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RESEARCH ARTICLE

Growth, yield, nutritional quality and nickel accumulation in cassava (*Manihot esculenta* Crantz) under nickel-amended soil

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Abstract

Heavy metal contamination is a growing concern for sustainable agriculture and global food security. Among various heavy metals, nickel (Ni) presents a unique challenge due to its dual role in plant physiology-it is essential in trace amounts but becomes toxic when present in excess. This study investigates the effects of different Ni concentrations on cassava (*Manihot esculenta* Crantz), with a focus on growth performance, yield attributes and nutritional composition. A controlled pot experiment was conducted using five Ni treatments (0, 50, 100, 150 and 200 mg kg^{-1}) to evaluate plant responses across morphological and biochemical parameters. At a sub-toxic concentration of 50 mg kg^{-1}, Ni significantly improved plant height, stem diameter and enhanced nutritional quality by increasing protein, starch and total carbohydrate contents suggesting a beneficial role in metabolic and physiological processes. However, exposures to higher Ni concentrations (≥100 mg kg^{-1}) led to notable reductions in growth and yield parameters such as plant height, stem diameter, tuber diameter, fresh tuber weight, etc., along with increased accumulation of Ni in edible tissues. This not only impairs plant development but also poses serious risks to food safety and human health. The findings highlight the balance between Ni's essentiality and toxicity. While low-level Ni exposure enhances agronomic benefits, the results underscore the critical need for monitoring and regulating heavy metal concentrations in agricultural soils to ensure sustainable cassava production and protect consumer health.

Keywords: bioaccumulation; cassava; food chain; heavy metal; micronutrient

Introduction

Manihot esculenta Crantz is commonly known by different names such as cassava, tapioca, manioc and youca is a starchy tuber crop of the Euphorbiaceae family. Cassava can thrive under abiotic and biotic stress and adapt to the conditions of marginal and nutrient-poor soils (1,2). Due to its ample carbohydrate content in the tubers, cassava is a staple crop for over 800 million people worldwide and is particularly important in developing nations (3). Leaves are also edible and serve as a staple food in certain countries due to their nutritional abundance (4). Additionally, cassava leaves are preferred as an alternative feed for eri silkworms (*Samia ricini* Donovan), especially when castor leaves (*Ricinus communis* L.), their primary host plants are unavailable (5). However, cassava contains highly toxic compounds, primarily cyanogenic glycosides, whose levels are influenced by genotype and environmental conditions such as drought (6). Globally, Heavy metals and Metalloids (HMs) are acknowledged as significant environmental contaminants that pose a serious threat to human health and ecosystems. Agricultural soils are particularly vulnerable to HM contamination due to various anthropogenic activities such as excessive use of chemical fertilizers and pesticides, irrigation with contaminated water, etc. (7). The elements such as chromium (Cr), nickel (Ni), cadmium (Cd), lead (Pb), mercury (Hg), copper (Cu) and zinc (Zn) are commonly found in contaminated agricultural soils and have hazardous effects on plants at high concentrations (8). Although HMs are not intrinsically toxic, they can be detrimental to plants when present in concentrations exceeding permissible limits. Some HMs, such as Ni are essential micronutrients that play important roles in plant growth and development, but only within a narrow range of concentrations (9).

Nickel is classified among the 23 HMs to be of significant concern for the environment and human health (10). It is the 22nd most prevalent element in the Earth's crust and an important trace metal making up around 0.008 % of its composition (11). It is therefore a naturally occurring component of water and soil parent material (12). Ni is a widespread trace metal pollutant in the environment, originating from both natural sources and various human activities (9). Anthropogenic activities significantly increase Ni accumulation in soils through various sources such as fossil fuel combustion, excessive fertilizer use, mining, smelting, vehicular emissions, cement factories and waste disposal (household, industrial and municipal) (13). Ni is a vital micronutrient for plant growth and development, playing key roles in various physiological processes (14). Although Ni is essential in trace amounts, elevated concentrations can induce toxicity and result in various harmful physiological and biochemical changes in plants (14). High concentrations of nickel can induce toxicity in plants, characterized by leaf chlorosis, stunted growth and disruptions in key physiological processes such as photosynthesis, respiration, nutrient uptake, sugar transport and water balance. Excessive accumulation of Ni in soils not only harms soil organisms but also leads to its uptake by plants, which enables it to enter the food chain through food crops (15,16). Previous studies have indicated that cassava is more susceptible to heavy metal contamination and other pollutants compared to other tuber crops, potentially posing greater health risks (17). According to previous studies, when cultivated in crude oil-contaminated soils, cassava can accumulate heavy metals in its tissues (18). Additionally, cassava tubers grown near cement factories have been reported to contain elevated levels of various heavy metals including chromium, nickel, lead, zinc, copper, iron, arsenic often exceeding the permissible limits established by the Food and Agriculture Organization (FAO) and the World Health Organization (WHO) (19). Interestingly, cassava has demonstrated the ability to phyto-extract HMs such as mercury and gold from bio-solids and mine tailings containing these elements (20).

While the effects of water and salinity stress on cassava growth and yield are well-studied, limited study exists on the impact of HM contamination, particularly nickel, which is considered to an essential micronutrient as well toxic HM, on its growth, yield and nutritional quality. It is essential to comprehend the physiological and biochemical responses of cassava to HM stress such as Ni, because of its high accumulation potential and the risks of HM transfer into the food chain. Therefore, this study aims to evaluate the impact of Ni contamination on the growth, yield and nutrient composition of cassava, with a focus on Ni uptake, accumulation and translocation in various plant tissues. By assessing bioaccumulation in edible and vital organs, the research highlights potential health risks, plant-metal interactions and the viability of cassava for cultivation or remediation in Ni-contaminated soils.

Materials and Methods

Plant materials and Ni treatments

The present investigation was carried out for two successive years (2021 & 2022), under greenhouse conditions in Bongaigaon, Assam (India) (Latitude 26.3440758° N and Longitude 90.5153918° E). The area is situated at an altitude of 63 m above mean sea level and falls in a sub-tropical to humid climate. The mean ambient temperature varied from 27.1–30.9 ^{o}C during cassava (March to November) cultivation. The average relative humidity varied from 42.74–66.43 % during cassava cultivation. The soil was sandy loam collected from fallow home garden and immediately analyzed the soil physico-chemical characteristics. Each pot was filled with 5 kg of soil that had been ground and passed through a 2 mm sieve.

Pot experiments were conducted with cassava stem cuttings irrigated with various concentrations of Ni solution. As the maximum permissible limit of Ni in the soil is 75 mg kg^{-1}, the Ni treatment levels of 0, 50, 100, 150 and 200 mg kg^{-1} soil were selected based on relevant literature for the present study (21). The lowest concentration (50 mg kg^{-1}) was chosen to observe any stimulatory effects, as certain trace levels of HMs can be beneficial for plant growth. Moderate to high levels (100–200 mg kg^{-1}) were included to mimic the escalating levels of HM stress that could arise in contaminated soils close to mining or industrial areas.

Disease-free, healthy mature cassava plant stem cuttings measuring 30 cm in length and containing 3 to 4 active buds were taken for the present experiment (22). The cuttings were then transplanted into large-sized grow bags filled with 50 kg of soil treated with varying concentrations of Nickel (II) sulphate heptahydrate ($NiSO_4{\cdot}7H_2O$) pure, 98 % (M.W. 280.85, SRL, India) as a source of Ni viz. 0 mg kg^{-1} (T_0), 50 mg kg^{-1} (T_1), 100 mg kg^{-1} (T_2), 150 mg kg^{-1} (T_3) and 200 mg kg^{-1} (T_4). Plants were watered periodically with Ni free water and recommended doses of NPKS @ 50, 22, 50 and 10 mg kg^{-1} and replicated thrice.

Determination of soil physico-chemical characteristics

The experimental soil that was used to fill the grow bags was collected, allowed to shade dry and then sieved using a 2 mm sieve. Three replications of each sample were examined. The pH and Electrical Conductivity (EC) values were measured using a digital pH and conductivity meter, respectively. The total Organic Carbon (OC) of the samples was measured by the Walkley and Black titration method where a known weight of finely ground soil was treated with potassium dichromate ($K_2Cr_2O_7$) and concentrated sulfuric acid (H_2SO_4) (23). Subsequently, 100 mL of distilled water and 10 mL of 85 % orthophosphoric acid were added, followed by 2–3 drops of diphenylamine indicator. The solution was then titrated against 0.5 N ferrous ammonium sulfate until the end-point colour change from violet-blue to dark green was observed. The total nitrogen content (N) was determined by the Micro-Kjeldahl method (23). 1 g of finely ground air-dried soil was digested with concentrated H_2SO_4 in the presence of a reaction mixture (potassium sulfate and copper sulfate). After digestion the contents transferred to a distillation unit. The ammonium ions were then liberated as ammonia by addition of concentrated sodium hydroxide (NaOH) and distilled into a boric acid solution containing mixed indicator. The trapped ammonia was subsequently titrated with H_2SO_4 until the endpoint colour change was observed. The total sodium (Na) and potassium (K) contents in the samples were measured in a flame photometer by digesting 1 g of air-dried soil sample with ammonium acetate overnight and the filtered solution was used for determination (24). The available phosphorus was determined spectrophotometrically using the stannous chloride technique (24). 1 g of air-dried soil was extracted with 200 mL of 0.002 N H_2SO_4 by shaking for 30 min. The suspension was filtered through Whatman No. 50 filter paper and to a known volume of the filtrate added 2 mL of ammonium molybdate solution and 5 drops of stannous chloride solution, resulting in the development of a blue-coloured complex. The absorbance of the solution was recorded at 690 nm using a UV–Vis spectrophotometer. Soil available Ni was determined using a flame atomic absorption spectrophotometer (25).

Plant growth characteristics

At the end of 9 Months After Plantation (MAP), growth parameters such as plant height (cm), stem diameter (cm), number of leaves per plant and leaf area (cm^2) were recorded (26). The height of the plant was measured from the base of the stem (at the soil surface) to the tip of the apical meristem using a standard measuring tape. The stem diameter was measured using a digital vernier calliper for precise measurement. To ensure consistency, measurements were made at a fixed position, approximately around 1 m above the soil surface. The values were recorded in centimeters (cm). Leaf area was calculated using the conventional graphical method. For each plant, fully expanded leaves were removed carefully and used right away for measuring to avoid wilting or curling. At harvest, the following yield attributes were recorded to evaluate the effect of treatments on tuber production: the number of tubers per plant, tuber diameter and fresh tuber weight per plant.

Determination of nutritional composition

Nutritional compositions were determined using the standard methodologies of the Association of Official Analytical Chemists (27). For the determination of moisture content, 1 g of fresh samples was weighed and placed in a petri plate and oven-dried to a constant weight at 105 °C (Eqn. 1).

$$\% \text{ MC} = \frac{\text{Wi-Wf final weight}}{\text{Wi}} \times 100 \qquad \text{Eqn. 1}$$

Where,

MC = Moisture content expressed as percentage

Wi = initial weight of sample (g)

Wf = final weight of sample (g)

Total Nitrogen content was determined following the methodology of Micro-Kjeldahl using Pelican Kelplus equipment (27) (Eqn. 2).

$$\% \text{ N} = \frac{14.01 \times (\text{mL of } 0.1 \text{ N } H_2SO_4 \text{ used-blank} \times 0.1 \times 100}{\text{W} \times 1000} \qquad \text{Eqn. 2}$$

Where,

N = nitrogen content expressed as percentage

W = weight of dried sample (g)

Crude Protein (CP) was calculated by multiplying the total nitrogen by the constant factor 6.25, as reported previously (27) (Eqn. 3).

$$\text{CP } \% = \text{N } \% \times 6.25 \qquad \text{Eqn. 3}$$

Where,

CP = crude protein expressed as percentage

N = total nitrogen expressed as percentage

Lipid was determined using a Soxhlet extraction apparatus (27) and calculated using the following equation (Eqn. 4).

$$\text{Lipid } (\%) = \frac{\text{Wf - Wi}}{\text{W}} \qquad \text{Eqn. 4}$$

Where,

Wi = initial weight of round bottom flask (g)

Wf = final weight of round bottom flask (g)

W = weight of substance taken (g)

Crude fiber content was determined from the defatted sample previously obtained through Soxhlet extraction (27). The crude fiber was calculated using the following equation (Eqn. 5).

$$\% \text{ of crude fiber} \frac{\text{W1-W2}}{\text{W}} \times 100 \qquad \text{Eqn. 5}$$

Where,

W1 = weight of crucible with dry residue (g)

W2 = weight of crucible with ash (g)

W = weight of substance taken (g)

Ash content was determined according to the standard procedure (27). After the moisture removed, the samples were incinerated at 550 °C to burn off all organic constituents (Eqn. 6).

$$\% \text{ of ash} = \frac{\text{Weight of the crucible with ash – initial weight of the crucible}}{\text{Weight of substance taken (g)}} \times 100 \qquad \text{Eqn. 6}$$

Where,

Wi = initial weight of the crucible (g)

Wf = final weight of the crucible (g)

W = weight of substance taken (g)

Total carbohydrate content and starch estimation were determined using the Anthrone method with slight modification (28).

Determination of Ni bioaccumulation

The dried plant samples were digested in the muffle furnace and the ash was dissolved in a 10 % nitric acid (HNO_3) solution. The dissolved ash solution was transferred to a 250 mL volumetric flask and the volume was adjusted up to 50 mL with distilled water and then filtered using Whatman filter paper. The filtrate was stored for further determination of Ni using Flame Atomic Absorption Spectroscopy (AAS) (23).

Data analysis

Data reported in this study are means of three replicates with standard deviations (±). Data were analyzed statistically by Analysis of Variance (ANOVA) using SPSS software at $p = 0.05$ (29). Graphical work was carried out using Origin software 8.0.

Results and Discussion

Physicochemical properties of soil

The physico-chemical parameters of soil, which include pH, EC, OC, total N, available P, total K, Na and available Ni have been recorded (Table 1). The soil was slightly acidic, with a pH of 6.2. For cassava cultivation, a pH range of 5.5–6.5 is generally considered optimal (30). The soil contained 1.27 % total OC and 0.08 % total N, reflecting a modest nutrient status. The presence of K (31 ppm) and Na (22 ppm) within desirable range ensured that the vital nutrient supply and ionic balance were not limiting factors for plant growth (31). The available Ni concentration was 0.45 mg kg^{-1}, which is well below the permissible limits for both soil and plant health (32).

Growth and yield parameters

The presence of Ni in the environment has a major impact on the plant growth and development (9). In this study, growth and

Table 1. Physico-chemical characteristics of experimental soil

Parameters	Values
pH	6.2 ± 0.002
Electrical conductivity (mS/cm)	0.3 ± 0.001
Total organic carbon (%)	1.27 ± 0.03
Total nitrogen (%)	0.08 ± 0.002
Available phosphorous (ppm)	37.0 ± 1.67
Total potassium (ppm)	31.0 ± 2.4
Total sodium (ppm)	22.0 ± 1.09
Soil available Ni (mg kg^{-1})	0.45 ± 0.067

yield of fully matured cassava plants, growing under varying levels of Ni stress were evaluated at 9 MAP and compared with the control plants. Plant growth parameters were significantly reduced overall by exposure to Ni, with the effects being most noticeable at higher Ni concentrations. Interestingly, a low dose of Ni stress (50 mg kg^{-1}) enhanced some growth characteristics when compared to the control.

Plant height and stem diameter

Plants exposed to a low Ni concentration (50 mg kg^{-1}/ T_1) showed a significant increase in height (396.53 cm), in comparison to the control (331.27 cm), suggesting a stimulatory impact of Ni at low levels (9). However, plant height decreased significantly as the Ni concentrations in the soil increased beyond 50 mg kg^{-1} (Table 2). Height of cassava declined to 286.90 cm at T_2 and then to 249.07 cm and 212.67 cm at T_3 and T_4, respectively. These findings suggest that Ni might serve as an essential micronutrient that promotes certain processes in cassava when it is present in trace amounts (16). However, at higher concentrations, Ni interferes with cell elongation and disrupts overall growth and metabolic activities, leading to stunted development (33,34).

Stem diameter followed a similar pattern, with cassava plants receiving the lowest Ni treatment (50 mg kg^{-1}) exhibiting the highest stem diameter of 3.68 cm, compared to an average of 3.42 cm in the control group. These results suggest that low levels of Ni may promote stem thickening in cassava.

Leaf area and number of leaves

In the present study, leaf area decreased with increasing Ni concentration, as compared to the control, except for the plants receiving the lowest Ni treatment (T_1), suggesting low level of Ni may promote leaf expansion (Table 2). The stimulatory effect of Ni at low amount may be attributed to the crucial role that Ni plays in enhancing metabolic processes, particularly nitrogen assimilation and urease activity, in plants, which can indirectly promote leaf development (16). However, there was a noticeable decrease in leaf area as the Ni content increased. The area of the leaves decreased to 206.33 cm^2 at T_2, then to 169.00 cm^2 at T_3 and 173.33 cm^2 at T_4. The significant decrease at higher Ni levels suggests that excessive Ni accumulation interferes with cell division and photosynthetic processes, resulting in smaller leaves (35). Along with leaf area, the numbers of leaves per plant were also found to be affected by higher dose of Ni. This can be attributed to the Ni induced phytotoxicity such as reduced leaf initiation and quicker leaf senescence (35).

Growth and yield of tuber

Ni exposure had a significant impact on the yield parameters of cassava tubers (Table 3). T_0 and T_1 did not show significant differences in tuber weight and diameter, indicating that lower Ni levels might not be detrimental to tuber development. However, all yield parameters gradually declined as the Ni content increased beyond 50 mg kg^{-1}. The higher Ni treatment (T_4) led to a significant reduction in tuber weight (4.02 kg), tuber diameter (5.87 cm) and the number of tubers per plant (3.33), all notably lower than those in the control group.

These findings suggest that high Ni levels interfere with normal tuber development, potentially through affecting photosynthetic allocation, nutrient uptake and root function. Abiotic stress in cassava can negatively hamper tuber yield, especially during the early stages of its development (36). It has been demonstrated that water stress lowers the average weight and length of individual tubers and the quantity of tuberous roots (37). Drought conditions can significantly affect cassava growth, development and overall tuber yield, with the most severe impact occurring during the tuberization stage, the phase when tubers enlarge and starch accumulation peaks (36). Although earlier studies have documented declines in cassava yield and starch content due to water stress (36,38), the present investigation is among the first to demonstrate comparable negative impacts resulting from heavy metal, Ni.

Nutritional composition

The nutritional composition of cassava leaves and tubers were analysed and reported (Fig. 1a–g). In the present study, moisture content showed a clear declining trend with increasing Ni

Table 2. Effect of Ni stress on plant height, stem diameter, leaf area and number

Treatments	Parameters			
	Plant height (cm)	Stem diameter (cm)	Leaf area (cm^2)	Number of leaves per plant
T_0	331.33 ± 8.65^a	3.42 ± 0.148^a	254.67 ± 13.07^a	357.17 ± 30.14^a
T_1	396.1 ± 12.39^b	3.68 ± 0.09^b	281.17 ± 22.66^b	380.03 ± 15.86^b
T_2	286.48 ± 23.69^c	3.03 ± 0.09^c	206.23 ± 14.52^c	270.99 ± 27.40^c
T_3	249.77 ± 17.02^d	2.58 ± 0.18^d	169 ± 9.79^d	219 ± 19.60^d
T_4	212.67 ± 13.2^e	2.18 ± 0.12^e	173.09 ± 22.89^e	158.5 ± 28.78^e

n=3; error bars indicate SD. Dissimilar letters in the same column in each parameter indicate statistically significant differences ($p < 0.05$)

Table 3. Effect of Ni stress on yield parameters of cassava tuber

Treatments	Tuber yield (kg)	Tuber diameter (cm)	Tuber nos/plant
T_0	6.26 ± 0.17^a	7.79 ± 0.1^a	5.67 ± 0.47^a
T_1	6.18 ± 0.19^a	7.86 ± 0.2^a	5.33 ± 0.47^b
T_2	5.08 ± 0.33^b	6.79 ± 0.14^b	4.67 ± 0.2^c
T_3	4.58 ± 0.09^c	6.42 ± 0.21^c	3.6 ± 0.09^d
T_4	4.03 ± 0.052^d	5.87 ± 0.53^d	3.33 ± 0.1^e

n=3; error bars indicate SD. Dissimilar letters in the same column in each parameter indicate statistically significant differences ($p < 0.05$)

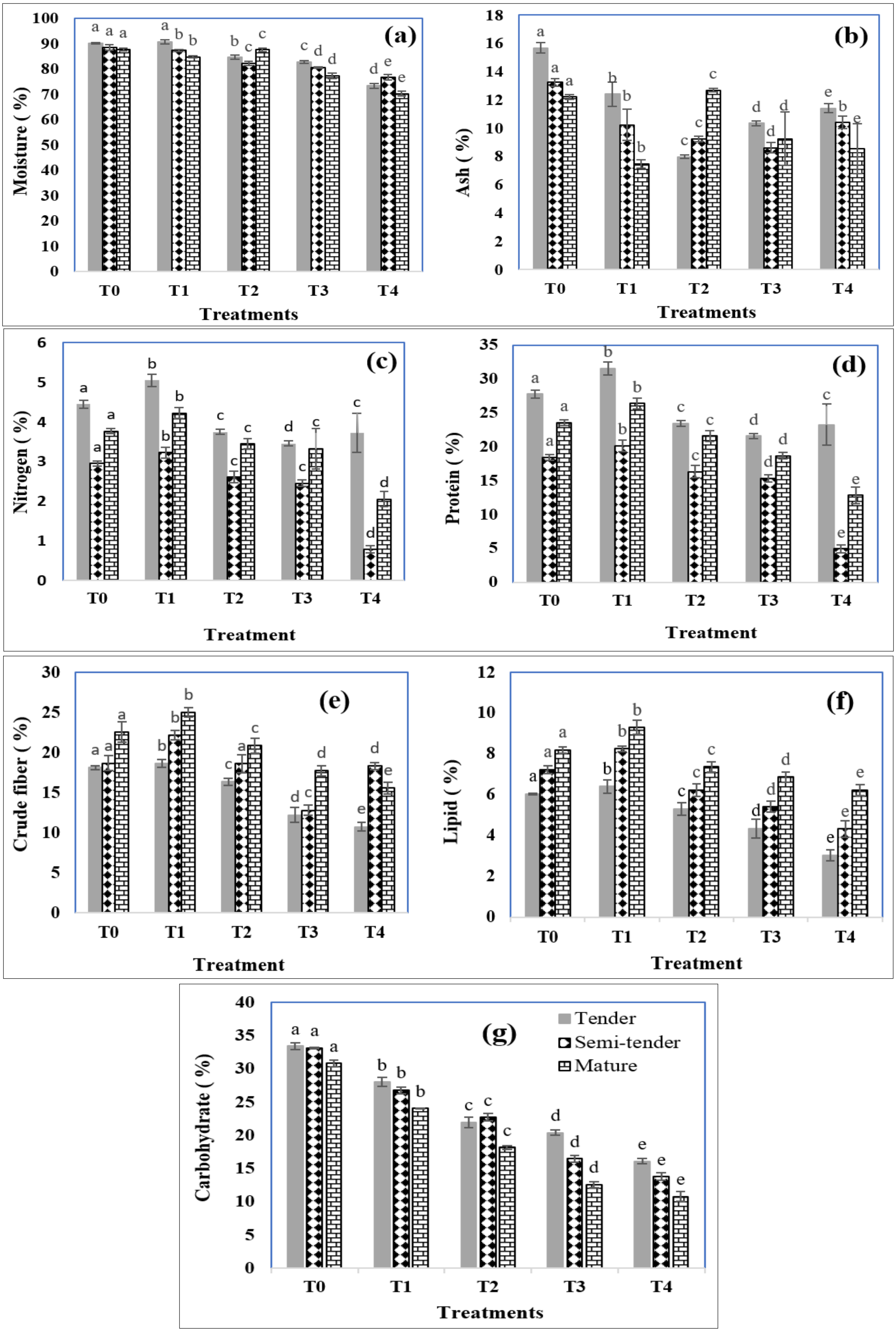

Fig. 1. Moisture, ash, nitrogen, protein, crude fiber, lipid and carbohydrate content respectively of cassava leaf under Ni stress.

n=3; error bars indicate SD. Dissimilar letters among the treatments for each leaf maturity stage indicate statistically significant differences ($p < 0.05$)

concentration across all leaf maturity stages tender, semi-tender and mature (Fig. 1a). No significant differences were observed in the values of moisture content of T_0 (90.073 %) and T_1 (90.607 %) of tender leaves. However, moisture content gradually decreased as Ni stress increased (T_2–T_4), reaching the lowest level in T_4 (73.340 %), an 18.6 % decrease from T_0, indicating toxicity at higher Ni concentrations. A similar decreasing trend with increased Ni content was observed for semi-tender and mature leaves. The findings show that, particularly at higher concentrations, Ni stress negatively impacts the physiological health of cassava leaves. In the present study, Ni stress exhibited a dose-dependent decrease in the moisture content of the tubers. T_0 showed the highest value (90.41 %) while T_4 represented the lowest (78.35 %). An increased transpiration rate, potentially triggered by Ni-induced disruptions in stomatal regulation and water balance mechanisms might result in reduced moisture content of both leaves and cassava in this study (39).

Ash content denotes the amount of total minerals present in plant tissues (40). Significant differences in ash content between treatment levels and leaf maturation stages were found in this study, suggesting differential uptake and allocation of minerals under Ni-induced stress (Fig. 1b). In tender leaves, T_0 exhibited the highest ash content (15.67 %), indicating normal mineral uptake. Moderate declines were observed in T_1 (12.41 %), T_3 (10.33 %) and T_4 (11.40 %), suggesting stress-induced disruption and possible adaptive responses at higher Ni concentrations. T_2 showed a marked reduction (7.97 %), pointing to significant impairment of mineral uptake due to Ni toxicity (35). A similar pattern was seen in semi-tender leaves, indicating that Ni interference with nutrient dynamics affects this developmental stage as well. Interestingly, mature leaves displayed a distinct trend: ash content dropped to 7.47 % in T_1 but increased sharply in T_2 (12.67 %), exceeding the control (12.2 %). This increase may reflect a detoxification mechanism, where excess Ni is immobilized in older tissues (41), indicating possible mineral reallocation or translocation under stress. However, ash content declined again in T_3 (9.23 %) and T_4 (8.53 %), suggesting that prolonged exposure to high Ni levels continues to suppress mineral accumulation.

Similarly, ash content in cassava tubers declined with increasing Ni concentrations, indicating a clear adverse effect of Ni on mineral accumulation in storage tissues. Ash content was highest in T_0, 1.69 %, followed closely by T_1 (1.56 %), indicating that low-level Ni exposure had only a marginal effect. However, there was a noticeable and steady decline with subsequent increases in Ni concentration (T_2–T_4), with the lowest value recorded at T_4 (0.68 %), signifying a 59.6 % decline in comparison to the control. The steep drop after T_1 implies that Ni stress limits the deposition of inorganic matter in tubers by interfering with mineral translocation and root function. These results are consistent with earlier observations that HM stress impairs root crop nutrient absorption and assimilation (42). Alongside decreased mineral absorption, the reduction in ash content may also indicate possible alterations physiological processes such as enzyme activity, respiration and tuber formation under metal stress (43,44).

Nitrogen is essential not only for plant growth but also for key metabolic processes such as protein synthesis, chlorophyll production and enzyme activity (45). In the current study, with increasing levels of Ni stress discernible variations in nitrogen content were observed (Fig. 1c). The nitrogen content was moderate under control conditions but slightly increased with low-level of Ni exposure i.e. T_1, suggesting a potential stimulatory effect at lower concentrations, most likely as a result of improved nitrogen absorption or increased enzymatic activity. Nitrogen levels, however, showed a steady decline with subsequent increases in Ni concentration (T_2–T_4), with the lowest values noted at T_4 for all leaf stages. However, its value in tubers did not show a significant difference ($p < 0.05$) between the T_0 (1.45 %) and T_1 (1.50 %), suggesting that low-level Ni exposure does not negatively affect nitrogen accumulation. However, with increasing Ni levels in the soil beyond 50 mg kg^{-1}, a marked decline in nitrogen content was observed, T_2 (1.16 %), T_3 (1.01 %) and T_4 (0.66 %). The reduced nitrogen accumulation observed in this study is attributed to Ni interference with protein metabolism and nitrogen-assimilating enzymes such as nitrate reductase (46). The inconsistent pattern across different leaf developmental stages suggests that both nitrogen uptake and internal translocation were disrupted by prolonged Ni exposure. The overall decline across treatments indicates a dose-dependent inhibition of nitrogen metabolism.

Protein content in cassava leaves exhibited a pronounced sensitivity to Ni stress, with values differing noticeably between treatments (Fig. 1d). Protein levels were moderate to high under control conditions (T_0), but under low-level Ni treatment (T_1), there was a discernible rise, indicating that Ni may have a stimulatory impact at sub-toxic quantities. And as Ni levels increased further (from T_2–T_4), the protein content gradually decreased, suggesting a disruption in protein biosynthesis and degradation pathways. T_4 had the lowest protein levels, particularly severe in semi-tender (4.96 %) and mature leaves (12.85 %). A similar trend was also observed for tubers. The protein content of tubers in this study, ranged from 4.12–9.4 %, with the highest value observed at T_1. Increased metabolic activity or the up-regulation of specific stress-related proteins may be the explanation of these sudden rises in protein content of both leaves and tubers (47). Furthermore, under increased stress levels, protein content declined significantly. The findings clearly demonstrate that increased Ni levels have a negative impact on cassava tuber protein biosynthesis, which reflects the deteriorating nutritional value of cassava when exposed to metal stress.

Under Ni stress, there was a significant variation in the fibre content across the leaf maturation stages (10.75–25.04 %) (Fig. 1e). Overall, the fibre content was found to increase with increase in leaf maturity stages, at all treatment levels. At T_0, fibre was highest in mature leaves (22.59 %), followed by semi-tender (18.69 %) and tender (18.16 %). However, at T_1, lipid accumulation increased across all stages, suggesting that low-level Ni exposure may have a stimulatory effect on lipid biosynthesis. However, as Ni levels increased beyond T_1, a steady decline in lipid content was observed. This could be because of excessive Ni induced oxidative stress which results in lipid peroxidation (48). The variety and age of cassava is known to influence its fibre content in the tubers. Like other parameters, fibre content in tubers markedly decreases with increased Ni concentration. The highest fibre content was observed in T_0 (5.32

%) showing no significant differences with T_1 (5.15 %). However, a sharp decline was recorded in higher Ni treatments, with T_4 showing the lowest value (2.62 %). However, the lipid values obtained in our study are notably higher than typical levels reported in earlier studies, approximately 1.5 % in fresh tubers and up to 4 % in root flour (6). The reason of these differences could be attributed to varietal differences, environmental factors, or differences in drying and analytical methods (6).

Although there was a slight stimulatory increase at low Ni exposure, the lipid content in cassava leaves showed a dose-dependent decline with increasing Ni concentration (Fig. 1f). At T_0, lipid levels were moderate and slightly increased at T_1, which may indicate a transient adaptation to mild stress. However, lipid content, significantly dropped with increasing Ni treatments (T_2-T_4), with the lowest values (tender- 3.033 %, semi-tender- 4.33 %, mature- 6.23 %) observed at the highest Ni concentration (T_4) (Fig. 1f). Similar patterns of lipid depletion under metal stress have been documented in other crops, underscoring the susceptibility of lipid metabolism to heavy metals (49,50). The lipid content in cassava naturally increases with leaf maturity, reflecting the accumulation of structural and storage lipids, which also align with our findings (51). However, in tubers, as Ni treatments increased, a significant decline in the lipid content was observed (Table 4). The highest average was recorded in the control (1.43 %), followed by 1.21 % at T_1 and the lowest value at T_4 (0.36 %). These biochemical alterations reflect broader physiological stress responses in cassava growing under heavy metal contamination, in addition to affecting the nutritional value.

In the present study, carbohydrate content decreased with increase in Ni stress and across the leaf maturity stages (i.e., tender > semi-tender > mature) (Fig. 1g). Carbohydrate content in tender leaves decreased from 33.46 % (T_0) to 16.12 % (T_4). Similarly, semi-tender leaves showed a reduction from 33.15 % at control (T_0) to 13.79 % at the highest Ni treatment (T_4). The same pattern was seen in mature leaves, with carbohydrate content declined from 30.84 % to 10.83 % between T_0 and T_4, respectively. A similar reduction under Ni stress in corn and broad beans were reported earlier (9,50). This decrease indicates to a disruption in carbohydrate metabolism possibly due to interference with photosynthetic efficiency or sugar transport mechanisms (51). There has been considerable variation in carbohydrate content in cassava leaves across studies. Carbohydrate content in cassava leaves ranges from 7 % to 18 % (52). In contrast, previously other researchers reported significantly higher carbohydrate content, ranging between 38 % and 45 % (dry weight) in cassava leaves (53).

In cassava tubers, approximately 80 % of the total carbohydrates are present in the form of starch, with only small amounts of sucrose, glucose, fructose and maltose (54). The starch content in tubers declined across treatments with highest (90.88 %) observed at 50 mg kg^{-1} Ni followed by 88.53 % at control (Table 4). However, beyond T_1, a gradual decline in starch content was observed. Although, cassava tubers typically contain 32-35 % on a fresh weight basis and from 80-90 % on a dry weight basis (6), exposure to increasing Ni stress in the present study led to a marked decline in starch accumulation, with values declining to as low as 65.19 % under the higher Ni stress (T_4). It is clear from these findings that elevated Ni levels could disrupt the processes involved in carbohydrate metabolism or starch biosynthesis pathways in cassava tubers. Reductions in starch content of tuberous root of sweet potato (*Ipomoea batatas*) under heavy metal stress have been previously reported in a similar study (55).

Nickel bioaccumulation

As soil Ni concentration increased, its bioaccumulation in cassava tissues also increased progressively, exhibiting clear differences between tubers and leaves at various maturity stages (Table 5). Ni levels in untreated plants (T_0) remained below the permissible limits. Mature leaves showed highest Ni content ranging from 3.7 mg kg^{-1} (T_1) to 12.1 mg kg^{-1} (T_4), among leaf maturity stages across all treatment. Our findings are consistent with previous findings which suggested that Ni accumulation is higher Ni in mature leaves compared to tender ones (56). Ni content in tender leaves increased sharply with increasing soil Ni levels, ranging from 3.3 mg kg^{-1} (T_1) to 13.3 mg kg^{-1} (T_4). Ni accumulation in semi-tender leaves ranged from

Table 4. Nutritional compositions of cassava tubers at the time of harvesting grown under different Ni treatments

Parameters (%)	Treatments				
	T_0	T_1	T_2	T_3	T_4
Moisture	90.41 ± 0.43^a	88.74 ± 1.24^b	84.17 ± 0.86^c	80.76 ± 0.57^d	78.36 ± 0.96^e
Ash	1.69 ± 0.07^a	1.56 ± 0.1^b	0.93 ± 0.1^c	0.93 ± 0.12^c	0.68 ± 0.10^d
Nitrogen	1.45 ± 0.07^a	1.50 ± 0.06^a	1.16 ± 0.10^b	1.01 ± 0.06^c	0.66 ± 0.09^d
Protein	9.04 ± 0.43^a	9.40 ± 0.38^b	7.27 ± 0.60^c	6.31 ± 0.37^d	4.12 ± 0.54^e
Crude fibre	5.32 ± 0.67^a	5.15 ± 0.14^b	2.95 ± 0.20^c	2.53 ± 0.41^d	2.62 ± 0.46^e
Lipid	1.43 ± 0.12^a	1.21 ± 0.12^b	0.75 ± 0.04^c	0.61 ± 0.04^d	0.36 ± 0.04^e
Starch	88.53 ± 1.10^a	90.88 ± 1.43^a	80.84 ± 1.46^b	70.23 ± 0.84^c	65.19 ± 1.11^d

n=3; error bars indicate SD. Dissimilar letters in the same row in each parameter indicate statistically significant differences ($p < 0.05$)

Table 5. Bioaccumulation of Ni in leaves and tubers of cassava

Treatments (Ni g kg^{-1})	Nickel Bioaccumulation (mg kg^{-1})			
	Leaf maturity stages			Tuber
	Tender	Semi-tender	Mature	
T_0	0.009 ± 0.0003	0.015 ± 0.0002	0.022 ± 0.007	0.05 ± 0.004
T_1	3.3 ± 0.013	2.5 ± 0.008	3.7 ± 0.06	1.4 ± 0.012
T_2	3.9 ± 0.078	3.8 ± 0.010	7.2 ± 0.084	2.1 ± 0.017
T_3	9.1 ± 0.063	5.1 ± 0.069	10.3 ± 0.962	2.9 ± 0.023
T_4	13.3 ± 0.052	6.6 ± 0.017	12.1 ± 1.016	3.6 ± 0.066

Maximum permissible limit of Ni in crops: 75–100 mg kg^{-1}; maximum permissible limit of Ni in soil: 10 mg kg^{-1} (21)

2.5 mg kg^{-1} (T_1) to 6.6 mg kg^{-1} (T_4). On the other hand, tubers accumulated significantly less Ni, with values ranging from 1.4 mg kg^{-1} (T_1) to 3.6 mg kg^{-1} (T_4). While Ni levels in tubers remained below permissible limits, the upward trend with increasing soil Ni suggests that prolonged cultivation on contaminated soils could lead to gradual Ni accumulation. The findings show that mature leaves serve as significant sinks for Ni bioaccumulation when grown in Ni-amended soil. This is consistent with previous findings that older leaves typically accumulate more heavy metals because of their longer exposure times and increased metal-binding capacity (57). These findings, when compared with the WHO prescribed maximum permissible limit of Ni in plants (10 mg kg^{-1}), are significant (32). At the higher soil Ni treatments (T_3 & T_4), both tender and mature leaves surpassed this threshold. This implies that cassava, when grown in Ni-amended soils, can accumulate Ni beyond the permissible limit, posing potential risks if used as animal or human feed.

Impact evaluation factors

Translocation Factor (TF)

TF >1 indicates that metals are easily transported by the plant to the aerial portions. However, the TF <1 suggests that the plant is mostly retaining the metals in its underground portions, such as its roots and tubers (58). In the present study, under all the stress treatments, TF of mature leaf: tuber was higher- 2.64 (T_1) to 3.361 (T_4) (Table 6). These findings indicate that Ni translocation to mature leaves is more pronounced than to tender and semi-tender leaves, suggesting that older tissues may accumulate more Ni from the tubers. Similar patterns have been reported in other crops, where age-related physiological and morphological features frequently result in older leaves accumulating larger amounts of HMs (59). The present investigation shows that the internal translocation of Ni within the tissues of cassava depends on leaf maturity. These translocation patterns are noteworthy from the standpoints of food safety and agronomy. While tubers are a main food source for human populations, cassava leaves are consumed as a leafy vegetable in some regions and utilized extensively as feed for eri silkworms (4,60). The high TF values (>1) suggest a significant risk of Ni transfer to above-ground biomass, which could lead to trophic chain contamination and dietary Ni exposure (61).

Bio-Concentration Factor (BCF)

Among the leaf maturity stages, mature leaves showed the highest BCF, with values ranging from 0.86 (T_4) to 1.23 (T_1) (Table 7). Tender leaves exhibited BCF values between 0.43–1.10, whereas semi-tender leaves showed the lowest BCF values, ranging from 0.42–0.83 across treatments. Mature leaves of cassava consistently showed the highest BCFs, suggesting a stronger tendency to accumulate Ni relative to soil concentrations. This suggests that mature leaves may function as preferential storage sites, where excess metals are sequestered to protect younger tissues.

Conclusion

This study highlights the dual role of Ni where low concentrations (50 mg kg^{-1}) promote growth and nutritional quality, however, higher levels cause sharp declines in yield and nutrient content. The narrow threshold between beneficial and toxic concentrations, coupled with Ni bioaccumulation in edible tissues, raises concerns for food safety and soil health. Therefore, although cassava can be grown on marginal soils, careful monitoring of Ni levels is necessary for both consumer protection and sustainable farming.

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Authors' contributions

The methodology was carried out by BD, NB and MC. Conceptualization was done by BD and MC, while BD performed the investigation. BD prepared the original draft of the manuscript and MC along with NB contributed to writing, review and editing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Table 6. Translocation factor of Ni in cassava tissues as influenced by different treatments of nickel

Treatments (Ni g kg^{-1})	Translocation factor of nickel		
	Tender leaf: Tuber	Semi-tender leaf: Tuber	Mature leaf: Tuber
T_0	0.18	0.3	0.44
T_1	2.357	1.785	2.64
T_2	1.857	1.809	3.428
T_3	3.137	1.758	3.551
T_4	3.694	1.833	3.361

Table 7. Bio-concentration factor of Ni in cassava tissues as influenced by different treatments of nickel

Treatments (Ni g kg^{-1})	Bio-concentration factor of nickel			
	Tender leaf: Soil	Semi-tender leaf: Soil	Mature leaf: Soil	Tuber: Soil
T_0	0.02	0.03	0.048	0.11
T_1	1.1	0.83	1.23	0.46
T_2	0.43	0.42	0.8	0.23
T_3	0.75	0.42	0.86	0.24
T_4	0.95	0.47	0.86	0.26

Ethical issues: None

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