

Differential foliar and root responses to cassava brown streak disease and their association with root yield: implications for cassava (*Manihot esculenta* Crantz) disease resistance breeding

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Abstract

Cassava Brown Streak Disease is a devastating viral disease threatening cassava production in Africa. While root necrosis causes direct economic loss, phenotypic screening often relies heavily on foliar symptoms. Furthermore, root bitterness (cyanogenic glucoside content) is frequently hypothesized to confer biochemical resistance against pathogens. The objective of this study was to characterize differential foliar and root responses to cassava brown streak disease, assess their association with root yield, and evaluate the influence of root taste on disease severity among cassava germplasm. A total of 138 cassava accessions were evaluated in a randomized complete block design with three replicates. Foliar and root CBSD severity (1–5 scale), root yield, and root taste (sweet, intermediate, bitter) were recorded. Data were analyzed using ordinal and linear mixed-effects models, with plant mortality and total root necrosis coded as zero yield to correct for survivorship bias. Ordinal mixed models revealed highly significant genotypic variation and high broad-sense heritability for both leaf (85%) and root (80%) CBSD traits. While population-level analysis showed a moderate positive correlation between leaf and root symptoms ($p = 0.45$, Odds Ratio = 4.37), accession-level predictions identified a critical 5.1% of genotypes exhibiting extreme phenotypic discordance. Notably, 'hidden susceptible' accessions displayed healthy foliage but severe root necrosis and zero yield. Linear mixed modeling demonstrated that root CBSD severity significantly reduced yield by $1.07 \text{ tonnesHa}^{-1}$ per unit increase ($p = 0.008$), whereas foliar severity had no direct effect on yield ($p = 0.90$). Crucially, Kruskal-Wallis tests revealed no significant differences in CBSD severity among sweet, intermediate, and bitter accessions ($p > 0.05$), indicating that resistance is independent of root taste. Root necrosis, rather than foliar mosaic, is the primary pathological constraint to cassava yield. Because CBSD resistance operates independently of root bitterness and foliar symptoms can be highly deceptive, mandatory root evaluation at harvest is indispensable. The identification of high-yielding, sweet, and root-tolerant accessions provided an elite parental material for developing consumer-preferred, disease-resilient cassava varieties.

Introduction

The plasticity of cassava (*Manihot esculenta* Crantz) edible biomass per unit area of land production is propelling the crop as a strategic food security and industrial raw material source (Manganyi et al., 2023). Moreover, cassava is a potential crop for feedstock for the production of biofuels. Therefore, bridging biofuel source gap since the stem contains about 11.62% hemicellulose and 21.43% cellulose fermentable sugars in the form of lignocellulose (Fathima et al., 2023). Its ability to produce under marginal climatic and soil conditions makes cassava a suitable climate adaptation, resilient livelihoods and income generation option for farmers in these environments (Belalcazar et al., 2016; Selvaraj et al., 2020; Wosula et al., 2024).

Cassava root has carbohydrate content of $320.0\text{--}350.0 \text{ gkg}^{-1}$ on a fresh weight (FW) basis and 800.0 gkg^{-1} on a Dry weight (DW) basis. This is higher than that of potatoes, but lower than that of wheat, rice, and sorghum (Li et al., 2017). The carbohydrate is used for food consumption for human and animal feeds, raw materials in industries like biofuel production (Koros et al., 2018). The high amounts of dietary

energy in cassava roots gives more returns per unit of input than any other staple crop in sub-Saharan Africa (Karim et al., 2020). As a result, the potential of cassava root processing opportunities is on positive growth trajectory (Szyniszewska, 2020). Cassava leaves provide protein, vitamins and minerals (Koros et al., 2018). This nutrient richness can improve dietary diversity, micronutrient and protein intake and health especially during drought period since they are available vegetable (Andersson et al., 2016; Szyniszewska, 2020). In various parts in Sub-Saharan Africa, young cassava leaves are consumed as a vegetable or as a constituent in a form of sauce eaten along with main staple meals. These leaves have a high level of protein which ranges from 21–39% depending on the cultivar (El-Sharkawy, 2004).

Damage to the leaves and roots causes economic losses to the farmer. One of the major threats to cassava production is constraint caused by cassava brown streak disease (CBSD) (Msimo et al., 2025; Sheat & Winter, 2023; Wosula et al., 2024). Leaf chlorosis and necrosis (Fig. 1), elongated necrotic lesions on stems and secondary and tertiary vein chlorosis and dry corky necrotic rot on starchy tissues and stunted growth on infected plants are the symptomatic characteristics of CBSD (Gondwe et al., 2003a; Masinde et al., 2018).

Severe cases of purple/brown lesions on the stems results into death of nodes, internodes and the axillary buds, resulting into dieback of some genotypes. Reduction of starch quality and quantities of amylose and amylopectin by 30% and 50% respectively as a consequence of CBSD infection in the roots. Furthermore, Transient symptom expressions have also been observed (Kawuki et al., 2016).

Cassava brown streak Ipomoviruses (CBSIs) which causes CBSD are among the most serious viruses that cassava is vulnerable to (Chikoti & Tembo, 2022). Moreover, cassava brown streak virus (CBSV) and Ugandan cassava brown streak virus (UCBSV) are two distinct viruses that cause CBSD. Although they cause similar symptoms in the plants, UCBSV has been reported to have lower pathogenicity which result in milder symptoms compared to CBSV (Masinde et al., 2016). The disease spread in the open field is rapid especially with the high population of infected polyphagous whitefly complex *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), which is the transmitting agent (Mkamilo et al., 2024; Munguti et al., 2021; Sheat & Winter, 2023b). Infected planting material is a source of disease inoculum in a new field. Planting material is often sourced from the previous generation which is a characteristic of cassava farming systems in Africa. This facilitates the wide spread of CBSD resulting into yield reductions, diminished seed quality, and a scarcity of disease-free planting materials (Apio et al., 2021; Ndung'u, 2010; Shirima et al., 2020). Root yield losses caused by CBSD in sub-Saharan Africa is estimated to be 30–70% and for susceptible genotypes up to 100% loss (Mware et al., 2009; Wosula et al., 2024). The yield losses are due to root constriction, splitting, and size reduction making them unfit for human and animal consumption (Mware et al., 2009).

CBSD was once thought to be confined to low-altitude coastal regions but has now been reported in areas above 1000 meters above sea level, indicating spread into previously unaffected zones. This expansion is largely attributed to the use of infected planting materials beyond coastal regions (Chikoti & Tembo, 2022; Mware et al., 2009). The severity of CBSD symptoms depends on various factors, including

plant genotype, age, the specific virus strain, and environmental conditions, all of which influence disease expression (Apio et al., 2021; Kayondo et al., 2018; Navangi et al., 2020; Rabbi et al., 2014). To curb virus proliferation, particularly through planting material, improved seed systems are essential. The production of clean planting material through plant tissue culture (PTC) is a crucial strategy in controlling the spread of cassava viruses (Apio et al., 2021; Shirima et al., 2020). Understanding the genetic basis of CBSD resistance is key to developing disease-resistant cassava varieties. Identifying resistance-associated genes can help breeders target effective traits (Okogbenin et al., 2013). Upon pathogen attack, plants activate multilayered defense mechanisms, including the phenylpropanoid pathway, which forms structural and chemical barriers against infection. This pathway is often upregulated during infection, leading to increased enzyme activity and accumulation of phenolic compounds (Kavil et al., 2021). In some studies, bitter cassava genotypes have shown lower CBSD impact, likely due to reduced whitefly populations. However, these genotypes are generally unpopular with farmers because of their extended maturity period (up to two years) and bitter taste. In contrast, sweet genotypes with shorter maturity cycles (9–12 months) are preferred but tend to be more susceptible to CBSD (Mware et al., 2009).

The main objective of the study is to characterize differential foliar and root responses to cassava brown streak disease and assess their association with root yield among cassava germplasm.

Materials and methods

Germplasm collection and experimental sites

A total of 138 cassava accessions representing farmer-named materials and introduced accessions were used in the study. The accessions were collected from different counties in Kenya where cassava is majorly grown. The counties of collections included: Kilifi (17), Makueni (7), Nakuru (1), Homa Bay (13), Migori (79), Kisumu (2) and Busia (19). The collection of the germplasm used single stem per germplasm and catalogued in a germplasm collection form as described by (Cox et al., 2014; Orek et al., 2022). The complete passport information, including accession identification, county of origin, collection location, source and farmer-reported preferred traits, is provided in Supplementary Table S1. The accessions were subsequently evaluated for differential responses to cassava brown streak disease under field conditions.

Cassava accessions were first multiplied to generate sufficient planting material. Single stems were cut into 15 cm segments and planted in single rows at Rongo University research farm (approx. 0.75°S, 34.6°E), Migori County. The site lies within the Lower Midland Agro-Ecological Zones IV and V (LM4-LM5), a transitional zone between highland and lowland systems. Soils are predominantly deep, well-drained Ferralsols and Acrisols, with loamy to clay-loam texture and moderate acidity (pH 5.5–6.5). The region experiences a bimodal rainfall pattern, with long rains from March to May and short rains from October to December. Average annual rainfall ranges from 1,200 to 1,800 mm, with mean daily

temperatures between 20°C and 28°C (International Center for Tropical Agriculture (CIAT), 2015; Jaetzold et al., 2006; KMD, 2024; Rongo University, 2024).

Experimental evaluation was conducted in two environments: (i) Rongo University farm in Migori County, and (ii) a farmer's field in Homa Bay County (approx. 0.36°S, 34.7°E). The Homa Bay site lies in the Lower Midland Zone III (LM3), at 1300–1500 m altitude, with deep, well-drained Ferralsols and Acrisols of moderate acidity (pH 5.5–6.5). Rainfall is bimodal, ranging from 1,200 to 1,600 mm annually, with mean daily temperatures between 22°C and 28°C, occasionally reaching 30°C during dry spells (International Center for Tropical Agriculture (CIAT), 2015; Jaetzold et al., 2006; KMD, 2024).

CBSD scoring procedure

CBSD was scored in two elements: foliar and root. For foliar, the incidence and severity were be recorded. Foliar incidences were calculated as a percentage of the plants showing symptoms while foliar severities will be recorded based on a scale of 1–5 for CBSD as shown in Table 1 and Fig. 1. Roots from each plant were harvested and chopped longitudinally and transversely to check for root necrosis on the starch bearing tissues. Scoring for root necrosis will be done based on a 1–5 scale by Gondwe et al. (2003) as shown in Fig. 2.

Table 1
Foliar and root symptom for CMD and CBSD chart

Scoring Scale	CMD Foliar Symptoms	CBSD Foliar Symptoms	CBSD Root Symptoms	General Description of Symptoms	Description of Varieties
1	No visible symptoms	No visible symptoms	No visible symptoms	No symptoms	Highly resistant
2	A mild distortion only at the base of leaflets with the remainder of leaflets appearing green and healthy/mild chlorotic pattern over entire leaflets	Mild foliar mosaic on some leaves and no stem lesions	< 5% of root necrotic	Mild	Resistant
3	Conspicuous mosaic pattern throughout leaf, narrowing and distortion of lower 1/3 of leaflets	Foliar mosaic with mild stem lesions and no die back	5–25% of root necrotic	Moderate	Tolerant
4	Severe mosaic, distortion of two-thirds of leaflets and general reduction of leaf size	Foliar mosaic and pronounced stem lesions and no die back	25–50% root necrotic & mild root constriction	Severe	Susceptible
5	Severe mosaic, distortion of $\frac{3}{4}$ of leaflets, twisted and misshapen leaves	Defoliation with pronounced stem lesions and die-back	> 50% root necrotic	Highly severe	Highly susceptible

Results

Descriptive Statistics and Phenotypic Variation

Descriptive statistics for CBSD severity and root yield revealed significant phenotypic variation within the evaluated germplasm collection (Table 2). Both foliar and root CBSD scores exhibited a pronounced right-skewed distribution. The median score for both traits was 1.0, indicating that the vast majority of accessions displayed high resistance to CBSD. However, the maximum scores of 5.0 for both leaf and root evaluations highlight the presence of highly susceptible genotypes within the population. The coefficient of variation (CV) was notably high for both leaf (64.64%) and root (63.21%) CBSD scores, demonstrating ample phenotypic variability for effective selection in breeding programs.

Table 2
Descriptive statistics for CBSD severity and root yield

Trait	Mean	Median	Min	Max	Range	SD	CV (%)
Leaf CBSD	1.61	1.0	1.0	5.0	4.0	1.04	64.64
Root CBSD	1.62	1.0	1.0	5.0	4.0	1.02	63.21
Root Yield (t/ha)	8.85	6.5	0.0	44.3	44.3	6.36	71.90
CBSD scores are on a 1–5 scale, where 1 = highly resistant and 5 = highly susceptible. Yield was measured in tonnes per hectare							

Root yield exhibited extensive variation, ranging from 0.0 to 44.3 tonnesHa⁻¹, with a mean of 8.85 tonnesHa⁻¹ and a median of 6.5 tonnesHa⁻¹. The minimum yield of 0.0 tonnesHa⁻¹ corresponds to accessions that experienced total crop failure due to CBSD-induced plant mortality or complete root necrosis prior to harvest. Conversely, the maximum yield of 44.3 tonnesHa⁻¹ underscores the presence of highly productive, vigorous genotypes within the collection. The high coefficient of variation for root yield (71.90%) further confirms the broad diversity of the population, providing a robust baseline for evaluating the specific impact of CBSD severity on economic output in subsequent analyses.

Phenotypic Variation and Distribution of CBSD Resistance

The phenotypic CBSD resistance within the germplasm collection was evaluated. The symptoms of severity were assessed across three replicates for both leaf and root traits. The results indicated that the scores were skewed towards resistance (score 1 and 2). This is an indication that most accessions possess effective resistance mechanisms against CBSD foliar and root necrosis. Conversely, higher severity scores (4 and 5) were infrequent, representing a minority of highly susceptible genotypes (Fig. 3).

Aggregation of these scores at the accession level confirmed the presence of substantial, albeit skewed, phenotypic variation. Boxplot analysis of the accession means (Fig. 4a) showed a tight interquartile range between 1.0 and 1.7 for both leaf and root traits, with a median of approximately 1.3. However, the presence of distinct outliers extending to the maximum score of 5.0 highlights the existence of extreme susceptibility within the population.

To better visualize the genetic architecture of this resistance, accessions were ranked based on their adjusted mean leaf CBSD scores (Fig. 4b). The resulting plot depicts a classic staircase distribution. A large proportion of the collection (over 60% of accessions) maintained a perfect resistance score of 1.0. Beyond this plateau, symptom severity increased in distinct step-wise increments (1.3, 1.6, 2.0, and 2.3), culminating in a sharp escalation to 5.0 for the most susceptible accessions, such as *KibandaMeno* and *Palsa*. This clear phenotypic stratification provides a robust foundation for selecting contrasting parental lines for future breeding initiatives.

Variation Among Cassava Accessions for CBSD Severity

The phenotypic variation of CBSD severity among the collected cassava accessions were evaluated by fitting Ordinal mixed-effects models that accounted for the block effects. The likelihood ratio tests revealed highly significant variation among accessions for both foliar ($\chi^2 = 170.68$, $df = 1$, $p < 0.001$) $\chi^2 = 170.68$, $df = 1$, $p < 0.001$) and root ($\chi^2 = 149.93$, $df = 1$, $p < 0.001$) $\chi^2 = 149.93$, $df = 1$, $p < 0.001$) CBSD symptoms.

The phenotypic variation was majorly driven by genotypic differences among the accessions rather than environmental heterogeneity as per variance component analysis. The estimated genotypic variance (σ_g^2) was 18.87 for leaf CBSD and 13.55 for root CBSD, while the block (environmental) variance was negligible (0.00 and 0.05, respectively). Consequently, the estimated broad-sense heritability (H^2) on the latent scale was high for both traits (85.2% for leaf CBSD and 80.2% for root CBSD), indicating that phenotypic selection for CBSD resistance in this germplasm collection will be highly effective (Table 3).

Table 3

Variance components and broad-sense heritability (H^2) for Cassava Brown Streak Disease severity traits based on ordinal mixed-effects models

Trait	² Genetic Variance (σ_g)	² Block Variance (σ_b)	Broad-Sense Heritability (H^2)
Leaf CBSD Score	18.87	0.00	0.85 (85%)
Root CBSD Score	13.55	0.05	0.80 (80%)

Heritability was calculated on the latent scale using the formula $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_b^2 + \sigma_e^2)$. Where the residual variance σ_e^2 is fixed at $\pi^2/3$ which is approximately 3.29 for the logit link function.

Discordance Between Foliar and Root CBSD Responses

Using a threshold of ≥ 1.5 difference between mean leaf and root scores, majority of the cassava accessions exhibited concordant responses. However, 5.1% ($n = 7$) of the accessions were classified as highly discordant. Thus, a distinct subset of genotypes displayed discordant phenotypic expressions. However, to capture biologically significant root-tolerant lines that exhibited clear phenotypic divergence (difference > 1.0) and high marketable yields, two additional accessions (Opoto and Tajirika) were included, bringing the total to 9 key discordant accessions. These discordant accessions were further categorized into two distinct groups. The first group exhibited foliar tolerance but root susceptibility. These were characterized by healthy foliage (scores ≤ 1.67) but severe root necrosis (scores ≥ 2.67) and drastic yield losses. The second group exhibited foliar susceptibility but root tolerance. These displayed severe foliar symptoms (scores ≥ 3.33) but maintaining relatively mild root necrosis (scores ≤ 3.33) and preserving high root yields (up to 17.60 tonnes ha^{-1}) (Table 4).

Table 4

Cassava accessions exhibiting discordant phenotypic responses between foliar and root Cassava Brown Streak Disease severity

Accession Name	Mean Leaf CBSD	Mean Root CBSD	Absolute Difference	Mean Root Yield (t/ha)	Category of Discordance
Mtwapa-01	1.67	5.00	3.33	0.00	Foliar Tolerant / Root Susceptible
F-19	1.33	4.33	3.00	11.20	Foliar Tolerant / Root Susceptible
Yellow-Rapongi	1.00	3.00	2.00	5.60	Foliar Tolerant / Root Susceptible
Agriculture-Ranen-01	1.00	2.67	1.67	6.37	Foliar Tolerant / Root Susceptible
Kamgundho	1.00	2.67	1.67	7.37	Foliar Tolerant / Root Susceptible
Selele-Rachar-Rapogi	1.00	2.67	1.67	6.50	Foliar Tolerant / Root Susceptible
Mzungu (Tanzania)	4.33	2.33	2.00	5.67	Foliar Susceptible / Root Tolerant
Opoto	4.67	3.33	1.34	17.60	Foliar Susceptible / Root Tolerant
Tajirika	3.33	2.00	1.33	17.47	Foliar Susceptible / Root Tolerant

Relationship Between Foliar and Root CBSD Severity

At population level, the Spearman's rank correlation analysis had a moderate, highly significant positive association between the foliar and root symptoms ($\rho = 0.45$, $p < 0.001$). This evaluation revealed that the foliar symptom severity could predict root necrosis. In addition, an ordinal mixed-effects regression model demonstrated that foliar severity is a strong predictor of root severity. For every one-unit increase in the foliar CBSD score, the odds of observing a higher root CBSD severity category increased by 337% (Odds Ratio = 4.37, 95% CI: (2.99, 6.38), $p < 0.001$). This confirms that while foliar scoring is a reliable proxy for root necrosis, the moderate correlation ($\rho < 1.0$) supports the necessity of direct root evaluation to capture the full phenotypic expression of the disease (Fig. 5).

At accession level, there was a discordant in this theory. A scatter and dump-bell plots were used to show the overall predictive power of the model. The green dots near the dashed line show that for most accessions, leaf scores accurately predict root scores. The red dots (Under-predicted) were the "hidden susceptibility" accessions such as F-19, Mtwapa-01, Kamgundho and Yellow-Rapongi (Fig. 6A). This is where the model expected a low root score but the actual roots were severely necrotic. The dumb-bell

plot (Fig. 6B) showed the gap between what the model predicted (blue dot) and what actually happened in the field (red dot) for the top 10 most discordant accessions. The longer the gray line connecting the dots, the more severe the discordance.

Impact of CBSD Severity on Root Yield

Evaluation of the CBSD on the agronomic impact was carried out by fitting a linear mixed-effects model with root yield as the response variable. An adjustment of correction for survivorship bias by coding plant mortality and total root necrosis as zero yield. The model revealed a highly significant negative relationship between root CBSD severity and yield ($F = 6.96$, $p = 0.0087$). Thus, an increase in one-unit of root symptom severity resulted in a reduction in yield by $1.07 \text{ tonnesHa}^{-1}$.

On the contrary, the foliar CBSD severity showed no significant relationship with yield ($p = 0.90$) once root necrosis was accounted for in the model. The marginal R^2 indicated that CBSD severity scores explained 2.68% of the total variance in root yield. This reflects the complex, multi-factorial nature of cassava yield, the statistical significance confirms that root necrosis is a primary pathological constraint to yield preservation (Fig. 7).

Estimation of Genotypic Yield Potential using Best Linear Unbiased Predictors (BLUPs)

The BLUP analysis revealed significant genotypic variation for root yield among the 132 evaluated accessions, with adjusted means ranging from 0.3 to $37.93 \text{ tonnesHa}^{-1}$ (Table 5). Six accessions: KibandaMeno-Branched-MidaCreek, KibandaMeno-MidaCreek, Unknown-Waite-Kegonga, Waite-Masaba, Nyamura and Palsa were not ranked due to total crop failure and inability to collect a number of phenotypic data after 6MAP. This is an indication of the devastating impact of CBSD on highly susceptible genotypes. The high yielding accessions were: MM96/0067 ($37.93 \text{ tonnesHa}^{-1}$), Agriculture-Maram (tonnesHa^{-1}) and Fumbachai ($22.87 \text{ tonnesHa}^{-1}$). While the lowest yielding accessions were: Wild-Ranen ($1.75 \text{ tonnesHa}^{-1}$), Agriculture-Masaba ($0.3 \text{ tonnesHa}^{-1}$) and Mtwapa-01 ($0.3 \text{ tonnesHa}^{-1}$). Mtwapa-01 had 'hidden susceptibility'. Furthermore, the broad variation among accessions provides a robust baseline for identifying accessions with the traits of interest for future breeding programs.

Table 5
Best Linear Unbiased Predictors (BLUPs) ranking for root
yield

S.no	Accession	Yield BLUP	Rank
1	MM96/0067	37.93	1
2	Agriculture-Maram	25.06	2
3	Fumbachai	22.87	3
4	Nyatanga-Nyamarere	21.68	4
5	Migyera-Busia	21.29	5
6	Kasukari-Mtwapa	19.78	6
7	ObaroDak-Nyamarere	19.23	7
8	MH95/0183	19.13	8
9	NyarMaseno	18.65	9
10	Bwana-Terana	18.46	10
11	Agriculture-Ranen-03	18.04	11
12	ObaroDak-Ranen	17.98	12
13	Agriculture-Mtwapa	17.43	13
14	Opoto	17.3	14
15	Tajirika	17.17	15
16	KBK-20	17.17	16
17	ObaroDak-Maram	17.11	17
18	KBK-4	17.07	18
19	Nyatanga-Rabuor	16.85	19
20	Nyatanga-Opapo	16.75	20
21	ObaroDak-Nyamarere-01	16.49	21
22	KBK-21	16.11	22
23	Agriculture-Maram-01	15.92	23
24	KME-4	15.05	24
25	Agriculture-Ranen-02	14.72	25
26	Selele-Ranen-01	14.63	26

S.no	Accession	Yield BLUP	Rank
27	Nyatanga-Uriri	14.43	27
28	MM96/0039	14.11	28
29	MM96/4872	13.92	29
30	Nyaodendo	13.6	30
31	Kazanzwara	13.11	31
32	Achuth	12.21	32
33	Nyar-ICIPE	12.02	33
34	Migyera-Sigiria	11.41	34
35	MM96	11.34	35
36	MM96/0031	11.28	36
37	F-19	11.12	37
38	Migyera-Rongo	11.02	38
39	Agriculture-Sigira	11.02	39
40	Karembo	10.12	40
41	Agriculture-Kitere	10.02	41
42	Kasukari-Kiboko	9.74	42
43	Nyatonge-Ranen	9.64	43
44	Nyanchama	9.19	44
45	KibandaMeno-Mtwapa	9.16	45
46	Katsuhanzala	8.8	46
47	AdhiamboLera-Mtwapa	8.45	47
48	Yellow-Busia	8.45	48
49	Agriculture-Busia-02	7.68	49
50	Agriculture-Rongo	7.48	50
51	Nyakakelo	7.45	51
52	Agriculture-Rapogi	7.42	52
53	Kamgundho	7.42	53
54	Agriculture-Uriri	7.39	54

S.no	Accession	Yield BLUP	Rank
55	Magana	7.39	55
56	MM96/4466	7.35	56
57	Nyakasamuel	7.13	57
58	Agriculture-Suba	7.06	58
59	Katune	6.97	59
60	Agriculture-Busia-01	6.9	60
61	Agriculture-Busia	6.87	61
62	Nyarkanyamkago	6.77	62
63	Agriculture-Opapo	6.58	63
64	Selele-Rachar-Rapogi	6.58	64
65	AdhiamboLera-Awendo	6.45	65
66	Agriculture-Ranen-01	6.45	66
67	Selele-Ranen	6.45	67
68	Agriculture-Kegonga	6.19	68
69	ObieroAbele	6.19	69
70	Mbale-Mida	6.13	70
71	Nyaranen	6.13	71
72	Nyakasani	6.1	72
73	Busia-03	6.07	73
74	Selele-Rongo	6.03	74
75	Unknown-Kehancha	5.9	75
76	Selele-Rakwaro	5.9	76
77	Agriculture-Ranen	5.87	77
78	Nyakanyamkago	5.87	78
79	Agriculture-Awendo	5.84	79
80	Mzungu (Tanzania)	5.78	80
81	Unknown-Rakwaro-01	5.78	81
82	Mary-Kaluorore	5.71	82

S.no	Accession	Yield BLUP	Rank
83	Yellow-Rapongi	5.71	83
84	Nyarkogutu-Ngothe-01	5.68	84
85	Selele-Sigiria	5.65	85
86	Nyarkogutu-Ngothe	5.58	86
87	Nyasuna-Masaba	5.58	87
88	Odiero	5.45	88
89	Nyagire	5.36	89
90	Ratena	5.36	90
91	Buria-Maram	5.33	91
92	Agriculture-Kegonga-01	5.23	92
93	Busia-02	5.23	93
94	Selele-Maram	5.16	94
95	Miida	5.1	95
96	Agriculture-Maeta	5.07	96
97	Bwong	5.07	97
98	Busia-04	5	98
99	Buria-Maeta	4.94	99
100	Rateng	4.81	100
101	Waite-Kegonga	4.81	101
102	Mufutu	4.78	102
103	Unknown-Rakwaro	4.59	103
104	Mbale-Uganda-Mida	4.55	104
105	Nyatonge-Sigiria	4.52	105
106	Unknown-Maram	4.46	106
107	Selele-Maram-01	4.36	107
108	Nyasega	4.33	108
109	Busia-01	4.3	109
110	Nyaeta	4.3	110

S.no	Accession	Yield BLUP	Rank
111	Amakuria	4.2	111
112	Nyarkadera	4.2	112
113	Unknown-Kegonga	4.2	113
114	Unknown-Maram-01	4.1	114
115	Machoberi	4.01	115
116	Selele-Busia	4.01	116
117	Agriculture-Dede	3.94	117
118	Buria-Rakwaro	3.94	118
119	Nyarkawuor	3.94	119
120	Mtwapa-02	3.91	120
121	Madam-Opapo	3.81	121
122	Otia	3.75	122
123	Kienyeji	3.56	123
124	Agriculture-Pembe	3.52	124
125	Nyasuna-Kokuro	3.43	125
126	Toji	3.43	126
127	Konono	2.43	127
128	Wild-Rusinga	2.07	128
129	Wild-KenduBay	1.88	129
130	Wild-Ranen	1.75	130
131	Agriculture-Masaba	0.3	131
132	Mtwapa-01	0.3	132

Influence of Root Taste on CBSD Severity

In order to determine whether root taste, a proxy for cyanogenic glucoside content influences CBSD resistance, disease severity scores were compared across Sweet (n = 276), Intermediate (n = 60), and Bitter (n = 60) taste categories. Descriptive analysis showed that similar mean CBSD scores across all taste categories. Sweet accessions exhibited mean leaf and root CBSD scores of 1.41 and 1.54, respectively, while Bitter accessions showed comparable scores of 1.57 and 1.30 respectively and Intermediate taste mean leaf and root CBSD scores of 1.57 and 1.43, respectively. The Kruskal-Wallis

test indicated a marginal significant difference in foliar CBSD severity among taste categories ($\chi^2 = 6.42$, $df = 2$, $p = 0.040$). However, post-hoc pairwise comparisons with Bonferroni correction revealed no statistically significant differences between any specific taste category pairs (Sweet vs. Bitter: $p = 0.07$; Sweet vs. Intermediate: $p = 0.34$; Intermediate vs. Bitter: $p = 1.00$). For root CBSD severity, no significant differences were detected among the taste categories ($\chi^2 = 2.82$, $df = 2$, $p = 0.245$), with all pairwise comparisons yielding non-significant p-values ($p > 0.05$) (Fig. 8).

Using the IQR method ($Q3 + 1.5 \times IQR$), 8 sweet-tasting accessions and 1 intermediate accession with extreme CBSD phenotypes were identified. These outliers fell into three distinct categories:

Foliar-susceptible but root-tolerant accessions: Mzungu (Tanzania) and Tajirika exhibited leaf CBSD scores significantly above the upper fence (> 3.5) but maintained normal root CBSD scores. These accessions represent valuable breeding material that preserves yield potential despite severe foliar symptoms. Foliar-tolerant but root-susceptible accessions: Mtwapa-01, F-19, Kamgundho, and Yellow-Rapongi displayed deceptively healthy foliage (scores 1.0-1.7) but exhibited root CBSD scores exceeding the upper fence (3.0–5.0). These accessions pose a significant risk to farmers, as selection based solely on foliar symptoms would inadvertently advance genotypes with severe root necrosis and yield loss. Highly susceptible accessions: KibandaMeno-Mtwapa and Opoto exceeded the upper fence for both foliar and root CBSD severity, confirming their extreme susceptibility. KibandaMeno-Mtwapa experienced total crop failure with plant mortality. Notably, all identified outliers were either sweet or intermediate tasting, with no bitter accessions classified as outliers. This further supports the conclusion that root taste does not confer resistance to CBSD (Table 6).

Table 6

Identified accession (8 sweet-tasting accessions and 1 intermediate) with extreme CBSD phenotypes

Accession	Taste	Mean Leaf	Mean Root	Interpretation
Foliar Susceptible but Root Tolerant Category				
Mzungu (Tanzania)	Intermediate	4.33	2.33	High leaf symptoms but roots protected
Tajirika	Sweet	3.33	2.00	Severe leaves but tolerant roots
Foliar Tolerant but Root Susceptible 'Hidden Danger' Category				
Yellow-Rapongi	Sweet	1.00	3.00	Looks healthy but roots damaged
Kamgundho	Sweet	1.00	2.67	Looks healthy but roots damaged
F-19	Sweet	1.33	4.33	Looks healthy but severe root damage
Mtwapa-01	Sweet	1.67	5.00	Looks healthy but total root failure (0 yield)
Highly Susceptible in Both Category				
Opoto	Sweet	4.67	3.33	Severe in both traits
KibandaMeno-Mtwapa	Sweet	5.00	5.00	Extremely susceptible - plant death

Discussion

Phenotypic Variation and Heritability of CBSD Resistance

There was a wide phenotypic variation of the collected germplasm for CBSD and root yield (Nandudu et al., 2023; Navangi et al., 2020). The CBSD scores distribution of this population was however skewed with a median of 1.0. This indicated that the accessions possess inherent resistance mechanisms against both foliar mosaic and root necrosis (Orek, 2014; Sichalwe et al., 2024). However, there was a subset of highly susceptible genotypes that scored 5.0, coupled with high coefficients of variation (> 63%).

Ordinal mixed-effects models analysis that was used to identify variance components demonstrated that the phenotypic variation was driven by genotypic differences rather than environmental heterogeneity, as evidenced by the negligible block variance. This was similar to previous studies by (Filho et al., 2024) in Iran and (Obare et al., 2024) in Kenya where they used different populations but had a similar outcome. Subsequently, the estimated broad-sense heritability (H^2) was exceptionally high for both leaf (85%) and root (80%) CBSD traits on the latent scale. High heritability estimates for CBSD resistance have been previously reported in cassava breeding populations (Ceballos et al., 2020; Pariyo et al., 2013). These

studies confirmed that visual phenotypic selection for these traits are highly reliable and that genetic gain can be rapidly achieved through recurrent selection. The clear phenotypic stratification observed in the ranked accession plots further validates the presence of distinct genetic architectures governing CBSD resistance, providing a robust foundation for selecting contrasting parental lines for future breeding initiatives (Filho et al., 2024).

The Misconception of Foliar Only Screening: Discordance Between Leaf and Root Symptoms

At the population level, there was a moderate positive correlation ($p = 0.45$) and a high odds ratio (4.37). This suggested that foliar severity can generally predict root necrosis at population level. Similarly, Kaweesi et al. (2014) observed that at population level, these correlations were significant. However, at genotype-specific level, there were inconsistencies between foliar CBSD severity and root. Where certain genotypes displayed severe foliar symptoms but minimal root necrosis, or vice versa.

In this study, a second level of analysis of accession specific was applied to quantify the theory of predictive relationship that foliar severity can generally predict root necrosis. Approximately 5.1% of the test population, exhibited extreme discordance. Therefore, breaking the said predictive relationship. This highlights the uniqueness of genotype-specific resistance mechanisms that have not been previously quantified. In addition, accessions such as Mtwapa-01, F-19, and Yellow-Rapongi displayed healthy foliage (scores ≤ 1.67). Their root necrosis scores were ≥ 3.0 with severe yield losses. This 'hidden susceptibility' phenomena are one of the driving factors of the accession level discordant prediction relationship. The quantification of the discordant relationship (5.1%) is the first empirical measure of hidden CBSD susceptibility at accession level, extending earlier qualitative observations by (Abe et al., 2023; Kaweesi et al., 2014; Ndyetabula et al., 2016; Ozimati et al., 2021). Therefore, CBSD material screening for resistance, reliance of foliar screening alone would lead to advancement of highly susceptible lines that would result in severe risk to the farmers livelihoods.

On the other hand, despite severe foliar symptoms in accessions such as Mzungu (Tanzania) and Tajirika maintained a high marketable yield ($> 17 \text{ tonnesHa}^{-1}$). This decoupling of foliar and root responses strongly reinforces the consensus that mandatory root evaluation at harvest is indispensable for accurate CBSD resistance screening and selection (Kayondo et al., 2018; Tomlinson et al., 2018).

Root Necrosis as the Primary Driver of Yield Loss

Root CBSD severity was a significant driver of yield loss. The yield reduction was by $1.07 \text{ tonnesHa}^{-1}$ for every incremental increase in disease severity. After accounting for root necrosis, foliar CBSD severity showed no significant relationship with yield ($p = 0.90$). This study agrees with a study by Ndyetabula et al. (2016) qualitatively demonstrated that cassava root necrosis severity is the primary driver of yield loss, while foliar severity alone showed weak or no correlation with productivity once root damage was accounted for. The model in this study provided a precise quantitative estimate ($-1.07 \text{ tonnesHa}^{-1}$ per

severity increment). Thus, establishing root CBSD severity as a statistically significant predictor of yield loss while foliar severity remains non-significant.

The study demonstrated that yield analysis was the evidence of agronomic impact of CBSD. This was done after correcting for survivorship bias by coding plant mortality and total root necrosis as zero yield, the model revealed that root CBSD severity is a highly significant driver of yield loss. Furthermore, R^2 (2.68%) was modest, it reflected on the high level of polygenic and environmentally sensitive nature of cassava yield. The statistical significance of the root CBSD coefficient confirms it as a primary pathological constraint. This aligns with previous economic and pathological assessments which establish that root necrosis, rather than foliar severity, is the direct cause of economic loss in cassava (Hillocks & Jennings, 2003; Legg et al., 2015). BLUP analysis identified MM96/0067 and Tajirika as high yielding and had some form of root tolerance to CBSD. These two genotypes have the potential of safeguarding food security, farmer incomes and livelihood security under high CBSD pressure environments.

Independence of CBSD Resistance from Root Taste (Bitterness)

Accumulation of cyanogenic glucosides is the driver of bitter taste of cassava. The bitterness has been hypothesized historically, to provide a biochemical defence mechanism against pests and pathogens (Easson et al., 2021; Ozimati et al., 2021). McKey et al., (2010) suggested that cassava bitterness may indirectly influence CBSD epidemiology by affecting vector feeding behaviour. However, this study demonstrated that CBSD resistance operates independently of root taste phenotypes. The statistical analysis showed that there was no significant differences in root CBSD severity among sweet, intermediate, and bitter accessions ($p = 0.245$). Furthermore, the study showed that extreme CBSD phenotypes (both highly susceptible and highly tolerant), outliers, were exclusively found in sweet and intermediate categories, with no bitter accessions classified as outliers.

The findings indicates that breeding pipelines do not have to rely on bitter, often less-preferred genotypes to achieve CBSD resistance. This quantified insight has a has profound implications in cassava breeding pipelines and farmer adoption of improved varieties. Furthermore, the historical trade-off between bitterness and pest resistance appears to be irrelevant for CBSD. Cyanogenic glucosides in cassava provide an effective biochemical defense against pests such as *Bemisia tabaci*, they do not confer direct resistance to viral pathogens like CBSD due to its evolution for herbivore deterrence rather than viral protection (Easson et al., 2021; McKey et al., 2010)

Conclusion and recommendation

The analysis carried out in this study confirmed that there was a substantial genotypic variation and high broad-sense heritability for both foliar and root CBSD traits, validating the efficacy of phenotypic selection for disease resistance in breeding programs.

A critical finding of this research was the decoupling of foliar symptom severity from economic yield loss. While foliar scoring is a useful population-level proxy, accession-level analysis revealed severe phenotypic discordance. The identification of 'hidden susceptible' genotypes, characterized by deceptively healthy foliage but catastrophic root necrosis and zero yield, highlighted the severe risk of relying exclusively on foliar screening. Conversely, the discovery of root-tolerant accessions that maintain high marketable yields despite severe foliar mosaic underscores the necessity of evaluating root necrosis to accurately capture the true agronomic impact of the disease. Statistical modelling confirmed that root CBSD severity is a significant and direct driver of yield reduction, whereas foliar severity has no independent effect on yield once root damage is accounted for.

Furthermore, this study definitively demonstrates that CBSD resistance operates independently of root taste phenotypes. The absence of significant differences in disease severity across sweet, intermediate, and bitter categories, coupled with the presence of extreme CBSD outliers exclusively in sweet and intermediate accessions, refutes the hypothesis that cyanogenic glucosides confer resistance to this viral pathogen.

In conclusion, to safeguard cassava yields and ensure farmer adoption, breeding programs must mandate root necrosis evaluation at harvest to avoid advancing hidden susceptible lines. The high-yielding, root-tolerant, and sweet-tasting accessions identified in this study, such as MM96/0067 and Tajirika, represent elite genetic resources. Deploying these genotypes will enable the development of consumer-preferred cassava varieties that do not compromise on disease resilience, ultimately securing food security and livelihoods in CBSD-endemic regions.

Declarations

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

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Author Contribution

MRM and APF contributed substantially to the conception and the design of the study; MRW drafted the manuscript and analysed the data; MRW, MRM, OME and APF edited and approved the version to be published.

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Figures



Figure 1

Cassava leaf with CBSD (Score 4)

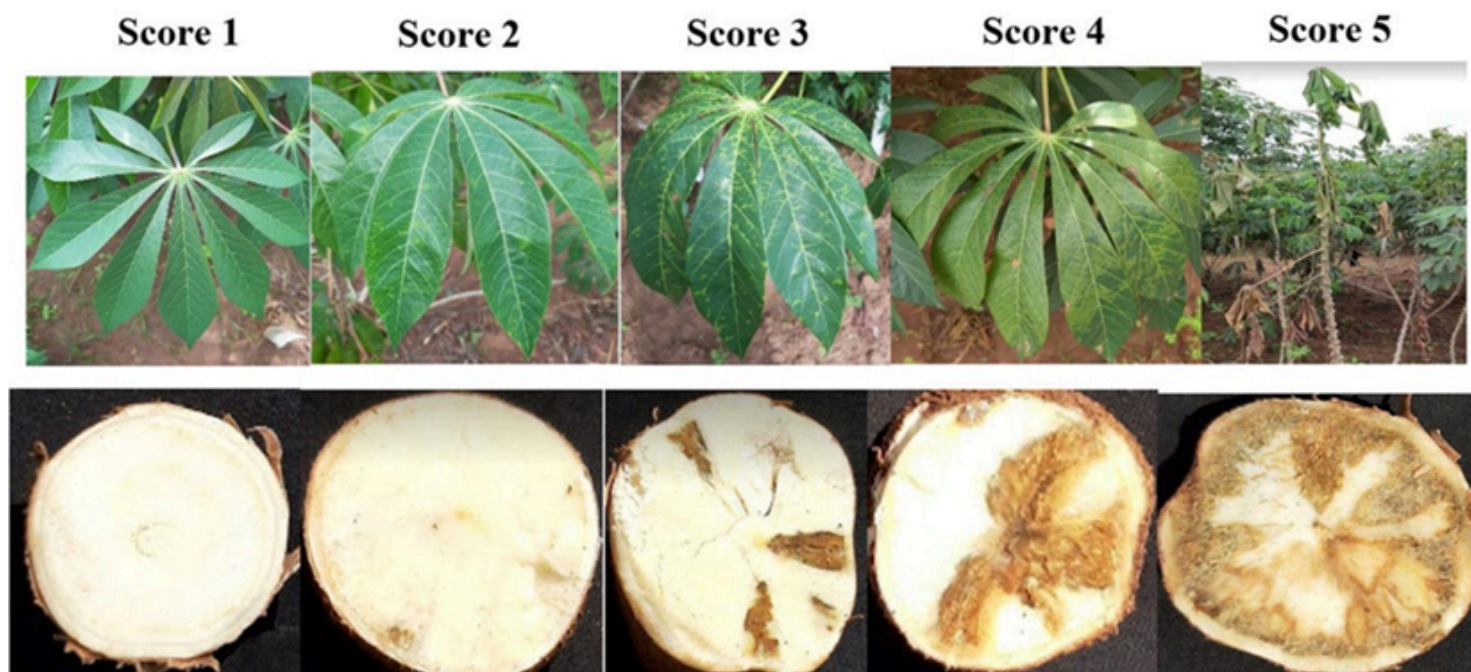


Figure 2

Pictorial representation of the foliar symptoms and root necrosis damage by CBSD scoring chart (Ano et al., 2021).

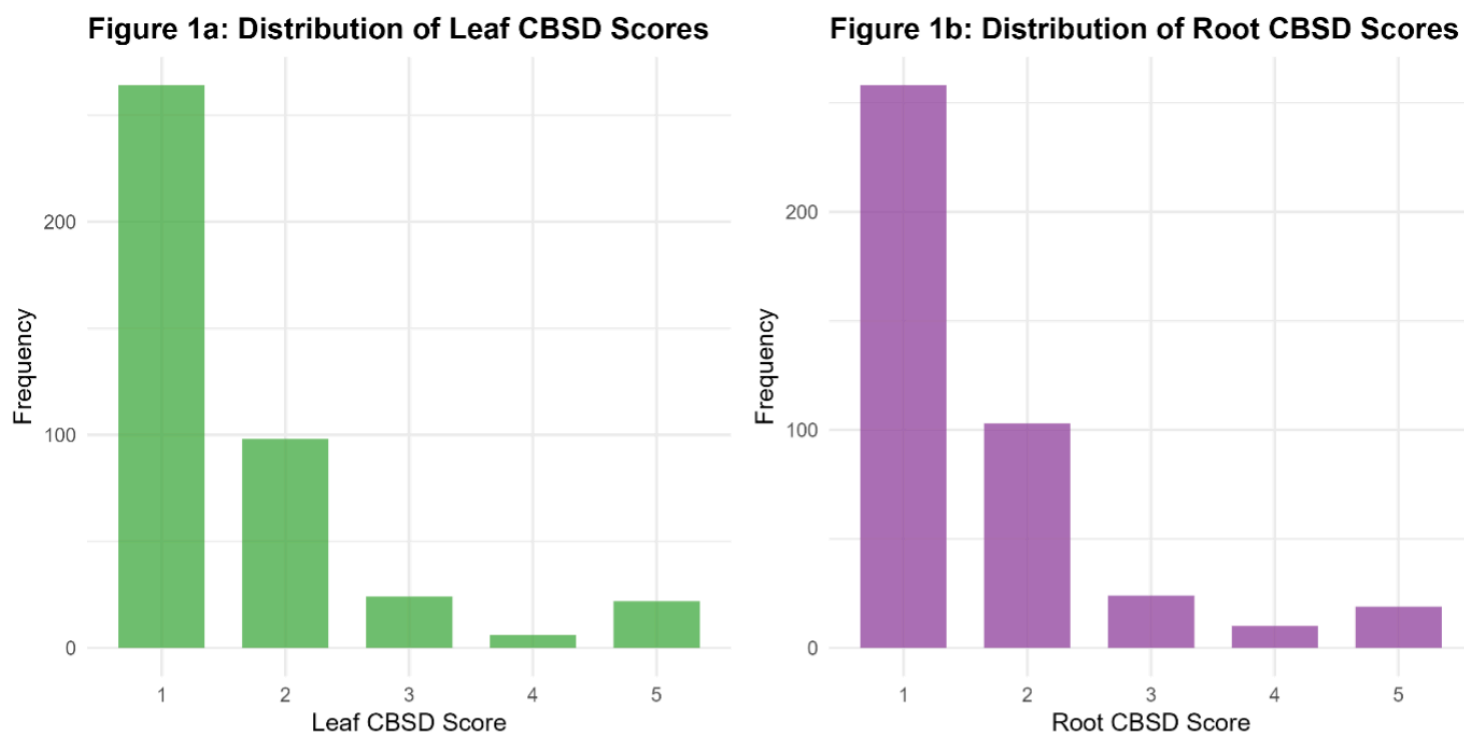


Figure 3

Distribution of CBSD scores on roots and leaves

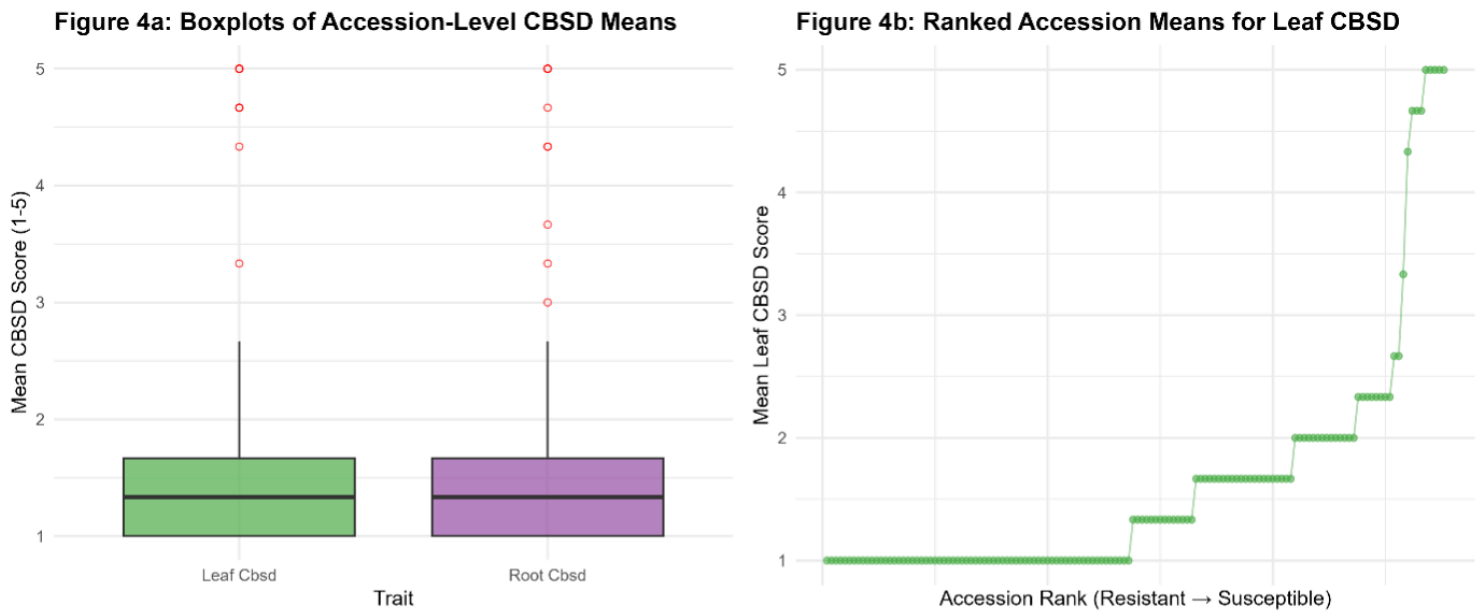


Figure 4

Boxplots at accession level of CBSD means and ranked accession means for leaf CBSD

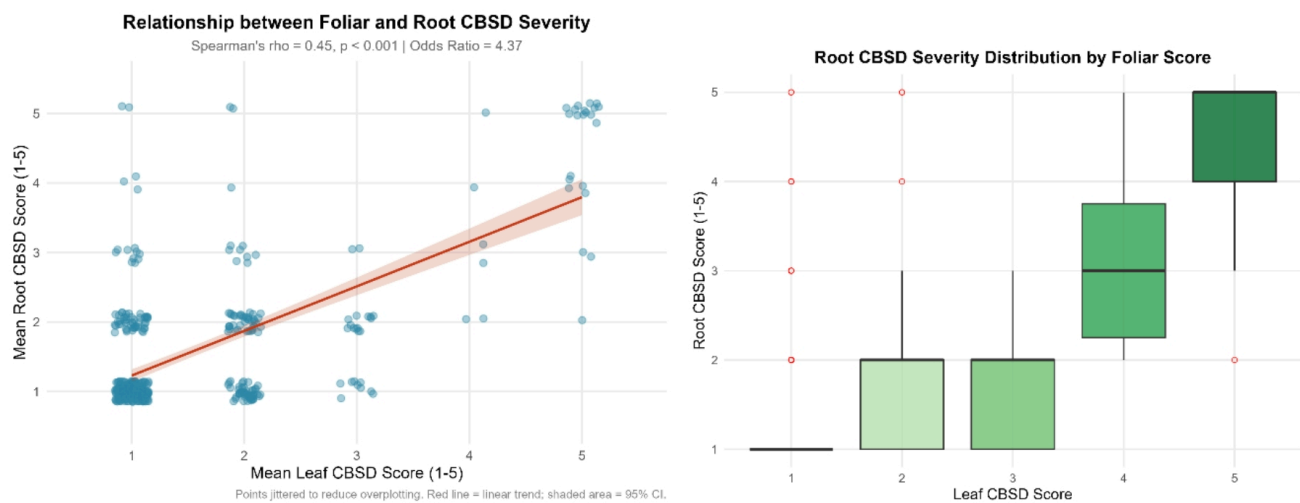


Figure 5

Relationship between foliar and root CBSD severity. **(A)**Jittered scatter plot illustrating the positive correlation between mean leaf and root CBSD scores, with a linear trend line and 95% confidence interval. **(B)**Boxplot distribution of root CBSD scores stratified by foliar CBSD severity categories.

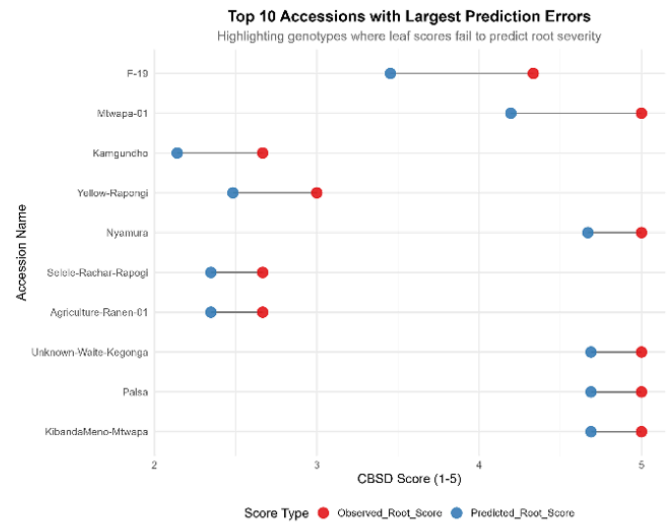
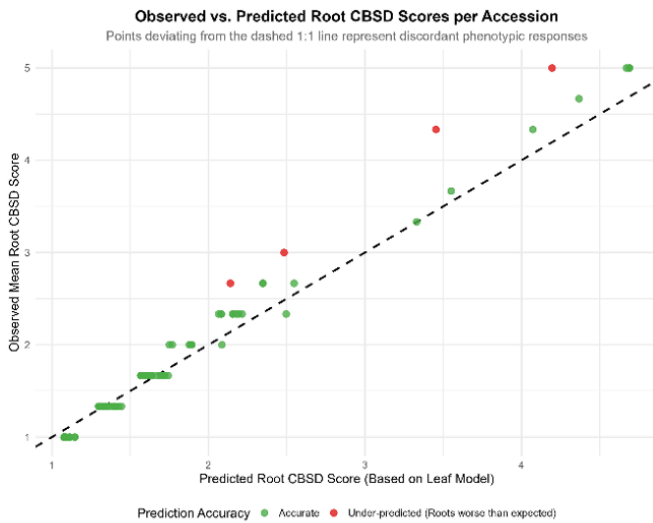


Figure 6

(A) Scatter plot of observed versus model-predicted root CBSD scores. **(B)** Dumbbell plot illustrating the top 10 accessions with the largest prediction errors, explicitly showing the divergence between predicted root scores (based on foliar symptoms) and empirically observed root necrosis.

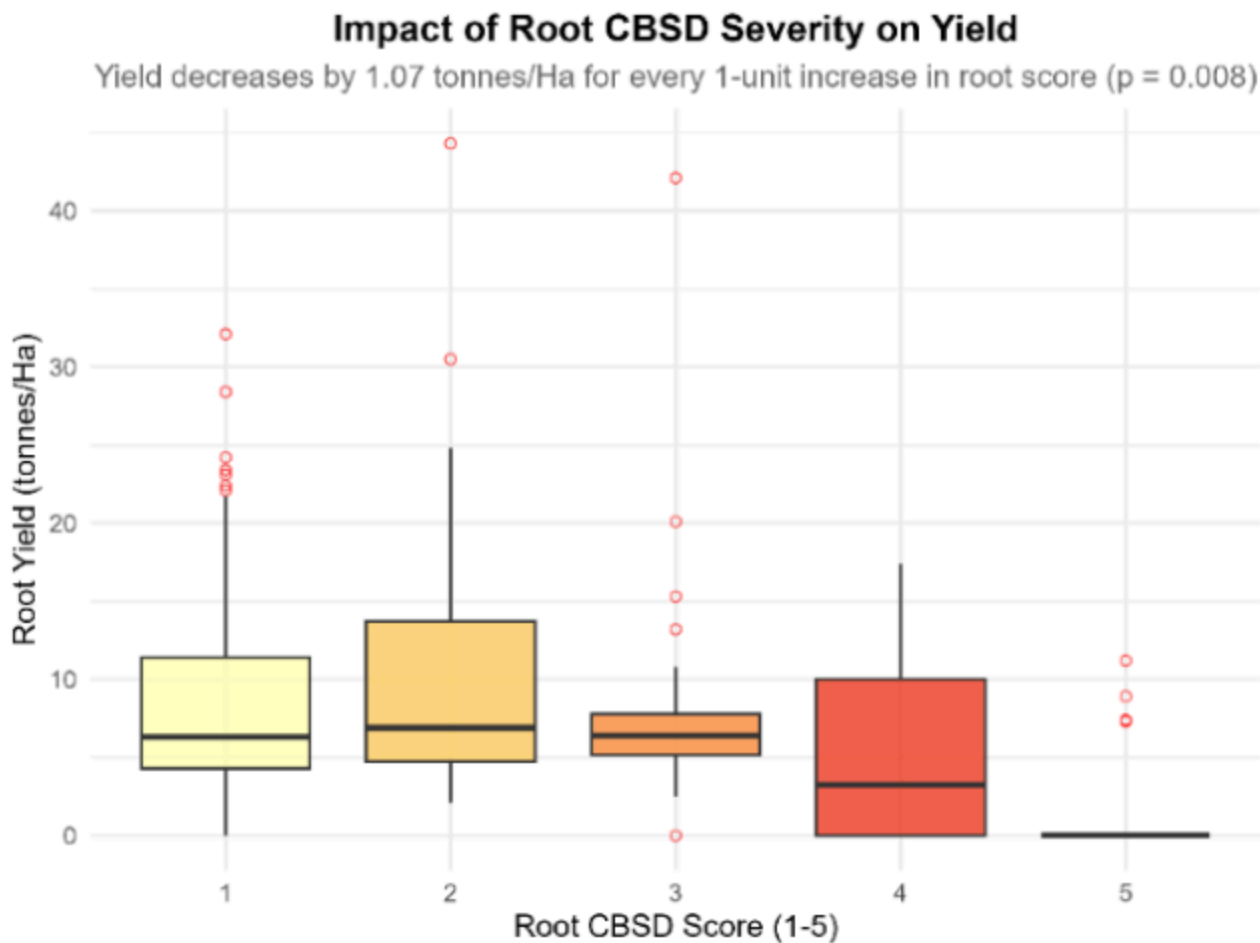


Figure 7

Root yield distribution across root CBSD severity scores (1-5)

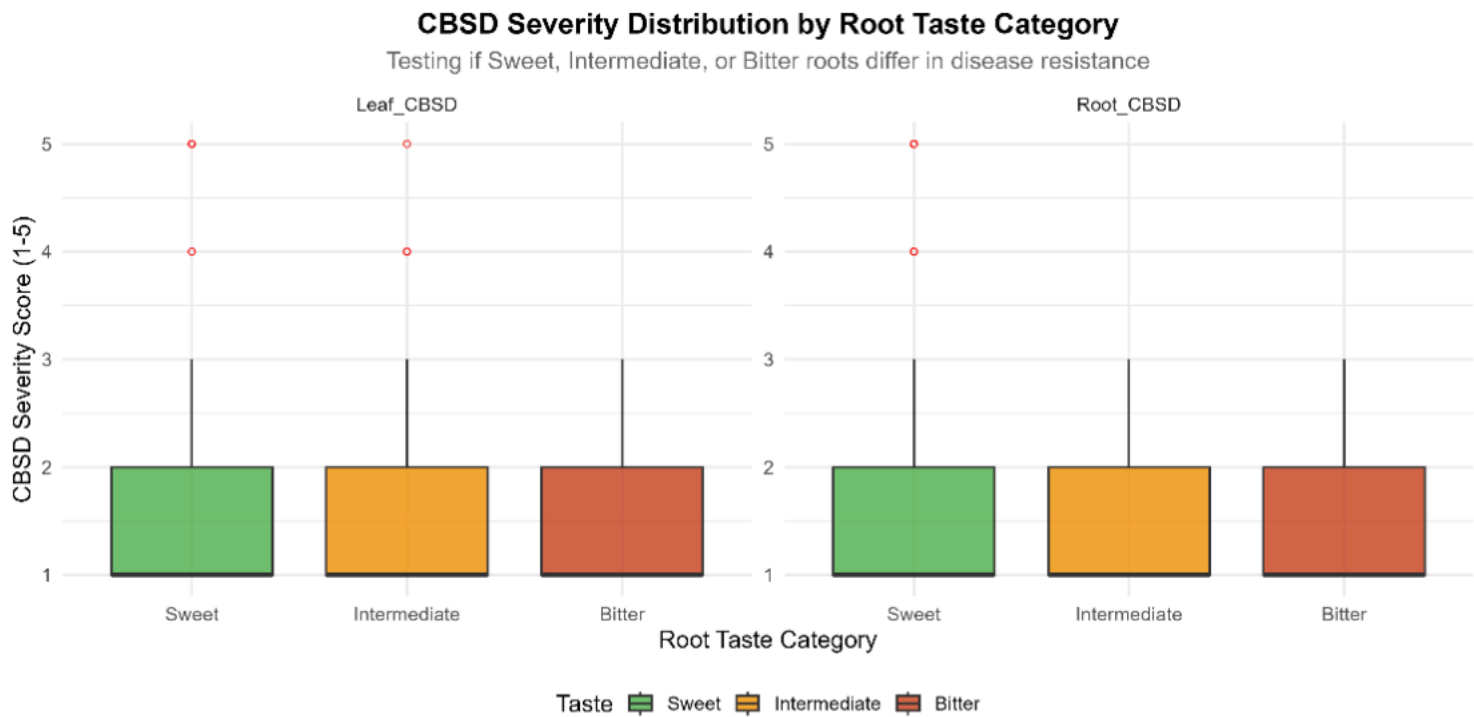


Figure 8

Distribution of foliar and root Cassava Brown Streak Disease (CBSD) severity scores stratified by root taste categories. Boxplots display the median (thick black line), interquartile range (box), whiskers (1.5× IQR), and outliers (red circles)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryData.docx](#)