil solution and by contacts generated through root growth and extension. The importance of root growth and morphology in nutrient access can not be adequately evaluated in agitated solution cultures [45], but genetic aspects related to P influx and efflux, rate of P transport in roots and shoots, affinity to uptake (K_m), threshold concentration C_{min}, could be evaluated using nutrient solution cultures which control the overall P recovery.

4.2.2 Utilization Efficiency

Nutrient utilization efficiency can be interpreted in many ways to characterize different species or genotypes into superior and inferior in utilization. Nutrient efficiency parameters are variable [11, 12] and could be misleading [14, 26, 29]. Efficiency ratio (ER) is the amount of biomass producing per unit of nutrient present in the tissues [46, 47]. The utilization index [47, 48], which is defined as biomass per unit of tissue nutrient concentration was proposed by Siddiqi and Glass [48] as an improved measure that, unlike the efficiency ratio, takes differences in the amount of biomass into consideration. Agronomic efficiency denotes the biomass, or harvestable product, produced per unit of nutrient applied [33, 43]. Measures used in this study to assess differences between the two species in term of P utilization efficiency included shoot dry mass response curve [43, 49] based on P accumulation which is homologous to P efficiency ratio based on P supply [11, 50], external P required to achieve certain percentage of yield [31] based on P supply, P utilization index [48], and shoot dry mass response curve based on the P concentration in DM which is similar to P utilization index, and finally P translocation by comparing both species in term of P concentration in lower and upper plant parts.

4.2.2.1 Growth Response Curve Based on P Accumulated in DM

The response of safflower and sunflower in terms of DM production based on P accumulation (Fig. 3)

interpreted according to M-M equation revealed that both species have the same K_m values which indicate that both crops have the same efficiency in utilizing internal P to produce 50% DM (low P supply). These results show that safflower is at least not more efficient than sunflower in utilizing absorbed P and hence not to be considered a low input cultivar compared to sunflower, as it needs the same P amount as sunflower to produce half maximum DM yield. A_{max} was higher in sunflower compared to safflower which indicates the maximum DM production potential and is not related to utilization efficiency. Accordingly, ER was calculated [28, 29], which is homologous to the growth response curve based on accumulated P in DM. It was reported that the ER values in pot experiment [15] reveal that sunflower was more efficient in utilizing absorbed P than safflower at optimal and moderate P deficiency supplies for the production of all yield parameters: DM, achenes, oil.

4.2.2.2 External P Requirement

The external P requirement to produce fixed amount of DM was higher by safflower compared to sunflower (Fig. 4). These data support the results obtained from the previous soil experiment [15] indicating that sunflower is more efficient in utilizing external P than safflower at suboptimal and optimal P supplies to express higher DM yield.

4.2.2.3 Utilization Index

This indicator showed the superiority of sunflower over safflower in the efficiency of utilizing internal P (similar to DM response curve based on P concentration) and supports the findings of the previous work conducted in soil [15]. The results obtained from this investigation and the previous work conducted in soil indicate that the difference between some efficiency indicators (efficiency ratio and utilization index) supports the conclusions of some authors that: ranking species for nutrient efficiency can vary according to the definition used [12, 13, 28, 29]. However, in our study, the difference between ER and UI was not conflicting. But the interpretation of utilization efficiency in terms of UI was clearer than that of ER. UI interpreted as DM production curve based on P concentration in DM revealed the lower K_m value in sunflower compared to safflower (Fig. 6) supporting the conclusion that safflower is less P efficient in utilizing internal P, while the ER shows no statistical difference between the two species in term of K_m values which also proves at least that safflower is not a low input crop compared to sunflower in terms of P.

4.2.2.4 Translocation/Remobilisation within the Plant

As a result of the inconsistency of the achene yield in sunflower, the real translocation efficiency was not possible to be calculated for this crop. But the ability of a cultivar to reduce the nutrient concentration of its lower parts or the supporting plant part as stem can indicate its efficiency in translocation [18]. Concerning our results, the ability of sunflower at anthesis to have the same P concentration in lower and upper leaves may indicate more translocation efficiency of P compared to safflower. The P concentration in lower and upper plant parts, along with the P concentration in total DM at both anthesis and maturity were not clear to conclude a difference in the efficiency in remobilisation between the two plants. Whether, the less P concentration in the lower leaves of sunflower is interpreted as efficiency of translocation, or as less P requirement is not clear from these data.

4.2.2.5 Relative Importance of Uptake and Utilization Efficiency in P Use Efficiency

Moll et al. [33] pointed out the possibility to quantify the relative contribution of the two components of nutrient use efficiency to the overall use efficiency. Provided a strict multiplicatory definition of the agronomic NUE is used, calculations may be based on an adaptation of the approach of Piepho [30] which was recently adopted by Gerendás et al. [29]. Coefficients c_i, based on the variance of

log-transformed uptake and utilization efficiency (components of PUE), were calculated to quantify the contribution of each component to final PUE variability (Table 7). It was found that, in safflower (regarded as inefficient in PUE), both uptake and utilization efficiencies contribute similarly to the overall P use efficiency with small differences. At anthesis, the utilization efficiency in safflower was marginally more important (53.28%) than uptake efficiency (46.72%), while at maturity, the opposite was observed (54.2% and 47.14% for uptake and utilization, respectively). When the data were pooled, the utilization efficiency (54.84%) overyielded the uptake efficiency (45.16%) in their relative importance in the overall P use efficiency of safflower. In sunflower (efficient P user), the utilization efficiency was much more important than uptake efficiency at anthesis (9.73% uptake, 90.27% utilization), maturity (15.49% uptake 84.5% utilization), and when data was pooled (11.02% uptake 88.98% utilization) in their relative contribution in the overall P use efficiency. Additionally, in an experiment conducted in soil in terms of K [29], safflower was found superior in K UE over sunflower at low and high K supplies, the contribution of the utilization efficiency was much more important than the uptake efficiency in the superior (safflower), while the opposite was observed in the inferior (sunflower). In this study, sunflower is superior over safflower in P use efficiency and the results prove the importance of the utilization efficiency determining this superiority in the overall P UE. It was reported that N use efficiency was mainly a function of N uptake efficiency in high N soils while, in low N soils, N efficiency was mainly related to N utilization efficiency [33]. The relative importance of nutrient uptake and utilization efficiency over the overall nutrient use efficiency has varied in different studies, according to the plant species and method used in the evaluation (nutrient solution, pot experiments, or field). Higher importance of N utilization efficiency than N uptake efficiency has been reported in oats [51]. The highest importance of P uptake efficiency has been reported in maize nutrient solution studies [52] and in pot experiments with green pepper [53]. In a study using 28 tropical maize genotypes evaluated at low and high P supplies, P uptake efficiency was much more important than P utilization efficiency to explain the variability observed in PUE at low and high P environments [54].

A better knowledge of the relative importance of P uptake and utilization efficiency would have implications in areas such as: plant physiology to prioritize studies in mechanisms of nutrient uptake or utilization, plant breeding to establish selection indexes including different nutrient efficiency selection criteria, and qualitative trait locus (QTL) mapping studies to choose traits to be mapped. It was reported that the higher P uptake efficiency in genotypes should be related either to root morphological traits [55], or to a higher capacity to associate with P solubilizing microorganism in the rhizosphere, especially, *Bulkhoderia* sp. [53]. It was documented that the main selection criteria for P internal utilization efficiency in maize should be towards reducing the grain P concentration [54], and this would have a positive impact on animal nutrition, since grain P is stored as the antinutritional factor phytate; and it would also reduce environmental pollution from high P manure produced by large animal feeding lots. However, the strategy of reducing grain P concentration should have a limit, since grain P is needed in the grain filling process and it is also important in seed germination.

The data reported in this work show that utilization efficiency should be considered in a breeding program to increase P use efficiency of safflower when establishing selection indexes for safflower traits.

5. Conclusions

Safflower is performing inferior to sunflower under P-limited conditions in terms of DM production.

Safflower is less efficient than sunflower in utilizing absorbed P at low P availability and at their respective optimal P supplies, and therefore can not be regarded as a low input species in terms of its P requirement. The results obtained using different efficiency indicators illustrate that the ranking of plants in terms of nutrient use efficiency may depend on the definition used. The calculation of utilization index includes however, both yield and plant nutrient concentration, is a good measure of utilization efficiency avoiding the dilution effect of nutrient under extreme nutrient supply, but also is likely to be complicating the identification of potential mechanisms associated with enhanced nutrient efficiency. The use of agronomic use efficiency as an efficiency indicator involves the uptake of the nutrient and its utilization to produce final yield and also does not indicate the mechanism through which the efficient cultivar interprets its efficiency. The better utilization efficiency of sunflower over safflower that contributed much more than uptake efficiency in the overall P UE is the cause of sunflower superiority in P UE. Indeed, little is known on the physiological mechanisms responsible for different utilization efficiency, further research efforts should aim at identifying the mechanisms responsible for differences in P utilization efficiency of sunflower (P efficient) and safflower (P inefficient). Breeding programs should emphasize utilization efficiency traits as selection criteria to improve safflower PUE.

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