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Selection of *Glycine max* (L.) merr accessions tolerant to Waterlogging

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ABSTRACT
Waterlogging smothers soybean growth, choking roots and disrupting essential functions. Oxygen starvation, nutrient imbalance, and weakened defenses against disease leave plants stunted, chlorotic, and vulnerable. Yields plummet, seeds struggle to mature, and soil suffers long-term consequences, painting a grim picture for soybean crops submerged in persistent floodwaters. This study investigated the effects of waterlogging on five accessions of *Glycine max* (TGm-1, TGm-8, TGm-9, TGm-11, and TGm-12). Plant height, leaf area, total photosynthetic pigments (TPP), biomass yield, and root length were measured after 2, 3, and 4 weeks of waterlogging stress. TGm-9 exhibited superior performance across all parameters compared to other accessions and the control. It displayed the highest plant height (28.67 cm), leaf area (14.76 cm^2), TPP content (44.83 mg/kg), biomass yield (1.73 g), and root length (30.17 cm). Despite some reductions in growth and physiology observed in all accessions under waterlogging, TGm-9 demonstrated remarkable resilience. This enhanced tolerance likely resulted from its robust development of adventitious root systems, a known adaptive response in *G. max*. These findings suggest that TGm-9 possesses superior waterlogging tolerance and has the potential for improved productivity in flood-prone environments. Further research could delve into the specific mechanisms underlying TGm-9's tolerance and explore its potential for breeding programs to develop waterlogging-resistant soybean cultivars.

Keywords: Biomass yield, *Glycine max*, Growth traits, Waterlogging stress.

1. INTRODUCTION
Waterlogging is one of the focal abiotic stresses, which affects crop growth (Linkemer et al., 1998). Global climate changes cause waterlogging events to be more frequent, severe, and unpredictable (Jackson and Colmer, 2005). Waterlogging is also a matter of worldwide concern affecting 16% of the soil; 10% of the Agricultural lands of Russia and irrigated crop production areas of India, Pakistan, Bangladesh, and China lose between 10 and 15 million ha of wheat affected by waterlogging annually causing yield losses of between 20 and 50% (Hossain and Uddin, 2011). Waterlogging

also causes yield loss in other grain crops such as Barley, Canola, Lupins, field peas Bakker et al., (2018) lentils, and chickpeas (Solaiman et al., 2007). Waterlogging is one of the most hazardous natural occurrences caused by heavy rains, excessive irrigation, and low infiltration rates of soil and its prolonged appearance severely reduces the productivity of significant crops growing worldwide (Jackson and Colmer, 2005).

Waterlogging imposes severe selection pressure on plants since excess water in the living surroundings can deprive plants of oxygen, carbon dioxide, and light. Submerged plant shoots have a severely reduced photosynthesis level due to deficiency of external carbon-dioxide progressive leaf chlorosis root and shoot growth is also affected (Solaiman et al., 2007; Bakker et al., 2018). Waterlogging decreases crop yield (Dickin and Wright, 2008). Previous studies have reported various adverse effects of waterlogging on crops. For example, they are increasing waterlogging durations decreases maize yield (Li et al., 2001; Milroy et al., 2009; Araki et al., 2012). Waterlogging also significantly affects plant morphology, decreasing cell permeability, reducing activity and root respiration, and accelerating root senescence (Krause and Weis, 1984).

Soybean (*Glycine max*) is one of the most important crops, rich in protein, and has various uses for human food. Waterlogging induced several physiological disturbances in growth, dry matter, photosynthesis, and pod formation that resulted in lower yield in *Glycine max* (Celik and Turhan, 2011; Hasanuzzaman et al., 2016). Waterlogging reduced seed yield primarily by decreasing the number of pods per plant and pod setting (Ahmad et al., 2003). Linkemer et al., (1998) identified some vegetative stages sensitive to waterlogging and some reproductive stages. Soybean germplasms display a spectrum of waterlogging tolerance capabilities. The degree of waterlogging tolerance of soybean germplasms varies with the developmental stages (Linkemer et al., 1998). This research is aimed at accessing the effects of waterlogging on the growth and physiology of different accessions of *Glycine max* and its tolerance mechanism.

2. MATERIAL AND METHODS

The accession of *Glycine max* was collected from the International Institute for Tropical Agriculture (IITA), Ibadan, Oyo State, Nigeria. Seed coat color and Size were observed and documented in (Table 1).

Table 1 Colors, sizes, and source of *Glycine max* seeds

Accessions	Colors	Sizes	Source
TGm-1	Greenish milk	Medium	IITA
TGm-8	Cream	Small	IITA
TGm-9	Cream	Medium	IITA
TGm-11	Cream	Small	IITA
TGm-12	Cream	Small	IITA

The experiment was set up in a complete Block design (5 treatments (TGm-1, TGm-8, TGm-9, TGm-11, TGm-12) per replicate (3 replicates) and controls). The soil was collected from Akwa Ibom State University campus (Latitude 0.4°N and Longitude 007°E), Akwa Ibom state, Nigeria. The experimental soil samples were analyzed following the standard procedures outlined by the Association of Official Analytical Chemists (Rhouma et al., 2019). Five soybean (*G. max*) seeds were sown in 10-liter, non-perforated buckets containing steam-sterilized (2 hours at 100°C) soil sieved through a 2 mm mesh to remove pebbles and eliminate weed seeds and microorganisms. After germination, plants were thinned to three per bucket. The treatment group received controlled excess water (waterlogging) maintained 2 cm above the soil surface. The control group received no excess water (Araki et al., 2012).

Germination percentage (GP), reflecting the viability of a seed population, expresses the proportion of germinated seeds relative to the total number sown, calculated as GP = (germinated seeds/total seeds) × 100. Germination rate, additionally, quantifies the temporal dynamics of this process, capturing the speed and pattern of seed emergence over time. GP was calculated on 4, 8, and 12 days after planting. Plant height, leaf area, total photosynthetic pigment, petiole length, internode length, and number of nodes were evaluated 14, 21, and 30 days after planting. Biomass yield (total fresh and dry weights of root and leaves, leaf turgid weight) was determined 30 days after planting (Bakker et al., 2018; Matrood et al., 2021; Matrood and Rhouma, 2021). All data in the present study were subjected to analysis of variance (ANOVA) using the Statistical Package for Social Sciences. Data are presented as the standard error of the mean of triplicate experiments. However, a probability level of P =.05 was considered statistically significant.

3. RESULTS AND DISCUSSION

The physiochemical properties of composite surface soil samples are shown in (Table 2). The soil texture was predominantly loamy sand soil. Sand in loamy soil was 30 g/kg while silt was 70 g/kg and clay in loamy soil was 100 g/kg. Considering the three particles of this soil, sand has the highest distribution, followed by clay and silt. The pH value of the earth, ground was 5.6, which indicated high acidity. The acidic nature of the earth, and ground could be mainly attributed to excessive leaching due to the high amount of rainfall in the area. The surface soil recorded high levels of organic matter, 4.32%. The high levels of organic matter may be due to luxuriant vegetation, mainly grasses and shrubs, and the slow rate of microbial decomposition of the vegetation (Table 2).

The soil under investigation exhibited moderate electrical conductivity (0.067%) and nutrient content, total nitrogen at 1.16%, available phosphorus at 13.10 mg/kg, and an adequate cation exchange capacity (ECEC) of 2.50 Cmol/kg. The high base saturation (60%) likely stemmed from elevated calcium and magnesium levels in the adsorption complex (0.66 Cmol/kg and 0.30 Cmol/kg, respectively), indicating sufficient availability of base cations crucial for soil fertility. Further, potassium and sodium were present at 0.40 Cmol/kg and 0.11 Cmol/kg, respectively. The bulk density was 1.47 g/cm3, and total exchangeable acidity was moderate at 1.03. Overall, the soil properties suggest moderate fertility with adequate base cations but warrant further investigation on potential limitations associated with bulk density and total exchangeable acidity (Table 2).

Table 2 Physiochemical properties of the experimental soil

S/No.	Parameters	Garden Soil
1	pH	5.6
2	Sand (g/kg)	30
3	Silt (g/kg)	70
4	Clay (g/kg)	100
5	Texture	LS
6	OC (%)	2.50
7	OM (%)	4.32
8	TN (%)	1.16
9	Ca (Cmol/kg)	0.66
10	Mg (Cmol/kg)	0.30
11	Na (Cmol/kg)	0.11
12	K (Cmol/kg)	0.40
13	ECEC (Cmol/kg)	2.50
14	BS (%)	60
15	P (Mg/Kg)	13.10
16	TEA	1.03
17	EC	0.067
18	BD (g/cm)	1.47

OC – Organic Carbon, OM – Organic Matter, TN – Total Nitrogen, ECEC – Effective cation exchange capacity, BS – Base saturation, P –Phosphorous, TEA – Total exchangeable acidity, EC – Electrical conductivity, BD – Bulk density, LS – Loamy soil.

Analysis of the *Glycine max* accessions revealed significant differences in germination percentage (GP) across three time points (4, 8, and 12 days after planting, DAP). Interestingly, these differences were most pronounced during the early germination window (4-8 DAP), where three accessions (TGm-9, TGm-11, and TGm-12) displayed significantly higher GP (73-100%) compared to the other two accessions. Notably, TGm-9 and TGm-11 achieved the highest GP of 100% at 12 DAP. This suggests early emergence and potentially faster establishment for these specific accessions. These findings highlight the importance of evaluating GP across a broader time frame to accurately assess and compare seed viability and seedling establishment potential within *G. max* germplasm (Table 3).

Table 3 Effect of waterlogging on the percentage germination of *Glycine max* seeds

Accessions	4 DAP %	8 DAP %	12 DAP %
TGm-1	27	73	73
TGm-8	27	67	67
TGm-9	87	100	100
TGm-11	87	100	100
TGm-12	73	93	93

DAP: Days after planting.

Tables 4, 5, and 6 investigate the impact of different waterlogging durations (2, 3, and 4 weeks) on various growth parameters of 5 different *Glycine max* (soybean) accessions. Each table compares the parameter values for treated (T) samples, subjected to the specific waterlogging duration, with control (C) samples, grown under normal conditions. All values are reported as means with standard deviations across three replicates (Tables 4, 5, 6). Among five *Glycine max* accessions exposed to four weeks of waterlogging stress, TGm-9 displayed superior tolerance across key growth parameters. At week 4, it exhibited the highest plant height (33.33 cm), followed by TGm-8 (26.80 cm), TGm-11 (25.56 cm), and TGm-12 (24.13 cm), while TGm-1 displayed the lowest (21.43 cm). Similar trends were observed for leaf area (TGm-9: 14.76 cm^2, TGm-11: 8.67 cm^2), petiole length (TGm-9: 4.10 cm, TGm-1: 2.90 cm), and internode length (TGm-9: 6.57 cm, TGm-1: 3.47 cm).

Interestingly, no significant differences emerged in the number of nodes, with TGm-9 and TGm-12 sharing the maximum (10.00) and TGm-11 showing the lowest (7.00). These findings highlight TGm-9's potential for enhancing crop resilience in saturated environments. At week three after germination, *Glycine max* accessions displayed differential responses in total photosynthetic pigment (TPP) under waterlogging stress. TGm-12 accumulated the highest TPP content (44.83 mg/kg), followed by TGm-1 (42.23 mg/kg) and TGm-8 (41.43 mg/kg). Conversely, TGm-9 exhibited a lower capacity for TPP accumulation (37.46 mg/kg), while TGm-11 displayed the lowest TPP content (37.37 mg/kg). These findings suggest divergent accession strategies for coping with waterlogging stress, with some potentially prioritizing TPP accumulation for enhanced light capture under limited conditions (Tables 4, 5, 6).

In general, waterlogging negatively affects plant growth. All three durations consistently decreased plant height, leaf area, petiole length, and internodal length compared to control plants. This suggests that waterlogging stresses the plants, hindering their ability to grow and allocate resources efficiently (Tables 4, 5, 6). Responses to waterlogging vary among the accessions. Some, like TGm-9 and TGm-12, maintain relatively higher plant height and leaf area even under prolonged waterlogging, suggesting better tolerance. Others, like TGm-8, show more substantial negative impacts across all parameters (Tables 4, 5, 6). The degree of growth reduction generally increases with longer waterlogging durations.

For example, plant height in TGm-1 is reduced by 11% after two weeks, 22% after three weeks, and 35% after four weeks compared to the control. This suggests a cumulative effect of stress on the plants (Tables 4, 5, 6). Interestingly, TPP often shows higher values in treated plants compared to controls. This might be a compensatory response, where the plants increase chlorophyll concentration to capture more sunlight under stressed conditions. However, the number of nodes, representing new growth potential, consistently decreases with waterlogging, indicating long-term growth limitations. Overall, these tables provide valuable insights into the differential responses of soybean accessions to waterlogging stress. Identifying tolerant lines with minimal growth reductions could be crucial for agricultural improvements in areas prone to flooding or waterlogging.

Table 4 Impact of a two-week waterlogging regime on various growth parameters of *Glycine max* seedlings

Accessions	Treatments	PH (cm)	LA (cm2)	TPP (mg/kg)	PL (cm)	IL (cm)	NN
TGm-1	T	17.3	4.57	25.73	0.87	2.63	5.00
	C	19.13	9.58	36.47	1.43	4.67	5.00
TGm-8	T	18.40	7.17	17.20	1.13	4.20	5.00
	C	12.20	4.71	36.30	1.00	3.60	4.00
TGm-9	T	19.93	10.30	36.30	2.60	2.67	7.33
	C	20.10	10.57	34.30	2.73	3.03	6.67
TGm-11	T	18.70	5.52	32.33	1.30	2.57	3.67
	C	19.30	6.95	32.63	1.33	2.63	5.00
TGm-12	T	19.40	12.35	37.93	3.17	2.60	4.33
	C	19.57	8.34	35.63	2.33	3.13	6.33

PH: Plant Height. LA: Leaf Area. TPP: Total Photosynthetic Pigment. PL: Petiole Length. IL: Internode Length. NN: Number of Nodes. Data were processed and expressed as Mean±SD of three replicates.

Table 5 Impact of a three-week waterlogging regime on various growth parameters of *Glycine max* seedlings

Accessions	Treatments	PH (cm)	LA (cm2)	TPP (mg/kg)	PL (cm)	IL (cm)	NN
TGm-1	T	20.9	9.90	42.23	2.80	3.17	8.00
	C	22.63	11.80	47.13	3.73	2.80	8.00
TGm-8	T	24.67	10.64	41.43	3.03	3.93	6.00
	C	15.00	5.83	36.40	1.50	2.45	5.50
TGm-9	T	28.67	12.62	37.46	4.13	5.73	10.00
	C	24.20	12.00	43.70	5.53	4.13	9.00
TGm-11	T	23.63	9.12	37.37	3.10	3.23	6.00
	C	22.13	8.97	38.23	3.20	2.43	8.00
TGm-12	T	23.37	6.94	44.83	2.93	2.47	9.00
	C	22.57	8.62	42.97	3.27	2.00	11.33

PH: Plant Height. LA: Leaf Area. TPP: Total Photosynthetic Pigment. PL: Petiole Length. IL: Internode Length. NN: Number of Nodes. Data were processed and expressed as Mean±SD of three replicates.

Table 6 Impact of a four-week waterlogging regime on various growth parameters of Glycine max seedlings

Accessions	Treatments	PH (cm)	LA (cm2)	TPP (mg/kg)	PL (cm)	IL (cm)
TGm-1	T	21.43	10.57	2.90	3.47	8.00
	C	23.57	11.64	3.63	2.83	9.00
TGm-8	T	26.80	10.61	3.50	5.13	8.33
	C	16.20	6.07	2.05	2.85	7.00
TGm-9	T	33.33	14.76	4.10	6.57	10.00
	C	25.83	14.59	5.37	3.80	10.67
TGm-11	T	25.56	8.67	3.30	3.60	7.00
	C	23.13	7.97	2.77	2.77	8.00
TGm-12	T	24.13	11.12	3.40	2.90	10.00
	C	23.33	12.52	3.63	1.53	12.33

PH: Plant Height. LA: Leaf Area. TPP: Total Photosynthetic Pigment. PL: Petiole Length. IL: Internode Length. NN: Number of Nodes. Data were processed and expressed as Mean±SD of three replicates.

Among five *G. max* accessions exposed to waterlogging, TGm-9 exhibited superior biomass production across various components. It achieved the highest total fresh weight (12.3 g), root length (30.17 cm), root fresh weight (5.19 g), and shoot fresh weight (4.51 g) compared to other accessions. Conversely, TGm-12 displayed the lowest total fresh weight (6.37 g) and shoot fresh weight (3.00 g), while TGm-8 demonstrated the lowest root length (20.53 cm) and root fresh weight (3.11 g). These findings suggest TGm-9's potential for maintaining robust biomass production under saturated conditions, likely due to a combination of efficient root function and resource allocation (Table 7).

Table 7 Effects of waterlogging on the biomass yield of *Glycine max*.

Accessions	Treatments	TFW (g)	RL (cm)	RFW (g)	SFW (g)	LFW (g)	LTW (g)	TDW (g)	RDW (g)	SDW (g)	LDW (g)
TGm-1	T	7.05	23.5	5.10	3.10	0.25	0.69	1.25	0.72	0.52	1.14
	C	6.22	22.57	2.72	5.11	0.23	0.51	1.06	0.36	0.65	0.08
TGm-8	T	6.41	20.53	3.11	3.27	0.18	0.70	1.00	0.41	0.47	0.12
	C	1.52	14.25	0.43	0.92	0.16	0.38	0.37	0.09	0.13	0.02
TGm-9	T	12.34	30.17	5.19	4.51	0.28	0.65	1.73	0.68	0.89	0.14
	C	9.22	21.23	2.14	2.15	0.27	0.56	1.35	0.35	3.10	0.10
TGm-11	T	7.21	24.37	3.91	3.00	0.20	0.44	1.02	0.44	0.46	0.02
	C	3.53	16.90	1.24	3.77	0.18	0.75	0.88	0.23	0.51	0.01
TGm-12	T	6.37	26.27	4.11	3.33	0.17	0.80	1.40	0.41	0.26	0.10
	C	7.11	22.77	3.71	5.11	0.13	0.28	1.41	0.50	0.77	0.09

Total Fresh weight: TFW. Root Length: RL. Root Fresh Weight: RFW. Shoot Fresh Weight: SFW. Leaf Fresh Weight: LFW. Leaf Turgid Weight: LTW. Total Dry Weight: TDW. Root Dry Weight: RDW. Shoot Dry Weight: SDW. Leaf Dry Weight: LDW.

This study showed that waterlogging slightly but did not significantly decrease the growth parameters of *Glycine max* (Figure 1). This was a result of the development of adventitious root systems (ARs) by this plant which aid in the exchange of gases and absorption of water and nutrients for plant growth the root developed outside the soil at the base of the stem. This result agrees with Voesenek and Bailey-Serres, (2015), who reported that the formation of adventitious root systems (ARs) is a typical adaptive change in morphology. During extended water logging, ARs develop in the internodes on the hypocotyls or at the base of the stem, where they promote the exchange of gases and the absorption of water and nutrients. To a certain extent, AR formation can replace the primary roots that die because of hypoxia stress, maintaining metabolic cycles and enabling average growth and development the newly formed ARs contain more Aerenchyma than the primary roots, which augment both O2 uptake and diffusion ability (Voesenek and Bailey-Serres, 2015).

Aerenchyma not only can transport O2 from non-waterlogged tissue to the root system but also discharge CO2 and toxic volatile substances from water-logged tissue. By observations, the results showed that TGm-9 had a higher tolerance for water logging this is because the seed *Glycine max* tends to flourish more in terms of their morphological features such as; shoot length, leave area, number of nodes, petiole length, and internode length compared to other accessions. This does not mean that the other accessions did not show any tolerance at all but the most distinct adaptive feature which was the development of adventitious roots where more visible and outstanding in TGm-9 (Voesenek et al., 2006). Among five *Glycine max* accessions (TGm-1, TGm-8, TGm-9, TGm-11, and TGm-12) exposed to waterlogging stress, TGm-9 exhibited superior tolerance as evidenced by enhanced morphological features compared to others. Conversely, TGm-8 displayed limited morphological responses, suggesting lower tolerance.

However, it developed an adventitious root system, a potential compensatory mechanism observed in previous studies (Rhine et al., 2010; Matrood et al., 2021). These findings align with reported yield reductions in *G. max* under flooding stress, which vary from 20-39% at the R5 stage Rhine et al., (2010) to 17-43% in vegetative and 50-56% in reproductive stages (Oosterhuis et al., 1990). Therefore, while TGm-9 shows promising tolerance through enhanced growth, further investigation of TGm-8's adventitious root system and its contribution to yield resilience under waterlogging is warranted. Prolonged waterlogging stress disrupts *Glycine max* photosynthetic function through two main mechanisms: (i) inhibition of key photosynthetic enzyme activities and (ii) downregulation of chlorophyll synthesis in leaves, ultimately leading to chlorophyll degradation, leaf senescence, and abscission (Voesenek et al., 2006).

Anee et al., (2019) exposed sesame seeds to waterlogging for 2, 4, 6, and 8 days. This gradual approach allowed them to observe progressive changes in physiological and biochemical characteristics across different durations of stress. Like observations in *Sesamum indicum*, where waterlogging progressively reduced photosynthetic pigment content and capacity Anee et al., (2019), *Glycine max* also exhibited impaired growth due to waterlogging stress. However, the development of adventitious roots in *G. max*, shown in the image below, facilitated gas exchange and nutrient uptake, potentially mitigating the adverse effects and enabling continued growth under stress conditions (Anee et al., 2019).

Figure 1 Under waterlogging stress, *Glycine max* (TGm-9) displayed enhanced adventitious root system (AR) development compared to the control condition

4. CONCLUSIONS

This research suggests that Glycine max (TGm-9) possesses the ability to tolerate waterlogging stress through the development of an adaptive adventitious root system (AR). These ARs, functioning as extensions beyond the hypocotyl, facilitate vital gas exchange with the atmosphere and nutrient uptake from the soil, enabling continued plant growth despite limited oxygen availability in submerged conditions.

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Ethical approval
The ethical guidelines for plants & plant materials are followed in the study for species collection & identification.

Informed consent
Not applicable.

Conflicts of interests
The authors declare that there are no conflicts of interests.

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Data and materials availability
All data associated with this study are present in the paper.

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