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A Meta-Analysis of Modifications of Root System Traits of Crop Plants to Potassium (K) Deprivation

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Abstract

Unlike nitrogen (N) and phosphorus (P), morphological responses of root systems of crop plants to potassium (K) dynamics in soils or growth media are only gaining currency. This is due to the realization of the instrumental role of K in several cellular and tissue level processes crucial for the growth, stress tolerance, metabolic functions, and yield of crop plants, and ultimately, food security and sustainable agriculture. This chapter used meta-analysis to synthesize the pooled evidence for modifications in several root system traits of different crop plants under conditions of K starvation in different growth media. In all, 37 studies that passed inclusion/exclusion criteria, from 1969 to 2019, were analyzed in aggregate and then disaggregated for root biomass, root length, and the number of roots. Three moderators were analyzed: type of soil or growth medium, crop, and K fertilizer applied in the included studies. The aggregated results show that the cumulative effect of K deprivation was a significant and large reduction (about $25.5 \pm 15.0\%$) in the bulk of root system traits considered, which was slightly lower than the reduction in shoot- or yield-related traits. Reductions of approximately $38 \pm 38.0\%$ in root biomass and $23.2 \pm 18.6\%$ in root length were observed, and the magnitudes of reduction were comparable to those observed from the disaggregated data. Though reductions in root system traits due to K starvation occurred under both greenhouse/lab and field conditions, the cumulative reduction in the former was significantly larger than that of the latter. Among the moderators, the effect of type of soil (or growth media) and crop on the scale of modification of root system traits to K deprivation are stronger compared to the effect of type of K fertilizer applied. It is concluded that, overall, K deprivation leads to significant reductions in root system traits, especially root biomass and length in soils and perlite regardless of the type of K fertilizer applied. Attention should be given to K management in cropping systems to avoid K starvation, especially at the early and vegetative stages, and to improve K reserves in soils. Further attention should be given to the responses of root system traits to K supply when matching crops to soils.

Keywords: potassium, deficiency, root growth, root system architecture, plant nutrition

1. Introduction

Potassium (K) is the 7th most abundant element in the Earth's crust. Recent increases in consumption of K fertilizers is leading to fast depletion of K reserves [1]. Potassium is a macro-nutrient that plays instrumental roles in the nutrition, physiology, growth and development of crop plants. It is essential for many cellular and tissue processes, including the regulation of stomatal aperture, photosynthesis, respiration, utilization of nitrogen (N) and protein synthesis, and transport of minerals and metabolites [2, 3]. Potassium contributes to osmotic pressure or turgor regulation, required in plants for cell expansion [2, 4] and osmotic adjustment to salinity. Potassium plays a role in the activation of over 60 enzymes, the balance of the microbial population in soil and is crucial for root growth and development [5, 6]. The major role of K in osmotic regulation and cell expansion implies K is instrumental in the growth and establishment of crop plants. Potassium also plays key roles in the physiology, nutrition and health of animals and humans, including the control of non-communicable diseases such as hypertension and other cardiovascular diseases [7, 8]. Humans and animals derive their nutritional K supply largely from crop plants, making K nutrition of crop plants critical to food security and human health, especially in reducing the global burden of non-communicable diseases [7, 8].

The K nutrition of crop plants derives from the dynamic balance between the labile and non-labile K, which are respectively responsible for the immediate or short- and long-term supply of K, in the soil or growth media [5, 6]. Labile K comprises the exchangeable and soil solution K while the non-labile K is made up of non-exchangeable and mineral K. Potassium limitation is a major problem of most soils and, even in fertile soils, root zone K supplies can be depleted rapidly early in the growing season or in few years of cultivation to create conditions of scarcity [5, 9]. The instrumental role of K in several cellular and tissue level processes, including efficient use of other macro-nutrients such as N, makes K deprivation critical to the growth and development of crop plants and food security.

Apart from carbon (C) and oxygen (O), the efficiency of plant uptake of water and most nutrients depends on the root system architecture (RSA, the arrangement and magnitude of roots in the soil) and physiology. Crop plants have evolved the ability to modify their RSA in response to resource scarcity [10], such as nutrients in the soil [9, 11]. This plasticity of RSA in response to the dynamics of soil resource supply has been exploited by plant breeders to enhance root traits to ultimately improve crop yield in variable environments [12, 13]. With nutrients, such as K, an understanding of the RSA-based response is particularly important for breeding and adapting crop plants to both natural and managed systems with low external input and highly unstable balance between depletion and supply over time and space. This is because the configuration of plant roots in the soil considerably influences the spatiotemporal distribution and exploration for resources in each soil layer or volume, and the effectiveness of plant acquisition of soil resources in response to concentration gradients [14, 15]. For example, it is known that RSA characterized by steep growth angles are vital for the uptake of nitrate and water which tend to be mobile in soils [16, 17] while shallow growth angles are more valuable for the uptake of P and K which tend to become immobile when fixed [18, 19].

Plant roots can respond metabolically [20], physiologically [21], and morphologically [9, 22] to nutrient deficiencies. As a result, crop plants would be expected to engage in the modification of their RSA to cope with or respond to conditions of low or deficient available K. However, the plasticity of RSA is highly random and not deterministic as it can give different results depending on the interaction of a given root phenotype with the prevailing environmental conditions, plant fitness and/or

underlying crop management practices [10, 13]. For example, local availability of K elicits local root growth and branching to K rich patches, although these adaptations may be moderate compared to root responses to local N or P [23, 24]. Under K limiting conditions, root elongation and the count of lateral roots are inhibited [9, 25, 26], but the magnitude of suppression varies among crop genotypes and root types [9, 27]. In *Arabidopsis*, for example, it has been reported that some accessions respond to low K supply by investing in the elongation of main roots to the detriment of lateral roots while the reverse is true for other accessions [9]. As a result, there is a need for cumulative evidence from several studies under different environmental conditions and with different crop plants to understand the most probable response of RSA of crop plants to K starvation.

While the magnitude of the morphological modifications of root traits remains to be quantified, studies involving root morphological responses to K starvation are not only a few compared to those involving N and P [28], but also patchy or sketchy and riddled with conflicting results. A pooled synthesis of the evidence from individual studies is required to show the most probable modifications and permit reasonable and reliable generalizations on the effect of K starvation on RSA of crop plants. Though a narrative review on the effect of K nutrition on root growth and development [28] exists, it has some of the limitations of narrative reviews that are addressed by meta-analysis [29, 30]. A key limitation is that the narrative review by [28] did not quantify the modifications in given root traits as a result of K starvation. The present study, therefore, used meta-analysis to (i) provide a pooled synthesis of the effect of K on RSA; (ii) quantify the reduction or otherwise in given RSA traits as a result of K starvation and (iii) assess how the effect of K on RSA traits is moderated by factors such as crop species and type of soil.

2. Methods

2.1 Data collection

We searched journal articles and grey literature that reported root trait responses to K application using Scopus (Elsevier B.V), Google Scholar and Google (Google Inc., Mountain View, CA, USA). Title searches included combinations of the terms: potassium OR K^+ OR KO_2 , “potassium superoxide” OR “potassium fertiliz*” OR potash AND “root growth” OR “root system architecture” OR “root morphology” OR “root hair” OR root*. In Google, we searched for ‘effect of potassium on plant roots’ and considered the first 200 hits. One investigator performed the search and two additional investigators explored the search results to decide on included studies. The two investigators had to agree based on predefined study inclusion criteria. The two investigators also had to agree on the extracted data from the included studies. Any discrepancies on an included study or data extracted from studies were resolved by the third investigator.

The predefined study inclusion criteria were: (i) the study had to report at least one root trait measured under both low or no K treatment (experimental treatment) and high or replete K treatment (control); (ii) the root traits should be reported on the same scale for both the experimental and the control treatments; (iii) the environmental conditions for the experimental and control groups, including plant species, and soil properties of each experiment were the same, and experiments were performed at the same temporal and spatial scales in the control and treatment groups; (iv) an included study must report means (\bar{X}) for the measured trait(s) and the reported \bar{X} , sample size (n) and a measure of dispersion (standard error [SE], standard deviation [SD], or 95% confidence interval [CI]) should be present as

numerical or graphical data, or it should be possible to estimate from the reported data. In studies where SEs were provided, SDs were computed as the product of the SE and the square-root of n . However, where SD or SE was not available, SD was reassigned as one-tenth of the X and the effect of this assumption on the results assessed via sensitivity analyses [29, 30]. To avoid multiple counting, the reported data must originate from primary research, and should not have been already included in another paper. Whenever it was available, we also collected data on three non-root traits, namely total biomass, shoot biomass and yield.

2.2 Handling of complex data structures

Complex data structures or non-independent observations were reported in some of the included studies. In such cases, a study reported root trait data from a plant using the same scale but at a series of distinct time-points. Thus, the same plant provided data for different time-points. Similarly, some studies also included several experimental treatment groups (increasing rate of K fertilization) and a single control group. For each of these complex data structures, the X, SD and n were respectively combined into single metrics because treating the data for the different time-points or subgroups as though they were independent would lead to incorrect estimates of the variance for the summary effect [31]. The n across subgroups or time-points was summed to get a combined n (i.e.: $n_1 = n_{11} + n_{12}$) and the combined mean was computed as the weighted mean, by sample size, across groups (Eq. (1)). Subsequently, the combined standard deviation was computed as shown in Eq. 2 [31].

$$\bar{X} = \frac{n_{11}\bar{X}_{11} + n_{12}\bar{X}_{12}}{n_{11} + n_{12}} \quad (1)$$

$$SD_1 = \sqrt{\frac{(n_{11} - 1)SD_{11}^2 + (n_{12} - 1)SD_{12}^2 + \frac{n_{11}n_{12}}{n_{11} + n_{12}}(\bar{X}_{11} - \bar{X}_{12})^2}{n_{11} + n_{12} - 1}} \quad (2)$$

Where \bar{X}_{11} , \bar{X}_{12} are the means in subgroups or time-points 1 and 2 of treatment group 1; SD_{11} and SD_{12} are the standard deviations, and n_{11} and n_{12} are the sample sizes; of subgroups 1 and 2 [31]. If a study, however, reported data on different crops or varieties of crops, these were considered as independent subgroups and were included separately in the meta-analysis if the data reported were single time-point data for the different crops species or varieties [29, 30].

2.3 Handling of dependent effect sizes

Most independent studies included multiple measures and therefore yielded multiple effect sizes. For example, a study could report on root traits such as biomass, length, diameter and branching density which were obtained on the same plants, each of which provided an estimate of the effect of K fertilizer application. Here, the data obtained from the included studies were subjected to two types of meta-analyses: a meta-analysis of aggregated outcomes of all these traits measured from same plants per study and a meta-analysis of the individual or disaggregated outcomes. We were mindful of the fact that often, a meta-analysis of aggregated outcomes is the recommended option due to the tendency of studies reporting more outcomes to be weighted heavier and biasing the summary estimate [32]. However, this option could lead to publication bias and

also provides limited control over the data within the context of the heterogeneity in the original studies. For example, heterogeneity due to subgroups within studies or variable categorizations is difficult to deal with in meta-analysis of aggregated outcomes. We, therefore, decided to employ the two approaches, albeit for different purposes, in this study. Accordingly, we firstly performed a meta-analysis including the multiple effect sizes from the same sample in individual studies in the meta-analysis and utilized this disaggregated dataset for moderator or subgroup analyses. Subsequently, we used the Borenstein, Hedges, Higgins, and Rothstein approach (BHHR; [31]) to aggregate dependent effect sizes (i.e. multiple root traits obtained from the same sample) to obtain one effect size per an independent study in each analysis. The BHHR method is the univariate method which is least biased and most precise in large simulation studies [32]. The aggregations were done using the MAd package [33] implemented in the R Project for Statistical Computing [34] and which averages all within-study effect sizes and variances, considering the correlations among the within-study outcome measures consistent with the BHHR procedures. Due to the non-availability of between-measure correlations within each of the studies, we assumed the default correlation for between within-study effect sizes of $r = 0.5$. Here, we conducted a meta-analysis for all the extracted traits. Subsequently, we conducted three independent meta-analyses, one each for root biomass, root length, and the number of roots. These root traits were the commonly measured root traits in the included studies.

2.4 Estimation of effect sizes and analysis of heterogeneity

We quantified the effects of K supply on root traits by calculating the response ratio (R), which is the ratio of the means of the experimental and control groups. The R was our preferred metric of effect size because we were interested in comparing the magnitudes of two means from the experimental and control treatments and we could back-transform it (i.e., $R = e^{\ln R}$) for ease in interpretation [30]. Given that ratios are said to generally have poor statistical properties; the R was subsequently log-transformed by Eq. 3 to obtain more desirable properties [35, 36].

$$\ln R = \ln \left(\frac{\bar{Y}_1}{\bar{Y}_2} \right) = \ln \bar{Y}_1 - \ln \bar{Y}_2 \quad (3)$$

where \bar{Y}_1 and \bar{Y}_2 are the mean of the root traits of the experimental group and mean of the root trait from the control group, respectively. The variance of the $\ln R$ is given Eq. 4.

$$v_{\ln R} = \frac{SD_1^2}{n_1 \bar{Y}_1^2} + \frac{SD_2^2}{n_2 \bar{Y}_2^2} \quad (4)$$

where n_1 and n_2 are the sample size of the experimental group and the control group, respectively, and SD_1 and SD_2 are the SDs of the experimental group and the control group, respectively [36]. A random-effects model of the meta-analysis was used to determine the grand mean and explore the continuous factors that may explain the response of root traits to K fertilizer application. The restricted maximum likelihood method (REML) was used to estimate the between-study variance. The mean effect size was considered significantly different from zero if its confidence interval did not include zero [35]. We estimated a summary effect and heterogeneity of the summary effect and when heterogeneity between studies was evident, a moderator analysis was performed via meta-regression to attempt an explanation of the heterogeneity.

2.5 Moderator analyses

Several explanatory variables (moderators), including soil factors, plant factors, and fertilizer and management practices, may affect the magnitude of the response of root traits to K fertilization. Study characteristics such as crop species (several), the agronomic purpose of crops (cereals, vegetables, fruits, industrial crops, etc.), texture of soil used for the experiment (several), growth media used (several), type of K used in fertilization (e.g.; muriate of potash, sulphate of potash, etc.), location of the experiment (field or greenhouse), among others, were collected from the primary studies. These moderators were extracted from primary studies when available; otherwise, it was marked as 'not provided'. The influence of any of these moderators on the effect size was assessed through analyses of heterogeneity [37] and was performed only when there were at least two studies for a given moderator. To examine whether root traits differed among treatments, variation was estimated by a Q statistic, a measure that partitions total heterogeneity (Q_T) into variance explained by the model (Q_M or Q_B) and residual error not explained by the model (Q_E or Q_W ; i.e. $Q_T = Q_M + Q_E$) [30, 35, 38]. Q_B and Q_W were tested against a X^2 -distribution (significance level $p < 0.05$) [35, 38]. Two moderators were significantly different if their 95% CI did not overlap [39]. A statistically significant Q_B suggests that there are differences among cumulative effect sizes for the categorical subgroups, while a significant Q_E implies that there are differences among effect sizes not explained by the model [30, 38]. There was no statistical justification for the further subdivision of the data if Q_B was not significant [40]. Also, we computed I^2 index as a complement to the Q estimates. The I^2 can be interpreted as the percentage of the total variability in a set of effect sizes because of differences between-study or between-comparisons (true heterogeneity) [30, 37].

2.6 Publication bias and sensitivity analysis

To test the publication bias, funnel plots were presented as scatter plots of the log ratio of means against their standard errors, in which case studies should be distributed symmetrically around the mean of the log ratio of means, in the absence of publication bias. If there was any evidence of publication bias, the 'trim and fill' method was used to assess the potential impact of bias on the overall effect size and the effect size re-calculated from the resultant model from the trim and fill [30, 41]. Due to reported limitations of the funnel plot approach, we further calculated the Rosenberg's fail-safe number (Nfs) for evidence of publication bias. The results were considered robust despite the possibility for publication bias if $Nfs > 5 \times n + 10$, where n is the number of effect sizes [29, 30, 42]. A sensitivity analysis was conducted to compare the robustness of results for primary studies that reported SDs and those for which SDs were estimated as one-tenth of the mean.

2.7 Data analyses

OpenMEE, the open-source, cross-platform software for ecological and evolutionary meta-analysis [43] and Metafor [44], the package for meta-analysis in the R statistical software [34] were used for statistical analyses and in producing forest plots. Some forest plots were produced in Microsoft® Excel 2016 using the results obtained with OpenMEE software.

3. Results

3.1 Overview of included studies

The included studies span 50 years, with the earliest published in 1969 and the latest in 2019. The recent years contributed the most number of studies and outcomes to the analysis (**Figure 1a**). The analyses included 37 studies (Appendix 1), consisting of 29 controlled-environment and 8 field-based experiments conducted in 16 and 7 countries, respectively (**Figure 1b**). There were 794 outcomes, consisting of 556 and 238 outcomes from the greenhouse- and field-based studies, respectively, and these were measured on 23 crop plants. Majority of the studies were conducted on cereals, mainly on maize and rice (**Figure 1c**). Included studies measured 23 root traits, with root biomass, length and numbers being the commonly measured root traits (**Figure 1d**).

3.2 Root system response to K fertilization

Root system traits and shoot biomass response to the growth media amended with K was compared with the non-K-amended media (**Figure 2**). The overall

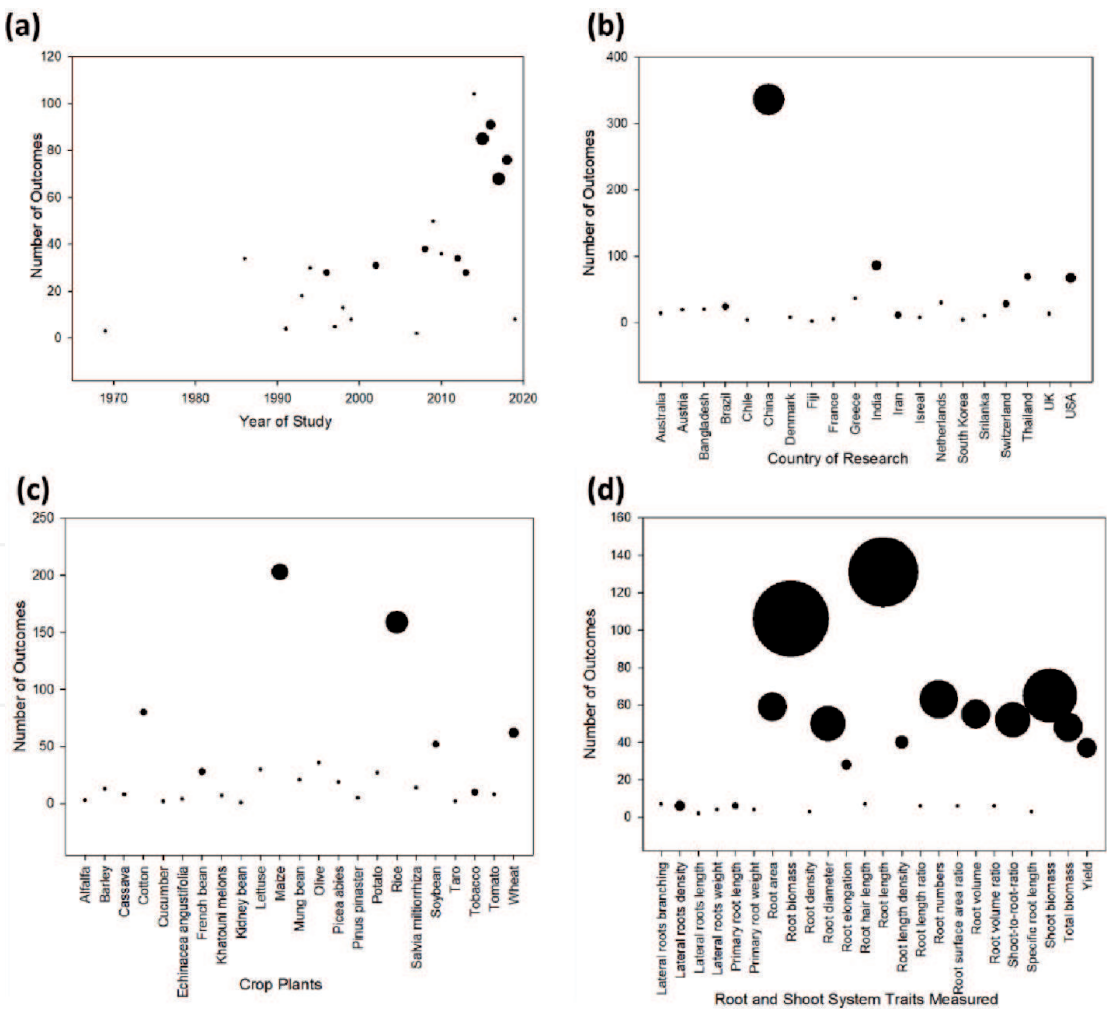


Figure 1. Overview of included studies used in the comparison of shoot biomass, yield and root system traits from crop plants grown on media or soils amended with K and those grown on non-amended soils or growth media. For each panel, the location of the bubble on the chart indicates the number of effect sizes or outcomes and the size of the bubble indicates the number of studies which yielded respective outcomes or effect sizes.

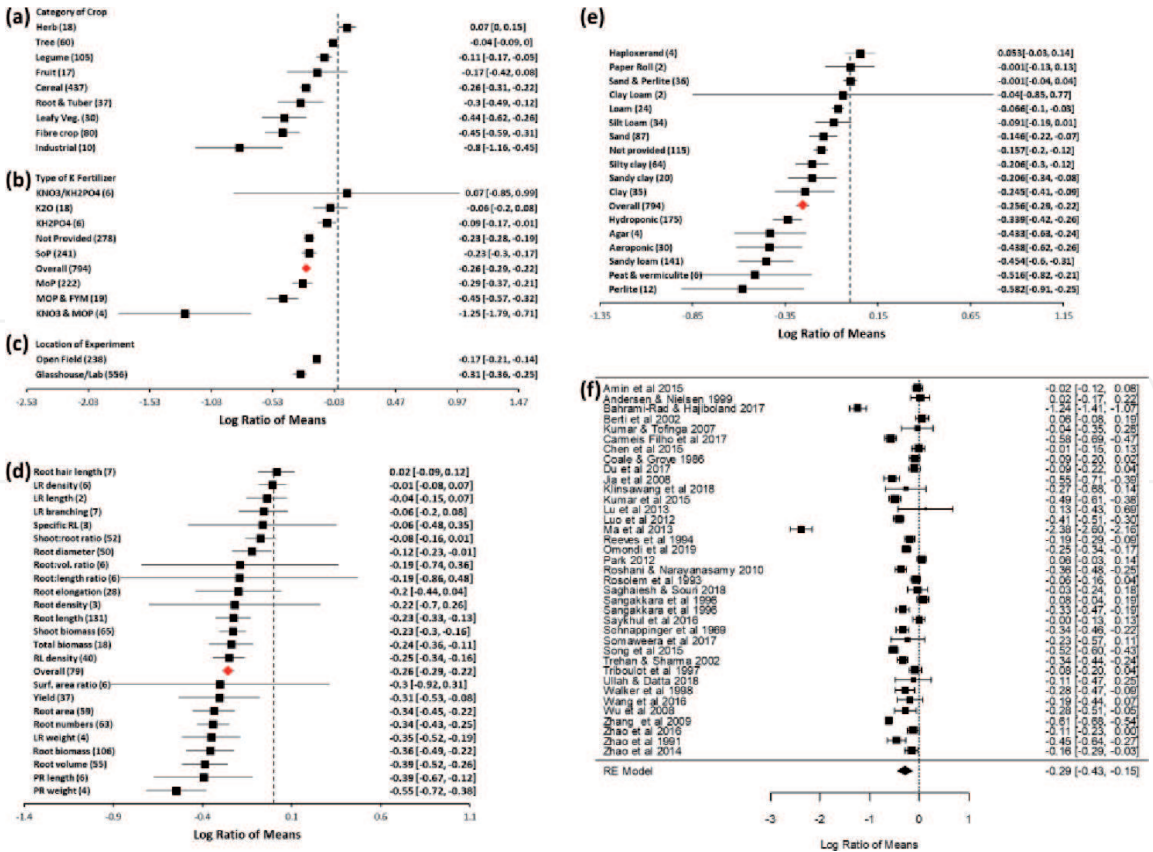


Figure 2. Effect of K deficiency on shoot biomass, yield and root system traits of crop plants. Figures (a) to (e) are the analyses of disaggregated data and presents the overall effect size and effect size as a function of various moderators. The effect of K deficit on extracted traits as moderated by (a) crop categories; (b) type of K fertilizer supplied to the replete K growth media; (c) location of the experiment; (d) type of trait that was measured and (e) growth media or soil texture on which plants were grown. (f) Effect of K deficiency on all extracted traits based on aggregated data, where dependent effect sizes were combined to obtain one effect size per study. The log ratio of means (dotted vertical line) = 0 indicates no effect; log ratio of means >0 indicates the larger size of the traits from crops grown on replete K media over those grown on deficient K media; log ratio of means <0 indicates the larger size of the traits from crops grown on K-deficient growth media over those grown on replete K media. Effect size is considered statistically significant if its 95% CI does not overlap zero.

effect size based on the disaggregated outcomes of $k = 794$, was -0.266 ± 0.020 (95% CI of -0.31 to -0.23 ; $I^2 = 98.91\%$; $p < 0.001$; **Figure 2a-e**), suggesting that the deficiency of K leads to approximately $23.3 \pm 4.0\%$ reduction in the size of root system traits compared to that on growth media with added K. The effect of K on root traits alone was comparable to the overall effect size and that of the shoot or yield-related traits. The effect size of root system traits alone was -0.263 ± 0.022 and that of shoot or yield-related traits was -0.283 ± 0.050 , suggesting that the deficiency of K leads to approximately $23.1 \pm 4.0\%$ reduction in the size of root system traits and $24.7 \pm 10.3\%$ in the size of shoot biomass or yield compared to that on soil or growth media with added K. Based on the I^2 (98.9%), there was a large inconsistency of effect sizes across the included studies, warranting the need for further examination of this variability.

There was a significant reduction in root traits on no or low K soils or growth media for all categories of crops, except those categorized as trees, fruits and herbs (**Figure 2a**). Meta-regression analysis suggested that the differences among cumulative effect sizes for the various categories of crops were significant ($Q_B = 46.8$; $I^2 = 98.8\%$; $df = 8$; $p < 0.001$). Thus, the predictive model (crop type) probably explains some of the variances in the effect size and the effect of K application on root traits of some of the species of crop plants significantly differs from that of cereals, the nominated reference subgroup. The error sum of squares (Q_E) was

insignificant ($Q_E = 817.2$; $df = 785$; $p = 0.207$), suggesting that the variation was accounted for by the crop species. But for potassium oxide (K_2O), potassium nitrate (KNO_3) or the combination of potassium nitrate and potassium dihydrogen phosphate ($KNO_3 + KH_2PO_4$), regardless of the type of K fertilizer applied, there was a significant increase in root system traits (**Figure 2b**) due to K application. Many studies did not provide the type of K fertilizer used but the effect size obtained for these studies was similar to the overall effect (**Figure 2b**). The Meta-regression indicated that the differences among cumulative effect sizes for the various types of K fertilizer were significant ($Q_B = 21.2$; $I^2 = 98.8\%$; $df = 7$; $p = 0.0034$) but only the estimates of the intercept (SoP; -0.280 ± 0.037 , CI: -0.352 to -0.208 , $p < 0.001$) and KNO_3 in combination with MOP (-0.966 ± 0.281 , CI: -1.516 to -0.416 , $p < 0.001$) were significantly different from zero.

Moreover, whether experiments were conducted under controlled conditions or field conditions, the lack of K in the soil or the growth media led to a significant reduction in the size of root system traits, yield, shoot and total biomass (**Figure 2c**). Although both were significantly different from zero, the meta-regression showed that there was a significant difference among cumulative effect sizes between greenhouse/lab- and field-based experiments ($Q_B = 9.41$; $I^2 = 98.9\%$; $df = 1$; $p = 0.0022$). The estimates were -0.307 ± 0.024 (CI: -0.354 to -0.26 , $p < 0.001$) and 0.133 ± 0.043 (CI: 0.048 to 0.218 , $p = 0.002$) for the greenhouse (the intercept) and field experiments, respectively, suggesting that there were larger reductions in root system traits due to K deficiency in greenhouse experiments ($26.4 \pm 4.8\%$) than there were under field experiments ($16 \pm 4\%$). Even so, about 99% of the observed variance comes from differences between studies which can be explained by other study-level covariates. About 50% of the traits extracted from the included studies were not significantly affected by K application. These included length of root hairs, density, length and branching of lateral roots, diameter and volume of roots, the ratio of length and surface area of roots (**Figure 2d**). The meta-regression showed that the differences among cumulative effect sizes for the different traits were not significantly different ($Q_B = 26.5$; $I^2 = 98.9\%$; $df = 24$; $p = 0.278$).

There were about 9 main plant growth media used in the experiments from the included studies. These included soil of various textures, peat and several non-soil growth media including perlite, vermiculite, paper roll, agar, hydroponics (water) and aeroponics (misty air). On the majority of these soil textures or growth media, there was a significant effect of K application on measured root system traits. The results suggested that there were larger reductions due to K deficiency on clay loam, loam and silt loam than on sandy clay, silty clay and clay (**Figure 2e**). The differences among cumulative effect sizes for the various soil textures of growth media were significant ($Q_B = 60.5$; $I^2 = 98.8\%$; $df = 16$; $p < 0.001$). Thus, soil texture or growth medium probably explains some of the variances in the effect size and the effect of K application on root traits might differ depending on soil texture or growth media. The residual sum of squares (Q_E) was insignificant ($Q_E = 806.3$; $df = 777$; $p = 0.226$), suggesting that the variation was accounted for by the soil texture or growth media. After within-study dependencies among outcomes have been addressed by aggregating outcomes within individual studies, the overall effect size based on the $k = 37$ was: $\ln R = -0.294$ (95% CI of -0.434 to -0.153 ; $p < 0.001$; **Figure 2f**), indicating that the deficiency of K in soils or growth media could lead to approximately $25.5 \pm 15.0\%$ reduction in the size of root system traits compared to that on high K soils or growth media amended with K. The $I^2 = 98.68\%$ of the aggregated data still indicated that there is a large degree of between-study heterogeneity.

3.3 Root biomass response to K fertilization

The overall effect size for root biomass for the disaggregated data of $k = 106$ was -0.389 (95% CI of -0.553 to -0.226 ; $I^2 = 99.5\%$; $p < 0.001$; **Figure 3**). Back-transforming the $\ln R$ suggested that K deprivation in a growth media leads to approximately $32.2 \pm 17.7\%$ drop in root biomass. When the data was analyzed based on crop species, significantly large root biomass due to K application was found for root and tuber crops ($\ln R = -0.394$; 95% CI = -0.640 to -0.148 ; $p = 0.002$), cereals ($\ln R = -0.573$; 95% CI = -0.857 to -0.289 ; $p < 0.001$) and fruits ($\ln R = -0.615$; 95% CI = -0.858 to -0.372 ; $p < 0.001$) (**Figure 3a**). However, the cumulative effect sizes of the different categories of crops were not significantly different ($Q_B = 8.77$; $I^2 = 99.4\%$; $df = 7$; $p = 0.269$). The analysis based on the type of K fertilizer indicated that the effect size for all K types except that of MoP was significantly different from zero (**Figure 3b**). According to the meta-regression, the cumulative effect sizes of the different types of K fertilizers were significantly different ($Q_B = 23$; $I^2 = 99.4\%$; $df = 5$; $p < 0.001$). Moreover, when growth media was used as a moderator, the effect sizes for root biomass did not significantly differ from zero for aeroponics and paper growth media but it was significantly different from zero for hydroponics, perlite and soil growth media (**Figure 3c**). Even so, there was no significant difference among cumulative effect sizes for the various growth media ($Q_B = 3.56$; $I^2 = 99.43\%$; $df = 5$; $p = 0.614$). After within-study dependencies among outcomes have been addressed by aggregating outcomes within individual studies, the overall effect size based on the $k = 24$ was -0.477 (95% CI of -0.799 to -0.154 ; $p = 0.004$; **Figure 3d**), indicating that the deficiency of K in soils or growth media could lead to approximately $38 \pm 38.0\%$ reduction in root biomass compared to that on high K soils or growth media amended with K.

3.4 Root length response to K fertilization

Under low K conditions, there is about $20.42 \pm 10.3\%$ reduction in root length compared to non-K-limited conditions ($\ln R = -0.228$, CI = -0.325 to -0.131 , $I^2 = 98.6$, $p < 0.001$). Using crop categories as moderators, the effect size of all groups was different from zero except that of legumes and herbs (**Figure 4a**) and there were significant differences in the estimates ($Q_B = 36$; $I^2 = 98.2\%$; $df = 8$; $p < 0.001$). The largest reduction in root length due to K deficiency was recorded by tobacco, here classified as an industrial crop and the least reduction in root length was recorded by tree crops (**Figure 4a**). Based on the type of K fertilizer, the effect size from SoP and K_2O were insignificant. Among the effect sizes which differed from zero, there were larger gains in root length if the source of K was a combination of KNO_3 and MoP compared with that of MoP alone (**Figure 4b**). The results of the meta-regression based on type of K fertilizer indicated that the estimates differed significantly ($Q_B = 33.2$; $I^2 = 98.2\%$; $df = 5$; $p < 0.001$). Thus, the relationship between root length and the effect of type of K fertilizer is stronger than would be expected by chance. Although the I^2 was very large, the Q_R suggested that with the type of K fertilizer in the model, the between-studies variance was largely explained ($Q_E = 122.7$; $df = 125$; $p < 0.001$). Having used growth media as a moderator, all effect sizes were significantly different from zero, except for that for germination paper (**Figure 4c**). There were significant differences among cumulative effect sizes for the various growth media ($Q_B = 22.1$; $I^2 = 98.3\%$; $df = 5$; $p < 0.001$), with perlite recording the biggest reduction in root length due to K starvation. The overall effect size based on the aggregated outcomes of $k = 23$ was -0.263 (95% CI of -0.433 to -0.094 ; $p = 0.002$; **Figure 4d**), indicating that the deficiency of K in soils or growth

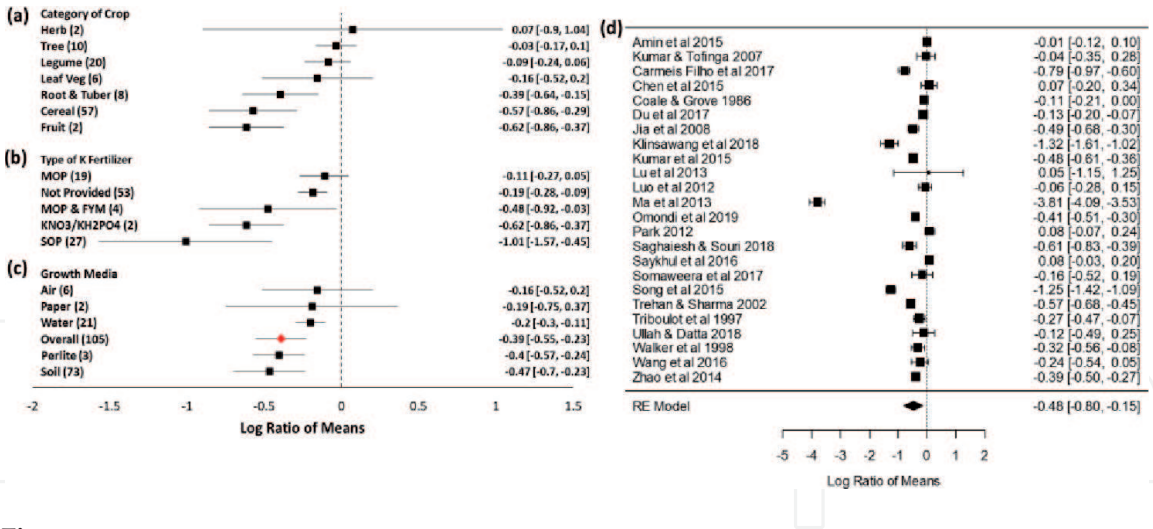


Figure 3. Effect of K deficiency on root biomass of crop plants. Figures (a) to (c) are the analyses of disaggregated data and presents the overall effect size and effect sizes a function of various moderators. The effect of K deficit on root biomass as moderated by (a) crop categories; (b) type of K fertilizer supplied to the replete K growth media; (c) growth media on which plants were grown. (d) Effect of K deficiency on root biomass based on aggregated data, where dependent effect sizes were combined to obtain one effect size per study. The log ratio of means (dotted vertical line) = 0 indicates no effect; log ratio of means >0 indicates larger root biomass of crops grown on replete K media over those grown on deficient K media; log ratio of means <0 indicates larger root biomass of crops grown on K-deficient growth media over those grown on replete K media. Effect size is considered statistically significant if its 95% CI does not overlap zero.

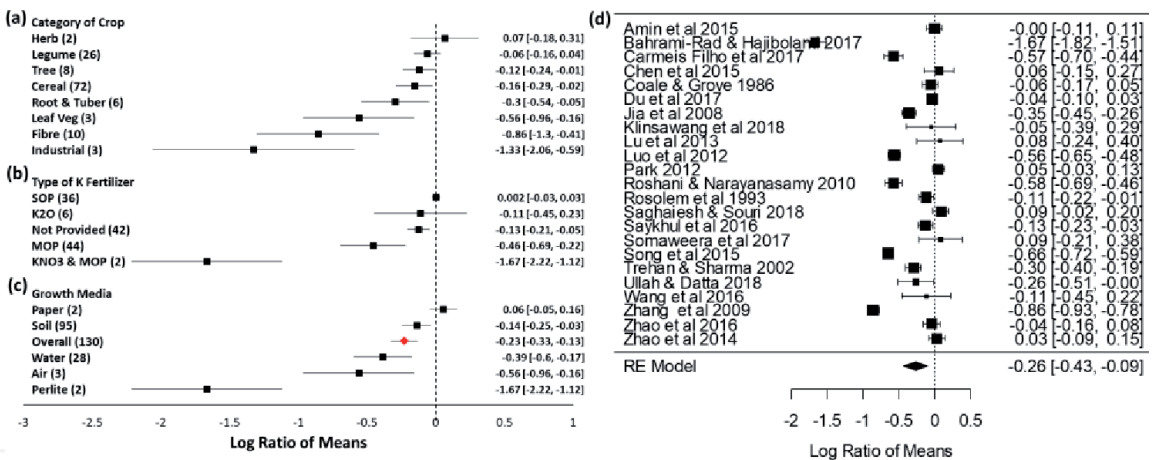


Figure 4. Effect of K deficiency on root length of crop plants. Figures (a) to (c) are the analyses of disaggregated data and presents the overall effect size and effect sizes a function of various moderators. The effect of K deficit on root length as moderated by (a) crop categories; (b) type of K fertilizer supplied to the replete K growth media; (c) growth media on which plants were grown. (d) Effect of K deficiency on root length based on aggregated data, where dependent effect sizes were combined to obtain one effect size per study. The log ratio of means (dotted vertical line) = 0 indicates no effect; log ratio of means >0 indicates the longer length of crops grown on replete K media over those grown on deficient K media; log ratio of means <0 indicates longer root length of crops grown on K-deficient growth media. Effect size is considered statistically significant if its 95% CI does not overlap zero.

media could lead to approximately $23.2 \pm 18.6\%$ reduction in root length compared to that on high K soils or growth media amended with K.

3.5 Root count response to K fertilization

The first meta-analysis for root count involving the disaggregated dataset showed that under K deficiency conditions, there is about $29.2 \pm 9.4\%$ reduction in root numbers compared to non-K-limited conditions ($\ln R = -0.345$, $CI = -0.434$ to -0.256 , $I^2 = 92.5$, $p < 0.001$). Using crop categories as moderators, the effect size of

all groups was different from zero except that of trees (**Figure 5a**) but there were no significant differences in the cumulative effect sizes of these species of crop plants ($Q_B = 11.8$; $I^2 = 89.44\%$; $df = 8$; $p = 0.158$). Based on the type of K fertilizer, the effect size from SoP was insignificant (**Figure 5b**). There were differences in the cumulative effect size ($Q_B = 13.3$; $I^2 = 90.13\%$; $df = 2$; $p = 0.0013$). Thus, the relationship between the number of roots and the effect of type of K fertilizer is stronger than would be expected by chance. All effect sizes were significantly different from zero, for all growth media in which the number of roots was counted (**Figure 5c**) but these cumulative effect sizes for the different media were not significantly different ($Q_B = 8.36$; $I^2 = 90.31\%$; $df = 5$; $p = 0.137$).

3.6 Sensitivity analysis of data with available and estimated dispersion around the mean

Here, we provide four sensitivity analyses of the data with available and estimated dispersions around the means. This includes the sensitivity analysis for the overall dataset involving all root traits ($k = 794$; number of studies = 37), the data for root biomass ($k = 106$; number of studies = 24), root length ($k = 131$; number of studies = 23) and root count ($k = 63$; number of studies = 12). For each of these analyses, we provide a sensitivity of results between the outcomes or studies that originally provided standard deviations (SDs), outcomes or studies that provided standard error of the mean (SEM) which had to be converted to SDs and those without any dispersion for which the SD was estimated as one-tenth of the mean.

For the entire dataset, similar to the overall effect size ($\ln R = -0.266$; 95% CI = -0.305 to -0.227 ; $p < 0.001$), the effect sizes for studies with measures of dispersion reported as SD ($\ln R = -0.248$; 95% CI = -0.42 to -0.077 ; $p = 0.005$), or SEM ($\ln R = -0.198$; 95% CI = -0.23 to -0.167 ; $p = 0.057$) or estimated as 10% of the mean ($\ln R = -0.35$; 95% CI = -0.429 to -0.271 ; $p < 0.001$) were all negative and significant (**Figure 6a**). This suggests that root system size reduces by approximately $22 \pm 18.6\%$, $18 \pm 3.2\%$, and $30 \pm 8.2\%$ due to K deficiency if, respectively, the study originally reports dispersion around mean as SD, SEM or dispersions are estimated as 10% of the mean. Meta-regression suggested that the cumulative effect

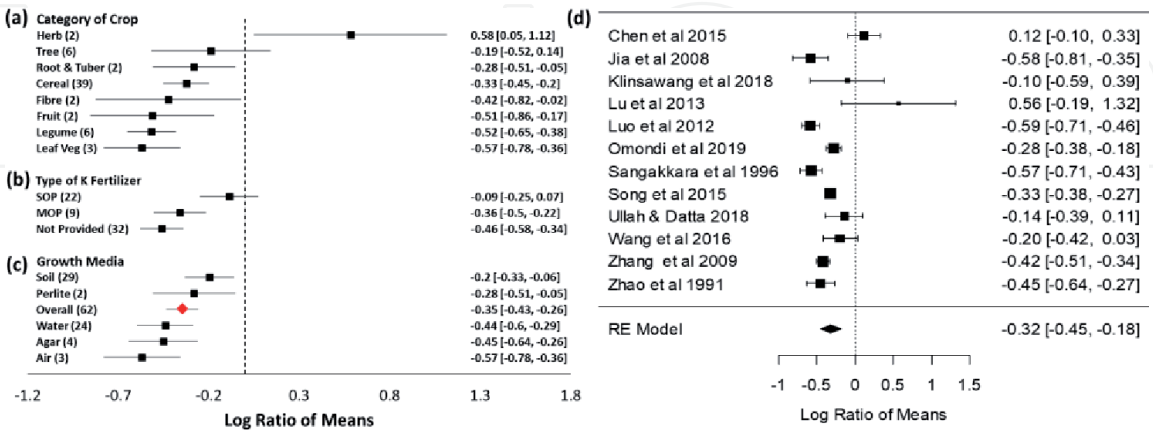


Figure 5. Effect of K deficiency on the root count of crop plants. Figures (a) to (c) are the analyses of disaggregated data and presents the overall effect size and effect sizes a function of various moderators. The effect of K deficit on root count as moderated by (a) crop categories; (b) type of K fertilizer supplied to the replete K growth media; (c) growth media on which plants were grown. (d) Effect of K deficiency on root count based on aggregated data, where dependent effect sizes were combined to obtain one effect size per study. The log ratio of means (dotted vertical line) = 0 indicates no effect; log ratio of means >0 indicates more roots from crops grown on replete K growth media over those grown on deficient K media; log ratio of means <0 indicates more root length of crops grown on K-deficient growth media. Effect size is considered statistically significant if its 95% CI does not overlap zero.

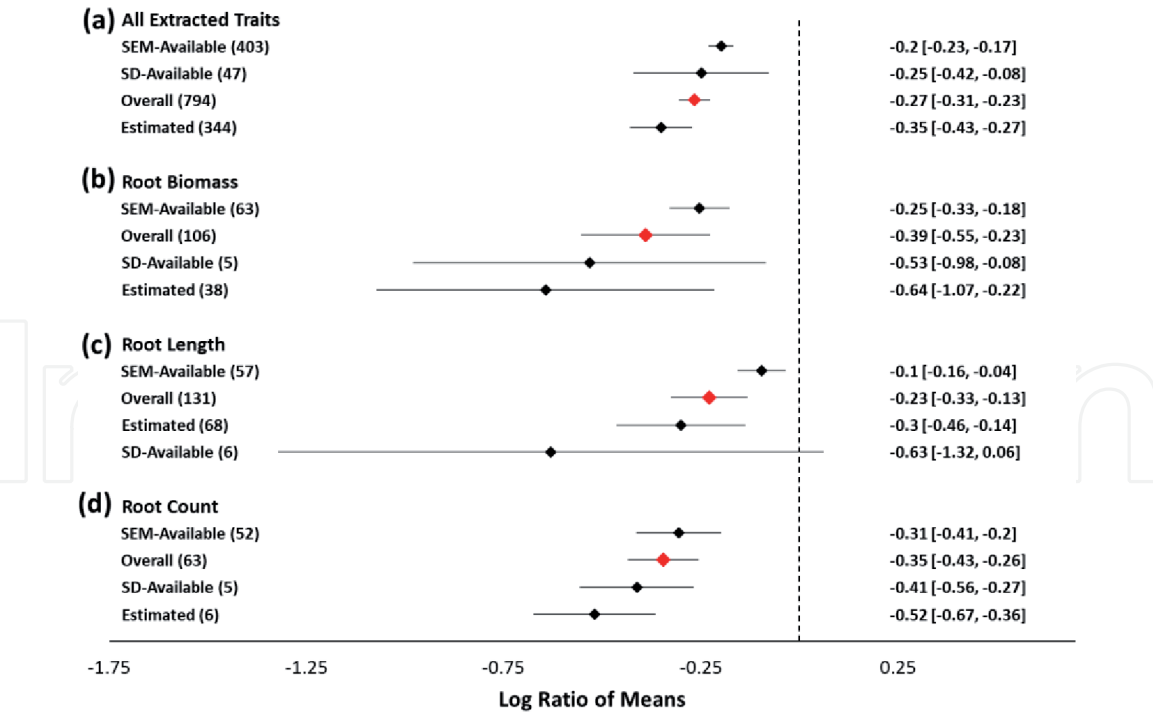


Figure 6. Sensitivity analyses of measures of dispersion for (a) data for all traits extracted from the included studies; (b) data for root biomass; (c) data for root length and (d) data for root count. The sensitivity analysis was conducted between primary studies that originally reported standard deviations, primary studies that originally reported standard error of the mean which had to be converted to standard deviations for the meta-analysis and primary studies which did not report any measure of dispersion and for which SDs were estimated as 10% of the mean. Effect size is considered statistically significant if its 95% CI does not overlap zero.

sizes for the different measures of dispersion were significantly different ($Q_B = 13.5$; $I^2 = 98.89\%$; $df = 2$; $p = 0.0012$).

For the root biomass data, all the three effect sizes, were negative and significantly different from zero (**Figure 6b**) and the meta-regression indicated that differences between their cumulative effect sizes were insignificant ($Q_B = 5.6$; $I^2 = 99.45\%$; $df = 2$; $p = 0.0609$). The sensitivity analysis for the root length data indicated that the three effect sizes for the different types of dispersion were all negative as was the overall effect size for the trait (**Figure 6c**). All effect sizes were significantly different from zero except for outcomes for which SDs were reported in the original study ($\ln R = -0.63$; 95% CI = -1.322 to 0.062 ; $p = 0.074$). The meta-regression for the root length data indicated that differences between the cumulative effect sizes were significant ($Q_B = 7.51$; $I^2 = 98.47\%$; $df = 2$; $p = 0.0234$). Similar to the overall effect size for the root count data ($\ln R = -0.345$; 95% CI = -0.434 to -0.256 ; $p < 0.001$), the effect sizes for studies with measures of dispersion reported as SD ($\ln R = -0.412$; 95% CI = -0.557 to -0.267 ; $p < 0.001$), as SEM ($\ln R = -0.305$; 95% CI = -0.413 to -0.197 ; $p < 0.001$) and estimated as 10% of the mean ($\ln R = -0.519$; 95% CI = -0.673 to -0.364 ; $p < 0.001$) were all negative and significant (**Figure 6d**). This suggests that root count reduces by approximately $34 \pm 15.6\%$, $26 \pm 11.4\%$, and $41 \pm 16.7\%$ due to K deficiency, respectively, if the study originally reported dispersion around mean as SD, SEM or SD was estimated as 10% of the mean. The meta-regression, however, suggested that the cumulative effect sizes for the different measures of dispersion around the means of root count were not significantly different ($Q_B = 2.61$; $I^2 = 91.57\%$; $df = 2$; $p = 0.271$).

3.7 Analysis of publication bias

For each of the analyses conducted here, Rosenberg's fail-safe numbers were computed for the disaggregated datasets and funnel plots produced for the

aggregated datasets. For the overall data involving all extracted traits, the fail-safe number for the disaggregated data was 2,232,020, which is approximately 193% greater than the threshold of 39,700 ($5 \times n + 10$) needed to consider the mean effect size robust. For the aggregated data of the overall dataset, the original funnel plot obtained was essentially asymmetrical, indicating the tendency for smaller sample sizes to be associated with stronger negative effects. Consequently, trim and fill analysis estimated that there were 13 (SE = 4) studies missing to the left side of the grand mean (**Figure 7a**). Although correcting for these with trim and fill method changed the magnitude of the effect size, it did not affect the significance and direction ($\ln R = -0.4498$; 95% CI = -0.5773 to -0.3224 ; $I^2 = 98\%$; $p < 0.0001$). This suggested that when the effect size is corrected for by trim and fill, there is about $36.2 \pm 13.6\%$ reduction in the size of various traits in crop plants grown under K deficient conditions compared to those grown under replete K conditions.

The Rosenberg's fail-safe number for the disaggregated data of root biomass (32081) was approximately 143.3% greater than the threshold of 5300 ($5 \times 106 + 10$) needed to consider the mean effect size robust. Similar to that of the general data, the original funnel plot for the analysis of root biomass was asymmetrical. The subsequent trim and fill analysis estimated 8 (SE = 3) missing studies on the left side of the mean (**Figure 7b**) and altered the magnitude of the effect size for root biomass, but not the significance and direction ($\ln R = -0.7088$; 95% CI = -0.9902 to -0.4273 ; $I^2 = 99\%$; $p < 0.0001$). Back-transforming the new effect

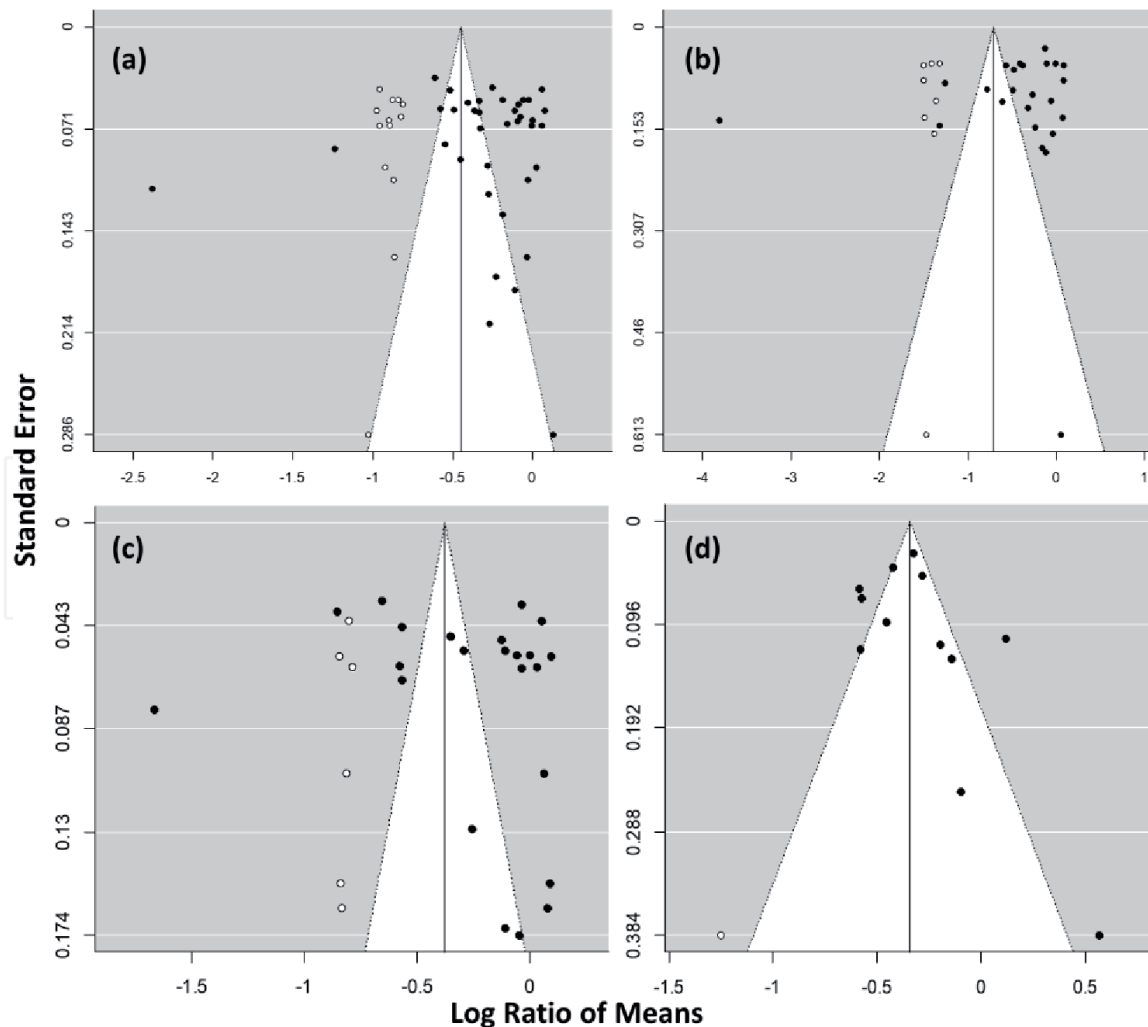


Figure 7. Funnel plots of average effect sizes (log ratio of means) for: (a) data for all traits extracted from the included studies; (b) data for root biomass; (c) data for root length and (d) data for root count. Effect sizes estimated missing on the left side of the grand mean and were corrected for with trim and fill method.

size showed that there is about $50.8 \pm 32.5\%$ reduction in the root biomass of crop plants grown under K deficient conditions compared those grown under replete K conditions.

The Rosenberg's fail-safe number for the disaggregated data of root length (67875) was an over 10-fold increase of the threshold of 6550 ($5 \times 131 + 10$) needed to consider the mean effect size robust. The funnel plot for the analysis of root length was equally asymmetrical and required correction by trim and fill, which estimated that 6 (SE = 3) studies were missing on the left side of the mean (**Figure 7c**). Back-transforming the trim and fill-corrected effect size ($\ln R = -0.3764$; 95% CI = -0.5339 to -0.2189 ; $I^2 = 98.2\%$; $p < 0.0001$) showed that there is about $31.4 \pm 17\%$ reduction in the root length of crop plants grown under K deficient conditions compared those grown under replete K conditions.

The Rosenberg's fail-safe number for the disaggregated data of root count (14840) was an approximately, 5-fold increase of the threshold of 3150 ($5 \times 63 + 10$) needed to consider the mean effect size robust. Funnel plots produced for the analysis of root count indicated a weak tendency for smaller sample sizes to be associated with stronger negative effects (**Figure 7d**). According to the trim and fill analysis, there was only 1 (SE = 2) study missing on the left side of the mean and correcting for the effect size ($\ln R = -0.3404$; 95% CI = -0.4807 to -0.2002 ; $I^2 = 90.5\%$; $p < 0.0001$) suggested that there is an approximately, $29 \pm 15\%$ reduction in the root count of crop plants grown on K deficient growth media compared to those grown on replete K growth media.

4. Discussion

Due to its crucial role in osmotic regulation and root expansion, potassium (K) starvation in soil or growth media during the early stages of plant growth can result in plant death or impaired establishment with adverse impacts on subsequent growth, performance and harvest index [45]. Potassium is indispensable in several cellular and tissue level processes that are critical to high harvest index and food and human health security. Potassium depletion can be rapid even in very fertile soils, resulting in conditions of starvation to crop plants [5]. However, morphological responses of plant roots to K starvation has not received as much attention as N and P [28]. In the current study, a meta-analysis of 37 included studies from 1969 to 2019 in 23 countries (Appendix 1; **Figure 1**) was done to quantify the net effect of K starvation (low or deficient K) on modifications of the root system architecture (RSA) of crop plants. Most of the included studies were done on cereals (mainly maize and rice) and root biomass, root length and number of roots were the commonest measured root traits. The use of inclusion/exclusion criteria, as a requirement of systematic review and meta-analysis, meant that some studies (and for that matter crops or root traits) were not covered in the current study if they did not meet the inclusion criteria.

Overall, results based on the aggregated data indicates a large effect size of K starvation, with substantial reduction ($25.5 \pm 15.0\%$) in the size of root system traits compared to K replete conditions. However, there were substantial heterogeneities between the included studies, which could be partly explained by the moderators identified in this study and others unaccounted for. The results of the disaggregated data also show significant reductions in root system traits under conditions of K starvation compared to K replete conditions. This magnitude of reduction in root system traits was comparable to that of shoot biomass and yield. A significant, net reduction in root system traits was observed for all categories of crop plants in the current study except those categorized as trees, fruits and herbs. The pooled

evidence suggests that, compared to the type of K fertilizer used, the type of crop and soil or growth media considerably mediated the scale of reduction in root system traits due to K starvation. Indeed, the crop genotype or species has been shown to mediate, if not confound, root system responses to conditions of K starvation. For example, it has been reported that even different accessions of *Arabidopsis* (*Arabidopsis thaliana*) responded differently to conditions of K starvation, in which one accession promoted main root elongation and diminished the elongation of lateral roots while the reverse was the case for the other accessions [9]. These differences were shown to be genetically controlled. A related study [46] found no effect of K starvation on the elongation of main roots but substantial reduction in lateral roots, while [25, 26] reported impaired elongation of main roots.

Type of soil (texture) also moderates the effect size of K starvation on root system traits. Larger reductions in root system traits, due to K starvation, were observed in clay loam, loam and silt loam compared to sandy clay, silty clay and clay (**Figure 2e**). This could be due to differences in K-specific binding sites in clay minerals and organic matter [5]. In soils with properties considerably influenced by clay, K can have a protective or competitive advantage for storage in the exchangeable or non-exchangeable but bioavailable form in clay minerals due to its low hydration energy compared to other antagonistic ions or competitive cations. This permits slow and progressive release of K in response to the concentration gradient, a situation more useful to the K nutrition of some crops. Besides, the K-bearing minerals of the sand and silt fractions (e.g. mica or alkali feldspars) can make large contributions to recharging the labile K pool. In contrast, soils with properties considerably influenced by organic matter would have much of its K in solution due to poor specific binding sites of organic matter for K [5, 45]. This could result in rapid depletion or loss of K from solution with attendant reductions in root system traits, especially in young roots.

The results also suggest that reductions in root system traits could be more drastic under greenhouse/lab conditions than under field conditions. Perhaps, field conditions present the typical dynamic balance between the labile and non-labile K pools, and depending on the soil and field conditions, can moderate the effect of K starvation due to potential recharge from non-labile sources [5]. This is in contrast to greenhouse/lab experiments where conditions are homogenized and potentially stable. The large variation in effect sizes from the included studies seems consistent with the heterogeneous results on morphological root system adaptation or responses to K starvation [9, 28] and this might be explained by crop and/or soil type. This inconsistency in the plasticity of root system architecture to K starvation, together with the variations observed across the included studies, suggests a need for extensive studies involving different crop plants and environmental conditions, complemented by elucidation of the metabolic activities that affect K uptake. It would also be critical to explore plant K content, due to its influence on plant water relations and metabolic processes and often serving as a regulator of various physiological processes.

4.1 Specific root traits and moderators

Results from both the aggregated and disaggregated data indicated a large, negative impact of K starvation on root biomass, root length, and the number of roots. Indeed, K is among the essential general regulatory factors of root growth. Contrary to previous results, recent findings show both systemic and localized root growth responses to K supply or deprivation in *Arabidopsis* though further studies are required to strengthen the evidence [28]. While roots have low preferential branching to K patches in a heterogeneous soil, local root growth is known to be promoted

by the close presence of K in the root zone [24, 47]. The general effect of K deprivation is inhibition of root elongation and reduction in the count of first-order lateral roots though this might vary by genotype or species [9, 26]. The role of K in osmotic regulation and maintenance of turgor pressure is critical for cell expansion in the elongation zone of roots [48] while K fluxes influence apical growth of root hairs [49, 50]. Also, the partitioning of assimilates or biomass between root and shoots is mediated by K through phloem transport [51]. Unlike other nutrients, K deprivation generally stimulates decreased (rather than increased) allocation of biomass to the root system, resulting in lower root biomass [52, 53]. This could be due to retarded phloem transport arising from a low supply of K [45, 51, 54]. Retardation of root growth would in turn limit further exploration and effective acquisition of K from the rhizosphere to redress the effect of K starvation. Hence, the effect of K starvation can be more drastic at early stages of plant growth, but this can persist to affect overall crop performance subsequently and harvest index. These physiological or metabolic roles of K in root system growth and development can account for the observed large reductions in root biomass, root length, and the number of roots in the current study as roots actively engage in functional and morphological modifications to cope with or respond to K starvation. The current study aimed at quantifying the effect size of K starvation on root system traits of crop plants using meta-analysis. A detailed treatment of the physiological basis of root system responses to K starvation can be found in the extensive narrative review by [28].

The type of soil (or growth media), crop and K fertilizer used were analyzed as moderators. Generally, the sign of the effect of K starvation on root system traits was independent of the type of K fertilizer used. It has been reported that different types of K fertilizers gave similar results, unlike the dosage, in a study with the rice variety IR 64 grown on Entisols [55]. However, unlike other types of K fertilizers in the disaggregated data, there was no significant difference between the effect size for root biomass of K-replete and K-starved plants when MoP was used. The largest reductions were observed in studies that used SoP or KNO_3 or KPO_4 . For root length, there was no significant difference between the effect size for K-replete and K-starved plants in studies that used SoP and K_2O . Studies that used MoP alone or KNO_3 + MoP showed significantly larger reductions in the K-starved group compared to the K-replete group. Because there were only two studies that combined KNO_3 and MoP and the confidence interval is wide, the cumulative effect on root length should be treated with caution due to weak statistical power. Similarly, the overall effect size of K starvation on the number of roots was not significantly different from the K-replete group when SoP was used but MoP and others were significantly different. These might suggest differences in sensitivities of different root system traits or crop plants to different types of K fertilizer. Perhaps, SoP or KNO_3 or KPO_4 substantially increased root biomass while MoP substantially increased root length or the number of roots. This could also be due to net interactive effect between soil, fertilizer and soil water regime. MoP is widely used but has a high potential for leaching. As a result, it could be more effective on soils with high K-specific binding sites and/or moderate rainfall or watering regime [45]. Besides, root system traits responses to K fertilizer could be different depending on whether the crop plant is chlorophobic or not. Compared to monocots, dicots are relatively poorer at extensive root growth for foraging under low K conditions [45]. Further studies would be required to substantiate this to inform breeding and, perhaps, fertilizer management practices to selectively enhance a target root system trait over others for specific purposes.

With crop type, the effect size of K starvation was significantly different from that of the K-replete group and the difference was largest for root and tuber crops, cereals and fruits. Cereals generally require sufficient K supply during the early or vegetative stage but little to no K during the regenerative stage [45]. The K supply at

the early stages is critical for the development of extensive root system that supports not only anchorage and crop establishment, but also foraging for soil resources, including K under low supply conditions, and phloem-xylem cycling during the regenerative stage. Analysis of previous experimental results showed that relative post-anthesis K uptake of maize, millet, rice, sorghum and wheat was significantly lower than N and P, but not different among the tropical cereals [56]. In roots and tubers, K is essential for the quantity and quality of roots or tuber yield [57]. The unique role of K in the synthesis and translocation of sugars and starches, as well as increasing sink capacity is much more pronounced in roots and tubers. Potassium enhances primary cambial activity to help storage root initiation. It also promotes enlargement of storage root and tubers. As a result, roots and tubers are heavy K feeders and, because they take up larger quantities of K than any other macro-nutrient, they can remove substantial amounts of K from the soil via harvesting. Cassava, for example, can take up about 146–167 kg K ha⁻¹ to produce root yield of 25 kg ha⁻¹, with about 87.8 kg K ha⁻¹ removed with the harvest [58]. In sweet potato, about 185 kg K ha⁻¹ might be required to produce 22 t ha⁻¹ tubers; and the roots can account for about 66% of total K removal from soil [59]. It is, therefore, not surprising that the cumulative effect of K starvation was negative and large for roots and tubers. K-starved legumes and herbs did not show any significant cumulative reductions in root length compared to the other categories of crop plants. Perhaps, this could be because the roots of legumes require K principally for root nodule formation. As observed for the number of roots in herbs, some herbaceous plants might increase the number of roots or root hairs in response to K deprivation [45].

In the disaggregated data, significant and large reductions in root biomass were observed under K starvation in studies that used soil and perlite as growth media, while germination paper and aeroponics did not produce cumulative effect significantly different from the K-replete condition (though these had much wider CIs). Similarly, the cumulative effect of K starvation on root length was not significantly different from the K-replete group in studies that used germination paper as growth medium but significant reductions were observed for all other growth media, with perlite showing the largest reductions. However, though significant reductions were observed in the number of roots of plants under K starvation for all growth media used, the cumulative effect sizes for the different growth media were not significantly different. These suggest differential mediation or moderation of root system traits responses to K starvation. Light textured or well-drained soils might facilitate K loss from the root zone via leaching depending on the intensity of rainfall or irrigation. Conversely, clay soils might fix K and reduce its availability to the roots [45]. Perlite, on the other hand, facilitates drainage which can contribute to leaching of K depending on irrigation or rainfall intensity. In both situations, conditions of scarcity would be created which can have marked effects even if the scarcity is short-lived. Germination paper might not be a good medium for studying the effect of K starvation on root system traits. Adu et al. [60] noted that when germination papers are used in screening root traits, significant paper effects on the root system data were recorded, possibly due to inadequate water absorption or some inherent minerals in the different papers.

4.2 Analyses of sensitivity, publication bias and heterogeneities

The Rosenberg fail-safe numbers generated from the analyses suggest that the results are more likely to be robust to publication bias. Thus, a relatively large number of unpublished data would be required to change statistically significant effects observed in the current meta-analysis [30]. Even so, the visual observation of the funnel plots indicates possible under-estimation of the original effect sizes,

as the 'trim and fill' suggested relatively bigger effect sizes. The sensitivity analyses of measures of dispersion indicated that the effect size from studies that originally reported SDs is comparable to the effect size from the overall data. However, while the conversion of SEM to SD seems to have underestimated the effect size, the estimation of SD as one-tenth of the mean may have significantly overestimated the effect size. This borders on quality of reporting practices in publications, where certain critical information such as standard deviation must be enforced in published papers, especially when continuous data are used. The analysis of heterogeneity also showed that the percentage of the total variability in a set of effect sizes, due to true heterogeneity between-study or comparisons rather than sampling error, was high. While this may point to large differences in experimental approaches, environmental variables and variations between studies, it is also possible that certain critical moderators were unaccounted for in the current study. Availability and uptake of K by plants is often complicated by many interacting components, including soil, plant, climate, and management factors. Critical moderators such as available and non-exchangeable K, cation exchange capacity (CEC), temperature and moisture content of the soil, plant population, placement of K fertilizer, tillage practices, among others were largely unreported in the included studies and may be implicated in the large heterogeneities or I^2 values observed.

5. Conclusion

Potassium plays critical roles in the growth and development of plant roots, which respond morphologically to K starvation. As agronomic use of K increases and becomes even more crucial for food security and sustainable agriculture in a changing climate, it is imperative to understand the extent of modifications in root system architecture in response to K starvation to inform efforts at improving crops and agronomic practices for efficient use of K. This meta-analysis sought to provide a pooled evidence on and quantify the effect of K starvation on modifications in RSA. Generally, the cumulative effect size of K starvation on pooled root system traits was significantly different from that of K-replete plants, resulting in about $25.5 \pm 15.0\%$ reduction in pooled root system traits. Similarly, K starvation can lead to a significant cumulative reduction of about $38 \pm 38.0\%$ in root biomass and $23.2 \pm 18.6\%$ in root length. The reductions were largest for the categories roots and tubers, cereals and fruits. Soils modified by organic matter showed large reductions compared to those modified by clay. Soil and perlite, as growth media, showed the largest reductions in root biomass and root length while germination paper might not be a suitable medium for assessing the response of these parameters to K starvation. Generally, the type of K fertilizer used in such studies is unimportant. The effect of K starvation on RSA might be invisible but the cascading effect on the quantity and quality of shoot biomass, harvest index, and food security could be palpable and costly. Hence, efforts at estimating optimal K management, in terms of timing, frequency, rate, and building K reserves in soils should be intensified vis-à-vis improvement in understanding of responses of root system traits in different crop genotypes and species, types of soil, and environmental conditions. In all this, special consideration should be given to responses of targeted root system traits to K starvation in matching crops to soil environments and adapting agronomic management practices.

Conflict of interest

The authors declare no conflict of interest.

Appendix 1: Reference list of included studies

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