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Mechanisms of potassium uptake efficiency and dynamics in the rhizosphere of safflower and sunflower in different soils

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ABSTRACT
Potassium uptake efficiency of safflower and sunflower was studied under semi-controlled conditions in loamy and sandy soils. Both species performed better in loamy soil. Safflower had higher agronomic efficiency and higher relative root length under suboptimal K supply. Safflower had higher specific root density and less root radius at all K levels. Safflower had higher relative root-shoot ratio under suboptimal K in loamy soil. Both species had similar K-influx at low and optimal K in loamy soil, while sunflower had higher influx under suboptimal and optimal supplies in sandy soil. Safflower had higher shoot demand in both soils under suboptimal and optimal K. Both species depleted similar amounts of soil solution-K under suboptimal K in sandy soil, while sunflower was more efficient under suboptimal levels in loamy soils. Sunflower depleted more extractable-K under both suboptimal and optimal K. Safflower could be considered K-uptake efficient crop.

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alternative crops; *Carthamus tinctorius*; K influx; potassium uptake efficiency; rhizosphere; safflower; shoot demand

Introduction

The rapid expansion of global human population which reached approximately 7.5 billion (United States Census Bureau 2018), requires a massive increase in crop production, potentially through expanding area under cultivation (Tilman et al. 2011), increasing yield per unit area (Wang et al. 2013) and applying intensive cropping techniques (Tilman et al. 2002). Both land clearing and more intensive use of existing croplands could contribute to the increased crop production required for such demand, but the tradeoffs of these alternative paths of agricultural expansion and their environmental impacts are unclear (Godfray et al. 2010). As a result of the intensification of agriculture and the introduction of high yielding varieties (Pretty and Bharucha 2014; Abbadi 2017a), the soils of many regions of the world are getting depleted in reserve K at a faster rate, making K deficiency one of the major constraints to crop production (White et al. 2010).

Potassium is a non-renewable resource (Guillou and Matheron 2014), quantitatively the most important inorganic cationic nutrient for crop productivity, unless supplied as fertilizer (Zörb, Senbayram, and Peiter 2014). As an essential macronutrient and the most abundant cation in higher plants (Wang and Wu 2013; Adams and Shin 2014), K plays a critical role in controlling ion homeostasis (Almeida, Oliveira, and Saibo 2017), osmoregulation (Anschütz, Becker, and Shabala 2014), protein metabolism (Marschner 2012), enzyme activity (Zahoor, Zhao, Abid, et al. 2017), membrane polarization (Nieves-Cordones, Al Shiblawi, and Sentenac 2016), photosynthesis (Zahoor, Zhao, Dong, et al. 2017), and various metabolic processes (Schachtman and Shin 2007). Although total K contents of most soils reach 2.6% of the lithosphere (Osman 2013), actual soil concentrations vary widely, ranging from 0.04 to 3% (Sparks and Huang 1985). This actual low

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availability of K is usually due to its enclosure in silicates and strong adsorption by K-specific binding sites (Britzke et al. 2012).

To fulfill crops requirements, applying K fertilizer is mandatory to ensure adequate K supply. However 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 (Bishopp and Lynch 2015). The use of efficient plant species is one of the possible strategies of sustainable land use, sustains resources and conserves the environment (Rao et al. 2016; Abbadi et al. 2017). Therefore, manipulating the genotypic differences in crops to adapt them to adverse soil conditions is one of the key strategies for the sustainable intensification of agricultural systems (Yang et al. 2005). Accordingly, species which are able to make use of the not readily available K could have a significant agronomic importance (Gerendás, Abbadi, and Sattelmacher 2008; Abbadi 2017b). However, cultivating K-efficient species to improve yields or developing genotypes that are more K-efficient may be possible if K efficiency mechanisms are elucidated (Dessougi, Claassen, and Steingrobe 2002).

Plant species and even cultivars within species differ in their nutrient use efficiency (NUE) (Dessougi, Claassen, and Steingrobe 2002; Bhadoria et al. 2004; Abbadi and Gerendás 2009). Definitions of NUE vary greatly and in some cases, may be misleading in terms of identifying the mechanisms for the NUE (Sattelmacher, Horst, and Becker 1994; Sadana and Claassen 1999; Steingrobe and Claassen 2000; Abbadi and Gerendás 2015; Abbadi 2017c; Abbadi et al. 2017). The ability of cultivars to tolerate low nutrient supply may be due to either high nutrient uptake at low nutrient concentrations and/or more efficient use of nutrient for more yield production (Abbadi 2007). NUE is a function of soil capacity to supply adequate levels of nutrients, and the ability of plants to acquire nutrients, transport them in roots and shoots and to remobilize 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 (Dessougi, Claassen, and Steingrobe 2002). Efficient plants in terms of utilization, can obtain relative high yield with a low K concentration in their dry matter, whereas uptake efficient plant can acquire sufficient K despite a low soil K supply level (Abbadi 2017b). The morphological characteristics of the root system (root length, root/shoot ratio, root radius, and root hairs), the physiology of uptake (the influx rate, maximum influx (I_{max}), Michaelis constant (K_m), and minimum solution concentration at the root surface at which influx equals efflux (C_{min})), and the ability of plants to increase K solubility in the rhizosphere are considered as mechanisms of K uptake efficiency (Steingrobe and Claassen 2000; Samal et al. 2010; Liu et al. 2014). Currently, there is no suitable efficiency index of crop response to K deficiency for breeding purpose (Jia et al. 2008).

Therefore, the identification of mechanisms of efficient species or cultivars with greater tolerance to suboptimal nutrient availability offers considerable promise for increasing the production potential on marginal land. Although, more efficient varieties of a given crop may be considered, large differences with respect to K demand between closely related, alternative crops may also be worth exploiting, in view of resource limitations. For instance, safflower (*Carthamus tinctorius* L.) and sunflower (*Helianthus annuus* L.), both belonging to the same family (*Asteraceae*), are important oil crops in temperate areas. Safflower was hypothesized as a low input cultivar in terms of K (Gerendás, Abbadi, and Sattelmacher 2008), but the mechanisms that outline this efficiency were not fully studied. Thus, the objective of this investigation was to study potassium uptake efficiency and its dynamics in the rhizosphere of safflower and sunflower when grown in different soils (sandy and loamy) under semi-controlled conditions.

Materials and methods

Experimental design

A pot experiment was conducted to evaluate the mechanisms of K uptake efficiency, in the rhizosphere of safflower (*C. tinctorius* L., variety "Sabina") and sunflower (*H. annuus* L., variety

"Peredovick E"), grown in two types of soil: loamy (obtained from Klein Elde, Lower Saxony, Germany) and sandy (obtained from Eickeloh, Lower Saxony, Germany), using four levels of K supplies. Before running the experiment, field-moist samples from the two types of soil under investigation were sieved to 2 mm particle size, from which, subsamples of soil were air dried and analyzed for extractable P, exchangeable K and 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} ammonium acetate exchangeable Mg. The loamy soil (pH 7.0 by water extraction) contained 16.5 mg kg^{-1} CAL-extractable P, 28 mg kg^{-1} CAL-exchangeable K, and 141 mg kg^{-1} ammonium 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} ammonium 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 3 g K pot^{-1}) were added in the form of K_2SO_4, 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 100 g^{-1}) was found 1.87, 4.72, 16.49, and 44.3 for sandy soil and 3.1, 5.2, 15.9, 43.8 for loamy soil in respective K supplies. Other nutrients added per pot were 2 g N (as NH_4NO_3), 1 g P (as solid $Ca(H_2PO_4)_2$), 0.8 g Mg (as $MgSO_4$). Micronutrients were added in adequate amount for both species 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 treatments (two plant types, two soil types, four K levels) were replicated four times in a non-orthogonal completely randomized design. One additional pot per each treatment was left unplanted as a control for the measurement of extractable and soil solution K and Mg concentrations during the experiment. The plants were watered daily to nearly a volumetric soil water content of 35%. The experiment was conducted in semi-controlled climate in a greenhouse; average day and night air temperatures ranged 20–22 °C and 18–20 °C with midday peak temperatures between 23 and 28 °C in July. Relative humidity varied between 40% and 80% and additional light was supplied with SON-T Agro 400 W bulbs, keeping the minimum photosynthetic photon flux density (PPFD) at 350 mmol m^{-2} s^{-1} at the plant canopy for a period of 14 h d^{-1}.

Harvesting and analytical procedures

Plants were harvested in two harvest times; plants of one pot in each treatment (plant species and soil type) was harvested in the first harvest after 35 days after planting and three pots in each treatment were harvested in the second harvest after 49 days after planting maintaining two weeks between the two harvests. At each harvest, after cutting the above ground plant parts, the soil of each pot was weighed (moist soil containing roots), then soil was cut to two identical parts. One part of the soil in each pot was sieved to exclude the roots and then was sub-sampled for the following measurements: a soil sample to measure the moisture content of the soil, another sample for measuring soil solution K and Mg, and finally a sample for measuring extractable K and Mg. The second half of the soil of each pot was preserved in sealed plastic bags at 6 °C and was washed within 24 hr for collecting the roots for root fresh weight, root length and root radius measurements.

Harvested plants were separated to stems, leaves and roots (half roots per pot were collected). Stems and leaves were measured for fresh and dry weight (g), then were analyzed for their K and Mg content. The roots in the cooled half of the pot (precisely weighed) were separated from the soil by washing them over a 0.2 mm sieve, then were preserved overnight in closed plastic bottle in a cold room (6 °C) to be measured for their fresh weight (g) and length (cm) within 24 hr.

K efficiency parameters

Shoot measurements

At harvest, the dry weight of plant parts was measured after drying at 60 °C till constant weight. Plant materials were grinded to pass a 1.5 mm sieve, of which, after thorough mixing, a subsample of 5 g was ball-milled to a fine powder. The samples were prepared for K analysis using wet microwave digestion with a concentrated tri acid mixture (HNO_3, $HClO_4$, and H_2SO_4 with a volumetric ratio of 8:2:1). Total K of the plant material digest was measured using flame photometer.

Soil solution K concentration, extractable K concentration, soil pH, soil water content, and buffer power

A column displacement method was used to collect the soil solution in order to determine initial soil solution K and Mg concentration. The method permits accurate determination of the unaltered composition of soil solution (Adams 1974). A sample of moist soil (350 g) was packed into a plastic column with a pore in bottom. Filter paper was placed in the bottom of each 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 tell 25 mL to insure not to collect diluted solution, and filtered through a 0.20 µm filter. The solutions were analyzed for K by flame photometer and for Mg using atomic absorption spectrometer. Soil solution K and Mg concentration was measured for planted and unplanted pots immediately at the time of each harvest. To determine solid phase (extractable) K, an air dried 10 g subsample of soil from each pot was extracted with calcium acetate lactate (CAL) method according to Schüller (1969). To determine extractable Mg, an air dried 10 g subsample of soil from each pot was extracted according to Schachshabel (1954). Potassium concentration in the extracts was determined using flame photometer, and Mg was determined using atomic absorption spectrometer. The pH was measured in water (1:2.5 soil:water ratio). Buffer power was calculated as the ratio of soil exchangeable K (mol cm^{-3} soil) and the soil solution K concentration (mol cm^{-3} soil solution).

Root length measurements

Fresh roots were dried gently between paper towels in fresh air at room temperature for 1 hr. After determining the root fresh weight (RFW), the root length (RL) was measured on six representative sub-samples per treatment. The root length measurement was done using the line intersection method of Tennant (1975). Assuming that the specific weight of roots is 1 g cm^{-3}, the mean root radius (r_0) was calculated as:

$$r_0 = \surd(\text{Root fresh weight (RFW)}/\pi \text{ Root length (RL)})$$

The root length density (RL_v) was calculated by dividing root length (RL) by the soil volume of the pot (cm root/cm^3 soil).

Shoot and root growth rate

This ratio relates the difference in shoot or root growth between the two harvests divided by the number of days between the two harvests: shoot growth rate (GR_s) $= \ln (SW_2 - SW_1)/(t_2 - t_1)$, root growth rate ($GR_r$) $= \ln (RW_2 - RW_1)/(t_2 - t_1)$, where SW is shoot dry weight, RW is root dry weight, and t is time.

Shoot demand

This ratio relates the K acquisition load imposed by shoot growth to each root segment. It is calculated by dividing the shoot growth rate (GR_s) by the average root length (aRL) assuming exponential root growth. $SD = ((SW_2 - SW_1)/(t_2 - t_1)) \times \ln((RL_2/RL_1)/(RL_2 - RL_1))$, where RL is the root length [cm] and SW is the shoot dry weight [g] at two harvest dates ($t_2 - t_1$).

Net K influx

The influx is the net amount of a nutrient that is taken up per unit root length (or root surface area) per unit time. Since direct measurement of the influx is not possible, only an average influx can be calculated for a given time period. At least two harvests are needed in which the nutrient content and root length of the plants are known. Assuming that the roots of young plants show exponential growth, the average influx was calculated after Williams (1948):

$$\mathrm{In} = ((SW_2 - SW_1)/(t_2 - t_1)) \times \ln((RL_2/RL_1)/(RL_2 - RL_1))$$

where In is the influx, U is the shoot K content [mol] at two harvest dates ($t_2 - t_1$) related to the root length between the two harvests ($RL_2 - RL_1$).

Statistical analysis

All statistical analyses were carried out using SAS (SA 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 to maintain an experiment-wise α of 5%.

Results

Growth and morphology

Oxidative necrosis and burns of lower leaves were observed in both species in both soils with low K supplies and these symptoms were more pronounced in sandy soils. Vegetative fresh weight (Table 1) of plant parts (leaves, stems, and roots) of both crops increased dramatically with increasing K supply in both soils. Fresh weights of plant parts of both species grown in loamy soil were significantly higher than those grown in sandy soil at all respective K supplies. In sandy soil with 0 added K, safflower leaves and stems were reduced similarly, but the reduction in roots was more pronounced. In sunflower, the most reduced part was the stem followed by roots followed by leaves. In sandy soil, root fresh weight of both species were reduced at suboptimal K supplies and high K supply. In K-deficient loamy soil, the most affected growth component in both species was the stem followed by the root followed by the leaves. In both species, root fresh weight was much less in plants grown in sandy soil as compared to those grown in loamy soils at all respective K supplies. Comparing both plant species in terms of relative fresh weight under low K availability, safflower was found superior as compared to sunflower in both soils. Both species grown in sandy soil with high K levels showed symptoms of Mg deficiency including oxidative necrosis and burns of lower leaves and reduced growth.

Regardless of the soil type, both crops responded strongly to increasing K supply with respect to dry matter (DM) production (Table 2, Figure 1). DM of both plant species was less in sandy soil as compared to loamy soil in all respective treatments. As fresh weight parameters, safflower relative dry weights of plant parts (leaves and stems) performed better than sunflower at sub-optimal K supplies. The best K supply in both sandy and loamy soils was less for safflower (0.2 g K pot^{-1}) as compared to sunflower (0.5 g K pot^{-1}) indicating that safflower is more K-efficient in producing relative dry weight under K deficiency as compared to sunflower.

Table 1. Effect of K supply on fresh weight (g pot^{-1}) of safflower and sunflower (absolute value without brackets and relative values between brackets).

	Soil type									
	Leaves		Stem		Shoot		Roots		TFW	
K supply(g pot^{-1})	Sandy	Loamy	Sandy	Loamy	Sandy	Loamy	Sandy	Loamy	Sandy	Loamy
Safflower										
0	8.90C* (44.5)	31.90C (65.1)	2.83C* (43.5)	10.35B (50.0)	11.73C* (44.3)	42.30B (60.7)	2.73C* (39.6)	11.98B (56.2)	14.93C* (45.6)	56.64C (59.1)
0.2	17.60BA* (88.2)	46.57BA (95.0)	6.17A* (94.9)	20.68A (100)	23.77A* (89.9)	67.25A (96.6)	6.89A* (100)	21.30A (100)	32.23A* (98.4)	91.04BA (95.0)
0.5	19.95A* (100)	34.80BC (71.0)	6.50A* (100)	10.10A (48.8)	26.45A* (100)	52.90B (76.0)	4.90B* (71.1)	16.20BA (76.1)	32.75A* (100)	71.87B (75)
3	12.03B* (60.3)	49.03A (100)	4.93B* (75.5)	20.60A (99.6)	16.97B* (64.2)	69.63A (100)	4.15B* (60.2)	19.18A (90.0)	21.47B* (65.6)	95.81A (100)
Sunflower										
0	20.97C* (24.6)	114.80C (53.5)	11.97C* (15.8)	91.57D (29.9)	32.93C* (20.5)	206.37D (39.6)	8.35C* (18.4)	60.89C (45.2)	42.51C* (19.9)	278.16C (41.5)
0.2	61.30B* (71.9)	154.77B (72.1)	52.13B* (69.0)	165.10C (53.9)	113.43B* (70.5)	319.87C (61.4)	27.30B* (60.3)	94.22B (69.9)	145.53B* (68.2)	430.57B (64.2)
0.5	85.20A* (100)	204.17A (95.2)	75.60A* (100)	260.93B (85.2)	160.80A* (100)	465.10B (89.3)	45.30A* (100)	132.05A (98.0)	213.54A* (100)	623.15A (92.9)
3	76.40A* (89.7)	214.53A (100)	72.45A* (95.8)	306.20A (100)	148.85A* (92.6)	520.73A (100)	34.82B* (76.9)	134.79A (100)	193.23A* (90.5)	670.77A (100)

For a given species and a given soil type, means within each column followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within different soil types. $P < 0.05$, $n = 3$.

Table 2. Effect of K supply on dry weight (g pot^{-1}) of safflower and sunflower (absolute value without brackets and relative values between brackets).

	Soil type			
	Leaves		Stem	
K supply (g pot^{-1})	Sandy	Loam	Sandy	Loam
Safflower				
0	1.42B* (47.2)	4.58B (62.1)	0.62B* (41.3)	2.20B (46.9)
0.2	2.45A* (81.4)	6.51BA (88.3)	1.40A* (93.3)	4.14A (88.2)
0.5	3.01A* (100)	4.96BA (67.3)	1.50A* (100)	3.94A (84)
3	2.03B* (67.4)	7.37A (100)	0.99BA* (66)	4.69A (100)
Sunflower				
0	2.56C* (27.5)	12.73C (54.7)	0.91C* (18.1)	5.80D (26.5)
0.2	6.81B* (73.1)	17.00B (73.1)	3.37B* (66.9)	10.59C (48.4)
0.5	9.32A* (100)	23.26A (100)	5.04A* (100)	18.79B (85.9)
3	8.63A* (92.6)	22.73A (97.7)	4.84A* (96)	21.88A (100)

For a given species and a given soil type, means within each column followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within different soil types. $P < 0.05$, $n = 3$.

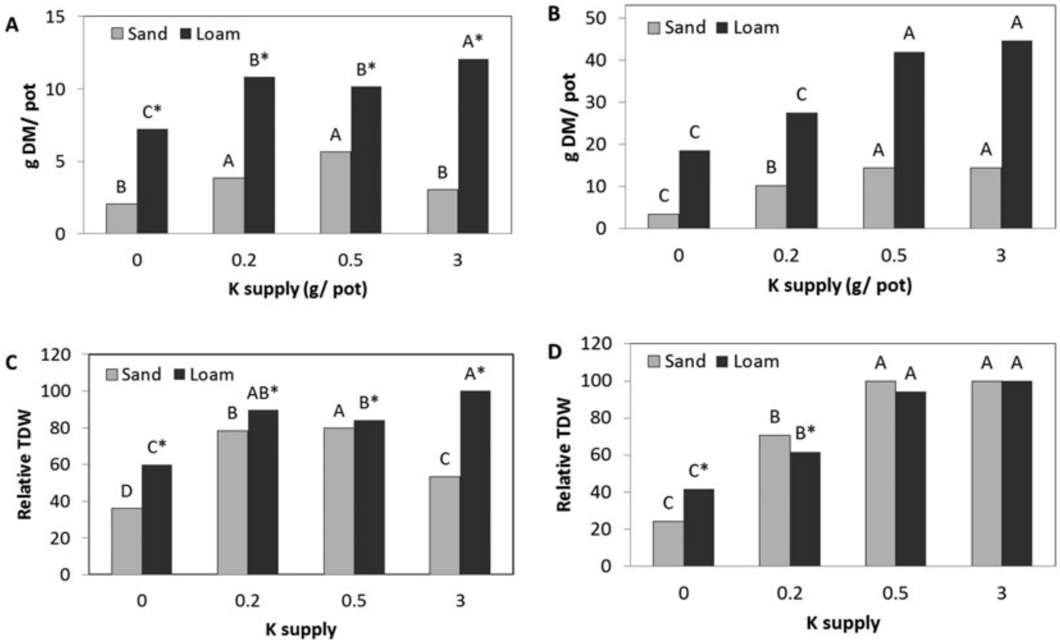

Figure 1. Effect of K supply on total dry weight (g pot^{-1}) and relative dry weight of safflower (A and C) and sunflower (B and D). For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at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

Shoot growth rate (GR$_s$)

Shoot growth rate (g DM day^{-1}) of sunflower was significantly higher than those of safflower at all respective K supplies in both soils (Figure 2). Safflower GR$_s$ was significantly higher in sandy soil as compared to loamy soil at all respective K levels, while the opposite was observed for sunflower. In sandy soil, relative GR$_s$ of both plant species was significantly reduced at suboptimal K levels as compared to that at best supplies. GR$_s$ was also reduced at higher K levels in safflower and maintained unchanged in sunflower. In loamy soils, sunflower maintained significantly similar relative GR$_s$ within K supplies while that of safflower was significantly reduced at high K

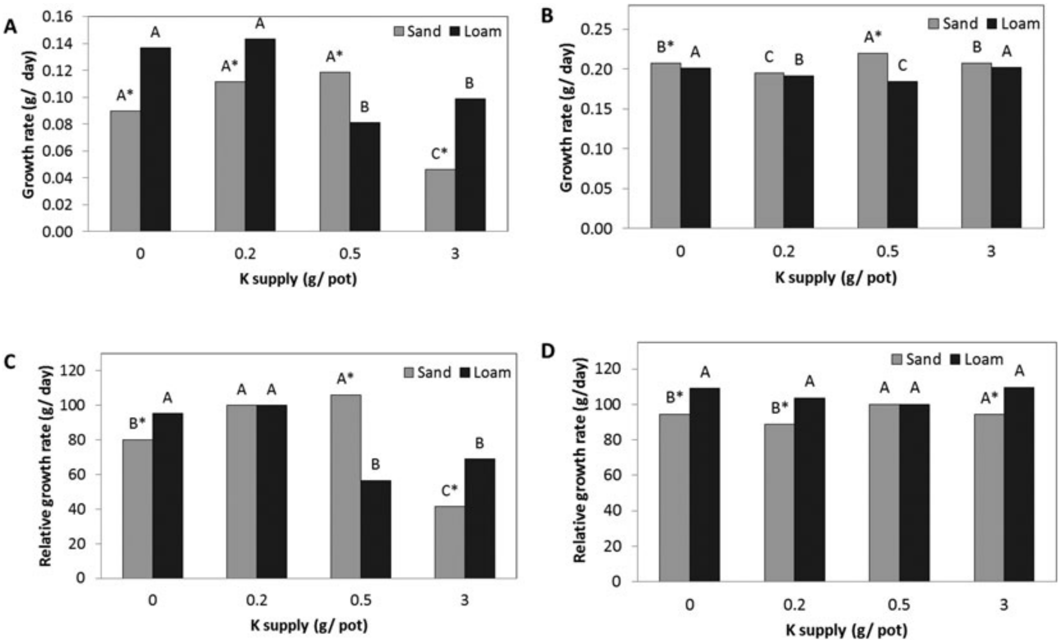

Figure 2. Effect of K supply on absolute growth rate (g dry matter day^{-1}) and relative growth rate (growth rate at a particular K supply related to growth rate at best K supplies) of safflower (A and C) and sunflower (B and D) shoot. For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

levels. In both soil types, there was no significant difference between both species in terms of relative GR_s, but safflower showed marginal reduction as compared to sunflower when grown at very low K supply in sandy soil.

Root parameters

Root length

In both species grown in both soil types, the longest roots per pot were recorded in plants grown at their respective best K supplies (Figure 3). Both species had significantly shorter roots at suboptimal and excessive K supplies in both soils. Sunflower had significantly longer roots than that of safflower at all respective K supplies in both soil types. Moreover roots of either plant species grown in loamy soil were significantly longer than those grown in sandy soils.

Specific root density and root radius

Specific root density and root radius of both species were not affected by different K supplies in both soils except for safflower in loamy soil for both traits, where specific root density was significantly increased and the root radius was significantly reduced when K supply was suboptimal (Table 3). In sandy soils, both species had similar specific root density or root radius values at 0 and 0.2 g K pot^{-1}. At 0.5 and 3 g K pot^{-1} in sandy soil, specific root density of safflower was higher than that of sunflower and the opposite was true for the root radius. Specific root density of safflower in loamy soil was significantly higher than that of sunflower at all respective K supplies, revealing that safflower roots were significantly thinner than that of sunflower at all respective supplies. Comparing both crops at their optimal supplies, the specific root density of safflower was significantly higher than that of sunflower, and the average radius of safflower roots was significantly smaller than that of sunflower.

Table 2. Effect of K supply on dry weight (g pot^{-1}) of safflower and sunflower (absolute value without brackets and relative values between brackets).

	Soil type			
	Leaves		Stem	
K supply (g pot^{-1})	Sandy	Loam	Sandy	Loam
Safflower				
0	1.42B* (47.2)	4.58B (62.1)	0.62B* (41.3)	2.20B (46.9)
0.2	2.45A* (81.4)	6.51BA (88.3)	1.40A* (93.3)	4.14A (88.2)
0.5	3.01A* (100)	4.96BA (67.3)	1.50A* (100)	3.94A (84)
3	2.03B* (67.4)	7.37A (100)	0.99BA* (66)	4.69A (100)
Sunflower				
0	2.56C* (27.5)	12.73C (54.7)	0.91C* (18.1)	5.80D (26.5)
0.2	6.81B* (73.1)	17.00B (73.1)	3.37B* (66.9)	10.59C (48.4)
0.5	9.32A* (100)	23.26A (100)	5.04A* (100)	18.79B (85.9)
3	8.63A* (92.6)	22.73A (97.7)	4.84A* (96)	21.88A (100)

For a given species and a given soil type, means within each column followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within different soil types. $P < 0.05$, $n = 3$.

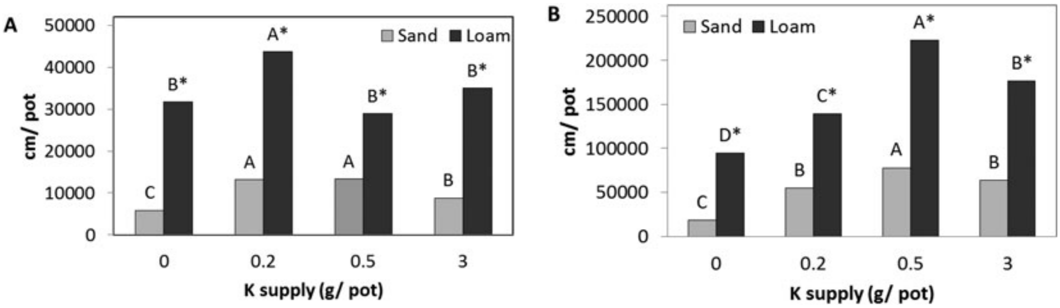

Figure 3. Effect of K supply on root length (cm pot^{-1}) of safflower (A) and sunflower (B). For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P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

Root growth rates (GR_r)

The maximum growth rate of safflower roots was obtained at best K supply in both soil types. Under suboptimal K level, this trait was similar to maximum rate in loamy soil but it was reduced significantly in sandy soil (Figure 4). At levels higher than optimal (0.5 and 3 g pot^{-1}), the growth rates of safflower roots were significantly reduced in both soil types. The maximum root growth rate of sunflower was recorded at the very low K level in both soils, then dropped significantly at 0.2 g K per pot in both soil types and then increased continuously with increasing K supply to a value similar to the maximum at the highest K level in sandy soil and maintained significantly reduced at all added K levels in loamy soil.

The root growth rates of safflower grown in sandy soil were significantly lower than that grown in loamy soils at all K levels. The growth rates of sunflower roots were lower in plants grown in sandy soils at optimal and suboptimal K levels but the difference was significant at 0.2 g K pot^{-1} only, while the opposite was recorded at the highest K supply. Root growth rate of safflower plants was significantly lower than that of sunflower at all respective K supplies and the difference was much pronounced in sandy soils.

The relative root growth rate of safflower grown in sandy soil was reduced significantly at suboptimal and high K supplies maintaining the highest rate at the best K level, while the same figure was reduced at high K levels only in loamy soil (Figure 5). Root growth rate of sunflower grown at the very low K level was significantly higher than that grown at the best K supply in

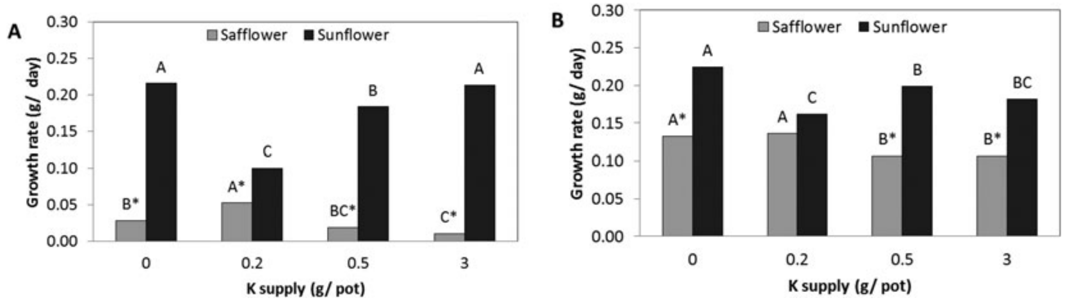

Figure 4. Effect of K supply on root growth rate (g day^{-1}) of safflower and sunflower in sandy (A) and loamy (B) soil. For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

both soil types, then it was significantly reduced at all added K levels except for plants grown at very high K supply in sandy soil where the value was similar to that grown with no added K.

Root shoot ratio (cm root/g shoot)

Safflower had significantly less root shoot ratio (RSR) than sunflower in all respective K supplies in both soil types and the difference was more pronounced in sandy soil (Figure 6). RSR for sunflower grown in either soil type was the highest at its best K supply, and the same was found in terms of safflower grown in sandy soil only. Safflower grown in loamy soil had the highest RSR under severe K deficiency, then decreased drastically as K supply increased. Safflower had significantly lower RSR in sandy soil as compared to loamy soil at all respective K supplies. In sunflower plants, the opposite was recorded except for the plants grown at very low K supply, where the RSRs in the two soil types were significantly similar.

As a general trend, the relative RSR was better at low and optimal K supplies than that at high K supply, and this response was significant in safflower in both soils. Both species had similar relative RSR when they were grown in either sandy or loamy soil at all respective K supplies except for safflower at very low K supply, where the relative RSR in loamy soil over-yielded that in sandy soil (Figure 7). At low K supplies, the relative RSR of safflower was lower than that of sunflower in sandy soil and the opposite was observed in loamy soil.

Root K influx

Potassium influx (pmol K cm $root^{-1}$ s^{-1}) in root cells of both species grown in both soil types increased with increasing external K concentration, except for that of safflower grown in sandy soil with high K supply where the influx was significantly decreased (Figure 8). In sandy soil, safflower roots had significantly lower K influx than those of sunflower at very low, respective optimal and high K supplies. The roots of both species had similar K influx when they were grown in loamy soil at suboptimal and respective optimal K levels, while sunflower out-yielded that of safflower at high K levels. K influx of safflower roots was significantly higher in loamy soils as compared to sandy soils at both extreme low and high K supplies and was similar in both soil types at intermediate K levels. K influx in sunflower root cells was significantly higher in sandy soils than that in loamy soil at all K supplies.

K concentration in dry matter

Both crops grown in both soils responded strongly to increasing K supply with respect to concentrating K in DM. In both soil types (Table 4), growth of safflower increased significantly up to 0.2 g K pot^{-1} external K supply, while sunflower optimal growth was achieved at 0.5 g K pot^{-1}

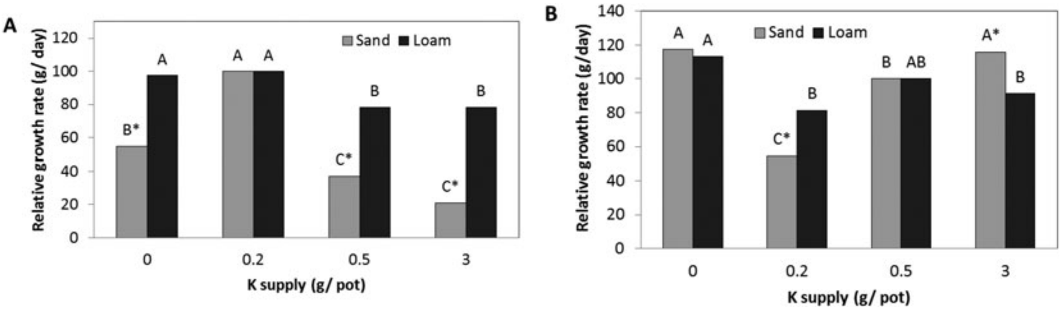

Figure 5. Effect of K supply on relative root growth rate (growth rate at each K level (g day^{-1}) related to optimal K level) of safflower (A) and sunflower (B). For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

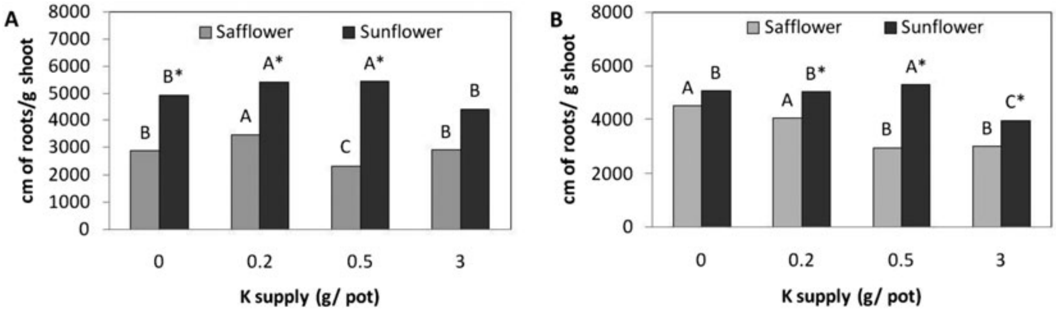

Figure 6. Effect of K supply on root shoot ratio (cm root/g shoot) of safflower and sunflower in sandy (A) and loamy (B) soil. For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

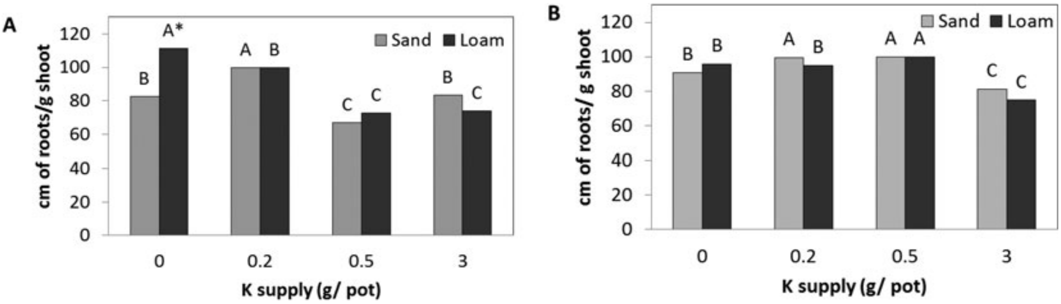

Figure 7. Effect of K supply on relative root: shoot ratio ((cm root) g shoot^{-1} related to optimal K level) of safflower (A) and sunflower (B). For a given plant species and different K level, means within followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

(Figure 1). At respective optimal K supplies, K concentration in leaves, stems and shoot DM 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 (leaves and stems) in both soil types as a result of the less DM produced per pot as compared to sunflower resulting in a concentrating effect, while the opposite was observed at high K supplies. Under the respective optimal K-supplies 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.

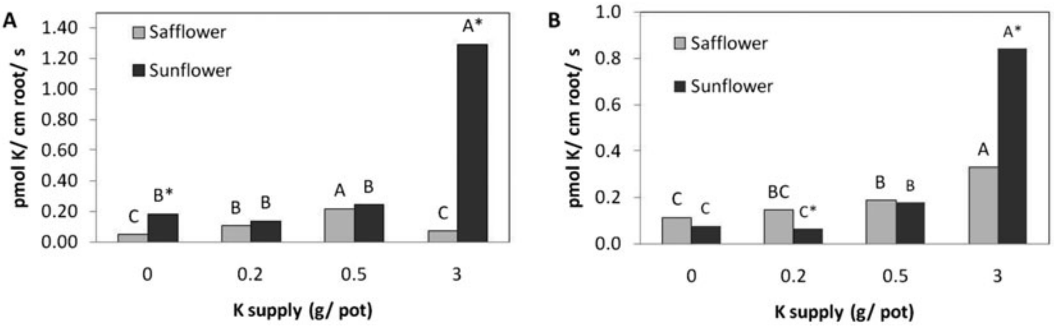

Figure 8. Effect of K supply on K influx of root cells (pmol K cm root^{-1} s^{-1}) of safflower and sunflower in sandy soil (A) and loamy soil (B). For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference for a given plant species at the same K level within soil types. $P < 0.05$, $n = 3$.

Table 3. Effect of K supply on specific root density (cm g root^{-1}) and root radius (cm × 1000) of safflower and sunflower.

	Specific root density		Root radius	
K supply (g pot^{-1})	Sandy	Loam	Sandy	Loam
Safflower				
0	2153.0A,a*	2677.3A,a	12.25A,a*	10.92B,b
0.2	1912.8A,a	2073.1BA,a	12.94A,a	12.49BA,b
0.5	1945.2A,a	1839.3B,a	12.82A,b	13.25A,a
3	2166.1A,a*	1800.6B,a	12.17A,b*	13.36A,b
Sunflower				
0	2107.6A,a*	1535.4A,b	12.45A,a*	14.56A,a
0.2	2052.4A,a*	1489.5A,b	12.48A,a*	14.64A,a
0.5	1744.2A,b*	1541.7A,b	13.59A,a	13.70A,a
3	1605.2A,b*	1373.5A,b	14.16A,a*	15.39A,a

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, *significant difference for a given plant species and a given K level within soil types. $P < 0.05$, $n = 3$.

Shoot demand (SD)

Shoot demand (SD) on the roots for K is the K acquisition load imposed by shoot growth on each cm of the root and is calculated by dividing the shoot growth rate by the average root length, assuming that the roots of plants grow exponentially. SD of both species was significantly higher when plants were grown in sandy soil as compared to those grown in loamy soil (Figure 9). In both soil types, shoot demand for K on the roots was significantly higher in safflower as compared to sunflower at all respective K supplies. SD of K on the roots of both species grown in either soil type at suboptimal K levels was much higher than that at optimal and high K levels. SD of both species in both soil types was the highest when plant grown in the most deficient K level, and decreased dramatically with increasing K availability in soil.

Soil parameters

Soil solution K and Mg

In the unplanted pots of both soil types, the soil solution contained increasing K amounts as a function of increasing external K supply. The solution obtained from sandy soils had significantly higher K than that obtained from loamy soil at all respective added K levels (Figure 10(A),

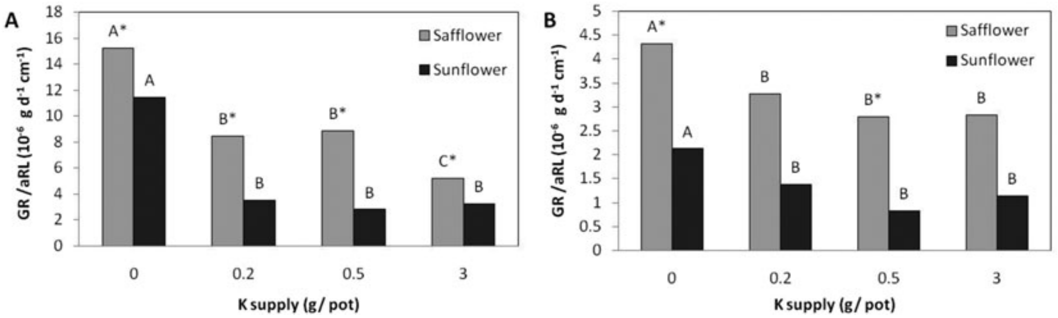

Figure 9. Effect of K supply on shoot demand for K of safflower and sunflower in sandy soil (A) and loamy soil (B). For a given plant species and different K level, means followed by the same letter are not significantly different, *significant difference within plant species at the same K level. $P < 0.05$, $n = 3$.

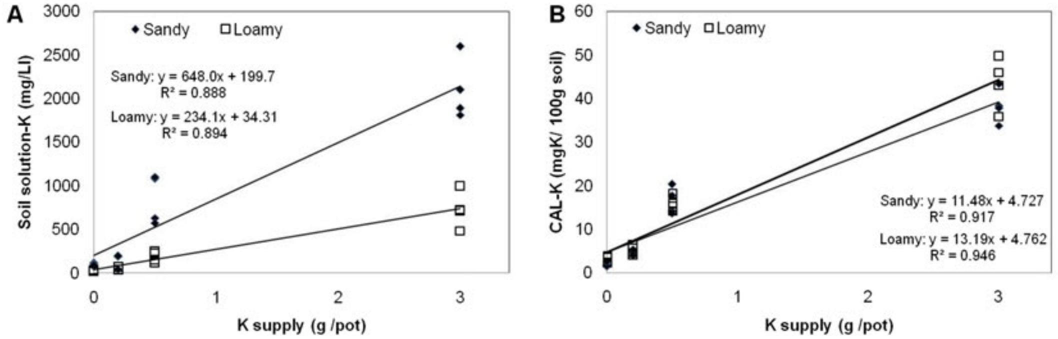

Figure 10. Effect of K supply (g pot^{-1}) on soil solution K (mg K L soil solution^{-1}) (A) and CAL-K (mg K 100 g soil^{-1}) (B) in unplanted pots of loamy soil (A) and sandy soil (B), $n = 4$.

"Materials and methods" section). Despite the fact that both soils had significantly similar extractable K (Figure 10(B), "Materials and methods" section) soil solution content of sandy soil was higher than that of loamy soil at all equivalent K levels.

The soil solution obtained from pots cultivated by four weeks and six weeks old safflower plants (the first and the second harvest respectively) contained increasing K contents with increasing K supply (Table 5). In terms of sunflower, only the highest K supply in both soils was corresponded with significant higher solution K in the second harvest while both optimal and high K supplies had significantly higher solution K at the first harvest. Soil solution obtained from safflower pots was significantly higher than that obtained from sunflower pots in both soils, but the difference between both species grown at zero added K supply in sandy soil was not significant. Soil solution K content was found significantly higher in sandy soils as compared to loamy soils and the difference was much pronounced in the case of sunflower pots.

As shown in Table 5, the soil solution obtained from sandy soils hosting both crops contained similar amounts of Mg contents among all K supplies except at the highest K supply, where Mg content was highly reduced. Additionally, soil solution Mg contents obtained from sandy soils were similar in all respective K supplies among species. Mg contents in soil solutions obtained from loamy soil hosting safflower was significantly reduced at the highest K supply only, while that cultivating sunflower, Mg contents at both 0.5 and 3 g added K were similar but significantly lower than those obtained from 0 and 0.2 g added K levels. The soil solution Mg values were significantly lower in sunflower pots as compared to safflower pots in all respective K supplies. For safflower pots, soil solution Mg obtained from sandy soil was significantly higher than that of loamy soils at all respective supplies except the highest added K level where the opposite was

Table 4. Effect of K supply on K concentration (g 100 g^{-1} DM) of safflower and sunflower.

	Soil type					
	Leaves		Stem		Shoot dry weight	
K supply (g pot^{-1})	Sandy	Loam	Sandy	Loam	Sandy	Loam
Safflower						
0	2.33C,a	2.12C,a	1.79B,a	1.87B,a	2.17C,a (65.6)	2.05C,a (86.5)
0.2	3.79B,a*	2.45BC,a	2.46B,a	2.20B,a	3.31B,a*	2.37BC,a
0.5	3.83B,a	3.28BA,a	2.84B,a	3.13A,a	3.50B,a	3.21BA,a
3	6.64A,a*	3.94A,b	4.43A,b	3.43A,b	5.92A,b*	3.75A,b
Sunflower						
0	2.16C,a	1.29C,b	1.34C,a*	0.77C,b	1.94C,b (63.8)	1.12C,b (39.7)
0.2	2.60BC,b*	1.51C,b	1.60BC,b	1.04C,b	2.27BC,b*	1.33C,b
0.5	3.44B,a	3.14B,a	2.29B,a	2.40B,b	3.04B,a	2.82B,b
3	7.32A,a*	6.08A,a	10.06A,a*	6.25A,a	8.28A,a*	6.17A,a

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, *significant difference for a given plant species and a given K level within soil types. $P < 0.05$, $n = 3$.

recorded. For sunflower pots, Mg contents obtained from sandy soils were significantly much higher than that obtained from loamy soils.

Extractable K and Mg, buffer power, and pH

For each species and each soil type, extractable K (mg K 100 g soil^{-1}) was similar in suboptimal and best K supply but increased significantly in high K levels (Table 6). Pots of either type of soil hosting sunflower plants contained significantly less amounts of extractable K than that contained safflower plants. Sandy and loamy soil hosting the same crop contained similar amounts of extractable K at all respective K levels except at the highest level, where sandy soil contained significantly higher K than that of loamy soils. For both species, sandy soils have similar values of extractable Mg concentration among different K supplies except at the highest K level where Mg concentration was highly and significantly reduced. Sandy soils hosting either safflower or sunflower contained similar amounts of extractable Mg at all respective K levels. In loamy soil, safflower pots contained similar amounts of extractable Mg in all K levels except the highest one where the value was significantly lowered, while that of sunflower, extractable Mg contents were drastically and significantly reduced with increasing K supply. Mg content in soil contained sunflower were significantly less than that contained safflower at all respective K levels. Comparing both soils within each plant type, sandy soils contained significantly higher exchangeable Mg than that of loamy soil at respective optimal and high K supplies.

Buffer power is normally calculated as the ratio of soil exchangeable K (mol cm^{-3} soil) and the soil solution K concentration (mol cm^{-3} soil solution). Figure 11 demonstrates the relation between both sources of K in both soil types that fitted the Langmuir isotherm showing the relationship between the adsorbed and equilibrium potassium concentration (quantity/intensity).

The pH values of soil did not change significantly within K supplies for each species in either soil type. Sandy soil had significantly lower pH values than that of loamy soil at all levels of K for both crops (Table 6).

Discussion

Growth and morphology

Biomass is frequently used in calculating net primary production and growth rates of plants to quantify their physiological responses to stress conditions (Cornelissen et al. 2003), and

Table 5. Effect of K supply on K and Mg soil solution (mg K L^{-1}) in unplanted pots (between brackets ()), and in the first harvest (between []), and at the second harvest (bold).

	Soil type			
	K (mg L^{-1})		Mg (mg L^{-1})	
K supply (g pot^{-1})	Sandy	Loam	Sandy	Loam
Safflower				
0	(93) [95] **51.4**C,a*	(30) [25] **15.6**C,a	(830) [1199] **756.4**A,a*	(317) [513] **568.3**A,a
0.2	(192) [149] **89.1**C,a*	(54) [27] **13.6**C,a	(829) [791] **631.9**A,a*	(314) [367] **474.3**A,a
0.5	(849) [273] **242.5**B,a*	(187) [50] **61.59**B,a	(104) [777] **691.3**A,a*	(97) [621] **354.8**BA,a
3	(2651) [3004] **2166.4**A,a*	(733) [747] **536.67**A,a	(274) [93] **44.8**B,a*	(123) [174] **144.5**B,a
Sunflower				
0	(92) [57] **36.5**B,a*	(30) [10] **2.47**B,b	(830) [951] **778.7**A,a*	(317) [345] **177.6**A,b
0.2	(192) [157] **28.8**B,b*	(54) [9] **0.617**B,b	(892) [1103] **708.2**A,a*	(314) [283] **138.4**A,b
0.5	(849) [225] **26.7**B,b*	(187) [48] **0.587**B,b	(104) [1081] **695.5**A,a*	(97) [57] **28.1**B,b
3	(2651) [3162] **1195.5**A,b*	(733) [343] **8.59**A,b	(274) [93] **37.9**B,a*	(123) [100] **16.45**B,b

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, *significant difference for a given plant species and a given K level within soil types. $P < 0.05$, $n = 3$.

considered as an important trait in growth analysis (Niklas and Enquist 2002). DM production is generally used as a good indicator for economic yield, thus differences of cultivars in this trait is a reliable method for screening efficient cultivars (Abbadi et al. 2017). In agreement with our findings (Tables 1 and 2, Figure 1), K nutrition benefits growth of sunflower and safflower by improving their stem and leaves growth and hence TDM (Gerendás, Abbadi, and Sattelmacher 2008; Abbadi, Gerendás, and Sattelmacher 2008) in both soils. The important growth traits determining yield of crops under study in response to K nutrition were previously determined using the path-coefficient analysis highlighting the tight correlation between yield and the size of the vegetative plant parts using standardized partial-regression and considered the stem DM as the most important trait in sunflower, while both stem and straw were equally important for safflower (Abbadi, Gerendás, and Sattelmacher 2008). These results are in accordance with our findings which affirmed the importance of stem DM for sunflower by its stronger response to different K supplies as compared to that of safflower, while both stems and leaves of safflower responded similarly to improved K supply. As a mobile nutrient in phloem, K is translocated to places of new growth, and under severe deficiency, the source organs become chlorotic and soon necrotic (Marschner 2012) as observed in K-deficient plants under investigation which was more pronounced in plants grown in sandy soils. In addition to its significance in water homeostasis (Anschütz, Becker, and Shabala 2014), K deficiency impair lignifications of vascular bundles (Pissarek 1973), representing an important factor contributing to susceptibility of K-deficient plants to lodging (Abbadi, Gerendás, and Sattelmacher 2008) as was documented in K-deficient sunflower plants under study indicating sunflower sensitivity to K deficiency as compared to safflower. Because sunflower plant is larger than safflower (Tables 1 and 2), the relative biomass production is a convenient tool to compare DM efficiency under suboptimal nutrient supplies (Abbadi 2017c). Safflower relative DM production at 0 added K supply (related to DM produced at 0.2 g K pot^{-1} as best supply) was 36% and 60% in sandy and loamy soil respectively, while the same figures for sunflower were significantly lower (24% and 41% considering 0.5 g K pot^{-1} is the optimal supply). This confirm the superiority of safflower over sunflower in terms of relative DM production under severe K deficiency which agrees with other reports concerning species under investigation (Abbadi, Gerendás, and Sattelmacher 2008; Gerendás, Abbadi, and Sattelmacher 2008). In the same line with previous

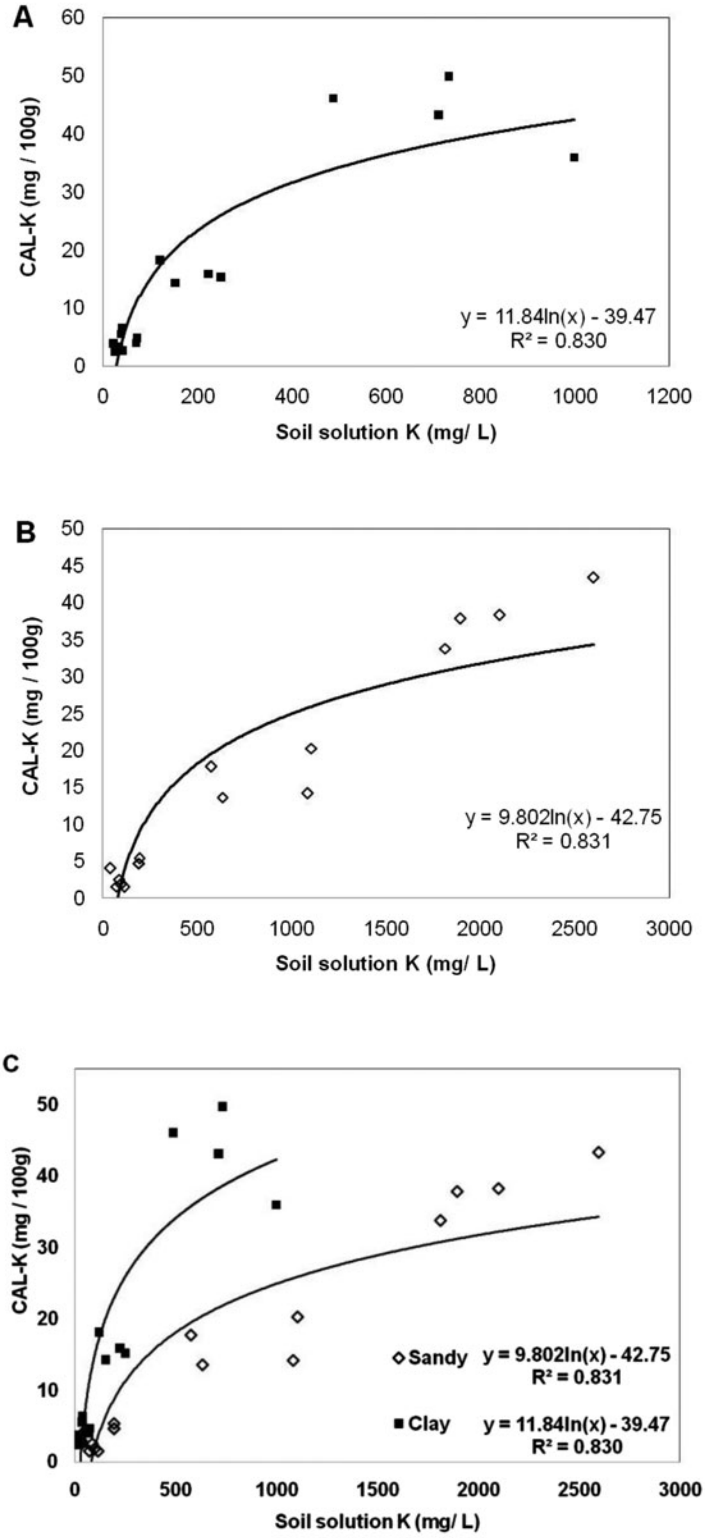

Figure 11. Relationship between extractable (CAL) K and soil solution K in unplanted pots of loamy soil (A) and sandy soil (B), in increasing K levels, $n = 4$.

findings, we find that sunflower biomass production was more sensitive than safflower under low K fertility (Abbadi 2007).

Shoot growth rate

Efficient plant species slow their shoot growth rates under suboptimal K supply (Dessougi, Claassen, and Steingrobe 2002), hence, safflower with a lower shoot growth rate in this study could be considered more efficient than sunflower with high growth rate (double values) at all respective K supplies including suboptimal levels (Figure 2). Differences in shoot growth rates in the same species in different soils and among species in the same soil indicate different adaptive strategies used by plants species under different growth conditions and can be discussed in terms of the availability of K in the rhizosphere that differ among soils K levels, and the shoot demand for K on roots that differ among species. Plants can respond to nutrient stress conditions in soil in terms of the ability of roots to sense low K availability and thence send inhibitory signals to shoots which harden the plants against the consequences of restrictive environment (Passioura 2002).

Traits affecting K uptake efficiency

Nutrient uptake efficiency is influenced by factors related to plant parameters and others associated with soil parameters (Fageria and Moreira 2011). Plant parameters under study include root length (Steingrobe 2001), root diameter (Dessougi Claassen, and Steingrobe 2002), root-shoot ratio (Yang et al. 2005), specific root length (Bhadoria et al. 2004), nutrient influx (Samal et al. 2010), and shoot demand for K on roots (Claassen and Jungk 1984; Pearse et al. 2006). Soil parameters cover soil solution K (Bhadoria, Singh, and Claassen 2001), extractable K (Trehan and Sharma 2005), and pH (Castañeda Ortiz 2006).

Root parameters

Nutrient supply to plants results from the interactions between plant roots and soil, depending on the nutrient quantity, availability, mobility in soil, and the uptake kinetics of the root system (Jungk 2001; Lambers et al. 2006; Zörb, Senbayram, and Peiter 2014). The root traits evaluated in this investigation include root biomass, length, radius, length density, root/shoot and K influx which are frequently discussed in the literature (Lynch, Lynch, and Jonathan 2007; Bishopp and Lynch 2015). K uptake by plants is affected by root morphological characteristics (Fageria and Moreira 2011), from which the root size (Table 1), and length (Figure 3) have been shown to influence nutrient uptake efficiency (Jia et al. 2008), and the root radius (Table 3) was found a root property affecting the contact between soil nutrients and root surface (Barber 1984). Root length density (Table 3) affects root distribution in soil and transport distance of K, because the amount of K absorbed by each root segment partly depends on the soil volume it can exploit by reducing distance between neighboring roots (Samal et al. 2010; Yang et al. 2005). Generally, plants enhance their efficiency of nutrient acquisition to overcome nutrient deficiency, by being flexible in biomass allocation (root shoot ratio), root morphology (length and radius), root distribution pattern (specific density), and influx as adaptive mechanisms to exquisite nutrients (Rengel and Marschner 2005; Lynch, Lynch, and Jonathan 2007). Plant species respond differently to K deficiency (Dessougi, Claassen, and Steingrobe 2002) by either increasing or decreasing root system (Jia et al. 2008). Our results showed that both studied species reduced root systems under suboptimal K supplies maintaining the longest roots at respective best K levels in both soil types. Safflower relative root fresh weight (Table 1) was significantly higher than that of sunflower at suboptimal levels indicating it's superiority in enlarging root system to explore more soil volume.

However, different K supplies in both soils didn't significantly affect specific root density and root radius of sunflower, these traits were improved in safflower under suboptimal K supply. Safflower was more efficient that sunflower in increasing its specific root density and producing finer roots at all respective K supplies in both soils (Table 3). Because roots are responsible for feeding shoots, higher root growth rate could be associated with higher efficiency of the plant to provide the shoot with required K. Both species showed the trend to increase their root growth rate under suboptimal K supply in sandy soil and this response was significant in both species in loamy soil. Sunflower GRr was significantly higher than that of safflower at all respective K supplies in both soils (Figures 4 and 5).

The ratio of root length to unit shoot weight (Figures 6 and 7) and the influx of K per unit root length (Figure 8) have been shown to be factors determining nutrient supply of plants (Claassen and Jungk 1984). Therefore, the combinations of root: shoot ratio (RSR) and root influx could be very different among plant species (Dessougi, Claassen, and Steingrobe 2002; Samal et al. 2010). The better K uptake efficiencies of plant species could be due to either high root: shoot ratio or/and high influx (Dessougi, Claassen, and Steingrobe 2002; Jia et al. 2008). In this investigation, sunflower out-yielded safflower in terms of absolute RSR in both soil types under all respective K supplies (Figure 6). The relative RSR of both species in both soils was higher at low than that at high K supplies, and this response was more pronounced in safflower as an adaptive response to low K availability. Potassium influx of the roots of both species grown in both soil types decreased drastically at suboptimal K levels (Figure 8) indicating that this trait is controlled genetically more than environmentally. At low K supply, safflower roots K influx was marginally higher than that of sunflower in loamy soil but the opposite was recorded in sandy soil indicating the similarity of both species in tuning their K influx at low K supply. At the very high K supply, sunflower roots K influx was much higher that of safflower because sunflower grow much larger that safflower at optimal K supply and demand more K to sustain its optimal growth.

K concentration in dry matter

Nutrient content in plant tissues is used as a measure for nutrient acquisition ability of plants (Dessougi, Claassen, and Steingrobe 2002; Abbadi et al. 2017). Plant species that accumulates more nutrient in its tissues as compared to a standard line, is superior in the uptake of that nutrient and considered as a better accumulator (Abbadi, Gerendás and Sattelmacher 2008; Gerendás, Abbadi, and Sattelmacher 2008). Contradictorily, the concentration of a nutrient in tissues of growing plants is usually used as a measure for the demand of the plant on that nutrient (Abbadi 2017c), thence the lower nutrient concentration in the vegetative parts to produce optimal yield express a higher utilization efficiency (Abbadi and Gerendás 2009, 2015). In consequence, the better nutrient accumulator may be oppositely concerned as plant high demanding on that nutrient for its physiological processes and therefore inferior utilizer. These two assumptions could be misleading in quest of uptake and utilization efficiency of plants. Both species in both soils responded strongly in terms of concentrating K in DM as influenced by increasing K supply (Gerendás, Abbadi, and Sattelmacher 2008). Safflower concentrated more K in their whole plant than sunflower did in both soil types under suboptimal K supply. Safflower accumulated 65.6% and 86.5% of its optimum required K concentration in sandy and loamy soils, respectively, while the same figures for sunflower were significantly lower (63.8% and 39.7) (Table 4). Under their respective best K-supplies, K concentration in DM of safflower over-yielded that of sunflower in sandy soil (3.31% for safflower and 3.04% for sunflower) but the opposite was observed in loamy soil (2.37% for safflower and 2.82% for sunflower). Therefore, safflower may be considered as a better accumulator than sunflower in both soils under low K supplies. However sunflower accumulated significantly more K (mg K pot^{-1}) 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. Safflower and sunflower differ in size (Tables 1 and 2), therefore relative biomass production should be used to compare their efficiency in DM production under suboptimal nutrient supplies (Abbadi 2017c). Safflower relative DM production at 0 added K supply was 36% and 60% in sandy and loamy soil respectively; while those respective figures for sunflower were significantly lower (24% and 41%). Therefore, safflower could be considered as a better K accumulator and more K utilizer under suboptimal K supply when relative values of K accumulation and DM accumulation were used.

Shoot demand for K on roots

The absorption rate for K is almost proportional to the GR_s per unit of root (Hunt and Burnett 1973). Roots have mainly to meet the nutrient demand exerted by shoot growth (Claassen and Jungk 1984; Engels and Marschner 1993). This demand, the shoot is putting on each root segment is a measure of the shoot growth rate together with the required K concentration in the shoot (Figure 9). Therefore, shoot demand (SD) on the root is represented as the K acquisition load imposed by shoot growth on each cm of root and is estimated by dividing the shoot growth rate (GR_s) by the average root length (RL). SD of safflower was higher than that of sunflower at all respective K supplies and was more pronounced at deficient K supply (Figure 9). Although safflower had half GR_s than sunflower at all K supplies (Figure 2), it had much less root length as compared to sunflower (Figure 3) resulting in significantly higher K demand per unit root length of safflower as compared to sunflower. The lower relative GR_s, could be the reason behind the efficiency of some crops such as wheat and rye because of its negative correlation with the SD. However, lower GR_s was found not necessarily associated with high efficiency in spinach and winter barley which were considered inefficient because of their high shoot demand for K as a result of their low K influx (Dessougi, Claassen, and Steingrobe 2002). The efficiency of sugar beet over wheat and maize was because it had four times higher influx, although it had the highest GR_s, and hence high SD (Sadana and Claassen 1999). The uptake efficiency of elephant grass was mainly because of a low shoot demand on the roots stemming from a high K influx (Dessougi, Claassen, and Steingrobe 2002). Hence, neither GR_s nor RL alone can explain the differences in nutrient efficiency of different crops, but the combination of both traits and the physiological activity of the root (influx) decide whether the plant has high or low SD. Even though safflower had the advantage of slower shoot growth rate (GR_s) as compared to sunflower, it had the disadvantage of lower RSR at suboptimal and all respective K supplies, and also its shoot K concentration was higher than that of sunflower at suboptimal and respective optimal supplies. However both species were similar in terms of K influx at suboptimal and optimal K supplies in loamy soil, safflower had higher influx than sunflower at suboptimal and respective optimal levels in sandy soil (Figure 8). Therefore the cause of the high SD in safflower stems from its low RSR that overpasses the advantageous trait of having low GR_s as compared to sunflower.

Soil parameters

Soil is a heterogeneous medium of solid, liquid and gas, in which the actual portion for ion transport is the liquid phase (Zaehle and Friend 2010). A potassium ion diffuses from solid soil material surface, to soil solution and moves towards the root cell, a process that release ions adsorbed at the soil particles to nourish the plant (Oliveira et al. 2010). Diffusion occurs when the initial ion concentration in the soil solution around roots is depleted, creating a concentration gradient from soil solution toward the root, disturbing the equilibrium between nutrients on the solid phase with those in the liquid phase (Tinker and Nye 2000; Giehl and von Wirén 2014). The soil particles act as a source for nutrient ions and plant roots act as the sink. The amount of ions that arrives at a plant root surface depend on different factors including the concentration of nutrients in soil solution, the volume of soil that is filled with water, the geometry of the soil pore system, the size of root system, root length, root radius, and root distribution in the soil profile (Giehl and von Wirén 2014; Rashmi et al. 2017). It is the plant that initiates nutrient transport from soil to root (Ticconi et al. 2009). As plant roots absorb a nutrient ion, soil solution concentration decreases at the root surface creating a depletion zone, the equilibrium in soil is thus disturbed, a gradient created, and the adjacent soil particles release nutrients into solution, and nutrient diffuse from the bulk soil to the root to be depleted again (Johnston 2001; Syers, Johnston, and Curtin 2008). Potassium uptake by roots from the rhizosphere is affected by desorption of K from soil particle surface, transport of K in the soil solution towards the root surface and inflow of K into root (Schenk 2006). This process depends on soil parameters, plant parameters as well as the nutrient characteristics (Jungk 2001), as a result of interactions between K availability (quantity and mobility) in soil and the ability of plant to acquire it (Johnston 2001). The contact between plant roots and K ions in soil is a prerequisite of K uptake, which develop by root growth to the places where nutrients are located and concurrently the transport of nutrients through the soil to the root surface (Steingrobe 2001). Thus, plants develop large root systems to expose large areas of root surface to the soil (Koevoets et al. 2016; Tron et al. 2015).

Soil solution K and Mg

Soil solution K in arable soils varies in the range of 100–1000 µmol L^{-1} (Jungk and Claassen 1986). K levels used in this investigation had 7.6, 13.0, 47.9, and 187.9 for loamy soil and 23, 49, 217, and 679 µmol K L^{-1} for the respective treatments (0, 0.2, 0.5, and 3 g K per pot) measured before planting. The availability of potassium depends on soil texture, where loamy content had a strong influence on K soil depletion (Claassen, Hendriks, and Jungk 1981). Similar to our findings, 66% of the applied Rb was released at the root surface by the sandy soil but this figure was 20% only by loam soil, therefore, the sandy soil release a much higher percentage of the applied K into solution as compared to soils containing clay (Jungk and Claassen 1986). At the highest K supply, soil solution K in sandy soil was 3.6 times as that of the loamy soil and also it was three times higher in unfertilized sandy soil as compared to soil containing clay.

Potassium concentration of soil solution measured at plant harvests (4 and 6 weeks after germination) varied depending on the plant species and soil type (Table 5). Sunflower depleted significantly more K from the soil solution than safflower did at all respective K levels including optimal supplies in both harvests in both soil types indicating that sunflower's demand for K is much higher than that of safflower. The concentration of K in the soil solution obtained from loamy soil was much more less than that obtained from sandy soil for both plants because of the higher CEC of loamy soil having much more K absorption sites on their surfaces that can sustain the release of K. At the second harvest, sunflower retained constant K (around 30 mg L^{-1}) in the soil solution at suboptimal and optimal levels in sandy soil, while almost all released K in all external supplies in loamy soil were depleted by sunflower plants. The same figures in safflower were found higher (less depleted) in the soil solution of both soils, indicating the high demand of sunflower on K in soil solution in addition to its higher K influx under high K levels as compared to safflower (Figure 8).

Although both crops under study grew with the same initial K supply in both soil types, the concentration of soil solution K, differ among pots of harvested crops (Table 5) as well as soil type. This indicates that K depletion depends on plant characteristics as well as soil conditions, affecting K concentration in soil solution at the root surface (Jungk and Claassen 1986). Young growing roots in soil start to absorb K at a rate close to $I_{\max}$ and hence K in the soil solution in contact with the roots can be thoroughly exhausted of K, thus plants adapt to low nutrient supply by increasing the efficiency of their uptake system at low concentration. Higher K concentration at the root surface enables a greater decrease of this concentration by increasing $I_{\max}$, resulting in a greater gradient and a higher influx, and consequently a higher uptake rate (Dessougi, Claassen, and Steingrobe 2002).

In contrast to other cations (K, Ca, and NH_4^+), Mg is comparatively mobile in soils (Gransee and Führs 2013), that can be ascribed to its unique chemical properties by having smaller ionic radius and larger hydrated radius than that of Ca, K, or Na (Gardner 2003). One consequence of these properties is that Mg is less strong bound to soil charges (CEC) leading to higher Mg concentrations in the soil solution compared to other cations.

Soil exchangeable K and Mg

Whereas plants take up K exclusively from soil solution pool, this pool is in a dynamic equilibrium with the exchangeable and, to a lesser extent, the non-exchangeable pools (Grimme and Nemeth 1979). The exchangeable K can be rapidly released from exchange sites on the surfaces of clay minerals and organic matter to replenish K-depleted soil solution (Steingrobe and Claassen 2000). The ability of plant roots to deplete their surroundings to very low concentrations appear to be essential for the release of non-exchangeable K from soil particle layers (Jungk and Claassen 1986). Both crops under study were able to decrease the initial exchangeable K (Table 6) in both soil types to different levels in respective K supplies. Sunflower was able to reduce exchangeable K to levels that are significantly lower than that of safflower at all respective K supplies in both soil types, revealing that safflower is less efficient in depleting soil solution K as well as extractable K from both soils, and in the same time indicating the high demand of sunflower for K.

Soil pH

Roots induce pH changes in the rhizosphere and lead to acidify soil by releasing protons which may replace K and contribute to its desorption from the non-exchangeable pool (Kuchenbuch 1983). Therefore, the capability of plants to change the pH in soil-root interface appears to be important in influencing K availability, a situation was not so clear in this investigation, where there was no clear trend in pH change in the same soil type with different plants or different K levels.

Conclusion

Plant species vary in their K use efficiency under different conditions using various strategies. Uptake efficiency depends on plant and soil parameters. Mechanisms related to plant include increasing some traits (root length, specific root density, root-shoot ratio, and K influx) and decreasing others (root diameter, shoot growth rate, and shoot demand on roots). The ability of the crop species to increase K solubility in the rhizosphere (K intensity and capacity) and to deplete more soil solution and extractable K are considered as mechanisms of K uptake efficiency in terms of soil parameters.

Under suboptimal K supplies safflower had higher agronomic K efficiency than sunflower in both soils indicated by a greater relative biomass. Safflower had higher relative root length, higher specific root density, thinner roots, but less root shoot ratio in both soils. K influx was similar in both species in loamy soil and safflower was inferior in sandy soil. Although safflower had slower shoot growth rate it had higher shoot demand on root because of the less root length and not having higher K influx. Safflower had similar ability to deplete soil solution in sandy soil and was inferior in loamy soil. Safflower depleted less extractable K from the rhizosphere in both soils as compared to sunflower. Safflower could be considered more efficient than sunflower at suboptimal K supply in sandy and loamy soils in terms of plant parameters and non-efficient in terms of soil parameters. Using different measures of uptake efficiency parameters to differentiate plant species and genotypes to superior and inferior could be in some cases misleading.

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