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Potassium Use Efficiency of Safflower and Sunflower Grown in Different Soils

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Abstract Using alternative crops that use supplied nutrients efficiently is a possible approach in land use sustainability. Plant species vary in their potassium (K) use efficiency in soils of low K availability by using different strategies. Growing K efficient species to improve yield may be desirable if K efficiency mechanisms are illustrated. Therefore K use efficiency of the alternative oil crops safflower and sunflower was investigated under semi-controlled conditions in sandy and loamy soils using four K supplies. Both species reacted strongly to increasing K supplies in both soils and performed better in loamy soil, although they contained less K concentration in loamy soil. Under suboptimal K supply in both soils, safflower was superior over sunflower by having higher agronomic efficiency (greater relative yield), higher internal K concentration, better relative K accumulation in dry matter. Both species had similar K efficiency ratio (KER) in sandy soil, but sunflower was more efficient in loamy soil. Sunflower was superior over safflower in terms of utilization index (UI) in both soils. Sunflower had less external K requirement and recovered more K than safflower in both soil types. The K use efficiency of crops is based on different competitive components. Thus using different measures of utilization efficiency parameters to differentiate plant species and genotypes to superior and inferior could be in some cases misleading. Neither safflower nor sunflower showed a combination of high values of all K uptake and utilization efficiency components in both soils at studied K levels.

Keywords: sustainable agriculture, potassium, utilization efficiency, alternative crops, *carthamus tinctorius*, *helianthus annuus*, safflower

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1. Introduction

Potassium (K) is an essential inorganic nutrient for all living organisms [1]. It is the most abundant cation in higher plants [2] comprising up to 10% of a plant's dry weight, although it has no structural functions. K is the main osmoregulator in plant cells, important in photosynthesis by acting in transpiration and CO₂ uptake, controlling the stomatal conductance, functions in sugar transport, enzyme activation, and resistance to draught [3,4,5,6]. After nitrogen, K is quantitatively the most required inorganic nutrient for plant growth that limits primary productivity in natural and cropping systems, unless supplied as fertilizer [5,7,8,9,10,11]. Although many soils have large reserves of total K, only a small fraction is phytoavailable making many agricultural areas deficient with available K [12]. Potassium availability is usually low due to its enclosure in silicates and its strong adsorption by K-specific binding sites on clay particles [13,14,15]. As a result of the intensification of agriculture and introduction of high yielding varieties, the soils are getting depleted in reserve K at a faster rate, therefore K deficiency is becoming one of the major constraints to crop production [12]. Although, in view of limited P resources [16] and serious environmental and economic

consequences [12,17,18,19,20], a considerate use of K is mandatory to correct nutrient deficiencies [21] and to fulfill the requirements of modern cultivars [22]. But in developing countries, where the proportion of less fertile soil is particularly high, it may be difficult to fulfill the nutritional requirements of high yielding crops [23]. For these reasons, K-fertilizers must be deployed efficiently [12].

Plant species and even cultivars within a species differ in their nutrient use efficiency (NUE) [5,8,9,24-31]. Crops differ in their ability to grow or yield well at suboptimal K supply [24,26,27,32,33,34,35]. Therefore, one of the possible strategies of sustainable land use, which enables maximum output with minimum input, sustains resources and conserves the environment, could be the use of efficient plant species [21,36,37]. Accordingly, plant species which are able to make use of the normally not readily available K could have a significant agronomic importance [27,38]. However, cultivating nutrient efficient species to improve yields may be possible if K efficiency mechanisms are elucidated [24,37]. Definitions of NUE vary greatly [31,39,40,41,42] and in some cases, may be misleading in terms of identifying the mechanisms for the nutrient use efficiency [26,27]. NUE is generally defined as the ability of species or cultivars to grow and yield better in a substrate containing suboptimal nutrient supply that would limit the production of other standard lines [43].

Other definitions of NUE, is the production of dry matter or harvestable products per unit of nutrient applied, and referred to as agronomic efficiency [44]. In like manner, the external nutrient requirement refers to the amount of nutrient in the media required to achieve a given percentage of maximum yield [45,46]. Additionally, the yield response per unit of added nutrient has also been used as a measure of NUE [29,30]. The ability of cultivars to tolerate low nutrient supply may be due to either high nutrient uptake ability at low nutrient concentrations and/or more efficient use of nutrient for more yield production [12,41]. Therefore, NUE may be broken down mechanistically into uptake efficiency and utilization efficiency. In other words, overall NUE in plants is a function of capacity of soils to supply adequate levels of nutrients, and the ability of plants to acquire nutrients, transport them in roots and shoots and remobilise them to other parts of the plant, involving various soil and plant mechanisms that contribute to genetic variability in efficiency of uptake and utilization of nutrients [12,47].

The use of alternative oil crops that differ in their response to K supply is a possibility to meet the increasing global demand for vegetable oil, and may be possible if K efficiency mechanisms are characterized [40,41]. For instance, safflower (*Carthamus tinctorius* L.) and sunflower (*Helianthus annuus* L.), both belonging to the same family (*Asteraceae*), are important oil crops in tropical areas. Safflower was hypothesized as a low input cultivar in terms of K [27] and N [28], but not P [30,31,48]. The mechanisms that outline the K efficiency of safflower as compared to sunflower grown in different soils were not investigated. Therefore, the objective of this investigation was to study the efficiency mechanisms of potassium utilization of safflower and sunflower in pot experiment using two soil types (sandy and loamy) low in K status under greenhouse conditions.

2. Methodology

2.1. Experimental Design

A pot experiment was conducted to evaluate K utilization efficiency of safflower (*Carthamus tinctorius* L., variety 'Sabina') and sunflower (*Helianthus annuus* L., variety 'Peredovick E'), grown in two soil types (loamy and sandy), using four levels of K supply. The experiment was conducted in a Semi-controlled climatic conditions in a greenhouse in the period between June and September 2012. Before conducting the experiment, field-moist soil samples were sieved to 2-mm particle size, from which, subsamples of soil were air dried and were analyzed for extractable P, exchangeable K, Mg, and pH. Initially, the sandy soil (pH 5.6 by water extraction) contained 26 mg kg⁻¹ CAL-extractable P, 22 mg kg⁻¹ CAL-exchangeable K, and 28 mg kg⁻¹ NH₄-acetate exchangeable Mg. The loamy soil (pH 7.0 by water extraction) contained 16.5 mg kg⁻¹ CAL-extractable P, 28mg kg⁻¹ CAL-exchangeable K, and 141 mg kg⁻¹ NH₄-acetate exchangeable Mg.

Mitscherlich pots (6 L) were filled with 3 kg sand (0 mg kg⁻¹ CAL-extractable P, 3 mg kg⁻¹ CAL-exchangeable K, and 1.8 mg kg⁻¹ NH₄-acetate exchangeable Mg, pH in

water was 7.3) and 3 Kg either sandy or loamy soil. Four K levels (0, 0.2, 0.5, and 3g K pot⁻¹) were added in the form of K₂SO₄, resulting in solution K concentrations (mg K L⁻¹ soil solution) of 92.6, 192.3, 848.9 and 2651 for sandy soil and 29.9, 53.8, 187.3 and 732.5 for loamy soil in consecutive added K levels. The CAL-extractable K (mg K kg⁻¹) was found 18.7, 47.2, 164.9 and 443.0 for sandy soil and 31.0, 52.0, 159.0, 438.0 for loamy soil in respective mentioned K supplies. Other nutrients added per pot were 2 g N (as NH₄NO₃), 0.8g Mg (as MgSO₄), and 1.0 g P (Ca (H₂PO₄)₂.H₂O). Micronutrients were added in adequate amount in both soil types (mg pot⁻¹: 17.5 B, 2.5 Mo, 8 Cu, 50 Mn, and 40 Zn). Three safflower or two sunflower plants were planted in each pot (because sunflower is larger than safflower). The plants were watered daily to nearly a volumetric soil water content of 35%. The experiment was conducted using completely randomized design with three replicates of each treatment.

2.2. Harvesting and Analytical Procedures

The plants were harvested after 56 days from sowing for both species in both soil types. Harvested plants were separated to stems and leaves. Stems and leaves were measured for dry weight, then were analyzed for their K, Ca, and Mg contents.

Shoot measurements and nutrient (K, Ca, and Mg) contents analyses

At harvest, the dry weight of plant parts were determined after drying at 70°C till constant weight. Dried plant materials were 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 plant samples were prepared for K, Ca, and Mg analyses using wet microwave digestion using concentrated tri acid mixture (HNO₃, HClO₄, and H₂SO₄ with a volumetric ratio of 8:2:1). Total K of the plant material digest was measured using flame photometer. Total contents of Mg and Ca of the plant material digest were measured using atomic absorption.

Measurement of soil solution K, extractable K concentration and pH

The column displacement method [49] was used to collect the unaltered composition of soil solution K concentrations, in which a sample of moist soil equivalent to 350g was packed into a plastic column with a pore in its bottom. Filter paper was placed in the bottom of each soil column to avoid soil particles losses during the collection. The samples were allowed to equilibrate for 24 h; then, deionized water was pumped to each column at a rate of 4 ml h⁻¹ until the soils reached field capacity water content. The displaced solution was collected till 25 ml to insure not to collect diluted solution, and then filtered through a 0.20µm filter. The solutions were analyzed for K by flame photometer. Soil solution concentration was measured immediately at the time of harvest.

To determine solid phase (extractable) K, a 10-g subsample of soil was air dried then extracted with calcium acetate lactate (CAL) according to [50]. To determine solid phase (extractable) Mg, an air dried 10-g subsample of soil from each pot was extracted according to [51]. Potassium concentration in the extracts was determined using flame photometer, Ca, and Mg was

determined using atomic absorption spectrometer. The pH was measured using ion electrode after water extraction.

2.3. Calculating Efficiency Indicators

Different measures of K efficiency were determined at each K level. Nutrients accumulated ($\text{mg nutrient pot}^{-1}$) in plant parts were calculated by the multiplication of plant parts weight in g (leaves, stems) with plant tissue nutrient concentration multiplied by 100. Total mg nutrient accumulated per pot was calculated as the sum of the mg nutrient accumulated in each plant part per pot. Nutrient concentration [$\text{mg nutrient g}^{-1}$ dry matter (DM)] in the plant was obtained from dividing the total mg nutrient accumulated per pot by the total dry matter of the plant per pot (g) divided by 10. K recovery (uptake efficiency) was calculated by dividing total K accumulated per pot (g pot^{-1}) by external K supply interpreted as added K supply, soil solution-K, and CAL-K (g pot^{-1}) according to [52]. External K requirement termed [$\text{g K required (g DM produced)}^{-1}$] at each K level was obtained by dividing the K supply (g K pot^{-1} interpreted as K supply, soil solution K or CAL extractable K) by DM yield at that K level. Potassium efficiency ratios (KER) was calculated as total plant dry mass (g pot^{-1}) divided by total K accumulation (g pot^{-1}) according to [53]. K utilization index [54] was calculated by dividing DM yield (g pot^{-1}) by K content in whole plant [$\text{g nutrient (g DM)}^{-1}$].

2.4. Statistical Analysis

All statistical analyses were carried out using SAS (SAS Institute Inc., Cary, USA, Release 8.02, 2001). Comparisons of means between different treatments were carried out using the GLM procedure considering a fully randomized design. With multiple t-test, the Bonferoni procedure was employed in order to maintain an experiment-wise α equals 5%.

3. Results

3.1. Effect of K Supply on Growth and Morphology

Dry matter (DM) weight of both species responded strongly to increasing K supply in sandy and loamy soils (Figure 1). DM of both species performed better when plants were grown in loamy soil as compared to sandy soil. In both soil types, growth of safflower increased significantly up to 0.2g K pot^{-1} , while sunflower optimal growth was achieved at 0.5g K pot^{-1} . Under low K supplies, typical K deficiency symptoms characterized by oxidative necrosis and burns of lower leaves were observed in both species in both soil types and the symptoms were more pronounced in both crops in sandy soils. Both species grown in sandy soil at the highest K supply showed lower leaves oxidative necrosis typical for Mg deficiency (Figure 2).

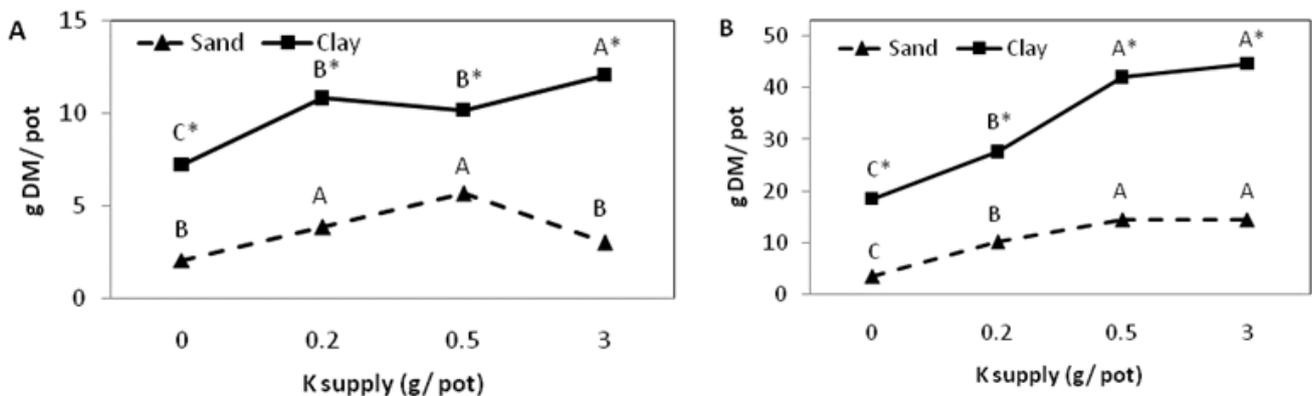


Figure 1. Effect of K supply on dry matter (g pot^{-1}) of safflower (A) and sunflower (B). For a given species and a given soil type, means within each column followed by the same letter are not significantly different, * indicates significant difference for a given plant species and a given P level within soil types. $P < 0.05$, $n=3$



Figure 2. Potassium induced Mg deficiency in sunflower (left) and safflower (right) grown at 3g K pot^{-1} in sandy soil (right for each species) as compared to loamy soils (left for each species)

3.2. Effect of K Supply on Nutrient Concentration in Dry Matter

3.2.1. K Concentration

Both crops grown in both soil types concentrated $[\text{mg K (g DW)}^{-1}]$ increasing K contents in DM of plant parts (stem and leaves) with increasing K supply (Figure 3). At respective optimal K supplies (0.2 and 0.5 g pot^{-1} for safflower and sunflower respectively in both soils), K concentration in plant parts was higher in safflower than those of sunflower when grown in sandy soil, but the opposite was found in loamy soil. Under sub-optimal K supply, safflower concentrated more K than sunflower in their whole plant and plant parts in both soil types, while the opposite was found at high K supplies. Under the respective optimal K supply for both crops, K concentration in DM of safflower marginally over-yielded that of sunflower in sandy soil but the opposite was observed in loamy soil.

3.2.2. Mg Concentration

Mg concentration in plant parts DM of both species decreased consequently with increasing K supply in both soil types (Figure 4). Mg concentration in safflower was significantly less than that of sunflower at all respective K levels in both soil types. At respective optimal K supplies, Mg concentration in shoot DM of safflower was less than that of sunflower in both soils. Safflower plants grown in

sand concentrated more Mg in their shoot than those grown in clay soil under sub-optimal K supply, while the opposite was found under high K levels and similar values were recorded in safflower shoots in different soil types when K levels were optimal. Mg concentrations in sunflower shoots were significantly higher in plants grown in sandy soils as compared to those grown in clay soils at all respective K levels.

3.2.3. Ca Concentration

Calcium concentration in leaves of both crops decreased with increasing K supply in both soil types, while Ca concentration in stems in safflower didn't change significantly as affected with K supply in clay soil and the same was recorded for sunflower grown in sandy soil. Stems of safflower grown in sandy soil increased marginally in the highest K supply while that of sunflower grown in loamy soil showed dramatic decrease with increasing K supply (Figure 5). Calcium concentration in all plant parts of safflower grown in sandy soil was significantly lower than that of sunflower at respective K supplies. Sunflower grown in loamy soil concentrated more calcium in their stems as compared to safflower stems at their respective K supplies except for the highest K level where the difference was not significant. All plant parts of both species concentrated more calcium when grown in clay soil as compared to sandy soil.

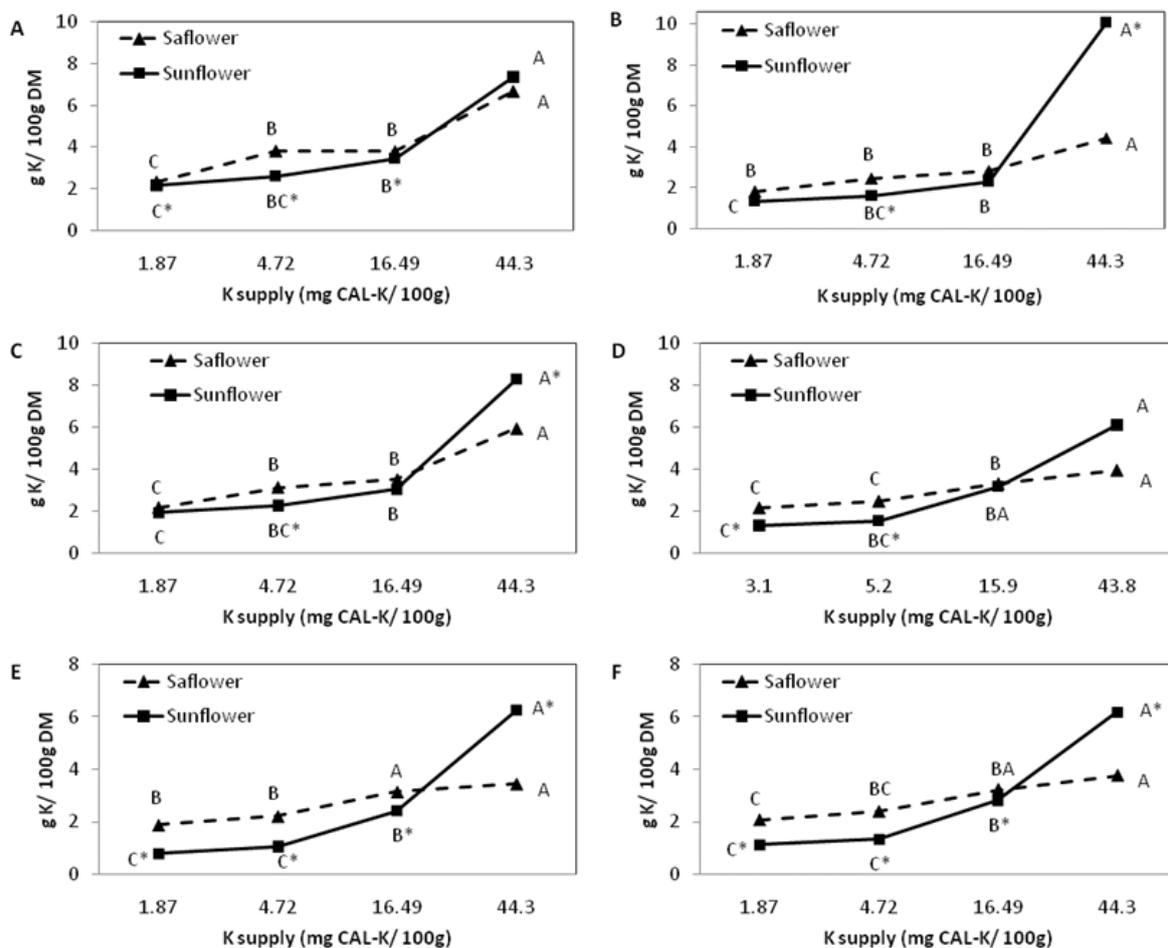


Figure 3. Effect of K supply on K concentration ($\text{g K } 100\text{g}^{-1} \text{ DM}$) of safflower and sunflower leaves (A, D), stems (B, E), and dry matter (C, F). For a given graph, means within each line followed by the same letter are not significantly different, means, * indicates significant difference in each graph between the two plant species at a given K level. $P < 0.05$, $n=3$

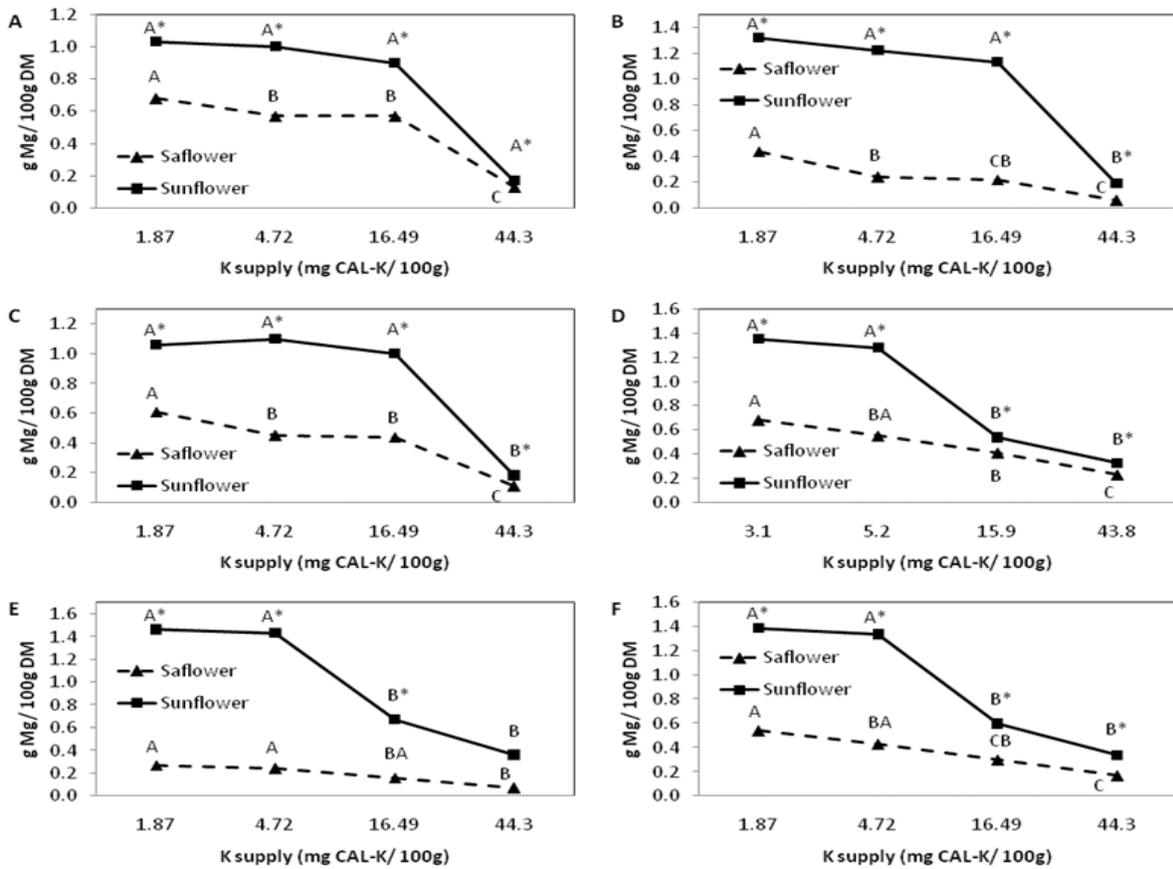


Figure 4. Effect of K supply on Mg concentration (g Mg 100g⁻¹ DM) of safflower and sunflower leaves (A, D), stems (B, E), and dry matter (C, F). For a given graph, means within each line followed by the same letter are not significantly different, means, * indicates significant difference in each graph between the two plant species at a given K level. P < 0.05, n=3

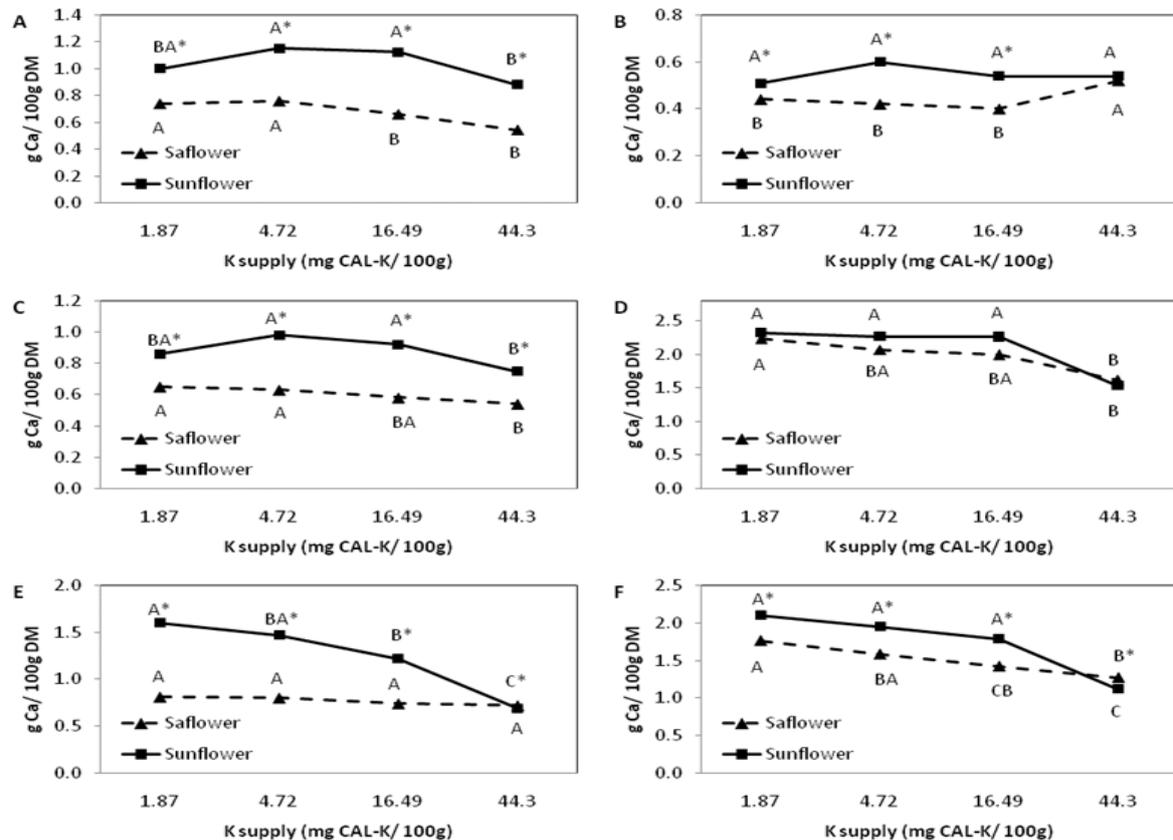


Figure 5. Effect of K supply on Ca concentration (g Ca 100g⁻¹ DM) of safflower and sunflower leaves (A, D), stems (B, E), and dry matter (C, F). For a given graph, means within each line followed by the same letter are not significantly different, means, * indicates significant difference in each graph between the two plant species at a given K level. P < 0.05, n=3

3.2.4. K Accumulation

Both crops accumulated significantly increasing amounts of K in DM as K supply increased in both soil types (Figure 6). Both species accumulated significantly higher amounts of K per pot in loamy soil as compared to those grown in sandy soil. Sunflower shoot K content (mg K pot^{-1}) was higher than that of safflower at all respective K supplies including respective optimal levels in both soils.

3.2.5. Mg and Ca Accumulation

The total accumulation of Mg and Ca in plant parts and whole plants of both species responded in the same

manner as a function of increasing K supply in both soil types (Table 1, Table 2). Mg or Ca content in each treatment (plant species or soil type) showed a bill shaped cubic significant response as affected by K supply, with the maximum accumulation at the respective optimal K supplies for each plant species. As larger plant, sunflower accumulated more contents of Mg or Ca than safflower did, at all respective K supplies in both soil types. In both species, Mg or Ca contents in plant parts and shoot was significantly much higher in plants grown in loamy soils as compared to sand soil at all respective K levels.

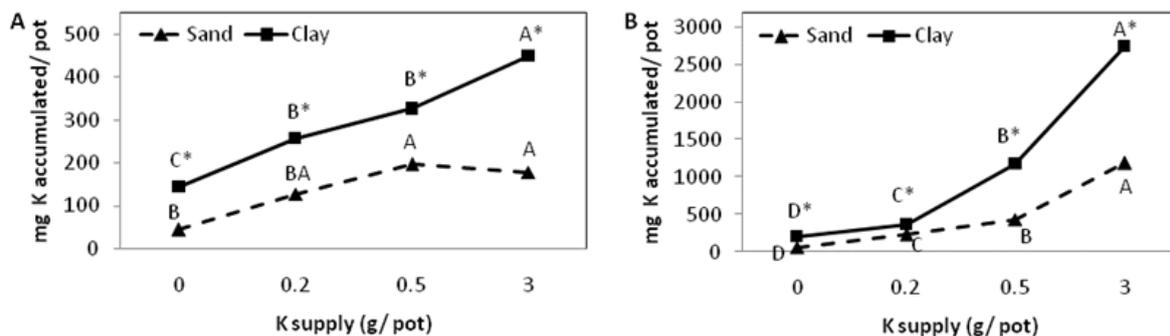


Figure 6. Effect of K supply on K accumulation (g/pot) of safflower (A) and sunflower (B). For a given graph, means within each line followed by the same letter are not significantly different, means, * indicates significant difference in each graph between the two soils at a given K level. $P < 0.05$, $n=3$

Table 1. Effect of K supply on Mg content (mg Mg pot^{-1}) of safflower and sunflower. For a given species and a given soil type, means within each column followed by the same capital letter are not significantly different, means in the same soil type and the same K level and different plant species followed by the same small letter are not significantly different, * indicates significant difference for a given plant species and a given K level within soil types. $P < 0.05$, $n=3$

K supply (g pot^{-1})	Leaves		Stem		Shoot Dry Weight	
	Sand	Loam	Sand	Loam	Sand	Loam
Safflower						
0	9.79 BA, b *	30.56 BA, b	2.58 A, b	5.84 BA, b	12.38 B, b *	36.39 BA, b
0.2	13.86 A, b *	35.75 A, b	3.28 A, b *	10.10 A, b	17.14 A, b *	45.82 A, b
0.5	17.12 A, b	20.33 BC, b	3.28 A, b *	6.10 BA, b	20.4 A, b *	26.42 BC, b
3	2.74 B, b *	16.51 C, b	0.67 B, b *	3.54 B, b	3.40 C, b *	20.05 C, b
Sunflower						
0	26.72 B, a *	174.67 BA, a	9.95 C, a *	83.62 C, a	36.67 B, a *	258.29 B, a
0.2	67.99 A, a *	216.51 A, a	44.32 B, a *	150.70 A, a	112.31 A, a *	367.20 A, a
0.5	83.88 A, a *	126.20 BC, a	61.34 A, a *	126.08 B, a	145.20 A, a *	252.28 B, a
3	14.71 C, a *	74.74 C, a	9.44 C, a *	78.73 C, a	24.14 B, a *	153.47 C, a

Table 2. Effect of K supply on Ca content (mg Ca pot^{-1}) of safflower and sunflower. For a given species and a given soil type, means within each column followed by the same capital letter are not significantly different, means in the same soil type and the same K level and different plant species followed by the same small letter are not significantly different, * indicates significant difference for a given plant species and a given K level within soil types. $P < 0.05$, $n=3$

K supply (g pot^{-1})	Leaves		Stem		Shoot Dry Weight	
	Sand	Loam	Sand	Loam	Sand	Loam
Safflower						
0	10.86 B, b *	100.34 B, b	2.69 B, b *	17.49 B, b	13.55 B, b *	117.83 B, b
0.2	18.55 A, b *	134.26 A, b	5.61 A, b *	33.77 A, b	24.16 A, b *	168.04 A, b
0.5	19.77 A, b *	98.15 B, b	6.25 A, b *	28.85 A, b	26.02 A, b *	127.00 BA, b
3	10.86 B, b *	118.49 BA, b	5.05 A, b *	33.61 A, b	16.01 B, b *	152.11 BA, b
Sunflower						
0	25.18 C, a *	297.13 B, a	4.47 B, a *	92.27 C, a	29.65 C, a *	389.40 B, a
0.2	79.25 B, a *	384.00 BA, a	20.25 A, a *	155.25 B, a	99.50 B, a *	539.25 B, a
0.5	104.45 A, a *	527.34 A, a	27.26 A, a *	229.06 A, a	131.70 A, a *	756.40 A, a
3	75.47 B, a *	346.87 B, a	26.29 A, a *	150.96 B, a	101.76 B, a *	497.83 B, a

3.3. Effect of K Supply on K Utilization Efficiency

3.3.1. K Efficiency Ratio (KER)

Nutrient utilization efficiency with respect to K is frequently described by the K-efficiency ratio (KER), which is defined as the biomass production per unit K accumulated. Safflower and sunflower showed statistically similar KER values at suboptimal and respective optimal K supplies when grown in sandy soils, while safflower KER was significantly higher than that of sunflower at the highest K supply (Figure 7). In loamy soil, sunflower KER was higher than that of safflower at suboptimal K supply, but safflower was found more efficient than sunflower at their respective optimal K supplies and also at the highest K level. The K efficiency ratio of both species in both soils decreased dramatically with increasing K supply. Both species were found more efficient at most respective K levels when they were grown in loamy soil in comparison with sand soil.

3.3.2. K Utilization Index (KUI)

In contrary to the KER, the K-utilization index is based on DM yield per unit nutrient concentration rather than nutrient accumulation presented in KER. Sunflower had significantly higher KUI at all respective K supplies including their optimal K supplies (Figure 7). KUI didn't change significantly with increasing K supply in safflower in both soils, while it decreased in sunflower at the highest K supply in loamy soil and at both lowest and highest K levels in sandy soil. KUI for both plants was significantly higher in loamy soil than that in sandy soil at all respective K levels.

3.3.3. Agronomic K Efficiency

The external or agronomic K requirement is defined as the amount of K in the substrate required to produce

a given relative or absolute yield. Agronomic K requirement in terms of K supply, CAL-K, and soil solution K of both crops in both soils decreased significantly when the K supply was reduced (Table 3). Safflower's agronomic K requirement was higher than that of sunflower at all respective K supplies in both soil types. At respective optimal K supplies (0.25 and 0.5 g K pot⁻¹ for safflower and sunflower respectively), agronomic K requirement in both soils were found similar in both crops for each soil type independently. Agronomic K requirement for all K supply forms (K supply, CAL-K, soil solution K) was significantly higher when plants were grown in sandy soils as compared to that grown in loamy soils.

3.3.4. K Recovery

Both species recovered decreasing amounts of all forms of soil K fertility (K supply, CAL-K, soil solution K) with increasing K supply in both soil types (Figure 8). Safflower recovered significantly less amounts of all K fertility forms as compared to that of sunflower in both soils at all respective levels including their optimal supplies. The recovery percentage of all K fertility forms was found lower in sandy soils as compared to loamy soils for both species. In loamy soil, both species recovered more K amounts than added quantities at optimal and at suboptimal K levels in both species, and the figures were more pronounced in sunflower. In sandy soil, only sunflower recovered K more than the added quantity at suboptimal K supply. When interpreting K supply as extractable K, sunflower recovered more added extractable K in all K levels when it was grown in loamy soil. But when the external K supply was interpreted in terms of nutrient solution both species grown in loamy soils recovered exceeded amounts of soil solution K at their respective optimal and suboptimal supplies but at K supply higher than optimal, only sunflower recovered more K than supplied as soil solution.

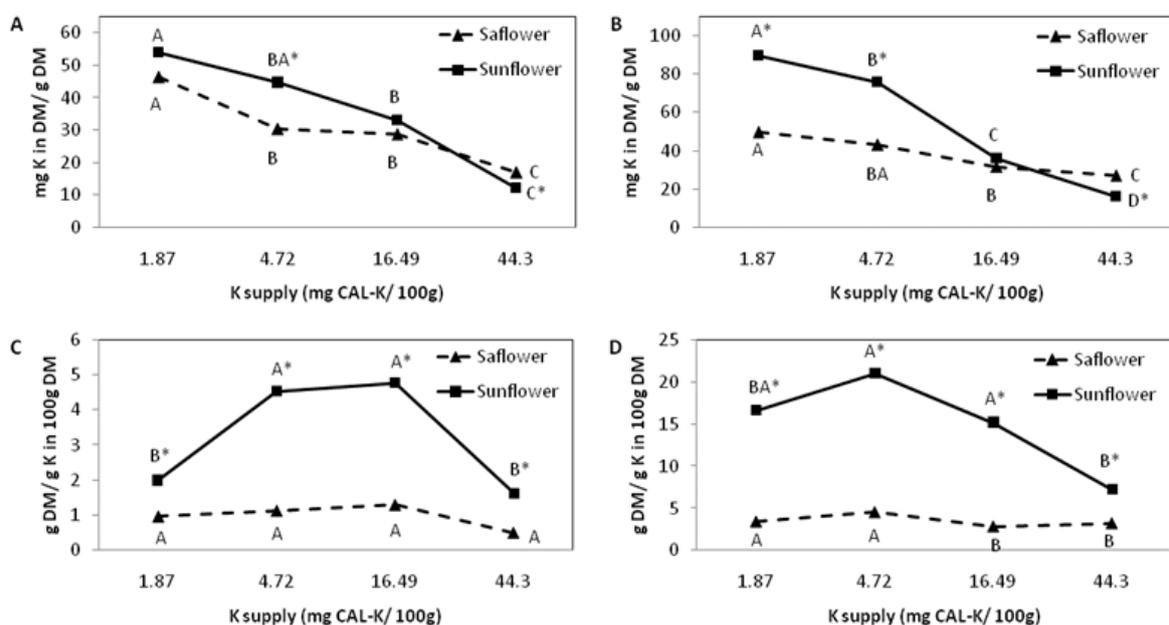


Figure 7. Effect of K supply on KER ($\text{mg K in DM (g DM}^{-1}\text{)}^{-1}$) (A and B), and KUI ($\text{g DM (g K 100g DM}^{-1}\text{)}^{-1}$) (B and C) for safflower and sunflower in sandy (A and C) and loamy (B and D) soil. For a given graph, means within each line followed by the same letter are not significantly different, means * indicates significant difference in each graph between the two soils at a given K level. $P < 0.05$, $n = 3$

Table 3. Effect of K supply on external K requirement (g external K to produce 1 kg of DM) for safflower and sunflower. For a given species and a given soil type, means within each column followed by the same capital letter are not significantly different, means in the same soil type and the same K level and different plant species followed by the same small letter are not significantly different, * indicates significant difference for a given plant species and a given P level within soil types. $P < 0.05$, $n=3$

K supply (g pot ⁻¹)	G added K/ 1 kg DM		g CAL-K/ 1 kg DM		g soil solution-K/ 1 kg DM	
	Sandy	Loam	Sandy	Loam	Sandy	Loam
Safflower						
0	-	-	65.19 C, a *	28.33 C, a	107.63 C, a *	9.244 C, a
0.2	55.23 C, a *	18.80 B, a	78.23 C, a *	29.32 C, a	106.24 C, a *	10.11 C, a
0.5	111.43 B, a *	56.30 B, a	220.48 B, a *	107.42 B, a	378.32 B, a *	42.19 B, a
3	1252.9 A, a *	250.70 A, a	1109.03 A, a *	219.34 A, a	2214.3 A, a *	122.41 A, a
Sunflower						
0	-	-	27.839 C, b *	9.882 C, b	37.81 C, b *	3.23 C, b
0.2	19.67 B, b *	7.27 C, b	37.059 C, b *	11.337 C, b	61.18 C, b *	3.91 C, b
0.5	34.90 B, b *	11.97 B, b	69.048 B, b *	22.833 B, b	118.48 B, b *	8.97 B, b
3	223.50 A, b *	67.23 A, b	197.833 A, b *	58.848 A, b	394.99 A, b *	32.84 A, b

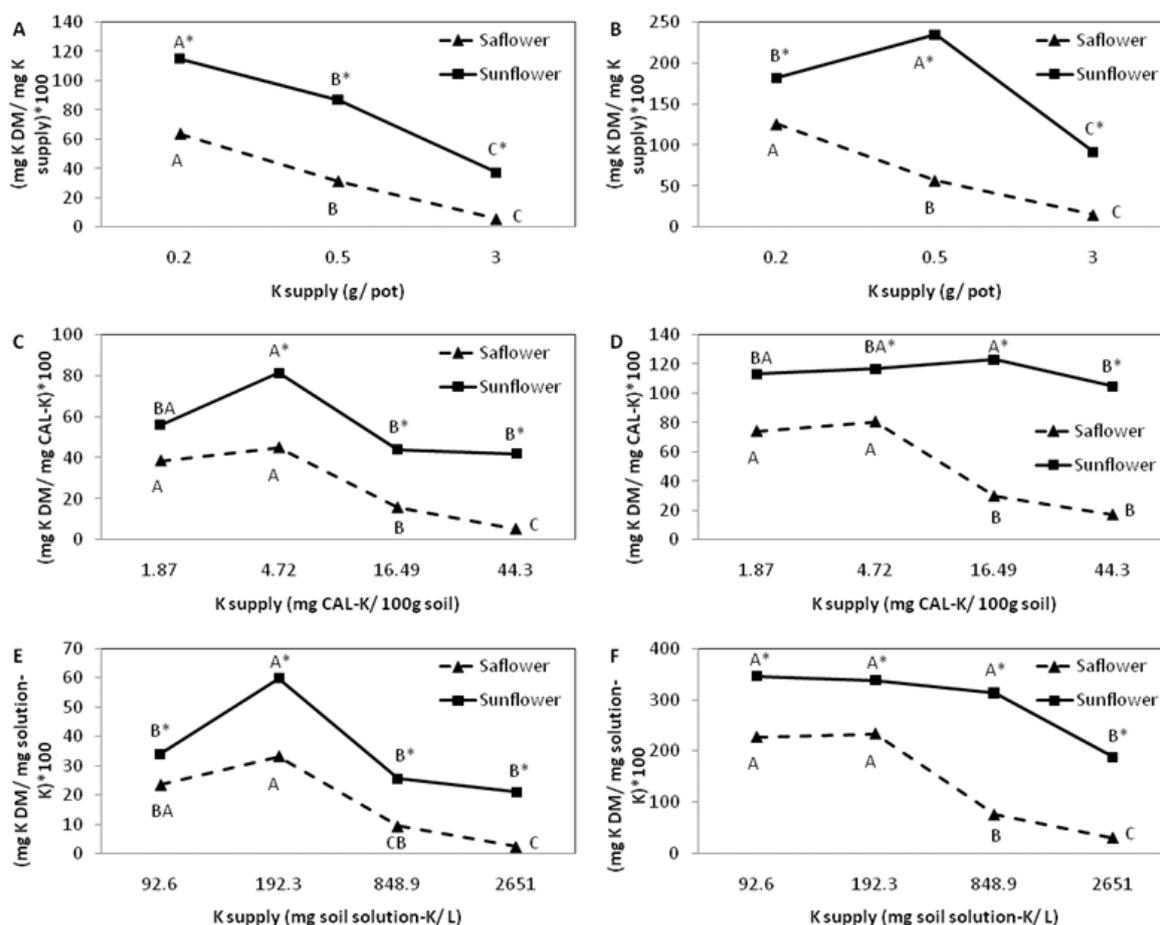


Figure 8. Effect of K supply on K supply recovery (mg K TDW⁻¹ / (mg K supply)*100) (A and B), CAL-K recovery (mg K TDW⁻¹ / (CAL mg K)*100) (C and D), soil solution-K recovery (mg K TDW⁻¹ / (Soil solution mg K)*100) (E and F) for safflower and sunflower in sandy (A, C and E) and clay (B, D and F) soil. For a given graph, means within each line followed by the same letter are not significantly different, means, * indicates significant difference in each graph between the two soils at a given K level. $P < 0.05$, $n=3$

4. Discussion

4.1. Growth and Morphology

Biomass is an important plant trait in growth analysis [55,56], where its measurements are the basis for quantifying the physiological responses of plants to environmental conditions, and thus indicating the net primary production and economic yield of crops [57,58,59,60]. Therefore cultivars differences for relative

shoot dry matter production indicate that this trait can be used as reliable parameter for screening nutrient efficient cultivars [61, 62]. Because safflower and sunflower differ in size (Figure 1), relative biomass production should be used to compare their efficiency under suboptimal nutrient supplies [31]. Safflower relative DM production at 0 added K supply (related to DM produced at 0.2g K pot⁻¹ as optimal supply) was 36% and 60% in sandy and loamy soil respectively, while those respective figures for sunflower were significantly lower (24% and 41%

considering 0.5g K pot^{-1} is the optimal supply). This indicates the superiority of safflower over sunflower in terms of relative DM production under severe K deficiency which agrees with other reports concerning safflower and sunflower [26,27]. In the same line with previous findings, we find that sunflower biomass production was more sensitive than safflower under low K fertility [38].

4.2. Nutrients Accumulation

4.2.1. K Accumulation

The concentration of a nutrient in tissues of growing plants is used as a measure for the demand of the plant on that nutrient [31]. The lower nutrient concentration in shoots to produce optimal yield is an indication for higher utilization efficiency of the plant [27,28,30]. In the other hand, uptake efficiency is usually expressed as the total nutrient content in plant tissues [24]. These two contradictory assumptions could be misleading in quest of the whole efficiency of the plant (uptake and utilization). If a plant accumulated more nutrient in its tissues as compared to a standard line, we may consider this plant as superior in the uptake of that nutrient and therefore a better accumulator of that nutrient or may be oppositely concerned as plant high demanding on that nutrient for its physiological processes and therefore inferior in the use of absorbed nutrient. In this investigation, safflower concentrated more K than sunflower did in their whole plant in both soil types under sub-optimal K supply, while under the respective optimal K-supplies, K concentration in DM of safflower marginally over-yielded that of sunflower in sandy soil but the opposite was observed in loamy soil (Figure 3). Therefore, safflower may be regarded as a better accumulator than sunflower in both soils under low K supplies, but could be less efficient in using absorbed K. However sunflower accumulated significantly more K than safflower at all respective K supplies, the relative accumulation of K (related to that at optimal K supply) reveals that safflower is better K accumulator than sunflower at suboptimal levels, performed similar to sunflower at respective K supplies but accumulated significantly less relative amounts than sunflower at high K levels. This can be discussed in view of the larger biomass production in sunflower demanding larger amounts of K in the tissues [27].

4.2.2. Mg and Ca Accumulation

Magnesium (Mg) concentration and its total content decreased drastically in dry matter of both species with increasing K supply in both soils (Figure 4). In principle, there are two reasons for Mg deficiency to occur, absolute deficiency and cation competition. The later reason is a consequence of nutrient imbalances in soils and is most likely to occur on sandy soils with low cation exchange capacity (CEC), or some soils of high potassium status as documented in this study [63]. It was frequently mentioned that, the rate of Mg uptake can be strongly depressed by other cations, such as K^+ , NH_4^+ , Ca_2^+ , Mn_2^+ , H^+ [3,64] and Al_3^+ [65], causing a cation competitive effects which lead to Mg deficiency. Accordingly, each of K or Mg can reduce the uptake of the other when the

"normal" soil balance does not exist in soils with low cation exchange capacity [3] as was clearly observed for both species under study grown in sandy soil (Table 1). Furthermore, over-fertilization with potassium induce magnesium deficiency in some soils as we observed in this investigation in both soils at the highest K supply in sandy soil (Figure 2). We observed that Mg deficiency was not compensated for by moderate supply of K but was aggravated by excess K supply. It is assumed that the disturbed metabolite (carbohydrates and amino acids) partitioning under Mg deficiency is a consequence of impaired phloem loading of metabolites [66]. When the root system serve as an important sink for metabolites, it suffers from limited carbohydrate supply under K induced Mg deficiency, and the reduced root growth further enhances the risk of other nutrient deficiencies and environmental stresses (e.g. drought stress) due to less explored soil volume and, therefore, less access to soil resources [67].

Increasing concentrations of K generally depress Ca content of plants [3]. This depressive effect of the monovalent cations such as K on Ca was attributed to reduced transpiration at high monovalent ion concentrations with a consequent reduction in Ca transport to tops [68]. Generally, excess supply of one of K, Ca or Mg result in a lower concentration of the remaining two cations, as was observed in our findings (Table 1 and Table 2). Therefore, high activity ratio between potassium and calcium induced Ca-deficiency [69].

4.3. K Use Efficiency

Different species and cultivars among species vary widely in their ability to thrive in nutrient- deficient environments, and therefore differ greatly in their nutrient efficiencies [24,31,38]. Genotypes that can acquire and use scarce nutrient resources more efficiently from less fertile soils could improve and stabilize agricultural production [70]. These genotypic differences are related to differences in efficiency of acquisition by the roots or in nutrient use by the plant, or both [38,71]. Different concepts of nutrient efficiency have been developed, some giving emphasis to productivity and others to internal nutrient requirement [39], and in some cases their interpretations are misleading [26,31,71]. To characterize different plant genera, species or genotypes for nutrient use efficiency (NUE), researchers use many criteria, including the presence or absence of deficiency symptoms [72], absolute growth at a limiting nutrient level [73], relative growth obtained by comparing growth at limiting and adequate nutrient levels [74,75], efficiency ratio (ER) or amount of biomass produced per unit of nutrient present in the tissues [74], the use of yield response curves in terms of the functional relationship between yield and nutrient accumulated in the aboveground biomass, or nutrient supply in nutrient media using Michaelis-Menten-type equation [26,27,28,29,76], and utilization coefficient as the inverse of the whole plant nutrient concentration being expressed on a dry matter basis [77]. The plants' nutrient efficiency could be also assessed by other terms like the "external" and "internal" nutrient requirements for plant growth and yield under limited nutrient availability in soil. The internal requirement is the

minimum uptake by a plant associated with a specific yield, usually near maximum growth [27,30,46]. It is also defined as the critical concentration for optimal crop growth or yield i.e. the nutrient concentration in plants sufficient to produce a certain proportion, e.g. 90%, of maximum dry matter yield [30,45,78]. Therefore, plants growing under limited K conditions with a low internal K requirement may have a low external K requirement or may be inefficient acquiring nutrient, but they should be efficient in using the nutrient taken up to produce dry matter. The external nutrient requirement of plants is the nutrient concentration in soil solution associated with adequate nutrition or growth [46]. As a convenient mean of expressing K utilization efficiency in this study, nutrient accumulation and concentration, efficiency ratio (ER), utilization index (UI), agronomic efficiency, external K requirement, and K recovery were used.

4.3.1. K Efficiency Ratio (KER)

The continuously increasing values of KER to produce DM, exhibited by safflower and sunflower (Figure 7), in response to decreasing nutrient supply, represents the general response of the adaptation of different species to nutrient-poor environments by enhancing their nutrient use-efficiency [27,79]. Similar observations have been found for safflower as compared to sunflower [27,28,29,30,31]. However, the ability of safflower and sunflower grown in sandy soil to utilize K in similar efficiency at low and optimal K supplies indicates that both crops are good responsive in increasing their utilization efficiency in sandy soils of poor K status. Additionally, safflower was found more efficient in utilizing K as compared to sunflower at their respective K supplies in loamy soils but it was inferior under low K supply.

4.3.2. K utilization Index (UI)

The utilization index [27,28,54] is defined as biomass produced per unit tissue nutrient concentration, that unlike the efficiency ratio, takes differences in the amount of produced biomass into consideration. UI was proposed [54] to avoid the interpretation of the dilution effect under low nutrient supply as utilization efficiency when interpreted in terms of ER [27,28,30,31]. Our findings in terms of K utilization index supports the superiority of sunflower over safflower at all respective K supplies including optimal and low K levels in both soil types (Figure 7). The comparison of the results of both efficiency parameters (UI and KER) indicates that the high values of efficiency ratios obtained at very low K levels could be a reason of dilution effect of K rather than an actual efficiency in K utilization when K is very limiting because K concentration in the biomass is low (Figure 7).

It was stated that a nutrient is needed at a threshold concentration to reach maximum growth; not threshold quantity, therefore, the utilization index could be considered as a reliable estimate of K utilization efficiency [27,30,31,54]. Furthermore, using different measures of utilization efficiency parameters to differentiate plant species and genotypes to superior and inferior could be in some cases misleading [26,71].

4.3.3. External K Requirement

An agronomic definition of nutrient efficiency relates plant productivity to nutrient supply [52]. It has also been calculated on the basis of the amount of nutrient available [53], therefore the term “external nutrient requirement” refers to the amount of nutrient in the media required to produce a given percentage of maximum yield [45]. Accordingly, a calculation used in this study [31] that defines the required external nutrient quantity in different forms (soil solution P and K, extractable P and K, and finally P and K supply) to produce 1 kg of DM.

Safflower’s agronomic K requirement in terms of external K supplies and CAL extractable K was higher than that of sunflower at all respective K levels including their respective optimal supplies, which indicates the higher K requirement in terms of K supply and exchangeable K for safflower as compared to sunflower at optimal growth (Table 3). While the K requirements to sustain optimal yield in terms of soil solution K was found less for safflower as compared to sunflower in sandy soil and the values were statistically similar for both crops when grown in loamy soils. Safflower had a higher agronomic K efficiency than sunflower under suboptimal K fertilization levels, indicated by lower external demand to express relative optimal yield and greater relative yield under low K supply.

4.3.4. Potassium Recovery

The enhanced recovery of supplied K with decreasing external K levels was reported previously for both crops in terms phosphorous in both soils [31] and also when grown in nutrient solution experiment [29]. Potassium starvation is known to activate K^+ uptake in plants [80,81] by the induction of expression of high affinity transporters which was considered as a major mechanism of adaptation to K deficiency. Growing roots continuously experience variations in potassium availability, to which they have to adjust their physiology and growth pattern. In order to optimize their performance as nutrient uptake organs and to compete for K^+ uptake in the dynamic and heterogeneous environment, plant roots developed mechanisms of acclimation to the current K^+ status in the rhizosphere. All these acclimation strategies enable plants to survive and compete for K in a dynamic environment with a variable availability of K [82].

Both crops recovered more amounts of K than supplied in loamy soil at deficient K levels (Figure 8). The ability of sunflower to recover more K than supplied in terms of extractable K in loamy soil indicate that sunflower is able to dissolve part of the nonexchangeable K held between the layers of the loamy particles. Furthermore, the exceeded recovery amounts by both plants as compared to supplied levels interpreted as soil solution reveals that the plants can deplete K from the soil solution many times and this nutrient is continuously supplied to the soil solution from the exchangeable pool [31].

The availability of potassium for the plant is highly variable, due to complex soil dynamics, which are strongly influenced by root-soil interactions. In accordance with its availability to plants, soil K is ascribed to four different pools: soil solution, exchangeable K,

nonexchangeable K and lattice K [83]. As plants can only acquire K^+ from solution, its availability is dependent upon the K dynamics, and total K content, as well as the concentration of other macronutrients in the soil solution [84]. The release of exchangeable K is often slower than the rate of K^+ acquisition by plants [85] and consequently, soil solution K^+ concentration in some soil is very low [86]. Plant roots can experience transient shortages of K because of spatial heterogeneity and temporal variations in the availability of this nutrient. The main source of soil heterogeneity is often the plant roots themselves, the K^+ transport activity of which creates zones with elevated or reduced nutrient concentration. Contact between a root and nutrient may occur because of root growth into the area where a nutrient is located (root interception), and transport of a nutrient to the root surface through the soil [87]. Root interception constitutes less than 1-2% of total K^+ uptake because of rapid removal of K^+ at the root surface [88,89]. The second process is the K^+ translocation through the soil to the root surface, is facilitated by diffusion and mass flow [90]. Diffusion is the most dominant mechanism of K^+ delivery to the root surface [91] and constitutes up to 96% of total soil K^+ transport [92].

Usually, only K in solution and K sorbed at loamy minerals (are in equilibrium), count as plant available. However, it has been shown that non-exchangeable K can also be used by plants when the available fraction is too low for sufficient supply. It is not fully clear in which way plants increase the availability of nonexchangeable K and why some plant species perform better than others. Plant species with increased capacity to render sparingly soluble nutrient forms into plant available ones or with a higher capacity to transport nutrients across the plasma membranes are considered to possess high nutrient uptake efficiency [36]. However, if the rate of nutrient replenishment at the root surface is much lower than the capacity of the root cells to take up nutrients, uptake will be governed by the nutrient supply rather than by the nutrient uptake capacity of the root cells [3].

4.3.5. Mechanisms of K Use Efficiency

Both species under investigation showed both efficiency and inefficiency traits in the same time, indicating that, the nutrient use efficiency is a process composed of competitive components and each component contributes to the overall efficiency to a certain positive or negative extent [28,29,30,31]. Researchers quantified the relative contribution of the two components of the agronomic potassium use efficiency as uptake efficiency and the utilization efficiency [27]. The calculation adapted based on a statistical approach [93], using results of two consecutive years comparing safflower and sunflower, and demonstrated that the contribution of the K utilization efficiency was much more important than its uptake efficiency in safflower, while the opposite was observed in sunflower. Consequently the uptake efficiency is based on different components which could be in a competitive manner. Therefore none of the crops under investigation showed a combination of high values of all uptake components. Therefore, using different measures of utilization efficiency parameters to differentiate plant species and genotypes to superior and inferior could be in some cases misleading [26,71].

5. Conclusion

Both species grown better in loamy soils than in sandy soils. To select low input species, the performance of the crops under suboptimal K supply is highlighted in this conclusion. Safflower performed better than sunflower in terms of relative biomass in both soils. Safflower concentrated more K than sunflower in their tissues in both soil types. Safflower had higher relative K concentration in DM than sunflower. Both species depleted similar amounts of the soil solution K in sandy soil but sunflower was more efficient in loamy soils. Sunflower depleted more extractable K than safflower in both soils. Both species had similar efficiency ratio in sandy soil but sunflower was more efficient in loamy soil. Sunflower was found superior over safflower in terms of utilization index in both soils. Sunflower had less external K requirement than safflower in both soils types. NUE parameters under K deficiency are genetically controlled and are affected by environmental factors under study. Neither safflower nor sunflower showed a combination of all KUE components in both soils, and interpreting KUE using different calculations may be misleading, therefore it is difficult to consider in straightforward conclusion one of the crops under study as a low input species as compared with the another under our experimental conditions.

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Competing Interests

None declared.

Abbreviations

K- Potassium, NUE- Nutrient use efficiency, CAL- Calcium acetate lactate, DM- Dry matter, KER- Potassium efficiency ratio, ER- Efficiency ratio, UI- Utilization efficiency, TDM- Total dry matter.

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