Does plant root architecture respond to potassium nutrition under water stress? A case from rice seedling root system architectural and growth responses

Authors:

Dipika S.Patel[a], Bardhan Kirti*[b], Patel Dhiraji P[c], Parekh Vipulkumar[b]

***Corresponding author**
kirtivardhan@nau.in

ABSTRACT

The root is the primary sensing organ for potassium (K) and water availability and thus we test the hypothesis that K may influence root architecture and contribute to drought tolerance under moisture stress. Rice seedlings failed to maintained favourable root architecture with low K under water stress and more reduction was observed in root projected area, maximum width, width to depth ratio. High K helps to maintain root top and bottom angle and reduce root steepness under mild water stress, however, high K supply does not warrant higher water productivity. In severe water stress, the steepness was more regulated by water than K availability.

Keywords:

Potassium, drought, root system architecture, *Oryza sativa* L.

INTRODUCTION

In rice, root traits such as root thickness, root density, rooting depth and root distribution have been considered as common drought tolerance contributing traits, depending upon the target environment[1,2]. Early stage changes in root angle promote the development of deep root system and has been considered as an important trait for drought avoidance in rice[3].Potassium (K) fertilization is adopted as a strategy for alleviating the ill effect of water stress in many crops, including rice[4-7].High level of K increases root diameter and dry matter[8]. Effect of K on root is also attributed to phytohormones balance[9] such as abscisic acid production[10,11]. In brief, literature suggests that roots and potassium both are interact for drought tolerance and thus we hypothesized that besides potassium playing a key role in plant cell water potential[12,13], stomatal conductance[14] and neutralizing reactive oxygen species[15,16] during moisture stress, it may also influence root architecture and contribute in alleviation of drought effect. Moreover, the knowledge gap still exists concerning influence of potassium on root architecture under moisture stress as most of the studies either focused on root growth[17]or conducted under no water stress[8]. The main objective of the present study was to study the effect of potassium on rice seedling root architectural features and seedling growth under moisture stress.

MATERIALS AND METHODS

Rice (*Oryza sativa* L.) variety NAUR-1 of subspecies Indica was used in this study. This variety has high adaptability for upland and lowland rice cultivation under the south Gujarat region. The experiment was conducted in naturally ventilated ploy house of the institute (20.9248° N,72.9079° E) in 2017-18.

The experiment was set up in complete randomized design with a factorial concept and was replicated thrice in two different periods to avoid time and labour constraints for periodical observations. The seeds were pre-soaked in deionized water for 24 hours. Five

seeds per bag were sown in semi-transparent polythene bags (32 cm x 20.5 cm) filled with 1.2 Kg growing media of uniform mixture of sand and perlite (2:1, 800g +400g). After emergence, only two seedlings were retained per bag.

The experiment consisted of three levels of water stresses, hereafter called as NWS (No water stress), MWS (mild water stress) and SWS (severe water stress), respectively, corresponding to 100%, 60% and 40% of moisture content based on field capacity (FC) which is defined as the amount of maximum water retained by growing media after darning excess water. The FC was estimated by gravimetric approach. Four filled bags saturated with water and covered at the top to prevent evaporation, were kept overnight to drain the excess water. In the next morning, the saturated bags were weighted and the differences between saturated and oven-dried media (105°C ±1°C in hot air oven for overnight and then till constant weight) was used to estimate amount of water retained at 100%FC by using formula: [(weight of saturated media–weight of oven-dried media) /weight of oven dried media] x 100. Average daily water loss (evapotranspiration) was estimated by daily weighing the four bags identical in each manner to experimental bags which were placed near the experimental repetitions and their weight differences from 100% FC was recorded. Initially all bags were daily replenished by the unmodified Yoshida solution[18] to maintained100% FC up to seed emergence and thereafter modified Yoshida solution was used for imposition of desired water stress(Figure 1 A, B, and Figure 2).

The Yoshida solution was modified for three different potassium levels, hereafter called as K- (Yoshida solution of 50% low K), K0 (Yoshida solution of normal K) and K+(Yoshida solution of 50% high K), which corresponding to 20 ppm K (35.7 g/l K_2SO_4), 40 ppm K (71.4 g/l K_2SO_4) and 60 ppm K (107.1 g/l K_2SO_4), respectively. The sulphur concentration was maintained in different treatments by adjusting amount of H_2SO_4 (Sp. gravity: 1.84, purity: 98%) according to K_2SO_4 concentration as 50ml/l in K0 treatment,

61.14 ml/l in K- and 38.85 ml/l H_2SO_4 in K+ treatments. All other nutrient concentrations of Yoshida solution were remained unchanged. The solution pH was adjusted to 5.5 before the application.

Total 405 roots were scanned during the experiment representing root architecture from five individual seedlings per treatment at three different time intervals (7, 14 and 21 days after emergence, DAE) from three repetitions. Individual seedlings root was immersed underwater in a scanner acrylic tray ($23.1 \times 15.5 \times 7 cm^3$) for 45 min before the scanning. The immersed roots were stained with natural red dye (0.25g/l) to increase contrast and reduce scanner light diffraction from the root surface. The root images were captured by HP Scanjet G2410 scanner at a resolution of 600 dots per inch. A circle scale marker of 40 mm diameter was placed beneath the scanner tray and all images were captured with the scale marker (Figure 1 C). At 21 DAE, the root samples were used to record their dry weight (65°C ±1°C in hot air oven, initially for overnight and subsequently till constant weight).

Root architectural features were computed by open access image-based root trait estimation platform: DIRT (Digital Imaging of Root Traits)[19]. All scanned images were calibrated at the masking threshold level of 3 before computation (Fig 1 D and E) and submitted for computation. The output datasets (in pixels) were converted, except average root density (ratio of foreground to background pixels within the root shape), in metric units by using the following formulas:

$$\text{Calibration factor} = \frac{\text{scale marker diameter}}{\text{Circle ratio(in pixel)}}$$

Where circle ratio (in pixel) computed by DIRT platform.

$Root\ depth\ (mm) =$ length in pixel x calibartion factor

$Maximum\ width\ (mm) =$ Maximum width in pixel x calibartion factor

$Projected\ Root\ Area\ (mm^2) =$ area in pixel x $calibartion\ factor^2$

At 21 DAE, shoot length (cm) and shoot dry weight (g) were measured from the same five seedlings from each treatment which were used for root analysis. Shoot length was measured from root shoot juncture to the leaves tip. The shoots samples were dried in a hot air oven at 65°C ±1°C initially for overnight and subsequently up to constant weight to compute seedling total dry weight. Treatments water productivity (mg/ml) was estimated as total dry weight of seedling (mg) divided by total water applied (ml) during the experimentation. Indirectly root thickness was estimated by specific root length (SRL)(m/g) as root depth divided by root dry weight[20].

The mean derived from five individual seedlings per treatments per replicate were taken periodically for parametric observations and non-parametric observations viz. maximum width to depth ratio, specific root length, water productivity, were calculated based on associated parametric means. The mean datasets were subjected to analysis of variance (ANOVA)[21] and mean differences at $LSD_{p=0.05}$ were considered statistically significant.

RESULTS

Vertical Root Architectural Features

Projected root area (PRA) was influenced by WS and K ($p \geq 0.05$) at 7, 14 and 21 DAE and by their interaction WS x K ($p \geq 0.05$) at 21 DAE (Table 1). The PRA was decreased with WS and at 21 DAE, the decreased was of 35.39% and 54.7% in K0MWS and K0SWS, respectively, as compared to K0NWS. Increased K availability increased the PRA. At 21 DAE, the increase in the PRA from K+NWS was a tune of 13.8 % as compared to K0NWS while decreased in the PRA from K-NWS was 30.1% over K0NWS. (Figure 3 A, B, C). The reduction in the PRA was more distinct under combined deficit treatments and at 21 DAE, 51% and 66% reduction were from K-MWS and K-SWS, respectively, over K0NWS. In the seedlings from K-MWS and K-SWS, the PRA was reduced by 25.3% and 25%, respectively,

over K0MWS and K0SWS. However, the PRA from K+MWS and K+SWS were not distinct ($p \geq 0.05$) than the counterpart K0MWS and K0SWS.

Seedling rooting depth (RD) at 7, 14 and 21 DAE were influenced by WS and K ($p \geq 0.05$) and by WS x K ($p \geq 0.05$) at 21 DAE (Table 1)(Figure 3 D, E, F). WS increased the RD by 13.5% and 15.8%, respectively, inK0MWS and K0SWS as compared to K0NWS at 21 DAE. However, RD were statistically equal ($p \geq 0.05$) between K0MWS and K0SWS at 7, 14 and 21 DAE.RD was reduced ($p \geq 0.05$) due to K limitation and at 7, 14 and 21 DAE and the reduction reached up to 17% at 21 DAE in K-NWS over K0NWS. Under NWS condition, higher K (K+NWS) does not exhibit any effect and RD was statistically equal to normal K (K0NWS) at 7, 14 and 21 DAE. Opposite to no water stress condition, K+ increased RD under MWS and SWS by 9.3 and 10% over K0 supply at 21 DAE. Though the RD from K+MWS and K+SWS were statistically not distinct ($p \geq 0.05$) from each other at 14 and 21 DAE. Effect of K- was more distinct under water stress treatments and RDs from K-MWS and K-SWS recorded 28.7% and 31.1% reduction, respectively, over K0MWS and K0SWS.

The availability of water and potassium both were found to increase average root density (ARD) ($p \geq 0.05$) (Table 1)(Fig 3, G, H and I). At 14 and 21 DAE, under MWS and SWS, seedlings ARD were reduced ($p \geq 0.05$) over NWS and at the end of the experiment, the reduction was up to 22.5%to 33%, respectively in K0MWS and K0SWS over K0NWS. The K- treatments reduces ($p \geq 0.05$) the ARD and at 21 DAE, reduction was up to 18.7% in K-NWS while 26.5% increase ($p \geq 0.05$) was observed in K+NWS as compared to K0NWS. Detrimental effect of combined deficit was observed ($p \geq 0.05$) at 14 and 21 DAE where seedlings grown under K-MWS, recorded around 33% less ARD as compared to K0MWS. However, in SWS, the effect of K was not discrete and ARD from K- or K+, were statistically equal ($p \geq 0.05$) to K0, at 14 and 21 DAE.

Horizontal Root Architectural Features

Maximum width (MW) of the root system was influenced ($p \geq 0.05$) by WS and K at 7, 14 and 21 DAE (Table 1) (Figure 4 A, B, C). WS decreased the MW, at 21 DAE decrease was tune of 20% and 60%in K0MWS and K0SWS, respectively, over K0NWS. However, K found to increased MW and at 21 DAE, K+NWS seedlings recorded 10.6% higher MW while K-NWS seedlings were recorded 26.5% less MW over K0NWS. A significant ($p \geq 0.05$) influence on MW was observed due to WS x K only at 21 DAE (Table 1). The reduction due to WS was more pronounced in seedlings with K- treatments and in K-MWS and K-SWS, the MW were 41% and 43% less as compared to K0MWS and K0SWS, respectively. Though, seedlings from K+MWS and K+SWS exhibited 20% and 48%, respectively higher MW over their counterparts K0MWS and K0SWS treatments, respectively.

Root top angle (RTA), an average angle of two sides angle between the root surface and soil horizon at 10% root depth, was influenced ($p \geq 0.05$) by WS and K at 7, 14 and 21 DAE and by WS x K at 21 DAE (Table 1). The RTA was increased with the progression of seedling age (Fig 4 D, E, F) which indicate decreasing the horizontal spread of roots at 10% of depth from the media surface. WS increased the RTA and at 7, 14 and 21 DAE narrower RTA were found with NWS while widen RTA was associated with SWS seedlings. At the end of the experiment, RTA was increased in K0MWS and K0SWS by 6° and 17.2°, respectively, over K0NWS. K- also had widened RTA and 18.7% increase was found in seedlings from K-NWS as compared to K0NWS at 21 DAE. The RTA from K+NWS was similar ($p \geq 0.05$) to K0NWS. The RTA from K-, K0 and K+ under MWS were not distinct ($p \geq 0.05$) from each other, however, in SWS, seedlings with K+ supply had shown 20% narrower RTA than K-SWS and was similar to K0MWS ($p \geq 0.05$) at 21 DAE.

Root bottom angle (RBA), the average angle between two sides angle of root and the horizontal soil plane at 80% of the root depth, was influenced ($p \geq 0.05$) by WS and K at 7, 14

and 21 DAE and by WS x K at 21 DAE (Table 1). The RBA increased with seedling age (Fig 4 G, H, I) and it was more widen than corresponding RTA of 7, 14 and 21 DAE. Similar to the RTA, WS widens the RBA and roots become less spread at the depth under WS. At 21 DAE, most widen RBA was observed in roots of K0SWS followed byK0MWS ($p \geq 0.05$), which were widen by 34.7% and 15.8%, respectively than K0NWS. K-found to increase RBA ($p \geq 0.05$) and 17.8% more widen angle was observed with K-NWS than K0NWS at 21 DAE. However, K+ application does not influence ($p \geq 0.05$) RBA and the RBA from K+NWS and K0NWS were similar ($p \geq 0.05$). The RBA of seedlings from K-MWS and K-SWS had 12.5% and 7.1%, respectively, more widen than their counterpart K0MWS and K0SWS, respectively. K+ supply in MWS did not restrict widening of RBA, though, seedlings from K+SWS show 13.6% narrower RBA than K0SWS.

To know the influence of WS and K, on root preferential elongation in the horizontal and vertical direction, maximum width to root depth (MW/RD) ratio was calculated and the ratio was influenced ($p \geq 0.05$) by both WS and K at 7, 14 and 21 DAE (Table 1) (Figure 6). However, the influence of WS x K ($p \geq 0.05$) on MW/RD ratio was observed at 7 and 14 DAE. The seedlings root was elongated more in a vertical direction than horizontally with increasing age as indicated by a gradual decrease in MW/RD ratio (Figure 5). WS reduces the MW/RD ratio and at 21 DAE, 31.1% and 65.2% less MW/RD ratio were recorded for roots of K0MWS and K0SWS, respectively, over K0NWS. K increased MW/RD ratio by 6.5% in K+NWS while in K-NWS, the ratio was 12.3% lower than K0NWS at 21 DAE.

Root growth

Root dry weight (RDW) at 21 DAE was influenced ($p \geq 0.05$) by WS, K and WS x K (Table 1) (Figure 6 B). WS reduced ($p \geq 0.05$) the RDW and maximum RDW was observed in K0NWS while 28% and 61% reduction were observed in K0MWS and K0SWS, respectively. The RDW of seedlings from K+NWS was similar ($p \geq 0.05$) to K0NWS while in K-NWS,

47% reduction was observed in the RDW. The RDW from K-MWS and K-SWS were 52% and 32% less than the counterpart seedlings of K0MWS and K0SWS, respectively. Under MWS, the RDW of K+ treatment was similar ($p \geq 0.05$) to K0MWS while in SWS it was 46% higher than counterpart K0SWS. At the end of the experiment, SRL influenced ($p \geq 0.05$) by WS and K (Table 1). WS increased ($p \geq 0.05$) SRL and in SWS, seedlings showed two-fold increase over NWS. Seedlings from K- and K+ had similar SRL to K0 (Figure 7).

Seedling growth

The shoot length (SL) of seedlings (Figure6 A and D) was influenced ($p \geq 0.05$) by WS, K and WS x K (Table 1). At the end of the experiment, SL under K0MWS and K0SWS were 16% and 30% lower than K0NWS. Supply of K- and K+ under NWS condition did not influenced ($p \geq 0.05$) SL. Though under MWS and SWS, seedlings from K- treatments recorded 21% and 24% lower SL, respectively, and 12.8% and 24.8% higher with K+ treatments, respectively, as compared to K0MWS and K0SWS.Seedlings total dry weight (TDW) at 21 DAE, was influenced ($p \geq 0.05$) by WS, K and WS x K (Table 1) (Figure 7 C). WS decreased TDW by 18 % and 46 %, respectively, in K0MWS and K0SWS as compared to K0NWS. Seedlings which were grown under K+NWS, had similar ($p \geq 0.05$) TDW to K0NWS, though 35% reduction was observed with K-NWS over K0NWS.Seedlings with K- treatment under MWS and SWS showed 46% and 26%reduction, respectively, in TDW over K0MWS and K0SWS, while TDW of seedlings from K+MWS and K+SWS were similar ($p \geq 0.05$) to K0MWS and K0SWS.

Water productivity

Water productivity (WP) was influenced ($p \geq 0.05$) by WS and K (Table 1) (Figure 8) and it ranged from 0.43 to 1.244 mg /ml of water in different treatments. WP was 17 % and 70 % higher in MWS and SWS, respectively. Seedlings with K- supply, showed decreased WP by 35% while seedling with K+ had similar ($p \geq 0.05$) WP as K0 treatment.

DISCUSSION

In the study, root architectural traits were influenced by WS, K and WS x K interaction (Figure 9), but at different proportion. Our results showed that under MWS, K limitation pronounced the ill effect of MWS and SWS on rice roots and more reduction were observed in root PRA, RD, ARD, MW, MW/RD ratio and RDW. Under K- condition of MWS and SWS, RTA and RBA were widened which indicate more steepness of the roots under WS. However, K+ supply under MWS, seems to suspend the negative effects of WS on PRA, RD, MW, MW/RD ratio and RTA. Though, under SWS, K+ supply had increased MW, MW/RD ratio, RDW and decreased root steepness by decreasing RTA and RBA (Figure 10).

Rice seedlings PRA, MW and ARD were reduced due to WS. It may be an energy adoptive strategy[23]of NAUR-1. In maize, recombinant inbred lines with fewer crown roots under WS had exhibited deeper rooting which helps in the acquisition of subsoil water and improved water status, stomatal conductance and leaf photosynthesis[24]. In the present study, the increased RD and SRL of NAUR-1 under WS, suggests the development of more acquisition unit (root length) per unit of dry mass as an energy adoptive strategy. The effect of WS on these parameters was more intense under K- which indicates that water and K both constitute additive limiting factor and maybe these traits regulated independently by these two resources. As sugar translocation is K dependent and triggers cell division[25,26] while cell elongation is turgor dependent process[24] and dependents on water content. Moreover, it seems that K sufficiency is important for PRA as even under NWS, K- treatment recorded the lower PRA. It may be due to limitation of turgor pressure due to low water absorption[27]and/or decreased auxin concentration[28]and disruption of auxin maxima in root tip[29,30] under K- condition.

Though besides increased RD under WS, the roots horizontal expansion was decreased as indicated by a reduction in MW and MW/RD ratio under MWS and SWS condition and roots were intended to more and more steep with increasing water stress. K found to encourage horizontal elongation by increasing root width as highest MW was observed with K+ treatments and lowest with K- treatments. The same was also reflected from the influenced of K on SRL where K+ supply decreased the development of root length per unit of dry mass investment. However, at the end of the experiment WS x K interaction was non-significant for MW/RD ratio. Though it seems that the ratio was more controlled by water under SWS than K, as WS x K interaction was significant at 7 and 14 DAE, but the ratio under K+ and K- was statistically equal. Moreover, increase steepness of roots also reflected by widens RTA and RBA under MWS and SWS, which indicate that the roots had lower contact surface area. K+ supply under MWS, alleviate the reduction of top and bottom angle but under SWS, K+ application failed to sustain this positive effect. It can infer from our study that besides increased translocation of mineral nutrients in xylem due to K[31], under MWS, K fertilization helps in maintaining RTA and RBA, and thus increases root-soil contact area and may contribute in the acquisition of other nutrients and soil resources. In a study of *Hibiscus rosa-sinensis* cv. Leprechaun, K application was reported to increase macronutrient content in leaves under WS condition[12].

As stele diameter play an important role in water conductance of root system, we observed K x WS effect on stele diameter (Figure 11). Our observations suggest that K+ increases stele diameter under water stress. K found to increase stele diameter in poplar, though under high nitrogen[32]. However, our results suggest further studies to distinguish the effect of genotype, WS and K on stele diameter as both increase or decrease diameter were adopted by diverse genotypes for drought tolerance in rice[33].

There was no significant interaction was found between WS x K for WP and also K+ application did not increased WP over K0, though K- application does reduced WP. Increase WP is expected under WS as more water would available in deeper soil horizons and less water was available for subsurface evaporation loss as compared to transpiration loss, which contributed in biomass gain. In our study, rice seedlings roots increase rooting depth with increasing water stress and thus seedlings were able to absorb more water, which was also reflected from seedling TDW. As seedlings take water from deeper horizons for transpiration and less water lost through evaporation, per unit of water loss, more biomass was accumulated. Similarly, as K+ essential for root growth[34], low availability of potassium decreases WP due to less efficient absorption of water. The decrease in water absorption may attribute to the low osmotic gradient between roots and growing media due to low K accumulation in roots under low K treatments[34]. However, K+ application over normal level, does not increase water productivity.

CONCLUSION

Our study shows that K and WS interaction influenced root spatial distribution which could have advantage for exploring underground resources for maintaining above ground rice seedling growth under mild water stress, depending upon K availability. Our results providing additional support for necessities to maintain adequacy of potassium soil status under moisture deficit scenario. These findings extend our knowledge on the role of K and open new research areas on how potassium could help in maintaining plant water status through root architecture moderation. Future studies should aim to evaluate the extent of the interaction on root architectural responses in diverse genetic background.

REFERENCES

1. Nguyen, H. T. Nguyen, T. H., Chandra Babu, R. and Blum, A., Breeding for drought resistance in rice: physiology and molecular genetics considerations. *Crop Sci.*, 1997, **37,** 1426-1434.

2. Kano, M., Yoshiaki, I., Kitano, H., Yamauchi, A., Root plasticity as the key root trait for adaptation to various intensities of drought stress in rice. *Plant Soil*, 2011, **342,** 117–128.

3. Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. *Nat. Gen.* 2013, **45**, 1097-1102.
4. Rezaei, E. E., Gaiser, T., Siebert, S., Sultan, B. and Ewert, F., Combined impacts of climate and nutrient fertilisation on yields of pearl millet in Niger. *Eur. J. Agron*., 2014, **55**, 77–88.
5. Fanaei, H. R., Galavi, M., Kafi M. and Bonjar, A. G., Amelioration of water stress by potassium fertilizer in two oilseed species. *Int. J. Plant Prod*., 2009, **3**, 41–54.
6. Martineau E, Domec JC, Bosc A., Denoroy, P., Fandino V. A., Lavres, J. Jr. and Linonel, J.C., (2017) The effects of potassium nutrition on water use in field-grown maize (Zea mays L.). *Environ. Exp. Bot*. 2017,**134**, 62–71.
7. Zain, N. A. M. and Ismail, M. R., Effects of potassium rates and types on growth, leaf gas exchange and biochemical changes in rice (Oryza sativa) planted under cyclic water stress. *Agricultural Water Management*. 2016, **164**, 83–90.
8. Filho, A. C. A.C., Crusciol, C. A. C., Nascente, A. S., Mauad, M. and Garcia R. A., Influence of potassium levels on root growth and nutrient uptake of upland rice cultivars. *Rev. Caatinga*, 2017, **30 (1)**, 32 – 44

9. Tatsumi, J., Endo, N. and Kono, Y., Root growth and partitioning of 13C-labelled photosynthate in the seminal root of corn seedlings as affected by light intensity. *Jpn. J. Crop Sci*. 1992, **61**, 271–278.
10. Zhao, X.H., Yu, H.Q., Wen, J., Wang, X.G., Du, Q., Wang, J. and Wang, Q., Response of root morphology, physiology and endogenous hormones in maize (Zea mays L.) to potassium deficiency. *J. Integr. Agric*. 2016, **15**, 785–794.

11. Tavakol, E., Jakli, B., Cakmak, I., Dittert, K., Karlovsky, P., Pfohl, K. and Senbayram, M., Optimized potassium nutrition improves plant-water-relations of barley under PEG-induced osmotic stress. *Plant Soil*, 2018, **430**, 23–35.
12. Egilla, J.N., Davies, F.T. Jr., Drew, M.C., Effect of potassium on drought resistance of *Hibiscus rosasinensis c*v. Leprechaun: Plant growth, leaf macro- and micronutrient content and root longevity. *Plant Soil*, 2001, **229**, 213–224.
13. Mengel, K. and Arneke, W.W., Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of Phaseolus vulgaris. *Physiol. Plant***,** 1982, **54**, 402–408.
14. Benlloch-González, M., Arquero, O.J., Fournier, M., Barranco, D. and Benlloch, M., K+ starvation inhibits water-stress-induced stomatal closure. *J. Plant Physiol*. 2008, **165**, 623–630.
15. Cakmak, I., The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *J. Plant Nutr. Soil Sci.*, 2005, **168**, 521–530.

16. Battie-Laclau, P., Laclau, J.P., Beri, C., Mietton, L., Almeida Muniz, M.R., Arenque, B.C., Piccolo, M.C., Jordan-Meille, L., Bouillet, J.P. and Nouvellon, Y., Photosynthetic and anatomical responses of Eucalyptus grandis leaves to potassium and sodium supply in a field experiment. *Plant Cell Environ*. 2014, **37**, 70–81.

17. Jordan-Meille L., Martineau, E., Bornot, Y., Lavres, J., Abreu-Jr. H. C., and Domec, J. C., How does water-stressed corn respond to potassium nutrition? A shoot-root scale approach study under controlled conditions. *Agriculture*, 2018, **8**, 180.
18. Yoshida, S., Forno, D. A., Cock, J. H. and Gomez, K. A., *Laboratory Manual for Physiological Studies of Rice.* (2nd edition). The International Rice Research Institute, Philippines, 1976.
19. Das, A., Schneider, H., Burridge, J., Ascanio, A. K. M., Wojciechowski, T., Topp., C. N., Lynch, P. J., Weitz, J. S. and Bucksch, A., Digital imaging of root traits (DIRT): a high throughput computing and collaboration platform for field-based root phenomics. *Plant Methods.* 2015, 11, 51.
20. Figueroa-Bustos, V., Palta, J.A., Chen, Y. and Siddique, H. M. K., Early season drought largely reduces grain yield in wheat cultivars with smaller root systems. *Plants*, 2019, **8**, 305.
21. Gomez, K.A. and Gomez, A. A., Statistical procedures for agricultural research (2 ed.). John wiley and sons, New York, 1984.
22. Christina, M., Maire, G. L., Battie-Laclau, P., Nouvellon, Y., Bouilleti, J. P., Jourdan C., Goncalvess, J. L. M., and Laclau J. P., Measured and modeled interactive effects of potassium deficiency and water deficit on gross primary productivity and light-use efficiency in Eucalyptus grandis plantations. *Global Change Biology*, 2015, **21**, pp. 2022–20.
23. Gao, Y. and Lynch, J. P., Reduced crown root number improves water acquisition under water deficit stress in maize (Zea mays L.). *J Exp Bot.* 2016, 67(15), pp. 4545–4557.
24. Sebastian, J., Yee, M. C. and Goudinho V. W., Grasses suppress shoot-borne roots to conserve water during drought. *National Academy of Sci*., 2016, **113**, pp. 8861-88866.

25. Martineau, E., Domec, J.C., Bosc, A., Dannoura, M., Gibon, Y., Bernard, C., Jordan-Meille, L., The role of potassium on maize leaf carbon exportation under drought condition. *Acta Physiol. Plant*, 2017, **39**, 219.

26. Cakmak, I., Hengeler, C., Marschner, H., Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. *J. Exp. Bot*., 1994, **45**, pp. 1251–1257.

27. Gerardeaux, E., Jordan-Meille, L., Constantin, J., Pellerin, S. and Dingkuhn, M., Changes in plant morphology and dry matter partitioning caused by potassium deficiency in Gossypium hirsutum (L.). *Environ. Exp. Bot*., 2010, **67**, pp. 451–459.

28. Römheld, V. and Kirkby, E. A., Research on potassium in agriculture: Needs and prospects. *Plant Soil*, 2010, **335**, pp. 155–180.

29. Shin, R., Burch, A.Y., Huppert, K.A., Tiwari, S.B., Murphy, A.S., Guilfoyle, T.J. and Schachtman, D.P., The Arabidopsis transcription factor MYB77 modulates auxin signal transduction. *Plant Cell*, 2007, **19**, pp. 2440–2453.

30. Song, W., Liu, S., Meng, L., Xue, R., Wang, C., Liu, G., Dong, C., Wang, S., Dong, J. and Zhang, Y., Potassium deficiency inhibits lateral root development in tobacco seedlings by changing auxin distribution. *Plant Soil*, 2015, **396 (1/2)**, 163–173.

31. Li, J., Wu, W. H. and Wang, Y., Potassium channel AKT1 is involved in the auxin-mediated root growth inhibition in Arabidopsis response to low K+ stress. *J. Int. Plant Biol*., 2017, **59**, pp. 895–909.

32. Harvey H. P., and Van Den Driessche, R., Nitrogen and potassium effects on xylem cavitation and water-use efficiency in poplars. *Tree Physiology*, 1999, **19**, pp. 943-950.

33. Henry A., Andrew, J., Batoto T. C., Torres R. O. and Serraj R., Root attributes affecting water uptake of rice (*Oryza sativa*) under drought. *Journal of Experimental Botany*, 2012, **63 (13)**, pp. 4751–4763.

34. Hasanuzzaman, M., Borhannuddin B. M. H. M., Nahar, K., Hossain Md. S., Mahmud Al J., and Hossen Md. S., Masud C. A. A., Moumita and Fujita, M., Potassium: A Vital Regulator of Plant Responses and Tolerance to Abiotic Stresses. *Agronomy*, 2018, **8**, 31.

Table 1 Summary of analysis of variance at p≥ 0.05, for water stress (WS) and potassium (K) nutrition treatments and their interactions (WS x K) on root architectural characteristics and seedling growth parameters, specific root area and water productivity.

Parameters	p Values		
	WS	**K**	**WS x K**
Projected root area (mm^2) at 7 DAE	*	*	ns
Projected root area (mm^2) at 14 DAE	*	*	ns
Projected root area (mm^2) at 21 DAE	*	*	*
Rooting depth (mm) at 7 DAE	*	*	ns
Rooting depth (mm) at 14 DAE	*	*	*
Rooting depth (mm) at 21 DAE	*	*	*
Maximum width (mm) at 7 DAE	*	*	ns
Maximum width (mm) at 14 DAE	*	*	ns
Maximum width (mm) at 21 DAE	*	*	*
Average root density at 7 DAE	*	*	ns
Average root density at 14 DAE	*	*	*
Average root density at 21 DAE	*	*	*
Maximum width to depth ratio at 7 DAE	*	*	*
Maximum width to depth ratio at 14 DAE	*	*	*
Maximum width to depth ratio at 21 DAE	*	*	ns
Root top angle (°) at 7 DAE	*	*	ns
Root top angle (°) at 14 DAE	*	*	ns
Root top angle (°) at 21 DAE	*	*	*
Root bottom angle (°) at 7 DAE	*	*	ns
Root bottom angle (°) at 14 DAE	*	*	ns
Root bottom angle (°) at 21 DAE	*	*	*
Root dry weight (g/seedling)	*	*	*
Specific root length (m/g)	*	*	ns
Shoot length (cm)	*	*	*
Total dry weight (g/seedling) at 21 DAE	*	*	*
Water productivity (mg/ml)	*	*	ns

(* significant at p≥ 0.05, ns: not significant)

Figure Legends

Figure 1 Schematic diagram of experimental setup: (A) estimation of field capacity of growing media, (B) experiment treatment imposition after seed emergence, (C) data acquisition and analysis of root architectural features. Inset: (D) sample scanned root image (E) and masked (at 3 threshold level) root image.

Figure 2 Daily weight loss of bags (g) (values are average of four isolated bags identical to experimental bags) and corresponding amount of nutrient solution applied (ml/bag) in different water stress treatments.

Figure 3 Projected root area (mm^2) (A, B, C), rooting depth (mm) (D, E, F) and average root density (G, H, I) at 7, 14 and 21 DAE (days after emergence) of rice seedling growing under NWS (no water stress), MWS(mild water stress) and SWS (severe water stress) with three levels of potassium : K- low potassium, K0- normal potassium and K+- high potassium (mean ± S.Em.).

Figure 4 Maximum width (mm) at (A, B, C), root top angle (D, E, F) and root bottom angle (G, H, I) at 7, 14 and 21 DAE (days after emergence). NWS- No water stress (100% FC), MWS- Mild water stress (60% FC), SWS- Severe water stress (20% FC), K- (low potassium), K0 (Normal potassium), K+ (High potassium).

Figure 5 Maximum width to depth ratio (A, B, C)at 7, 14 and 21 DAE (days after emergence). NWS- No water stress (100% FC), MWS- Mild water stress (60% FC), SWS- Severe water stress (20% FC), K- (low potassium), K0 (Normal potassium), K+ (High potassium).

Figure 6 Shoot length(cm) (A), root dry weight (g/seedling) (B), total dry weight (g/seedling) (c) and representative seedlings growth (D) of rice growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.).

Figure 7 Specific root length (m/g) of rice seedlings at 21 DAE growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.). Alphabet represent significant differences (at $p \geq 0.05$).

Figure 8 Water productivity (mg/ml) of rice seedlings at 21 DAE growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.). Alphabet represent significant differences (at $p \geq 0.05$).

Figure 9 Representative root architecture of rice seedlings growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) at 7, 14 and 21 DAE (days after emergence).

Figure 10 Observed percent relative changes (%) at the end of the experiment in rice root architectural features due to varied availability of water, potassium. NWS- No water stress (100% FC), MWS- Mild water stress (60% FC), SWS- Severe water stress (20% FC), K- (low potassium), K0 (Normal potassium), K+ (High potassium).

Figure 11 Stele diameter (mean ± SD, n= 5) (A) and representative radial cross section from 3-4 cm of the seminal root tip (B) of rice seedlings growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium).

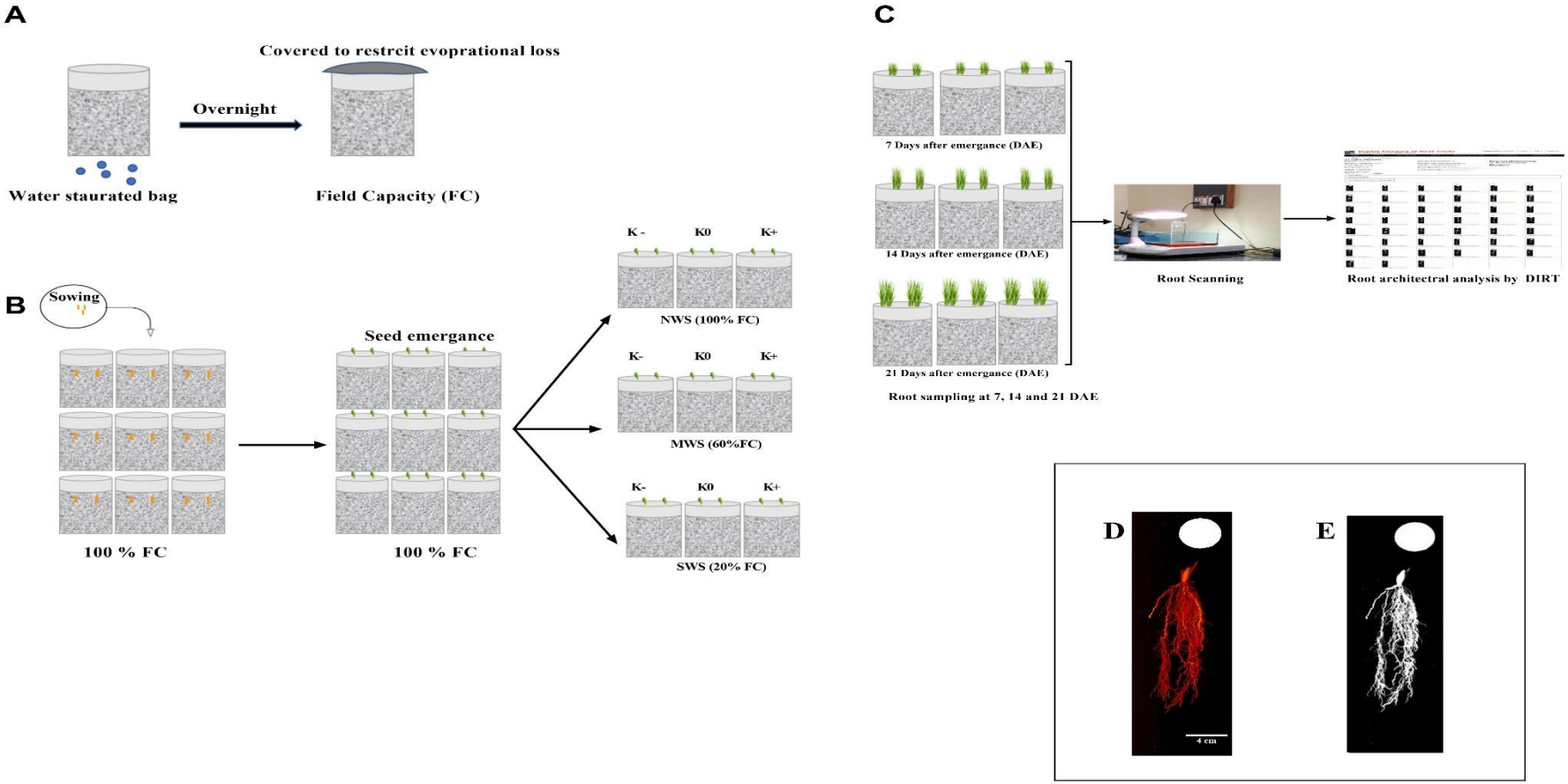

Figure 1 Schematic diagram of experimental setup: (A) Estimation of field capacity of growing media, (B) Treatment imposition after seed emergence (C) Data acquisition and analysis of root architectural features. Inset: (D) Sample scanned root image (E) and masked (at 3 threshold level) root image.

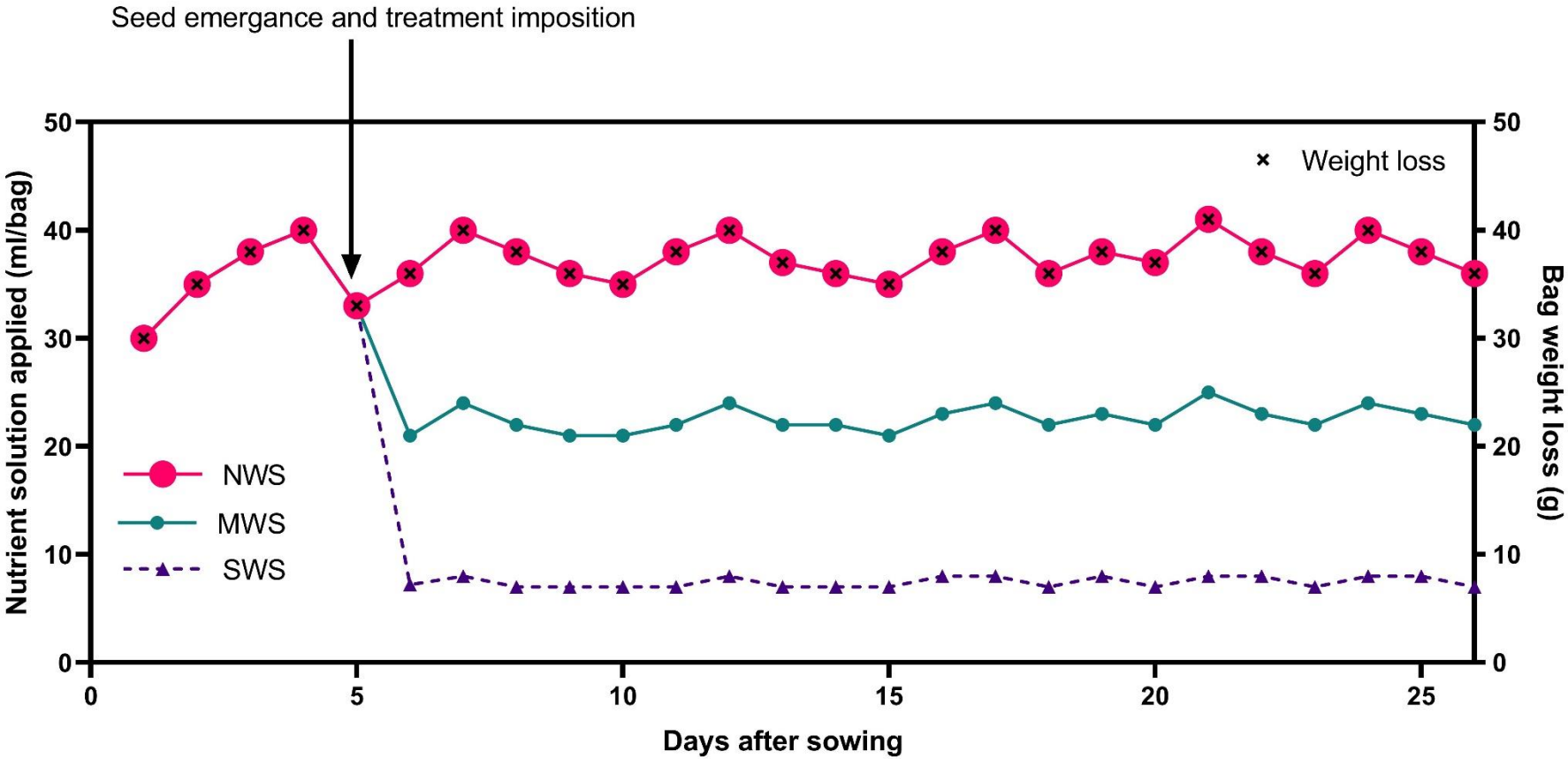

Figure 2 Daily weight loss of bags (g) (values are mean of four isolated bags identical to experimental bags) and corresponding amount of nutrient solution replenished (ml/bag) in different water stress treatments. NWS- No water stress (100% FC), MWS- Mild water stress (60% FC), SWS- Severe water stress (20% FC),

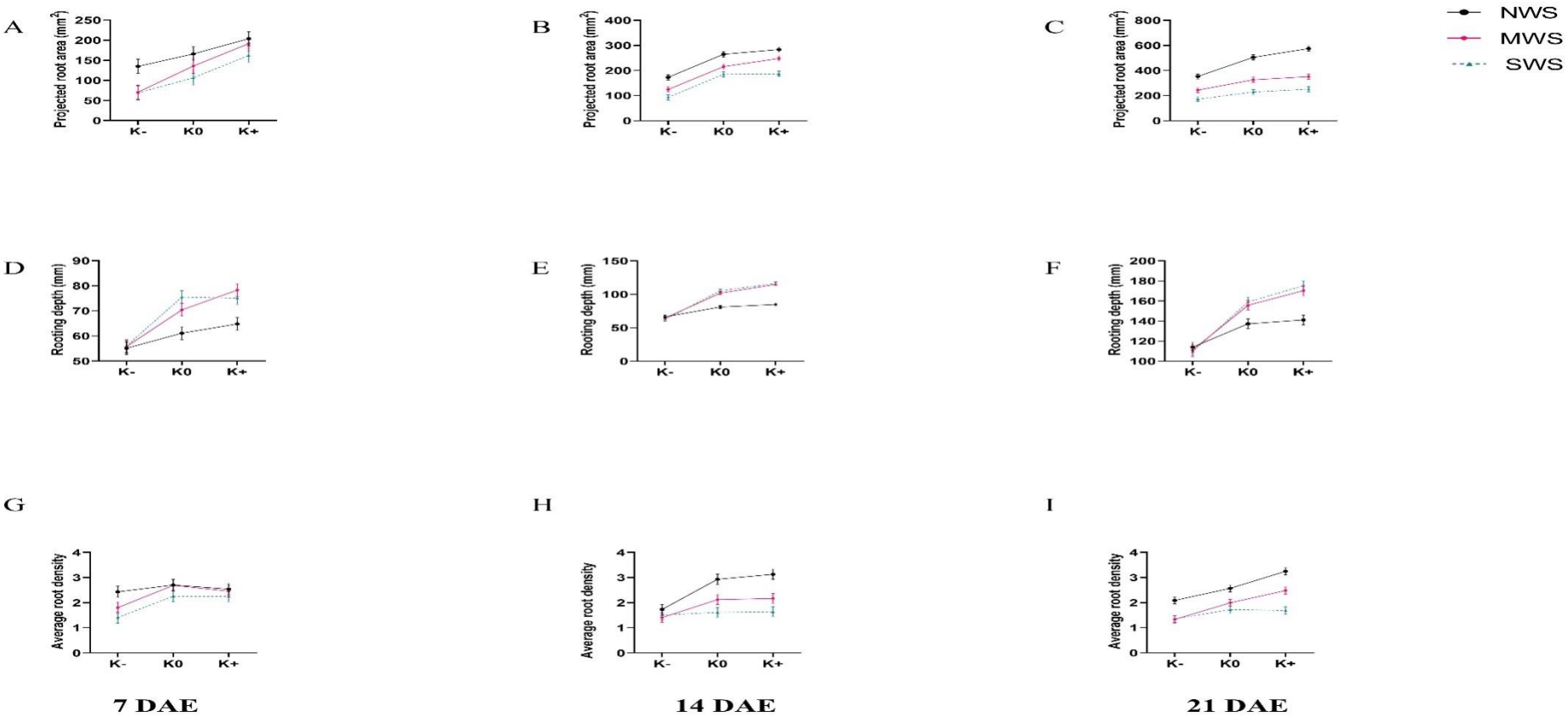

Figure 3 Projected root area (mm^2) (A, B, C), rooting depth (mm) (D, E, F) and average root density (G, H, I) at 7, 14 and 21 DAE (days after emergence) of rice seedling root growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium : K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.).

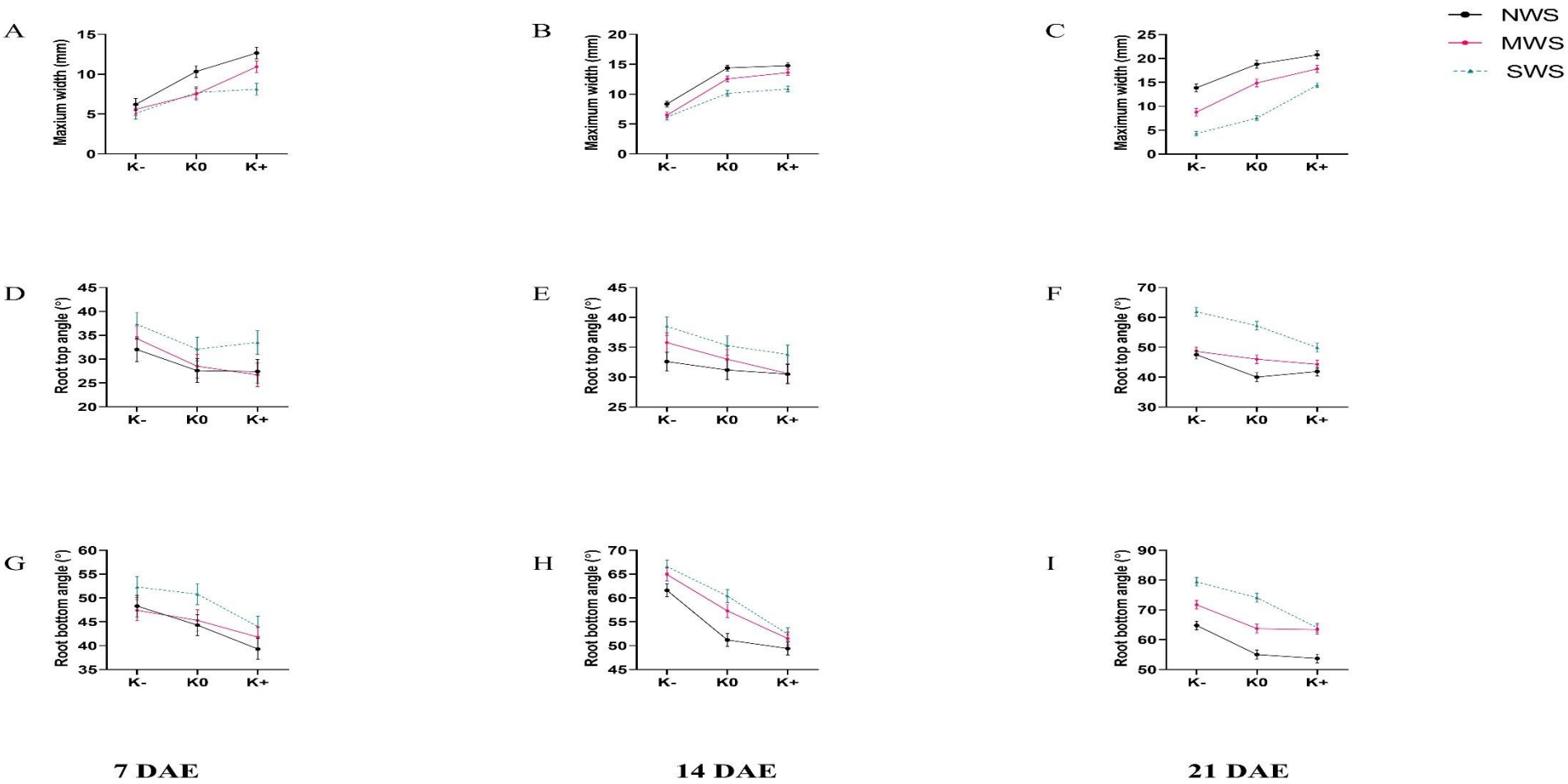

Figure 4 Maximum width (mm) (A, B, C), root top angle(°) (D, E, F) and root bottom angle (°) (G, H, I) at 7, 14 and 21 DAE (days after emergence) of rice seedling root growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.).

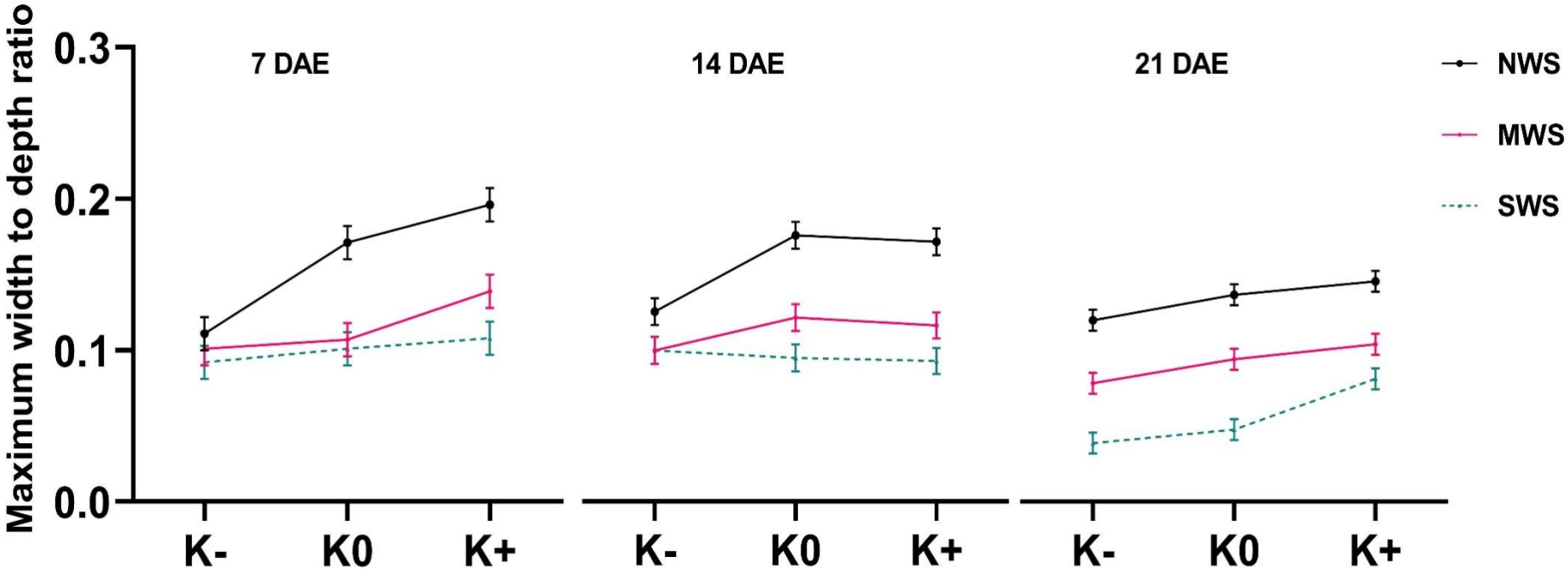

Figure 5 Maximum width to depth ratio at 7, 14 and 21 DAE (days after emergence) of rice seedling root growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium : K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.).

-

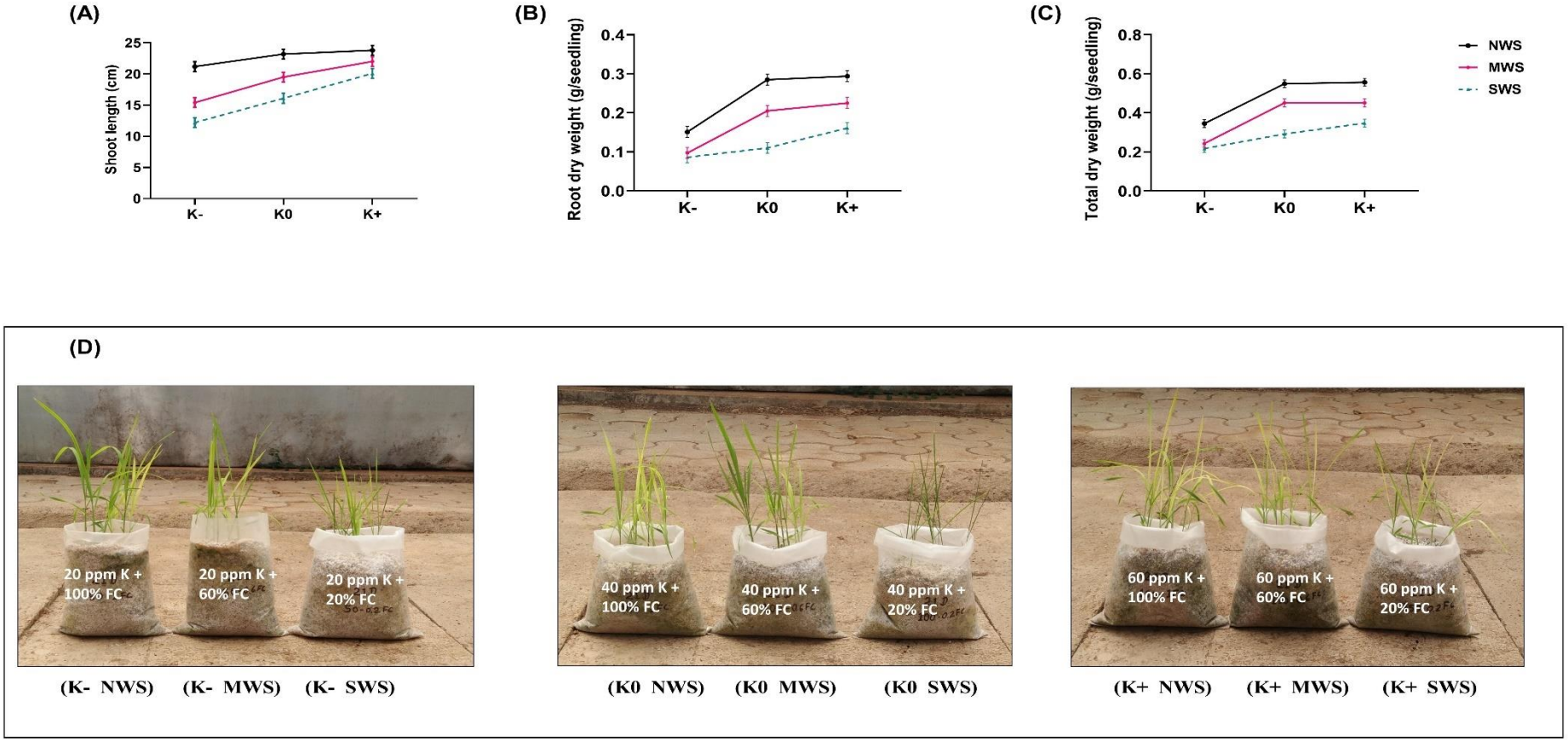

Figure 6 Shoot length(cm) (A), root dry weight (g/seedling) (B), total dry weight (g/seedling) (c) and representative seedlings growth (D) of rice growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.).

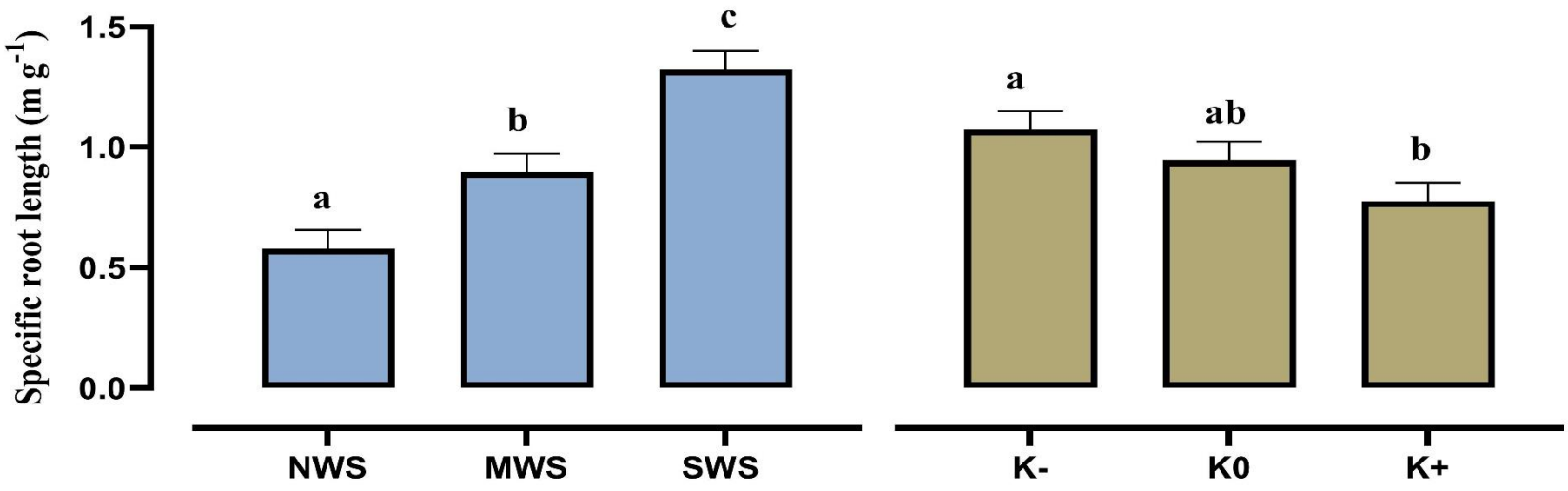

Figure 7 Specific root length (m/g) of rice seedlings at 21 DAE growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.). Alphabet represent significant differences (at $p \geq 0.05$).

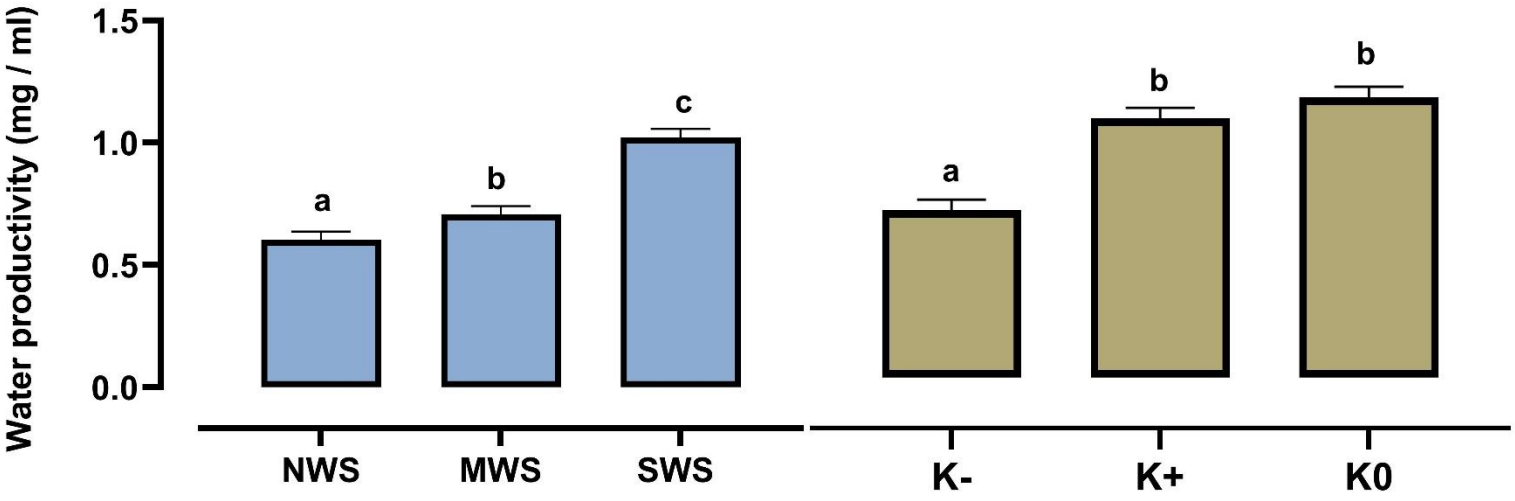

Figure 8 Water productivity (mg/ml) of rice seedlings at 21 DAE growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) (mean ± S.Em.). Alphabet represent significant differences (at $p \geq 0.05$).

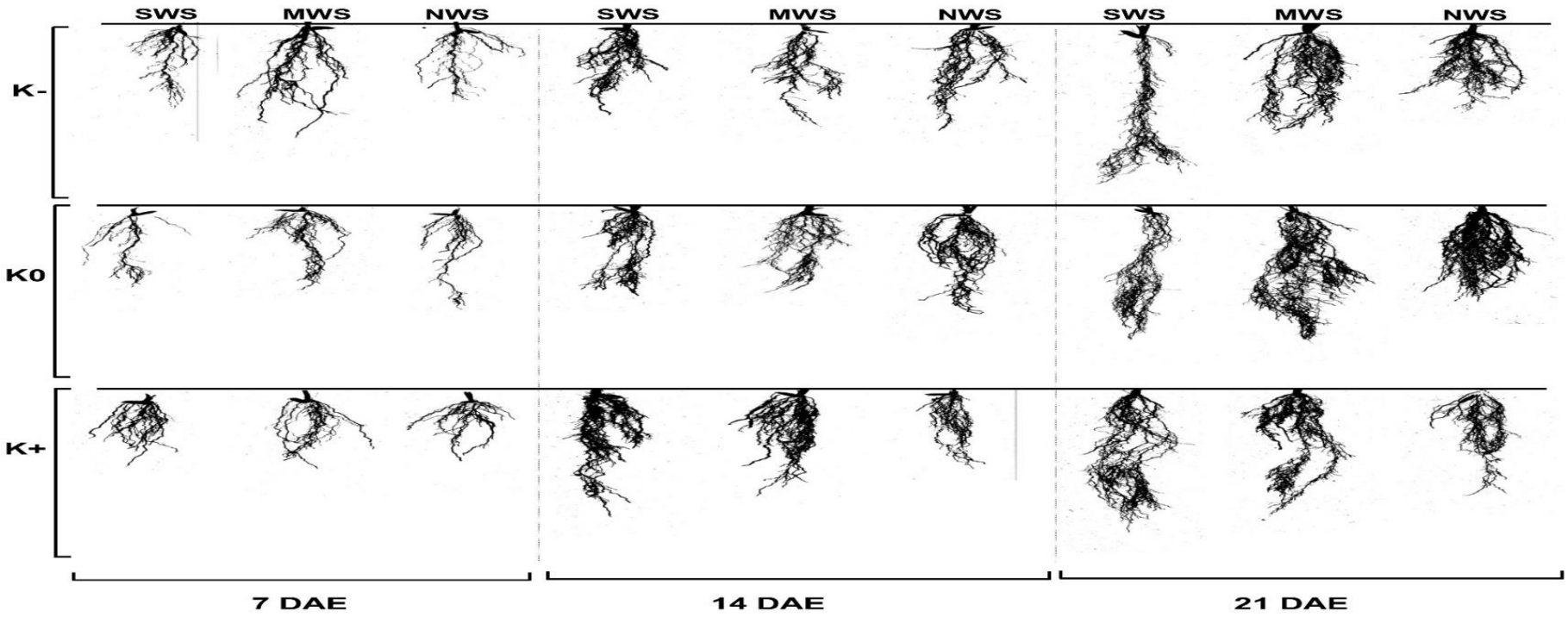

Figure 9 Representative root architecture of rice seedlings growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) with three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium) at 7, 14 and 21 DAE (days after emergence).

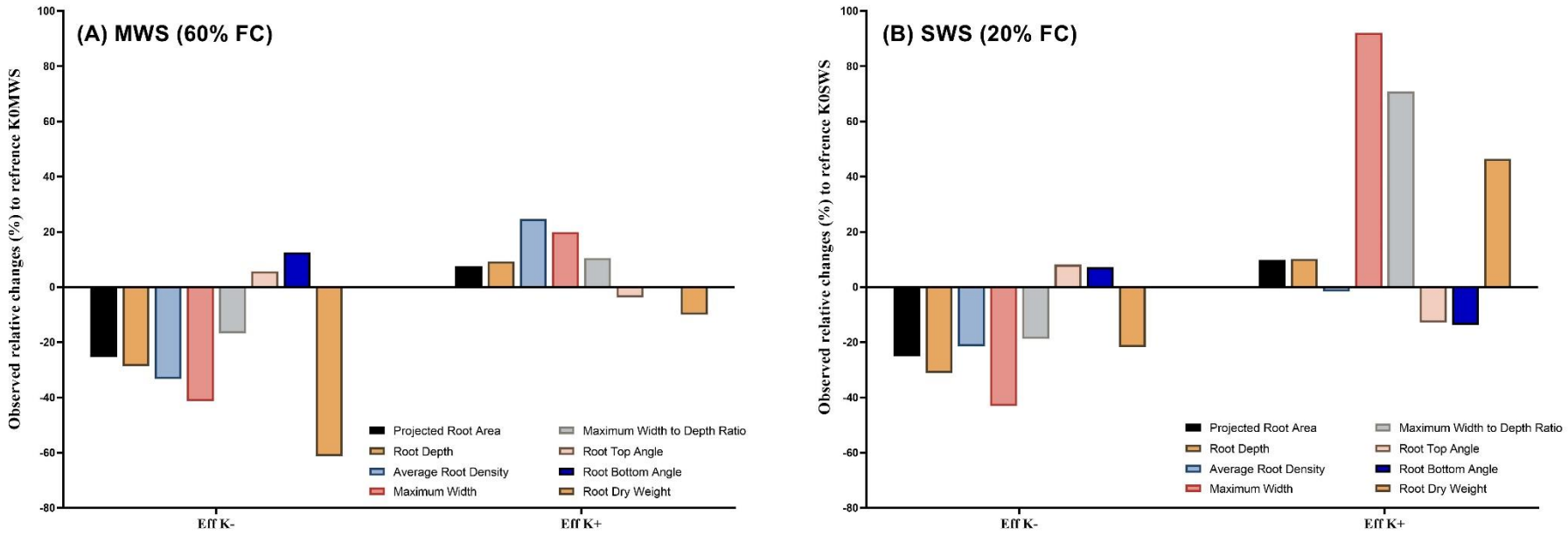

Figure 10 Observed relative changes (%) at the end of the experiment in rice seedlings roots due to effect of K- and K+ nutrition (A) under mild water stress (B) under severe water stress. Individual effect of K- and K+ are obtained by calculating the percent changes over optimal K nutrition under the respective water stress, as described in reference[22].

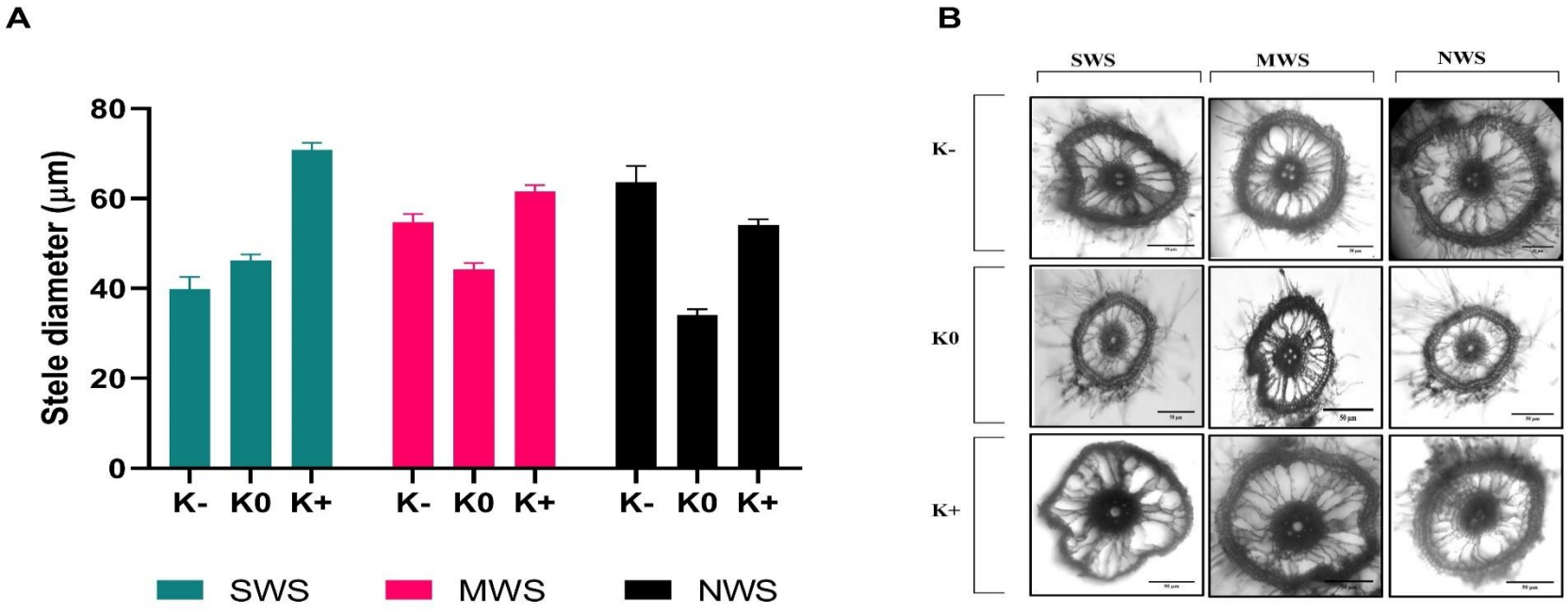

Figure 11 Stele diameter (mean ± SD, n= 5) (A) and representative radial cross section from 3-4 cm of the seminal root tip(B) of rice seedlings growing under NWS (no water stress), MWS (mild water stress) and SWS (severe water stress) and three levels of potassium: K- (low potassium), K0 (normal potassium) and K+ (high potassium).