agronomy

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# Growth Response of Cassava to Deficit Irrigation and Potassium Fertigation during the Early Growth Phase

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Received: 27 January 2020; Accepted: 24 February 2020; Published: 26 February 2020

**Abstract:** Cassava (*Manihot esculenta* Crantz) experiences intermittent water deficit and suffers from potassium (K) deficiency that seriously constrains its yield in the tropics. Currently, the interaction effect between deficit irrigation and K fertigation on growth and yield of cassava is unknown, especially during the early growth phase. Therefore, pot experiments were conducted under controlled greenhouse conditions using cassava cuttings. Treatments initiated at 30 days after planting included three irrigation doses (30%, 60%, 100% pot capacity) and five K (0.01, 1, 4, 16, and 32 mM) concentrations. The plants were harvested 90 days after planting. Decreasing irrigation dose to 30% together with 16 mM K lowered the leaf water potential by 69%, leaf osmotic potential by 41%, photosynthesis by 35%, stomatal conductance by 41%, water usage by 50%, leaf area by 17%, and whole-plant dry mass by 41%, compared with full-irrigated plants. Lowering the K concentration below 16 mM reduced the values further. Notably, growth and yield were decreased the least compared with optimal, when irrigation dose was decreased to 60% together with 16 mM K. The results demonstrate that deficit irrigation strategies could be utilized to develop management practices to improve cassava productivity by means of K fertigation under low moisture conditions.

**Keywords:** leaf area; *Manihot esculenta*; photosynthesis; tuber; water status

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## 1. Introduction

A global challenge for the agricultural sector is to produce more food with less water [1]. Developing new scientific strategies that allow crops to use water efficiently could be crucial in a world with a growing population [2]. Thus, water application strategies focused on increased agricultural water productivity, such as deficit irrigation coupled with potassium (K) fertigation to investigate multiple alternatives, have a pivotal role to play in sustainable crop production. Cassava (*Manihot esculenta* Crantz) is a major food crop for more than 800 million people in the tropics, providing more than 60% of daily calorific needs [3]. Cassava leaves are widely consumed, due to the high contents of protein, minerals, vitamins, lipids, and fiber, compared with roots that are mainly rich in carbohydrates [4,5]. Cassava is alternatively used as a processed food, animal feed, starch for pharmaceutical industries, and bioethanol for vehicles [6,7]. Even though cassava is considered drought-tolerant [8,9], the crop experiences intermittent water deficit [10] and suffers from K deficiency [11,12], which seriously constrains its yield in the tropics.

Water deficit restricts cassava growth and yield by decreasing the soil-water potential, which in turn limits stomatal conductance [13,14], resulting in reduced photosynthesis [15], number of leaves, and the individual leaf size [8,16]. It also leads to a reduction in shoot growth [17] and subsequent reduction in fresh and dry biomass [18,19]. Cassava shoot and root biomass can decrease by 70% under conditions of water deficit [20,21] but are more pronounced if the water deficit occurs during the first

1–5 months after planting [18,22] since plant leaf expansion and tuberous root development initiate during this period.

Cakmak and Engels [23] showed that water deficit increases the plant K requirement. K alleviates water deficit in plants by regulating the cell osmotic potential ($\Psi_s$) to maintain the turgor pressure ($\Psi_p$) required for cell functioning [24] and regulating the stomatal movement that aids in minimizing water losses during drought, leading to maintain the carbon dioxide ($CO_2$) fixation [25]. K also plays a key role in partitioning photosynthates to storage roots [26,27] and activation of enzymes [28]. It also increases heat tolerance in plants [26]. Byju et al. [29] estimated that cassava requires a total uptake of 15.6 K kg ha$^{-1}$ to produce a single metric ton of dry root yield. Thus, improving K nutrition in drought areas with low inherent soil fertility could increase cassava productivity. Lately, cassava yields have been improved through irrigation [30,31] and nutrient application [29,32]. Studies of K nutrition in cassava have also been performed [33,34] with granular K application. However, no studies have combined water deficit strategies and K fertigation in cassava to elaborate its effect on growth and yield. Moreover, understanding how young cassava plants respond to deficit irrigation and K fertigation during the early growth phase is essential for holistic agronomic management to ensure improvements in terms of growth and marketable yield under drought conditions. Therefore, the objective of this work is to assess the effects of interaction between deficit irrigation and K fertigation on growth and yield response of biofortified cassava during the early growth phase.

## 2. Materials and Methods

### 2.1. Plant Material and Growth Conditions

Four pot experiments were conducted with single-stem cuttings (25 cm) of yellow cassava "Mutura" cultivar (Kenya Agricultural and Livestock Research Organization (KALRO), Nairobi, Kenya). Cuttings were planted in 5-L pots containing 1.7 kg of pre-fertilized potting mix (pH 5.5, N–P–K: 17–4–25, organic matter: 25–40%, Kekkilä Karkea ruukutusseos, W R8014; Kekkilä Oy, Vantaa, Finland). The potting mix was saturated with water and allowed to drain overnight, and the maximum soil water holding capacity (1600 g pot$^{-1}$) was calculated as the difference between water applied and water drained. The pots were placed in the greenhouse at the University of Helsinki, Finland, under controlled conditions with day/night temperatures of 28/20 °C and relative humidity of 55% ± 5%. High-pressure sodium lamps (Master son-t; Philips Lighting N.V., Eindhoven, The Netherlands) provided a 12-h photoperiod with photosynthetic photon flux density (PPFD) of 600 µmol photosynthetically active radiation (PAR) m $^{-2}$ s$^{-1}$ at the top of the canopy. The plants were watered every second day on the soil surface until drainage for 30 days, and the side shoots were trimmed to maintain single-stemmed plants. At 30 days after planting (DAP), treatments lasting 60 days were initiated. There were three irrigation doses (30%, 60%, 100% pot capacity) in all four experiments that were further split into a range of K (potassium chloride (KCl); Sigma-Aldrich Chemie GmbH, Munich, Germany) concentrations of 0.01 mM (EXP. I, III, IV), 1 mM (EXP. I, II, III, IV), 4 mM (EXP. II, IV), 16 mM (EXP. I, II, III), and 32 mM (EXP. III, IV) of irrigation water. Plants were watered every second day with full-strength Hoagland solution [35] in which the K concentration was modified. The experiments were arranged in a completely randomized design with four (EXP. I, in total 36 pots) to eight (EXP. II, III, IV, in total 72 pots each) replicates.

### 2.2. Measurements

Morpho-physiological traits were measured at 15-day intervals, beginning 30 DAP between 11:00 and 13:00 h from the three uppermost fully expanded leaves of each plant. The leaf temperature was measured, using an infrared thermometer (Fluke 574; Fluke Corporation, Everett, WA, USA). The chlorophyll content was measured with an Apogee MC-100 meter (Apogee Instruments, Logan, UT, USA). Net photosynthesis and stomatal conductance were measured with a portable photosynthesis meter (LI-6400; LI-COR, Lincoln, NE, USA). The plant height was measured from the soil level to the tip of the plant. The leaf water potential ($\Psi_w$) was measured according to McCutchan and Shackel [36] by first covering the leaflets with bags made of black plastic on the inside and aluminum foil on the outside to prevent leaf transpiration. After 1 h, the leaflets were detached and leaf $\Psi_w$ was measured, using a pressure chamber (Soilmoisture Equipment Corp; Goleta, CA, USA). The osmolality was analyzed from the leaves used for the $\Psi_w$ measurements, using a freezing-point depression osmometer (Micro-Osmometer 3300 M; Advanced Instruments, Norwood, MA, USA) as described by Mäkelä et al. [37]. The osmotic potential ($\Psi_s$) was calculated from the osmolality values as $\pi$ (osmotic pressure, MPa) = $cRT$, where $RT$ ($R$ is the gas constant (J mol$^{-1}$ K$^{-1}$), $T$ is absolute temperature (K)) is 2.48 and $c$ the osmolality (osmol kg$^{-1}$). Leaf turgor ($\Psi_p$) was estimated as $\Psi_w$–$\Psi_s$. The pots were weighed every second day before irrigation and K treatment application to monitor water usage.

The plants were harvested at 90 DAP by cutting the stems at the soil surface. Leaves were detached from the plants, and the roots were carefully washed with water to remove soil. The fresh weight of the leaves, stems, and roots was recorded. The green and senescent leaves were then separated, and the green leaf area was measured with a portable leaf area meter (LI-3000; LI-COR, Lincoln, NE, USA). The green leaves and tuberous roots were divided into two subsamples. One subsample of each was snap-frozen in liquid $N_2$ and stored at −20 °C until further analysis. The other subsample was dried in a forced-air chamber at 70 °C for 72 h, weighed, ground to pass a 0.5-mm sieve using a centrifugal mill (ZM200; Retsch, Haan, Germany) and stored at room temperature until further analysis.

### 2.3. Potassium Analysis

The K content was analyzed from the ground leaf and root subsamples. Plant material (250 mg) was weighed into polytetrafluoroethylene (PTFE) Teflon tubes (CEM Corp; Matthews, NC, USA) and 6 mL of 15.2 M nitric acid (68% *w/v*; VWR International BVBA, Leuven, Belgium) and 1 mL of 9.8 M hydrogen peroxide (30% *w/v*; Merck KGaA, Darmstadt, Germany) were added for microwave digestion (MARS 240/50; MARSXpress, CEM). The digested samples were filtered through paper (Whatman grade no. 42, pore size 2.5 µm; GE Healthcare, Gloucester, Cheltenham, UK), diluted in purified water and stored at −20 °C. Elemental analysis was conducted with an inductively coupled plasma-optical emission spectrometer (iCAP 6200; Thermo Fisher Scientific, Cambridge, UK) with every 20th sample as standard.

### 2.4. Statistical Analyses

Data of the four experiments were combined and analyzed as one experiment, after subjecting to contrast analysis for experimental differences. To show the effects of irrigation doses, K concentrations, and their interactions as fixed effects on traits measured, a two-way ANOVA was carried out. Differences were considered significant when the $p$-values were <0.05, and means were compared using Tukey's multiple range test. In addition, a two-tailed Pearson correlation was calculated to measure the patterns of relationship among the traits measured. All statistical analyses were carried out using R program (version 3.5.1; R Development Core Team, Vienna, Austria) [38].

## 3. Results

### 3.1. Physiological Parameters

The irrigation and K doses showed significant interactive effects on leaf $\Psi_w$ and $\Psi_s$ (Figure 1). When irrigation dose was decreased to 30% together with 0.01 mM K, leaf $\Psi_w$ and $\Psi_s$ were each lowered to −2.7 MPa by 90 DAP but increasing the K concentration to 32 mM increased leaf $\Psi_w$ to −1.6 MPa and leaf $\Psi_s$ to −1.8 MPa. Conversely, when irrigation dose was decreased to 60% together with 0.01 mM K, leaf $\Psi_w$ and $\Psi_s$ were each lowered to –2.3 MPa; however, increasing the K concentration to 32 mM increased leaf $\Psi_w$ to −0.8 MPa and leaf $\Psi_s$ to −1.3 MPa by 90 DAP. In general, leaf $\Psi_w$ and $\Psi_s$ values remained maximum in full irrigated plants together with 32 mM K.

The different irrigation and K doses significantly affected leaf $\Psi_p$ but showed no interactive effects (Table 1). Leaf $\Psi_p$ greatly reduced when irrigation dose was decreased to 30% rather than to 60%, compared with full-irrigated plants (100%). Notably, increasing the K concentration to either 16 or 32 mM resulted in increased $\Psi_p$ by 90 DAP, regardless of the irrigation doses. In addition, the $\Psi_p$ loss point or the critical potential was observed at 90 DAP, where leaf $\Psi_p$ was greatly reduced when irrigation dose was decreased to 30% and K concentration was 0.01 mM.

**Table 1.** Leaf turgor ($\Psi_p$) of young cassava plants in response to deficit irrigation and K fertigation. The treatments were initiated 30 days after planting and lasted 60 days. The data from four separate experiments were combined and shown as the means ± standard error of 4–16 replicate plants.

| **Treatment** | | **Leaf Turgor (MPa)** | | | | |
|---|---|---|---|---|---|---|
| | | **30 DAP** | **45 DAP** | **60 DAP** | **75 DAP** | **90 DAP** |
| Irrigation | 30% | 0.46 | 0.39 | 0.29 $^{a}$ | 0.18 $^{a}$ | 0.11 $^{a}$ |
| | 60% | 0.48 | 0.43 | 0.37 $^{b}$ | 0.36 $^{b}$ | 0.30 $^{b}$ |
| | 100% | 0.48 | 0.49 | 0.50 $^{c}$ | 0.51 $^{c}$ | 0.55 $^{c}$ |
| | S.E.M (df = 3–15) | 0.017 | 0.036 | 0.039 | 0.034 | 0.038 |
| Potassium | 0.01 mM | 0.47 | 0.4 | 0.29 | 0.25 $^{a}$ | 0.10 $^{a}$ |
| | 1 mM | 0.48 | 0.42 | 0.35 | 0.30 $^{ab}$ | 0.24 $^{b}$ |
| | 4 mM | 0.46 | 0.43 | 0.38 | 0.34 $^{b}$ | 0.32 $^{c}$ |
| | 16 mM | 0.48 | 0.46 | 0.45 | 0.43 $^{c}$ | 0.45 $^{d}$ |
| | 32 mM | 0.48 | 0.48 | 0.47 | 0.46 $^{c}$ | 0.49 $^{d}$ |
| | S.E.M (df = 3–15) | 0.022 | 0.046 | 0.05 | 0.044 | 0.05 |
| *p*-value (<0.05) | I | 0.738 | 0.134 | 0.001 | <0.001 | <0.001 |
| | K | 0.964 | 0.710 | 0.068 | 0.004 | <0.001 |
| | I × K | 0.896 | 0.998 | 1.000 | 0.997 | 0.288 |

Means followed by different letters in the same column are different (Tukey's test $p < 0.05$). DAP = days after planting; I = irrigation; K = potassium; S.E.M. = standard error of the mean; df = degrees of freedom.

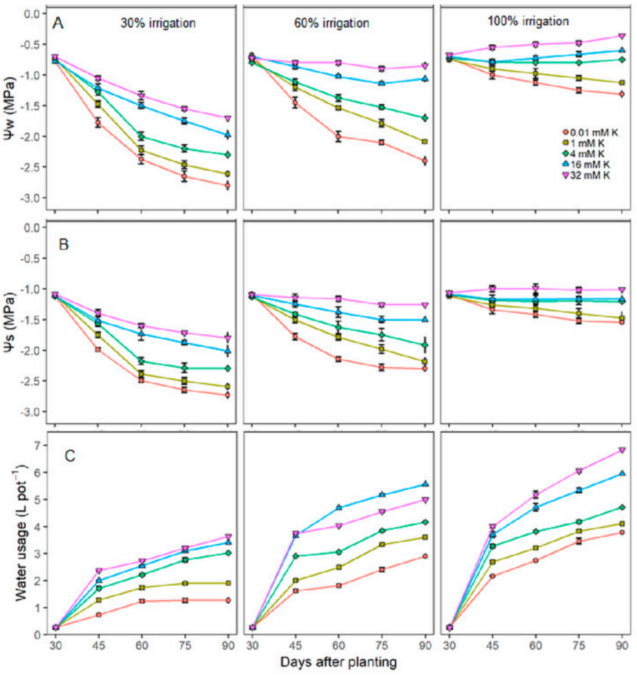

**Figure 1.** Leaf water potential $\Psi_w$ (**A**), leaf osmotic potential $\Psi_s$ (**B**), and water usage (**C**) of young cassava plants in response to deficit irrigation and K fertigation. The treatments were initiated 30 days after planting and lasted 60 days. The data from four separate experiments were combined and shown as the means ± standard error of 4 to 16 replicate plants.

Plant water usage followed a trend similar to that observed in leaf $\Psi_w$ (Figure 1)**.** Decreasing irrigation dose to 30% together with 0.01 mM K caused an 80% reduction in water usage between 30 and 90 DAP. However, when the K concentration was increased to 32 mM, water usage reduced by 45% compared with full-irrigated plants. Notably, decreasing irrigation dose to 60% together with 16 mM K only caused a 13% reduction in water usage compared with full-irrigated plants.

Moreover, the irrigation and K doses showed significant interactive effects on net photosynthesis, stomatal conductance, leaf temperature, and leaf chlorophyll (Figures 2 and 3). Decreasing irrigation dose to 30% together with 0.01 mM K reduced the net photosynthesis and stomatal conductance by 70% and leaf chlorophyll by 51% between 30 and 90 DAP. However, when the K concentration was increased to 16 mM, the net photosynthesis reduced by 35%, stomatal conductance by 41%, and leaf chlorophyll by 34% between 30 and 90 DAP, compared with full-irrigated plants. In contrast, decreasing irrigation dose to 60% together with 0.01 mM K reduced net photosynthesis by 56%, stomatal conductance by 42%, and leaf chlorophyll by 38% between 30 and 90 DAP. Moreover, increasing the K concentration to 16 mM reduced the net photosynthesis by 21%, stomatal conductance by 19%, and leaf chlorophyll by 18%. In all, decreasing irrigation dose to 60% together with 16 mM K resulted in the least reduction in net photosynthesis and stomatal conductance, although the least reduction in leaf chlorophyll was observed when irrigation dose was decreased to 60% together with 32 mM K.

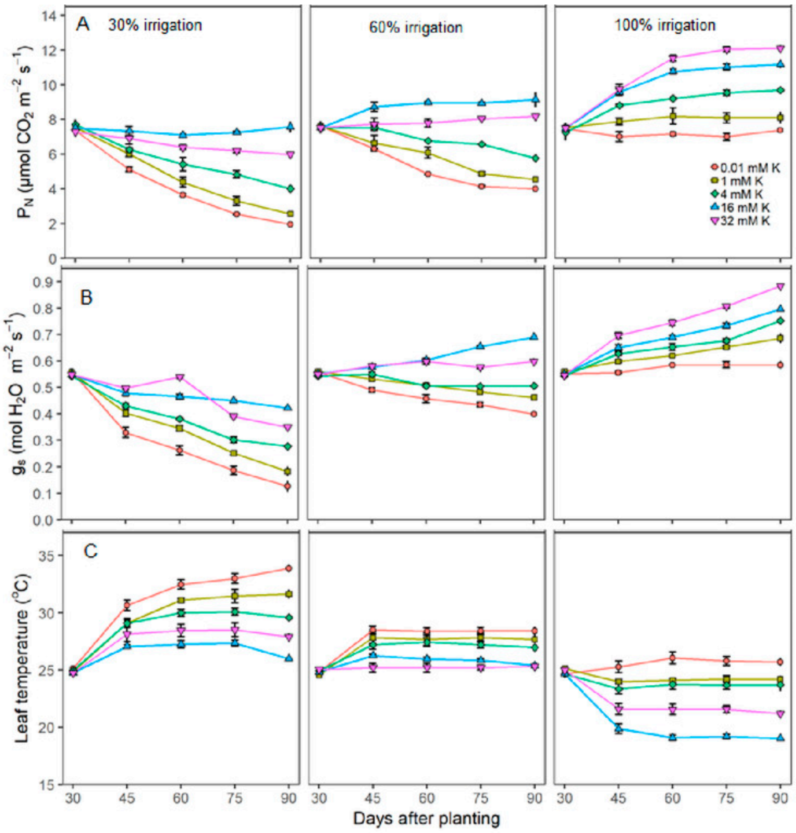

**Figure 2.** Net photosynthesis $P_N$ (**A**), stomatal conductance $g_s$ (**B**), and leaf temperature (**C**) of young cassava plants in response to deficit irrigation and K fertigation. The treatments were initiated 30 days after planting and lasted 60 days. The data from four separate experiments were combined and shown as the means ± standard error of 4 to 16 replicate plants.

The leaf temperature increased when the irrigation dose was decreased, but the leaf temperature declined when the K concentration was increased (Figure 2). At 90 DAP, the leaf temperature was highest (34 °C) when irrigation dose was decreased to 30% together with 0.01 mM K, but when the K was increased to 16 mM, the leaf temperature was low (26 °C). Likewise, when irrigation dose was decreased to 60% together with 0.01 mM K, the leaf temperature was 28 °C, but when K was increased to either 16 or 32 mM, the leaf temperature was 26 °C. In all, decreasing irrigation dose to 60% together with 32 mM K showed the lowest leaf temperature (25 °C) between 30 and 90 DAP compared with full-irrigated plants.

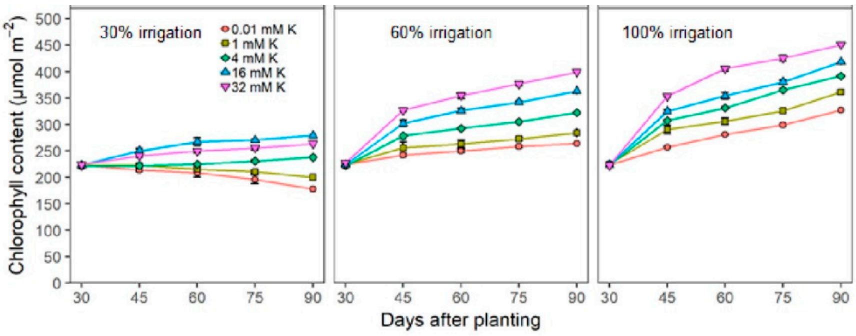

**Figure 3.** Leaf chlorophyll content of young cassava plants in response to deficit irrigation and K fertigation. Treatments were initiated 30 days after planting and lasted 60 days. The data from four separate experiments were combined and shown as the means ± standard error of 4 to 16 replicate plants.

### 3.2. Growth Parameters

The irrigation and K doses showed interactive effects on plant height (Figure 4). The plants were 49% shorter by 90 DAP when irrigation dose was decreased to 30% but 27% shorter when irrigation dose was decreased to 60%, compared with full-irrigated plants. Notably, lowering the K concentration below 16 mM resulted in shorter plants, regardless of the irrigation doses. The plants were 72% shorter when irrigation dose was decreased to 30% together with 0.01 mM K but were 52% shorter when K was increased to 16 mM K by 90 DAP, compared with full-irrigated plants. The smallest difference in heights was obtained when irrigation dose was decreased to 60% together with 32 mM K, compared with full-irrigated plants.

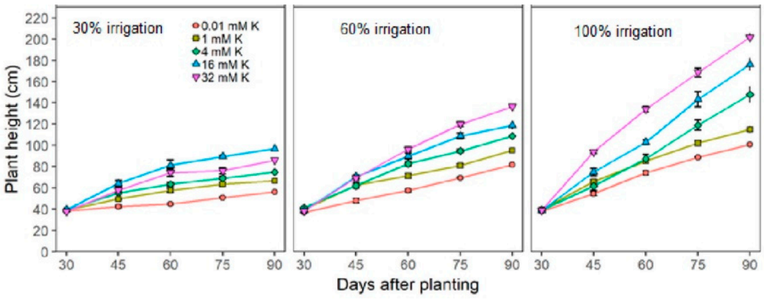

**Figure 4.** Plant height of young cassava plants in response to deficit irrigation and K fertigation. The treatments were initiated 30 days after planting and lasted 60 days. The data from four separate experiments were combined and shown as the means ± standard error of 4 to 16 replicate plants.

The plant leaf area, tuber number, leaf dry mass, stem dry mass, root dry mass, and whole-plant dry mass differed significantly with the irrigation and K doses and their interactions (Table 2). Decreasing irrigation doses substantially reduced these parameter values, while increasing the K increased their values. The plant leaf areas were 17% smaller and whole-plant dry mass was 41% lower when irrigation dose was decreased to 30% together with 16 mM K, compared with full-irrigated plants. In contrast, the plant leaf areas were 8% smaller and whole-plant dry mass was 13% lower when irrigation dose was decreased to 60% together with 16 mM K. This treatment combination showed the least decrease compared with full-irrigated plants. Otherwise, the largest leaf areas were obtained in full-irrigated plants together with 16 or 32 mM K, which were similar, whereas the highest whole-plant dry mass was obtained in full-irrigated plants with 32 mM K.

**Table 2.** Plant leaf area, leaf dry mass, shoot dry mass, root dry mass, and whole-plant dry mass of 90-day-old cassava plants in four pot experiments. Deficit irrigation and K fertigation were initiated 30 days after planting and lasted 60 days. The data from separate experiments were combined and shown as the means of 4 to 16 replicate plants.

| Treatment | | Plant Leaf Area ($m^2$) | Dry Mass (g) | | | |
|---|---|---|---|---|---|---|
| | | | Leaves | Shoot | Roots | Whole-Plant |
| Irrigation | Potassium | | | | | |
| 30% | 0.01 mM | 0.37 $^{a}$ | 16.9 $^{a}$ | 13.6 $^{a}$ | 11.0 $^{a}$ | 41.4 $^{a}$ |
| | 1 mM | 0.38 $^{a}$ | 20.0 $^{ab}$ | 24.6 $^{bcd}$ | 13.5 $^{ab}$ | 58.1 $^{b}$ |
| | 4 mM | 0.44 $^{ab}$ | 20.6 $^{ab}$ | 24.4 $^{bcd}$ | 17.7 $^{bc}$ | 62.7 $^{b}$ |
| | 16 mM | 0.57 $^{d}$ | 29.7 $^{c}$ | 29.4 $^{cde}$ | 25.5 $^{d}$ | 84.6 $^{c}$ |
| | 32 mM | 0.48 $^{bc}$ | 20.6 $^{ab}$ | 27.7 $^{bcd}$ | 27.5 $^{d}$ | 75.8 $^{c}$ |
| 60% | 0.01 mM | 0.38 $^{a}$ | 23.3 $^{b}$ | 19.0 $^{ab}$ | 22.8 $^{d}$ | 65.0 $^{b}$ |
| | 1 mM | 0.48 $^{b}$ | 33.6 $^{cd}$ | 33.3 $^{de}$ | 26.8 $^{d}$ | 93.6 $^{d}$ |
| | 4 mM | 0.59 $^{d}$ | 33.7 $^{cd}$ | 33.0 $^{de}$ | 34.7 $^{e}$ | 101.4 $^{de}$ |
| | 16 mM | 0.63 $^{de}$ | 39.9 $^{e}$ | 37.5 $^{ef}$ | 46.8 $^{gh}$ | 124.2 $^{h}$ |
| | 32 mM | 0.62 $^{de}$ | 33.6 $^{de}$ | 33.6 $^{de}$ | 41.3 $^{fg}$ | 108.6 $^{ef}$ |
| 100% | 0.01 mM | 0.42 $^{ab}$ | 34.8 $^{d}$ | 20.8 $^{abc}$ | 24.7 $^{d}$ | 80.3 $^{c}$ |
| | 1 mM | 0.56 $^{cd}$ | 32.1 $^{cd}$ | 44.5 $^{fg}$ | 38.5 $^{ef}$ | 115.2 $^{fg}$ |
| | 4 mM | 0.62 $^{de}$ | 35.3 $^{d}$ | 47.2 $^{g}$ | 39.1 $^{ef}$ | 121.6 $^{gh}$ |
| | 16 mM | 0.68 $^{e}$ | 40.5 $^{d}$ | 44.8 $^{fg}$ | 55.0 $^{i}$ | 140.3 $^{i}$ |
| | 32 mM | 0.68 $^{e}$ | 40.2 $^{d}$ | 50.9 $^{g}$ | 51.8 $^{hi}$ | 142.9 $^{i}$ |
| S.E.M (df = 3–15) | | 0.016 | 0.86 | 1.92 | 1.12 | 1.82 |
| *p*-value (<0.05) | I | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | K | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | I × K | <0.001 | <0.001 | 0.001 | <0.001 | <0.001 |

Means followed by different letters in the same column are different (Tukey's test $p < 0.05$). S.E.M. = standard error of the mean; df = degrees of freedom; I = irrigation; K = potassium.

The leaf, stem, and root dry mass followed trends similar to that observed with whole-plant dry mass. Decreasing irrigation dose to 30% together with 16 mM K resulted in fewer tubers. Conversely, the tubers were much fewer when the K concentration was lowered below 16 mM. Substantially high numbers of tubers were obtained when irrigation dose was decreased to 60% together with 16 or 32 mM K, which did not vary.

### 3.3. Correlation of Physiological and Growth Traits

Statistically significant relationships were observed among the traits measured (Table 3). Net photosynthesis was highly correlated ($0.906 \leq r \leq 0.980$; $p < 0.05$) with stomatal conductance, leaf $\Psi_w$, leaf $\Psi_s$, leaf chlorophyll, water usage, and whole-plant dry mass. Positive associations ($0.719 \leq r \leq 0.897$; $p < 0.05$) were also found between plant leaf area, plant height, tuber number, and water usage. However, the leaf temperature correlated negatively ($-0.923 \leq r \leq -0.772$; $p < 0.05$) with all traits measured.

**Table 3.** Pearson correlation matrix for morpho-physiological traits of young cassava plants in response to deficit irrigation and K fertigation.

| | LDM | RDM | WPD | TBN | LA | PLH | Chl | LT | $P_N$ | $g_s$ | $\Psi_w$ | $\Psi_s$ | $\Psi_p$ | WUS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LDM | 1 | | | | | | | | | | | | | |
| RDM | 0.826 ** | 1 | | | | | | | | | | | | |
| WPD | 0.875 ** | 0.951 ** | 1 | | | | | | | | | | | |
| TBN | 0.719 ** | 0.825 ** | 0.834 ** | 1 | | | | | | | | | | |
| LA | 0.736 ** | 0.832 ** | 0.887 ** | 0.743 ** | 1 | | | | | | | | | |
| PLH | 0.792 ** | 0.897 ** | 0.911 ** | 0.812 ** | 0.823 ** | 1 | | | | | | | | |
| Chl | 0.857 ** | 0.928 ** | 0.936 ** | 0.777 ** | 0.832 ** | 0.930 ** | 1 | | | | | | | |
| LT | −0.807 ** | −0.870 ** | −0.894 ** | −0.809 ** | −0.772 ** | −0.869 ** | -0.889 ** | 1 | | | | | | |
| $P_N$ | 0.838 ** | 0.915 ** | 0.933 ** | 0.823 ** | 0.835 ** | 0.928 ** | 0.939 ** | −0.912 ** | 1 | | | | | |
| $g_s$ | 0.881 ** | 0.906 ** | 0.940 ** | 0.781 ** | 0.786 ** | 0.892 ** | 0.951 ** | −0.923 ** | 0.939 ** | 1 | | | | |
| $\Psi_w$ | 0.825 ** | 0.896 ** | 0.915 ** | 0.759 ** | 0.819 ** | 0.890 ** | 0.953 ** | −0.898 ** | 0.941 ** | 0.956 ** | 1 | | | |
| $\Psi_s$ | 0.802 ** | 0.869 ** | 0.886 ** | 0.725 ** | 0.792 ** | 0.865 ** | 0.929 ** | −0.880 ** | 0.921 ** | 0.936 ** | 0.975 ** | 1 | | |
| $\Psi_p$ | 0.682 ** | 0.746 ** | 0.763 ** | 0.662 ** | 0.690 ** | 0.737 ** | 0.781 ** | −0.725 ** | 0.763 ** | 0.773 ** | 0.820 ** | 0.671 ** | 1 | |
| WUS | 0.831 ** | 0.935 ** | 0.933 ** | 0.775 ** | 0.864 ** | 0.931 ** | 0.964 ** | −0.868 ** | 0.931 ** | 0.923 ** | 0.946 ** | 0.928 ** | 0.761 ** | 1 |

**: differences between traits are significant at $p < 0.01$. LDM = leaf dry mass; RDM = root dry mass; WPD = whole-plant dry mass; TBN = tuber number; LA = leaf area; PLH = plant height; Chl = leaf chlorophyll; LT = leaf temperature; $P_N$ = net photosynthesis; $g_s$ = stomatal conductance; $\Psi_w$ = leaf water potential; $\Psi_s$ = leaf osmotic potential; $\Psi_p$ = leaf turgor; WUS = water usage.

### *3.4. Potassium Content*

The irrigation and K doses significantly affected the K content but showed no interactive effects (Table 4). When irrigation dose was decreased to 30%, the K content in the roots was 14% lower, but when irrigation dose was decreased to 60%, the K content in the roots was 9% lower. Increasing the K concentration to 32 mM resulted in the highest K content in both the leaves and roots. In general, K contents were all higher in the leaves than in the roots.

**Table 4.** Potassium (K) content in the leaves and roots of 90-day-old cassava plants in four pot experiments. Deficit irrigation and K fertigation were initiated 30 days after planting and lasted 60 days. The data from separate experiments were combined and shown as the means of 4 to 16 replicate plants.

| **Treatment** | | **K Content (g $kg^{-1}$ Dry Matter)** | |
|---|---|---|---|
| | | **Leaves** | **Roots** |
| Irrigation | 30% | 12.6 $^{a}$ | 9.9 |
| | 60% | 14.6 $^{b}$ | 10.5 |
| | 100% | 14.7 $^{b}$ | 11.5 |
| | S.E.M (df = 3–15) | 0.89 | 0.73 |
| | *p*–value (<0.05) | 0.01 | 0.061 |
| Potassium | 0.01 mM | 11.1 $^{a}$ | 3.6 $^{a}$ |
| | 1 mM | 12.2 $^{a}$ | 10.0 $^{b}$ |
| | 4 mM | 14.5 $^{ab}$ | 11.3 $^{b}$ |
| | 16 mM | 14.8 $^{ab}$ | 13.7 $^{c}$ |
| | 32 mM | 17.4 $^{b}$ | 14.7 $^{c}$ |
| | S.E.M (df = 3–15) | 1.08 | 0.49 |
| | *p*–value (<0.05) | <0.001 | <0.001 |

Means followed by different letters in the same column are different (Tukey's test $p < 0.05$). S.E.M. = standard error of the mean; df = degrees of freedom.

## 4. Discussion

Our findings show that water deficit and the K concentrations influence the water status of young cassava plants, thereby affecting the leaf gas exchange and causing a decline in growth and yield. Decreasing irrigation dose to 30% together with 0.01 mM K lowered leaf $\Psi_w$ and $\Psi_s$ greatly, while leaf $\Psi_p$ was five times lower at the end of our experimental period (90 DAP) compared with full-irrigated plants (100%). The decrease in $\Psi_s$ in response to the water stress imposed is an osmotic adjustment mechanism used by most plants to adjust to water-limited environments [39] and contributes to $\Psi_p$ maintenance at low $\Psi_w$ [40,41]. Osmotic adjustment enables leaf $\Psi_p$ maintenance for the same leaf $\Psi_w$, thus supporting stomatal conductance [42], and improves root capacity for water uptake [43]. Moreover, our results showed that increasing the K concentration to 32 mM increased both leaf $\Psi_w$ and $\Psi_s$. This effect could have been related to the high $K^+$ solute concentration in the leaves, which seemed to increase the $\Psi_s$, as evident from elemental K content analyzed in the leaves. Furthermore, K is one of the primary osmotic solutes that contribute to osmotic adjustment in plants by altering the $\Psi_s$ and enabling plant cells to retain water and maintain $\Psi_p$ [44,45].

Reduction in water usage parallelled the decrease in leaf $\Psi_w$. Significant positive correlations ($r = 0.923$) observed between water usage and stomatal conductance suggest that the reduction in water usage was probably induced by stomatal closure. Cassava responds to initial water deficit by partial stomatal closure and nearly complete stomatal closure during extreme water deficit [8,17]. Duque and Setter [46] suggested that stomatal closure protects the leaf from severe water loss and protects photosynthetic systems and cellular structures from irreversible damage. Our results showed that effective water usage was greatest when irrigation dose was decreased to 60% together with 32 mM K, given the high amount of dry mass observed relative to full-irrigated plants. High dry mass production under water deficit is achieved when plants divert a large portion of available soil moisture towards stomatal conductance [47]. The water usage and stomatal conductance data further suggest that partial stomatal closure occurred at about 60 DAP when the water level was decreased to 30% or 60% of pot capacity. The marked increase in water usage, regardless of the irrigation doses when the K concentration was increased to 32 mM, suggests that high levels of K increased the leaf $\Psi_s$ and consequently increased $\Psi_w$, resulting in $\Psi_p$ maintenance and increased water usage.

The observed depletions in net photosynthesis was significantly associated with a significant reduction in stomatal conductance. Our results showed that the decline in net photosynthesis was more pronounced when irrigation dose was decreased to 30% together with 0.01 mM K, but less pronounced when irrigation dose was decreased to 60% of pot capacity. Even more, the strong positive correlation observed between net photosynthesis and stomatal conductance ($r = 0.939$) and leaf $\Psi_w$ ($r = 0.941$) suggests that photosynthesis was limited by stomatal closure in response to a limited water supply. The decline in leaf chlorophyll due to decreased irrigation doses additionally limited photosynthesis. This decline in leaf chlorophyll is considered a non-stomatal limiting factor [48] and is prevalent under water-deficit conditions, causing decreased photosynthetic activity [49]. Chlorophyll degradation also occurs in K-deficient plants [25], which further inhibits photosynthesis. Conversely, low-K nutrition diminishes Hill reaction activity [50] and the rate of production of adenosine triphosphate (ATP) and reduces nicotinamide adenine dinucleotide phosphate (NADP) in chloroplasts [51], resulting in reduced net photosynthesis. In contrast, increasing the K concentration to 16 mM increased net photosynthesis by increasing leaf $\Psi_w$ and leaf $\Psi_p$, which in turn increased stomatal conductance, resulting in increased net photosynthesis. Moreover, $\Psi_p$ determines stomatal aperture and closure [52,53], and the extent of stomatal closure in cassava during water deficit levels corresponds to the decline in net photosynthesis [8,54]. The enhanced need for K by plants under water deficit appears to be related to the fact that K is required for the maintenance of photosynthetic $CO_2$ fixation [25].

The leaf temperatures increased above the ambient greenhouse temperature (27 °C) when irrigation doses were decreased. Our results showed that increased leaf temperature corresponded to decreased net photosynthesis as indicated by the significant negative correlations between leaf temperature and net photosynthesis ($r = -0.912$), and between leaf temperature and leaf $\Psi_w$ ($r = -0.898$). This observation implies that the rise in leaf temperature was occasioned by stomata closure in response to a decline in $\Psi_w$. High leaf temperature leads to heat stress, and photosynthesis is more sensitive to heat stress under water deficit [55]. Thus, $C_3$–$C_4$ plants such as cassava rely on evaporative cooling to lower leaf temperature [56]. Despite decreased irrigation doses, increasing the K concentration to 16 mM and above appeared to lower leaf temperature. This was attributed to the role of high K concentration, which increased stomatal conductance and, thus, prevented leaf temperature from reaching harmful levels [57].

Plant leaf area and plant height were greatly reduced when irrigation dose was decreased to 30% together with 0.01 mM K. These reductions could be linked to the decrease observed in leaf $\Psi_w$, low $\Psi_p$, decreased stomatal conductance, and declined net photosynthesis. Raza et al. [58] showed that water deficit initiates a series of biochemical and physiological processes that result in a reduction in crop growth and yield. The small leaf areas (0.37 $m^2$) and short plants (56 cm) observed at the end of the experiment when irrigation dose was decreased to 30% together with 0.01 mM K were probably due to the effects of low leaf $\Psi_p$. In comparison, plant leaf areas and plant height increased due to increased $\Psi_p$ when irrigation dose was decreased to 60% of pot capacity. These observations concur with Alves and Setter [9], who found decreased leaf area expansion in cassava 8 days after initiation of water deficit. Nesreen et al. [59] reported reduced leaf area, plant height, and stem diameter in cassava subjected to water deficit under greenhouse conditions. Moreover, optimal leaf area development is important to photosynthesis and dry mass yield [60].

Leaf dry mass, root dry mass, whole-plant dry mass, and tuber number were equally reduced when irrigation dose was decreased to 30% together with 0.01 mM K. These reductions can be largely attributed to the decline in net photosynthesis and reduced leaf areas that were influenced by the low $\Psi_w$, $\Psi_s$, and $\Psi_p$. Duque and Setter [46] reported a 78% loss in total plant dry weight in cassava after 31-days of water deficit treatment. El-Shakwy and Cadavid [61] observed reductions in leaf area index and shoot and root biomass when they initiated water stress in three cassava cultivars for 2 to 8 months after planting. Nevertheless, increasing the K concentration to 16 mM improved the growth and yield of young cassava plants, regardless of decreased irrigation doses. This could be ascribed to the high levels of K that reduced the negative effects on plant-water relationships and improved net photosynthesis. This observation agrees with the findings of Mengel and Arneke [44], who reported improved water status and high dry mass in cassava supplied with high levels of K (4 mM) in comparison to low-K (0.1 mM) treatments. There were no tubers when irrigation dose was decreased to 30% together with 0.01 mM K, whereas four tubers were observed when K was increased to 16 mM. High levels of K increase the translocation of photosynthates to the storage roots [62], and the photosynthates initiate cassava tuberous root growth during the early growth phase [8,21].

The critical nutrient contents of K observed in this investigation fall within the sufficient range as those obtained by Nguyeh et al. [63] in field-grown cassava at four months after planting. The decreased K contents observed when irrigation doses were decreased were probably due to the limited water supply, which possibly limited the K uptake from the rhizosphere. Plants experiencing both water and K deficiency tended to show decreases in K accumulation rates, while those grown in K-rich soil maintained high rates of K accumulation during most of the season [64]. Moreover, our findings show that increasing K from 16 to 32 mM did not result in additional growth and yield benefits, regardless of the irrigation doses. Thus, it appears that 32 mM K was excessive and could have limited the uptake of other cations, creating a nutrient imbalance [65].

## 5. Conclusions

Our investigation showed significant interactions between deficit irrigation and K, whereby decreasing irrigation dose to 60% together with 16 mM K resulted in the least reduction in growth and yield. Thus, it seems that deficit irrigation strategies could be used as a tool to develop management practices to improve cassava productivity by means of K fertigation under low moisture field conditions. The experiments allowed analytical investigation of the effects of the irrigation and K doses without interference from underlying abiotic and biotic factors. Nevertheless, the present investigation had certain limitations such as the use of pots, which could have constrained plant growth, and the use of a controlled greenhouse environment, which varies from field environments. Therefore, further tests with several cassava cultivars under field conditions are warranted to compare these findings.

**Author Contributions:** Conceived and designed the experiment D.O.W., P.S.A.M., and J.K.; contributed the reagents/materials P.S.A.M.; conducted the experiments D.O.W.; supervised the research P.S.A.M., J.K., and L.A.; performed the statistical analysis D.O.W., and P.S.A.M.; wrote the first draft of the manuscript D.O.W. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by CIMO Finland (TM-17-10552) and the Ella and Georg Ehrnrooth Foundation. The open access publication fee was covered by the University of Helsinki.

**Acknowledgments:** We gratefully acknowledge Markku Tykkyläinen, Afrane Yaw, and Marjo Kilpinen for their technical assistance with the greenhouse and laboratory activities. We thank the Kenya Agricultural and Livestock Research Organization (KALRO) for providing the cassava cuttings used in this investigation.

**Conflicts of Interest:** The authors declare no conflict of interest. The funders played no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript or in the decision to publish the results.

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