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Identification and Characterization of Putative Cassava Mutant Genotypes under Low-pH Hydroponic Conditions with Aluminum

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Abstract

Cassava is an important staple food and an alternative to rice that exhibits relative resilience to both abiotic and biotic stresses. The development of cassava genotypes through mutation breeding has been conducted by a research team from the Department of Agronomy and Horticulture, IPB University. Currently, approximately 10 putative mutant cassava genotypes of M1V14 have been obtained, including G6-2-15-1-1, G6-2-15-5-3, and G6-2-15-3-3, which have high leaf mineral content and substantial tuber yield. This research aimed to evaluate morphological responses and identify growth patterns of cassava mutant genotypes under low-pH conditions with aluminum. By comparing control plants with Al-treated plants. 'Vamas-1', 'Gajah' (wild type), and putative mutant G6-2-15-1-1, and G6-2-15-5-3 exhibited greater reduction in plant and root growth compared to the putative mutant G6-2-15-3-3. All genotypes showed varying degrees of growth inhibition at the highest Al treatment (6 mM), indicating differences in Al tolerance. Based on the PCA analysis, most root morphological traits and plant biomass were strongly associated with the putative mutant G6-2-15-3-3. In addition, traits such as root diameter, number, length, and biomass were characteristic of 'Gajah', whereas the number of shoots, time of shoot emergence, and leaf biomass were characteristic of 'Vamas-1'. In addition, based on leaf biomass and basal root morphology, the putative mutant G6-2-15-3-3 shows potential as a new superior genotype with high leaf and tuber production, offering additional economic value. The development of this variety could serve as an alternative for farmers in developing countries, especially in Indonesia, to address the challenges posed by acidic soils with high aluminum content.

Keywords: aluminum toxicity, morphological responses, putative mutant, root growth

Introduction

Indonesia ranks as the seventh-largest producer of cassava in the world, following Nigeria, the Congo, Thailand, Ghana, Cambodia, and Brazil (Food and Agriculture Organization, 2022). Nevertheless, there were a significant decrease in cassava cultivation area (about 39%) and cassava production (about 28%) in Indonesia over the past decade (Food and Agriculture Organization, 2023). Therefore, efforts to increase national cassava production could include expanding cassava cultivation onto marginal land, such as acid soils. In Indonesia, according to Ritung et al. (2015), acid soils cover approximately 107.36 million hectares, accounting for about 74.3% of the overall dry land. Kalimantan, Sumatra, and most of Papua having the highest prevalence of acid soils. Acid soils are usually associated with nutrient deficiency and metal toxicity. Aluminum (Al) stress is a major constraint in crop development on acidic soils, as most plants are sensitive to high levels of Al saturation.

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Aluminum (Al) ranks as the third most abundant element in the Earth's crust after silicon (Von Uexküll & Mutert, 1995). Al is generally not toxic to plants unless the soil conditions become sufficiently acidic (approximately pH 5 or below). Under normal conditions, Al occurs mainly in the form of silicates, phosphates, sulfides, and oxides. When the soil pH drops below 5.5, Al is solubilized into toxic forms such as $[Al(H_2O)6]^{3+}$, $AlOH^{2+}$, $Al(OH)_3$, and $Al(OH)_4$ (Chowra et al., 2016). Trivalent aluminum (Al^{3+}) is the predominant form in acid soils and can severely impede root elongation and inhibit plant growth in most plants (Nogueirol et al., 2015). High aluminum concentrations inhibit root growth, thereby limiting nutrient and water uptake in plants (Yamamoto, 2019; Yang et al., 2011). Al toxicity has been the main factor limiting crop production on acidic soils (Kochian, 1995; Kochian et al., 2015).

Cassava (*Manihot esculenta* Crantz) originated in Latin America and was subsequently introduced to Africa and other regions (Shigaki, 2016). It is a staple food alongside rice and maize in Asian and African countries, and it is cultivated by over 800 million people. Several studies have focused on cassava putative mutant genotypes of AGH-IPB. However, previous studies have mainly focused on morphological traits and tuber yield (Agustina, 2016; Khumaida et al., 2015; Maharani et al., 2015; Rambe, 2017; Sansurya, 2018; Yani et al., 2018). Pratama et al. (2023, 2023a) reported the variability of leaf traits and nutrient content (Zn and Fe) in mutant genotypes from the M1V11 generation, including three local varieties, one introduced from Thailand, and two national varieties. These findings suggest that AGH-IPB putative mutant genotypes have the potential to be developed into superior varieties with high nutrient and tuber yield; however, their adaptability to acidic soils has not been studied.

Research on cassava morphology under aluminum stress is crucial for developing selection methods for aluminum-tolerant genotypes. Nutrient culture or hydroponic techniques have been recognized as practical approaches for initial screening of various crop commodities under aluminum stress conditions (Bhukya et al., 2024; Mejia-Alvarado et al., 2023; Punpom et al., 2022). Therefore, this study aimed to identify cassava mutant genotypes capable of maintaining growth under aluminum stress and to evaluate their potential tolerance to Al.

Materials and Methods

Plant Growth Conditions and Aluminum Treatment

The experiment was conducted from September to November 2024 in a greenhouse at the Cikabayan Experimental Station, Department of Agronomy and Horticulture, IPB University. The cassava genotypes used in this experiment included 'Gajah', the wild-type genotype used as the reference; 'Vamas-1', a cassava variety known for its aluminum tolerance; and three putative mutant genotypes in the M1V14 generation, including G6-2-15-1-1, G6-2-15-5-3, and G6-2-15-3-3, which were obtained from Pratama et al., (2023). Stem cuttings approximately 25 cm long were collected from M1V13 plants grown in the field and classified according to their upper, middle, and lower stem positions (Figure 1a). The experiment was arranged in a random complete block design (RCBD) with two factors: cassava genotype and nutrient solution. Four level treatment of genotypes included 'Gajah', a wild-type of putative mutants; 'Vamas-1', a known Al-tolerant variety; and three putative mutant genotypes in the M1V14 generation, including G6-2-15-1-1, G6-2-15-5-3, and G6-2-15-3-3, while four levels of nutrient solution consisted of control (AB mix pH 5.5 without $AlCl_3$), AB Mix pH 4.0 without $AlCl_3$, AB Mix pH 4.0 + 3 mM $AlCl_3$, and AB Mix pH 4.0 + 6 mM $AlCl_3$, resulted 20 treatment combinations with three replications per treatment. The control nutrient solution was maintained at a neutral, soil-like pH (around 5.5) and represented standard hydroponic conditions; the pH 4.0 treatment served as the negative control for Al stress, allowing us to differentiate the effect of low pH itself from that of low pH combined with Al stress. In Al treatments, the pH was adjusted to 4.0 to simulate acidic soil conditions and ensure the solubility of Al^{3+} ions

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(Hao et al., 2022; Liu et al., 2020). Each replicate consisted of three growth container, with each bucket containing three cuttings, resulting in a total of 540 plant cuttings. The hydroponic culture preparation procedure was as described in Pratama et al. (2023).

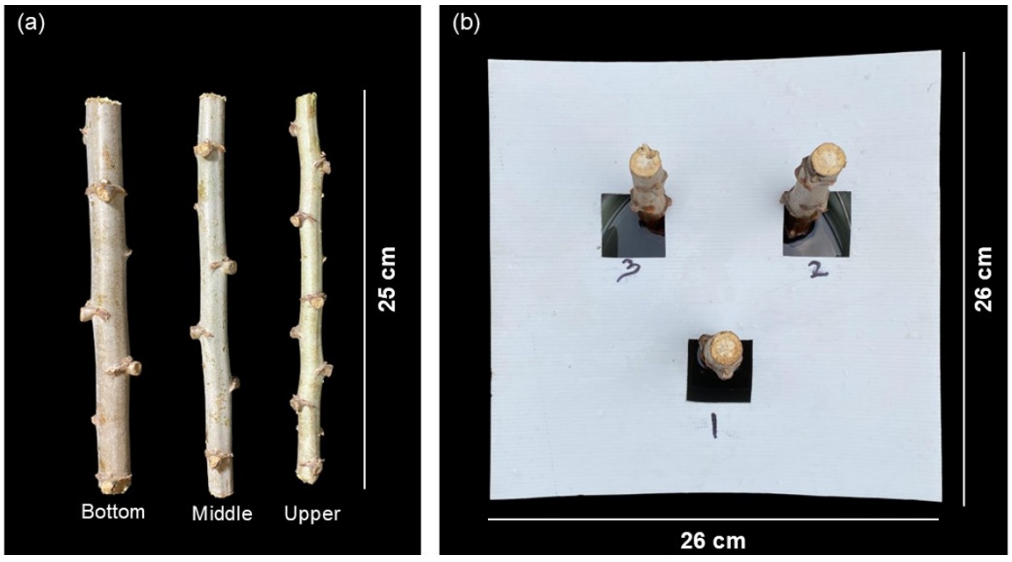
This experiment used a growth container (about 4 L), corrugated board (to support stem cuttings), a pH meter, and a camera. The growth container were approximately 17 cm high, with a top diameter of 26 cm, while the corrugated boards measured 26 × 26 cm, as shown in Figure 1. The experimental setup was prepared by punching three holes in each corrugated board. Nutrient solutions were prepared using AB-Mix fertilizer by separately dissolving 1140 g of nutrient A and 1140 g of nutrient B in water to create 5 L stock solutions. The AB solution contained N total (25.9%), Ca $(NO_3)_2 \cdot 4H_2O$ (18.1%), KNO_3 (31.2%), $MgSO_4.7H_2O$ (6.6%), KH_2PO_4 (6.4%), $C_{10}H_{12}FeN_2NaO_8$ (0.35%), $MnSO_4 \cdot 7H_2O$ (0.06%), $CuSO_4 \cdot 5H_2O$ (0.07%), $Na_2B_4O_7 \cdot 10H_2O$ (0.04%), $ZnSO_4 \cdot 7H_2O$ (0.07%), and $Na_2MoO_4 \cdot 2H_2O$ (0.01%) with modifications to the Al concentration as needed. The nutrient solution for each growth container was prepared by combining 1 L of water with the stock solution, following the recommended dosage according to plant age (5 ml A and 5 ml B for 1–4 WAP (weeks after planting); 10 ml A and 10 ml B for 5–8 WAP), as described by Pratama et al. (2023). For the control, the pH was adjusted to 5.5. In the Al treatment, the pH was set to 4, and aluminum chloride ($AlCl_3$) was added at a concentration of 0.4 g/L for 3 mM $AlCl_3$ and 0.8 g/L for 6 mM $AlCl_3$, resulting in 1.6 g/L and 3.2 g/L $AlCl_3$ per 4 L growth container from 1–8 WAP. We used 3 and 6 mM $AlCl_3$ based on our previous unpublished experiment, which showed that the 3 mM $AlCl_3$ did not cause any toxic effects; therefore the concentration was increased to 6 mM $AlCl_3$.

Plant Growth and Morphological Observation

The traits evaluated were the number of shoots, the number of leaves, plant height (in cm, measured from the base to the tip of the shoot), and the plant canopy fresh and dry weights (all plants were weighed for each genotype). The fresh leaf weight of the plant was also measured. The canopy fresh weight was determined by weighing all aboveground plant parts, excluding the roots, after which the samples were oven-dried at 80 °C for 3 days to determine canopy dry weight. In this study, the root morphological traits evaluated included root length, diameter,

Figure 1

(*a) The Segmentations of Stem Cuttings and (b) Culture Bucket with the Nutrient Solution Inside and Corrugated Board to Hold the Cassava Cuttings, Which are Used in this Research*



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and number of the upper nodal, lower nodal, and basal roots. The types of cassava roots were classified as described by Adu et al. (2020). The fresh and dry weights of the cassava roots were also determined. All root components were weighed to determine their fresh weights. Subsequently, the roots were dried in an oven at 80 °C for 72 hr to obtain the dry weight (Adu et al., 2020).

Data Analysis

Data normality was assessed using the Shapiro-Wilk test, and homogeneity using the Levene and Bartlett tests. Two-way ANOVA (for normally distributed data) and Mixed-Effects model ANOVA (for non-normally distributed data) were used to assess differences in the factor means (genotype and nutrient solution). Duncan's multiple range test (DMRT) was used for mean separation at $\alpha = 0.05$. Data analysis was performed using RStudio and SAS OnDemand for academics software. Pearson correlation analysis was performed in R (version 4.1.3) using the 'meta' package, while PCA was conducted in R (version 4.4.1) with the 'Factoextra' package. Analyses were run in RStudio, the integrated development environment.

Results and Discussion

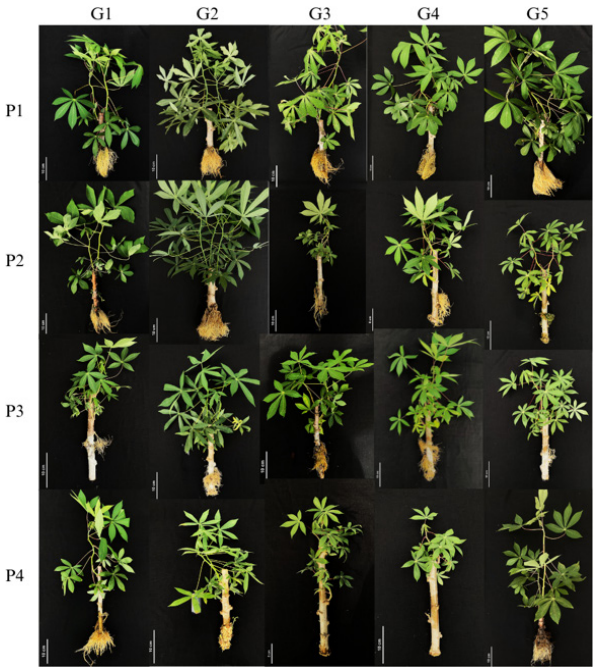
Effect of Aluminum on Cassava Vegetative Growth

The general condition of cassava plants grown in hydroponic culture is shown in Figure 2. Overall, all cassava genotypes grew well under control conditions and under the 3 mM Al treatment. In contrast, root growth inhibition was observed at pH 4.0 and under the 6 mM Al treatment. The simple hydroponic technique used in this study could serve as a preliminary screening method for evaluating crop species under Al stress (Bhukya et al., 2024; Mejia-Alvarado et al., 2023; Punpom et al., 2022).

As shown in Table 1, analysis of variance (ANOVA) revealed that while genotype did not affect the number of shoots, adversely

Figure 2

General Condition of Cassava Genotypes in Hydroponic Culture at 8 Weeks. G1: 'Gajah' (Wild Type), G2: 'Vamas-1', G3: G6-2-15-1-1, G4: G6-2-15-5-3, G5: G6-2-15-3-3, P1: AB Mix pH 5.5 (Control), P2: AB Mix pH 4.0 + 0 mM $AlCl_3$, P3: AB Mix pH 4.0 + 3 mM $AlCl_3$, P4: AB Mix pH 4.0 + 6 mM $AlCl_3$



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significantly affected the number of leaves at 6–8 WAP. On the other hand, nutrient solution had a significant effect on shoots and leaf number at 2–8 WAP. Interestingly, there is no interaction effect among genotype and nutrient solution on both parameters. Overall, the number of shoots across all nutrient solutions declined throughout the observation period. Notably, the control nutrient solution exhibited the lowest mean shoot number at 8 WAP (approximately 1.92), which was significantly lower than that of the other treatments. The highest number of leaves was observed in plants treated with the 3 mM Al and in the control treatments, while the lowest number of leaves was recorded in plants grown at pH 4.0 without $AlCl_3$ and in plants treated with the 6 mM Al, confirming the adverse impact of low pH on plant development (Iuchi et al., 2007; Sawaki et al., 2009). 'Vamas-1' and the putative mutant G6-2-15-3-3 produced the highest number of leaves (approximately 21.49 and 19.75, respectively), whereas the wild-type genotype 'Gajah' had fewer leaves (approximately 16.64) (Table 1). The interaction between genotype and nutrient solution significantly affected plant height according to DMRT at α = 0.05 (Figure 3). Overall, the control treatment significantly increased plant height across all genotypes, whereas the 6 mM Al treatment reduced plant height (Figure 3). These findings are likely attributable to Al toxicity, which can impair cassava vegetative growth. Similar results were reported in *Jatropha curcas* L. subjected to Al stress, which exhibited reductions in plant height and leaf area (Steiner et al., 2012).

After eight weeks of cultivation, cassava growth exhibited significant differences in both shoot and leaf biomass (Figure 4). 'Vamas-1' and the putative mutant G6-2-15-3-3 had the highest shoot biomass (81.24 g and 79.36 g, respectively), significantly higher than other genotypes. Similarly, these two genotypes had the highest leaf fresh weights (approximately 12.72 g and 12.67 g, respectively). A similar

Table 1

Effect of Genotypes and Nutrient Solutions on the Number of Shoots and Leaves in Cassava

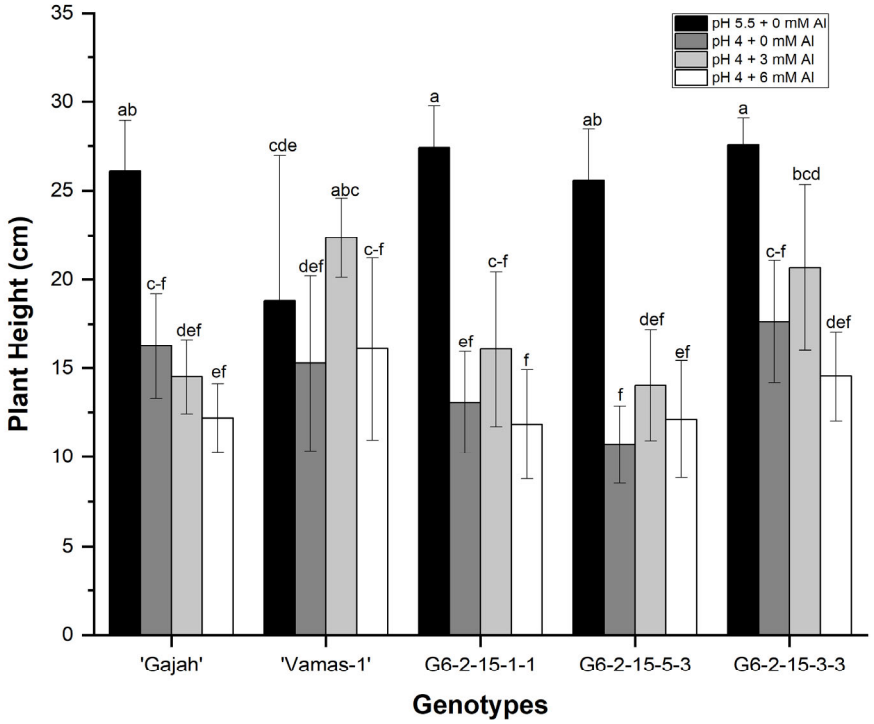
Treatments	Number of shoots				Number of leaves			
	2 WAP1	4 WAP1	6 WAP1	8 WAP1	2 WAP2	4 WAP2	6 WAP	8 WAP
Genotypes								
'Gajah'	3.27	2.42	2.54	2.55	4.75	9.23	13.55 c	16.64 b
'Vamas-1'	3.87	2.65	2.77	2.72	5.97	12.38	17.40 a	21.49 a
G6-2-15-1-1	3.71	2.68	2.46	2.49	6.3	11.32	14.92 bc	16.87 b
G6-2-15-5-3	3.54	2.62	2.45	2.45	5.29	11.27	13.89 c	15.82 b
G6-2-15-3-3	3.71	2.57	2.36	2.36	6.69	12.13	16.81 ab	19.75 a
Nutrient solutions								
pH 5.5 + 0 mM $AlCl_3$	3.83 b	2.17 b	1.94 b	1.92 b	7.49 a	12.51 a	17.28 a	20.19 a
pH 4.0 + 0 mM $AlCl_3$	3.14 b	2.30 b	2.51 a	2.51 a	4.92 bc	8.99 b	12.59 c	15.30 b
pH 4.0 + 3 mM $AlCl_3$	4.01 a	3.05 a	2.83 a	2.83 a	6.22 ab	12.59 a	16.52 ab	19.99 a
pH 4.0 + 6 mM $AlCl_3$	3.51 b	2.84 a	2.79 a	2.81 a	4.57 c	10.98 ab	14.86 b	16.97 b
Genotype	ns	ns	ns	ns	ns	ns	**	**
Nutrient solution	*	**	*	*	*	*	**	**
Genotype × Nutrient solutions	ns	ns	ns	ns	ns	ns	ns	ns

Notes. Numbers followed by the same letter within a column are not significantly different according to DMRT at α = 0.05. [1]Based on Mixed-effect model ANOVA, [2]data was transformed using √x+0,5. *: significant difference at α= 0.05, **: significant difference at α = 0.01. WAP: weeks after planting. ns: not significant according to the statistical test at α = 0.05.

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Figure 3

Plant Height at 8 Weeks of All Cassava Genotypes Induced by Varying Levels of Nutrient Solutions



Note. Error bars denote the standard deviation of three blocks. Mean values followed by different letters are significantly different according to DMRT at α = 0.05.

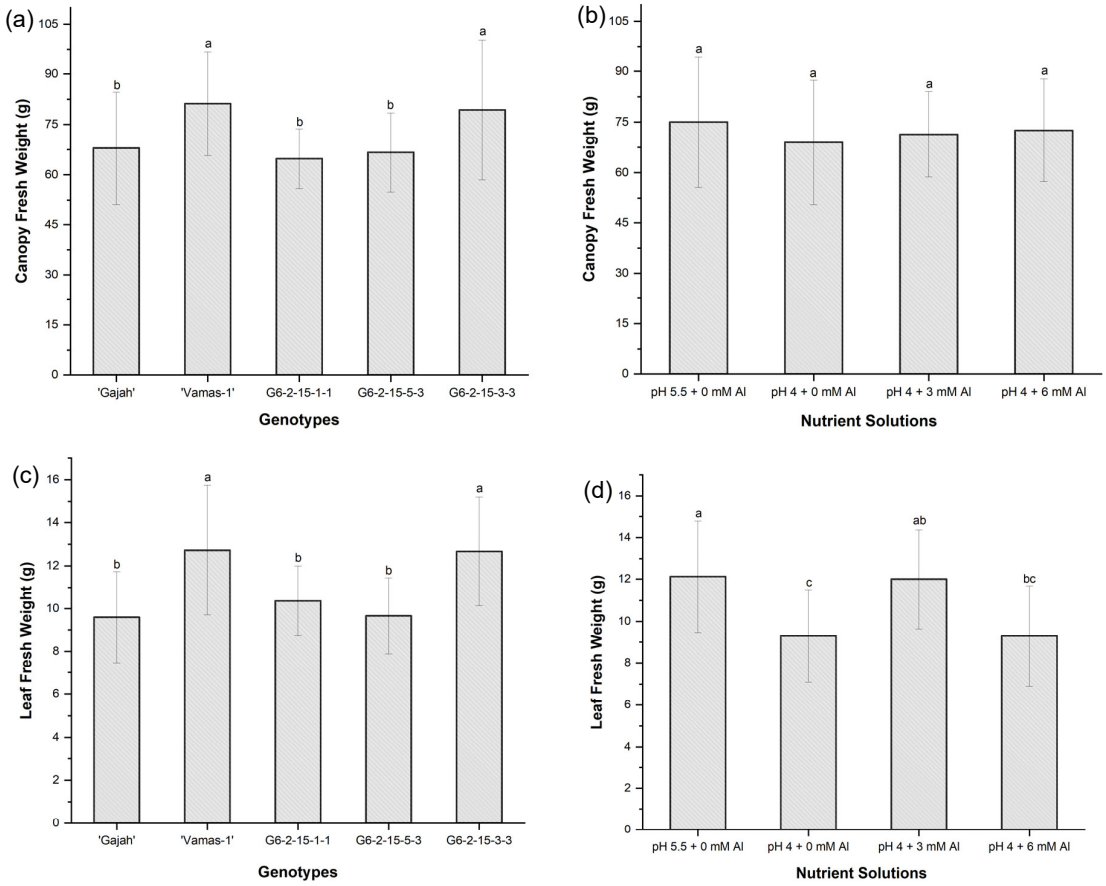
pattern was observed for canopy dry weight, with 'Vamas-1' and mutant G6-2-15-3-3 exhibiting significantly higher values than the other genotypes (Figure 5a). In contrast, no significant differences were observed among 'Gajah', putative mutant G6-2-15-1-1, and G6-2-15-5-3 (Figure 4a–c). Furthermore, analysis revealed no significant differences between the control (pH 5.5) and the 3 mM Al treatments. However, the pH 4.0 without Al and the 6 mM Al treatments significantly reduced leaf fresh weight by approximately 18% (Figure 4d). This result indicates that low pH itself negatively affected plant growth. Low pH has been associated with inhibition of root growth (Yang et al., 2005) by facilitating H^+ influx into roots, which impairs plant growth. An increased H^+ influx can depolarize the plasma membrane, thereby affecting cytoplasmic acidity (Babourina et al., 2001). Thus, low pH due to H^+ ions generally adversely affects root tissues, leading to reduced growth and development. Low pH combined with the 6 mM Al stress significantly reduced cassava growth (Figure 4d). In contrast, the combination of low pH (pH 4.0) and the 3 mM Al treatment significantly promoted vegetative growth, suggesting a possible hermetic response to Al stress. Hormesis is a biological phenomenon in plants characterized by growth stimulation at low doses of stressors such as aluminum, salinity, or heavy metals (Jabin et al., 2024).

Although the effect of Al treatments on nutrient uptake was not directly measured, we hypothesize that the inhibition may be related to alterations in nutrient uptake. Several studies have reported that Al stress reduces nutrient uptake in some species. Kichigina et al. (2017) indicated that Al reduced K, Mg, Zn, Mn, and S content in the roots and shoots of Al-treated plants. Guo et al. (2018) demonstrated that Al treatments not only reduced the uptake of N, P, K, Ca, Mg, and S but also decreased the relative

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Figure 4

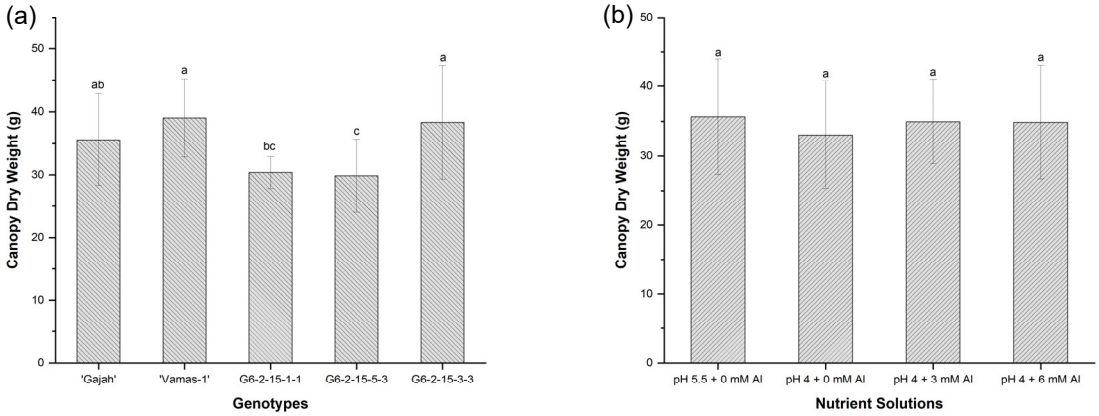
(a-b) Canopy Fresh Weight and (c-d) Leaf Fresh Weight of All Nutrient Solutions and Cassava Genotypes



Note. Error bars show the standard deviation of three blocks. Mean values followed by different letters are significantly different according to DMRT at α = 0.05.

Figure 5

Effect of Genotypes (a) and Nutrient Solutions (b) on Canopy Dry Weight



Note. Error bars denote the standard deviation of three blocks. Mean values followed by different letters are significantly different according to DMRT at α = 0.05.

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water content of citrus roots and leaves. In sugarcane, Al significantly reduced nutrient use efficiency of macro- and micronutrients (Borges et al., 2020). Additionally, P deficiency is a major concern in acidic soils, as Al has a high affinity for P and forms insoluble Al–P compounds (Magalhaes et al., 2018). This effect occurs because Al interacts with the negatively charged phospholipid bilayer of the plasma membrane, disrupting membrane potential and inhibiting H^+-adenosine triphosphatase (H^+-ATPase) proton-exclusion activity (Maejima and Watanabe, 2014). Consequently, ion transport is affected, including that of K^+, NH_4^+, Mg^{2+}, and Ca^{2+} (Gupta et al., 2013). Al-induced nutrient deficiencies and their impacts on plant height and biomass have also been identified in *Phaseolus vulgaris* and *Arabidopsis* (Pereira-Lima et al., 2023; Vasconcelo et al., 2020). These studies suggest that Al toxicity can cause nutritional imbalances in plants, potentially affecting crop growth and productivity.

Effect of Aluminum on Cassava Root Growth

During observation, we identified three types of roots in cassava plants: upper nodal roots, lower nodal roots, and basal roots (Adu et al., 2020). These root types were further examined to evaluate morphological changes induced by Al exposure. The putative mutant G6-2-15-3-3 exhibited the largest upper nodal root diameter (approximately 14.67 cm), a difference that was statistically significant (Table 2), suggesting a possible adaptive response to Al stress. Meanwhile, the wild-type genotype 'Gajah' had the highest fresh and dry weights of upper nodal roots (approximately 6.54 g and 1.77 g, respectively) (Table 2). We also measured the diameter of upper nodal roots. Although there were no significant differences between the putative mutant and wild-type genotypes, the putative mutant G6-2-15-3-3 exhibited the largest upper nodal root diameter (approximately 1.08 mm) (Figure 6).

Table 2

Effect of Genotypes and Nutrient Solutions on Root Length and Root Biomass

Treatments	Root length (cm)		Fresh root weight (g)		Dry root weight (g)	
	Upper nodal[2]	Lower nodal[2]	Upper nodal[1]	Lower nodal[1]	Upper nodal[1]	Lower nodal[1]
Genotypes						
'Gajah'	10.46 b	8.63	6.54 a	4.35	1.77 a	0.79
'Vamas-1'	10.94 b	10.94	3.29 b	3.46	0.70 c	0.67
G6-2-15-1-1	10.86 b	9.49	3.28 b	3.22	0.84 bc	0.80
G6-2-15-5-3	12.03 b	10.00	5.67 ab	2.53	1.33 ab	0.59
G6-2-15-3-3	14.67 a	10.30	5.33 ab	3.07	1.56 a	0.75
Nutrient solutions						
pH 5.5 + 0 mM $AlCl_3$	13.92 a	11.50 a	6.25 a	4.33 a	1.54 a	0.87 a
pH 4.0 + 0 mM $AlCl^3$	11.45 b	9.59 a	5.15 a	3.12 ab	1.50 a	0.86 a
pH 4.0 + 3 mM $AlCl^3$	12.45 ab	11.43 a	5.49 a	4.22 a	1.25 a	0.85 a
pH 4.0 + 6 mM $AlCl^3$	9.35 c	6.97 b	2.39 b	1.63 b	0.67 b	0.30 b
Genotype	**	ns	*	ns	**	ns
Nutrient solution	**	**	*	**	**	*
Genotype x nutrient solution	ns	ns	ns	ns	ns	ns

Notes. Numbers followed by the same letter within a column are not significantly different according to the DMRT at α = 0.05. [1]Based on mixed-effect model ANOVA, [2]data was transformed using √x+0,5. *: significant difference at α = 0.05, **: significant difference at α = 0.01, ns: not significant according to the statistical test at α = 0.05.

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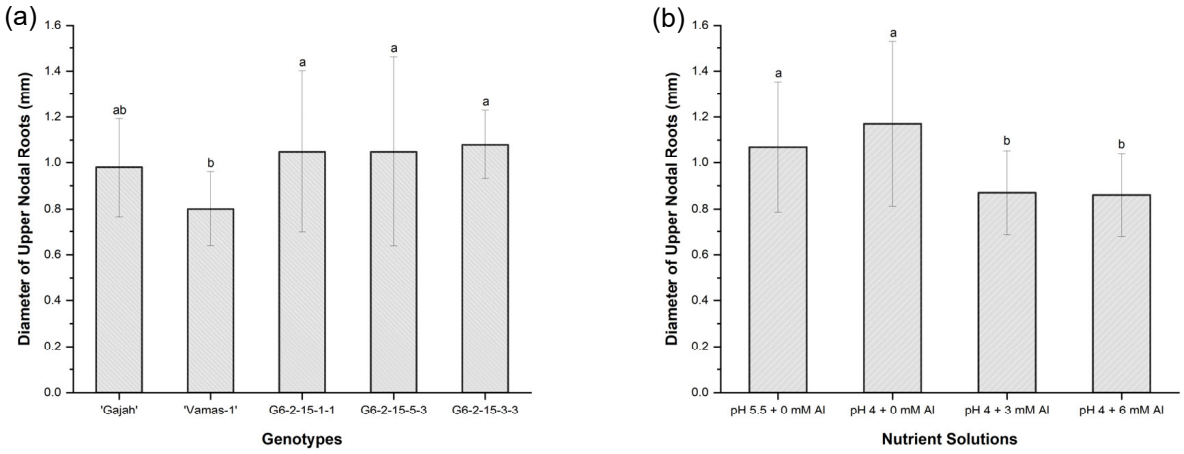
The interaction between genotype and nutrient solution significantly affected basal root morphology, including fresh weight, dry weight, root length, and number of roots (Figure 7). Notably, the 3 mM Al treatment enhanced basal root growth compared with the control across all genotypes (Figure 7a–d). For example, the 'Vamas-1' genotype significantly increased the fresh weight of basal roots (7.09 g) and the dry weight of basal roots (0.79 g) under the 3 mM Al treatment. By contrast, the 6 mM Al treatment drastically reduced the fresh and dry weight of basal roots in the putative mutant genotypes. In the mutant genotype G6-2-15-1-1, the fresh weight of basal roots decreased by 76.8% and the dry weight of basal roots by 86.6% compared with the control, while in the G6-2-15-5-3, the fresh weight of basal roots decreased by 82% and the dry weight of basal roots by 78.3% compared with the control (Figure 7a–b). Moreover, 'Gajah', 'Vamas-1', and the putative mutant G6-2-15-3-3 exhibited minimal reductions in response to Al-induced stress compared with the other genotypes.

Basal root length reduction was also observed in several genotypes under the 6 mM Al treatment. 'Gajah' and 'Vamas-1' exhibited reductions of 27.1% and 21.3% in basal root length, respectively, compared with the control. The putative mutant genotypes G6-2-15-1-1 and G6-2-15-5-3 showed reductions of 60% and 48.5%, respectively, in basal root length compared with the control. Interestingly, the putative mutant G6-2-15-3-3 showed a distinct response, significantly increasing basal root length even under high Al concentrations (6 mM) (Figure 7c). Furthermore, an increase in the number of basal roots was generally observed in several genotypes under the 3 mM Al treatment. However, 'Gajah' and the putative mutant G6-2-15-3-3 displayed a significant increase when exposed to the highest Al treatment (6 mM) (Figure 7d). These findings suggest that the 3 mM Al treatment appears to stimulate basal root growth, whereas the 6 mM Al treatment is associated with an inhibitory effect. In addition, we observed genotype-specific responses in basal root morphology. Notably, the putative mutant G6-2-15-3-3 demonstrated a significant increase in the length and the number of basal roots, even under high Al exposure conditions. These differences among genotypes suggest varying capacities to adapt to Al-induced stress.

Overall, our findings indicate that the 3 mM Al treatment significantly increased cassava root growth, suggesting a possible hormetic

Figure 6

Effect of Genotypes (a) and Nutrient Solutions (b) on the Diameter of Upper Nodal Roots in Cassava Plants

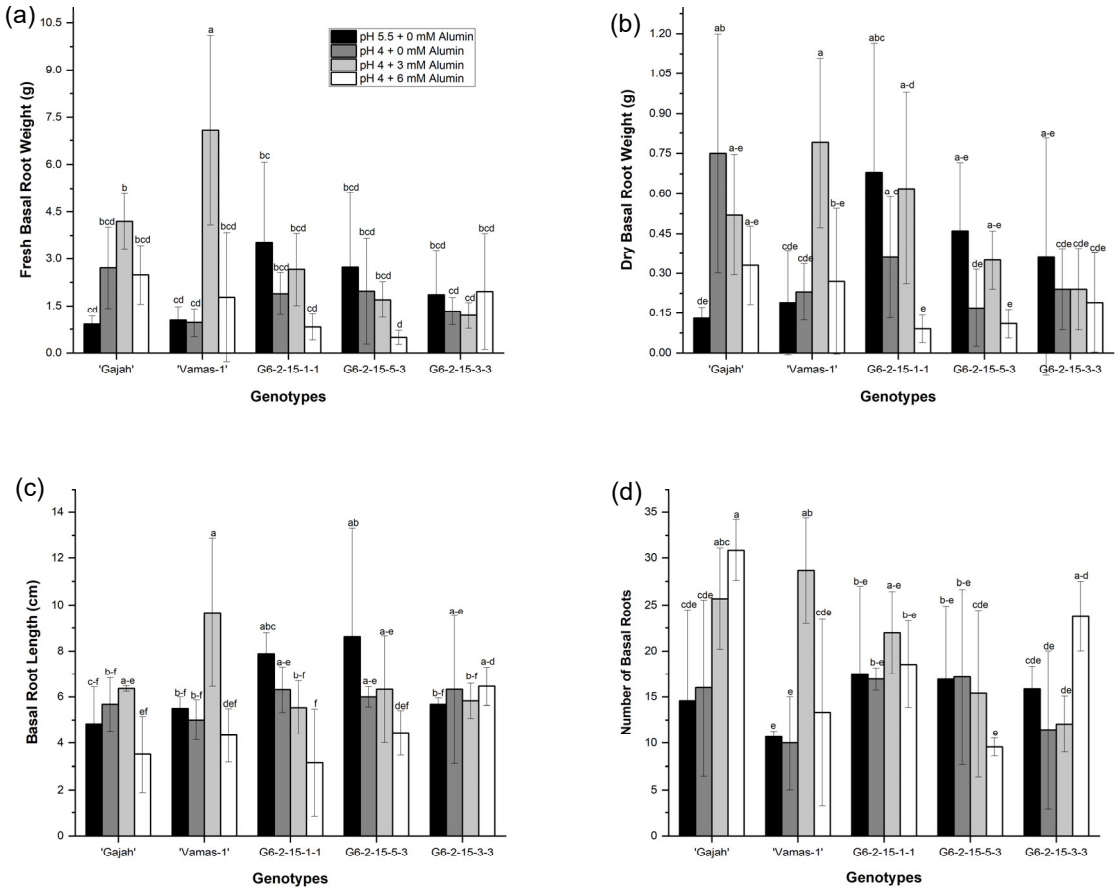


Note. Error bars denote the standard deviation of three blocks. Mean values followed by different letters are significantly different according to DMRT at α = 0.05.

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Figure 7

(a) Fresh Basal Root Weight, (b) Dry Basal Root Weight, (c) Basal Root Length, (d) Number of Basal Roots in Cassava Genotypes Grown under Different Nutrient Solutions



Note. Error bars denote the standard deviation of three blocks. Mean values followed by different letters differ significantly according to DMRT at α = 0.05.

response of cassava roots to Al exposure, in which growth stimulation occurs following exposure to low concentrations of an inhibitor (Hajiboland et al., 2013; Liu et al., 2020; Ofoe et al., 2022; Sun et al., 2020). Punpom et al. (2022) reported that at moderate concentrations (<50 μM), Al can trigger proton release from cassava roots, thereby enhancing Fe availability in the rhizosphere and Fe acquisition in plants, which may contribute to photosynthetic metabolism and root growth. Our findings are consistent with previous reports suggesting that exposure to low Al concentrations can induce growth responses in local plants, Al-hyperaccumulators, and plants adapted to acidic soils (Arasimowicz-Jelonek et al., 2014; Jiang et al., 2021; Punpom et al., 2022; Sun et al., 2020).

By contrast, under the highest Al treatment (6 mM), we observed significant inhibition of root and vegetative growth in cassava genotypes. These results indicate that high Al concentrations were toxic to the cassava genotypes. In line with this study, Zhang et al. (2019) reported that the primary symptoms of Al toxicity in plants include growth inhibition and root morphological disruptions. Growth inhibition was also observed in the pH 4.0 without Al, confirming the impact of low pH on plant development (Iuchi et al., 2007; Sawaki et al., 2009). Root growth reduction due to high Al exposure has been documented in various plant species, although the threshold concentration for Al toxicity can differ among

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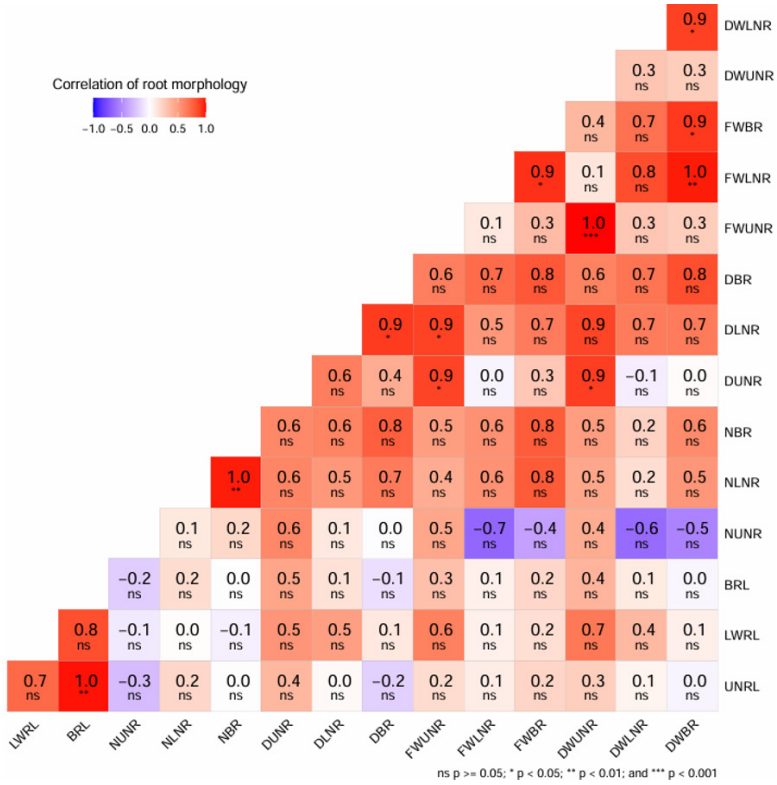
species. For example, the 1.25 mM Al treatment has been reported to inhibit root growth in *Trifolium* and tomato seedlings (Bortolin et al., 2020; Ofoe et al., 2022). In addition, the 2 mM Al also inhibited root growth in *Camellia japonica* (Liu et al., 2020). Furthermore, exposure to 100 µM Al has been documented to inhibit root growth in *Arabidopsis* and cassava (Pereira-Lima et al., 2023; Punpom et al., 2022). Meanwhile, the 5 mM Al was also reported to restrict root growth in tea plants (Hao et al., 2022).

Pearson Correlation of Root Morphology

Pearson correlation analysis of root morphological traits revealed strong associations among several traits (Figure 8). A significant positive correlation ($r > 0.9$, $p < 0.05$) was identified between DUNR (diameter of upper nodal roots) and the biomass of upper nodal roots. Meanwhile, DLNR (diameter of lower nodal roots) showed a significant positive correlation ($r > 0.9$, $p < 0.05$) with DBR (diameter of basal roots) and FWUNR (fresh weight of upper nodal roots). These data indicate that roots with larger diameters tend to have higher biomass. Physiologically, roots with larger diameters may have greater conductive and storage capacities and may exhibit greater secondary growth, thereby resulting in greater biomass accumulation. This is consistent with Wu et al. (2016), who reported that maize roots with larger diameters exhibited higher branching and elongation

Figure 8

Correlation Coefficients Among Root Morphological Traits of Five Cassava Genotypes under Aluminum Stress Conditions



Notes. UNRL = upper nodal root length, LNRL = lower nodal root length, BRL = basal root length, NUNR = number of upper nodal roots, NLNR = number of lower nodal roots, NBR = number of basal roots, DUNR = diameter of upper nodal roots, DLNR = diameter of lower nodal roots, DBR = diameter of basal roots, FWUNR = fresh weight of upper nodal roots, FWLNR = fresh weight of lower nodal roots, FWBR = fresh weight of basal roots, DWUNR = dry weight of upper nodal roots, DWLNR = dry weight of lower nodal roots, DWBR = dry weight of basal roots.

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rates, thereby increasing overall root biomass. Similarly, Wang et al. (2022) reported that root diameter plays an important role in biomass accumulation across various annual plant species. In cassava, Menegucci et al. (2024) showed that thicker roots contribute dominantly to total plant biomass. Thus, the correlation between root diameter and root biomass in this study could potentially be used as a selection trait for aluminum-tolerant genotypes.

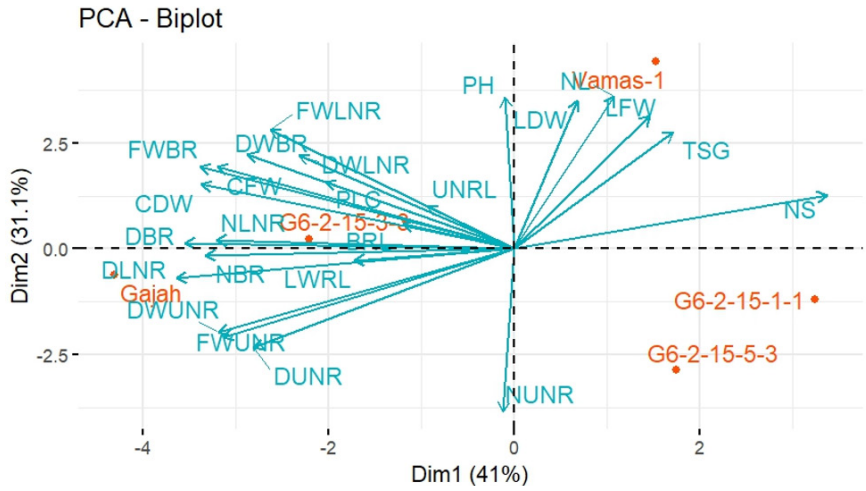
PCA Analysis

Figure 9 presents the results of principal component analysis (PCA), illustrating the diversity of genotypic responses to growth-related traits under aluminum stress conditions. The mutant genotypes G6-2-15-1-1 and G6-2-15-5-3 did not exhibit superiority in either vegetative traits or root morphology. The 'Vamas-1' variety demonstrated high performance in terms of the number of shoots, number of leaves, fresh leaf weight, and dry leaf weight. The 'Gajah' genotype was associated with the number of upper nodal roots, diameter of upper nodal roots, fresh and dry weight of upper nodal roots, root length of lower nodal roots, number of basal roots, and root diameter of basal roots. The mutant genotype G6-2-15-3-3 higher values for plant height, root length of upper nodal roots, root length of basal roots, number of lower nodal roots, diameter of basal roots, fresh and dry shoot weight, fresh weight of basal roots, and fresh and dry weight of lower nodal roots, as well as dry weight of basal roots. 'Vamas-1' was positioned in quadrant I (right), while the mutant genotypes G6-2-15-1-1 and G6-2-15-5-3 were located in quadrant II (right). The 'Gajah' genotype was positioned in quadrant III (left), whereas the mutant genotype G6-2-15-3-3 was located in quadrant IV (left). Genotypes located within the same quadrant indicate a high degree of similarity.

The PCA results explained the genetic variation among cassava genotypes across all vegetative and root morphological traits. Principal components with eigenvalues greater

Figure 9

PCA Analysis of Vegetative and Root Traits on All Cassava Genotypes in the 6 Mm Aluminum Concentrations



Notes. TSG = time to shoot emergence, NS = number of shoots, PH = plant height, NL = number of leaves, LFW = leaf fresh weight, CFW = canopy fresh weight, LDW = leaf dry weight, CDW = canopy dry weight, PLC = percentage of leaf chlorosis, UNRL = upper nodal root length, LNRL = lower nodal root length, BRL = basal root length, NUNR = number of upper nodal roots, NLNR = number of lower nodal roots, NBR = number of basal roots, DUNR = diameter of upper nodal roots, DLNR = diameter of lower nodal roots, DBR = diameter of basal roots, FWUNR = fresh weight of upper nodal roots, FWLNR = fresh weight of lower nodal roots, FWBR = fresh weight of basal roots, DWUNR = dry weight of upper nodal roots, DWLNR = dry weight of lower nodal roots, DWBR = dry weight of basal roots.

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than 1 and variation percentages greater than 4% were considered main PCs (Abimbola et al., 2016; Brejda et al., 2000). Principal component analysis described the variation among cassava genotypes across the evaluated traits. Eigenvalues represent the significance and proportion of variance explained by each component, whereas eigenvector coefficients denote the contribution level of individual variables associated with each principal component.

Principal components, eigenvalues, variance (%), cumulative variance (%), and variable loadings are presented in Table 3. In this study, four principal components had greater than 1 and together explained 100% of the cumulative variance (Table 3). The first PC (40.95%) and second PC (31.05%) accounted

Table 3

Eigenvalue, Variance, Cumulative Variance, and Variable Loadings of 5 Cassava Genotypes for Vegetative and Root Morphology Traits

Traits	Principal components			
	PC1	PC2	PC3	PC4
Eigenvalue	9.83	7.45	4.51	2.21
Variance (%)	40.95	31.05	18.79	9.21
Cumulative variance (%)	40.95	72	90.79	100
Variable loadings				
Time to shoot emergence (dap)	0.43	0.69	0.56	-0.10
Number of shoots	0.84	0.32	0.41	-0.08
Plant height (cm)	-0.02	0.90	-0.39	-0.17
Number of leaves	0.27	0.91	-0.32	-0.04
Leaf fresh weight (g)	0.36	0.79	-0.45	0.18
Canopy fresh weight (g)	-0.80	0.49	-0.03	0.34
Leaf dry weight (g)	0.17	0.88	-0.36	0.24
Canopy dry weight (g)	-0.84	0.38	-0.08	0.36
Percentage of leaf chlorosis (%)	-0.51	0.39	0.67	-0.36
Upper nodal root length (cm)	-0.23	0.25	-0.93	-0.03
Lower nodal root length (cm)	-0.43	-0.06	-0.67	-0.59
Basal root length (cm)	-0.30	0.14	-0.92	-0.15
Number of upper nodal roots	-0.03	-0.96	0.04	0.24
Number of lower nodal roots	-0.80	0.05	-0.02	0.59
Number of basal roots	-0.83	-0.04	0.17	0.52
Diameter of upper nodal roots (mm)	-0.70	-0.59	-0.38	0.11
Diameter of lower nodal roots (mm)	-0.91	-0.17	0.16	-0.33
Diameter of basal roots (mm)	-0.88	0.03	0.44	-0.07
Fresh weight of upper nodal roots (g)	-0.78	-0.52	-0.13	-0.29
Fresh weight of lower nodal roots (g)	-0.66	0.71	0.25	-0.01
Fresh weight of basal roots (g)	-0.84	0.49	0.11	0.16
Dry weight of upper nodal roots (g)	-0.79	-0.49	-0.18	-0.28
Dry weight of lower nodal roots (g)	-0.58	0.55	0.25	-0.53
Dry weight of basal roots (g)	-0.72	0.56	0.38	-0.11

Note. Bold values represent the main contributing traits for each PC.

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for 72.0% of the total variation. Time to shoot emergence, number of shoots, number of leaves, and leaf fresh weight were important traits contributing to PC1. As a result, the first component differentiated genotypes with high shoot number, leaf number, and leaf fresh weight. PC2 was mainly influenced by number of shoots, plant height, number of leaves, leaf fresh weight, leaf dry weight, fresh weight of lower nodal roots, dry weight of lower nodal roots, and dry weight of basal roots. PC3 was mainly determined by the time to shoot emergence, the number of shoots, the percentage of leaf chlorosis, the diameter of the basal roots, the fresh weight of the lower nodal roots, the dry weight of the lower nodal roots, and the dry weight of the basal roots. PC4 was largely governed by canopy fresh weight, canopy dry weight, number of lower nodal roots, and number of basal roots. Traits with large positive or negative loadings contribute substantially to the variation represented by the respective PCs. Traits with high variability can be used to select diverse genotypes along a particular principal component.

Conclusions

Overall, the putative mutant genotype G6-2-15-3-3 exhibited greater tolerance to Al toxicity than the other mutant genotypes evaluated. In this study, we identified a hormetic effect, in which growth was stimulated by exposure to low concentrations of an inhibitor. This condition was observed under the 3 mM Al treatment, which enhanced both cassava plant and root growth. By contrast, the highest Al treatment (6 mM) significantly inhibited the growth of cassava plants and roots. Therefore, we conclude that the 6 mM Al concentration used in this study is toxic to cassava genotypes. Based on the observed responses, the three putative mutant genotypes (G6-2-15-1-1, G6-2-15-5-3, and G6-2-15-3-3) can be tentatively classified according to their relative responses to Al stress. The putative mutant G6-2-15-3-3 showed the smallest reduction in both plant and root traits under Al stress, indicating that this genotype is more tolerant to Al toxicity than the other putative mutant genotypes evaluated. Based on these results, the putative mutant G6-2-15-3-3 genotype may have potential for high leaf and tuber production, although this requires validation under field conditions. Recommended follow-up studies include molecular validation to identify Al-tolerance–related genes, field evaluation under high-Al soil conditions, and physiological analysis of nutrient uptake efficiency. If confirmed, these traits could support the development of a superior cassava variety that combines Al tolerance with high productivity. Such a variety would offer a valuable alternative for farmers in developing countries, particularly in Indonesia, by enabling the productive use of marginal lands with elevated Al levels.

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