JEE Journal of Ecological Engineering

Journal of Ecological Engineering 2024, 25(11), 327–334
https://doi.org/10.12911/22998993/193409
ISSN 2299–8993, License CC-BY 4.0

Received: 2024.09.03
Accepted: 2024.09.23
Published: 2024.10.01

The Effects of Water Regimes on Morphological and Physiological Traits of Black Pepper (*Piper nigrum*)

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ABSTRACT

This research investigates the impact of drought and waterlogging stresses on the morphological and physiological characteristics of black pepper (*Piper nigrum*). The greenhouse experiment was laid out in a randomized complete block design (RCBD) with treatments consisting of three water regimes (drought, control, and waterlogging), all replicated three times. The results suggested that the root traits of black pepper, such as root length and surface area, showed considerable reductions under both stress conditions, with more severe impacts observed under waterlogging. The significant reductions were observed in plant height, number of leaves, number of branches, leaf area, and SPAD value, root and shoot dry weight of black pepper. Gas exchange parameters also decreased markedly under drought stress, with waterlogging causing an even greater reduction. The findings provide valuable insights into managing the effects of environmental fluctuations on black pepper cultivation.

Keywords: waterlogging, drought, black pepper, root traits, gas exchange.

INTRODUCTION

Black pepper (*Piper nigrum*), native to the Western Ghats of India, is one of the most widely used spices globally, valued for its flavor and medicinal properties (Reshma et al., 2022). It plays a significant economic role in many tropical countries where it is cultivated, including Vietnam, India, and Indonesia (Ahmad et al., 2020). However, the cultivation of black pepper is highly sensitive to climate conditions. Climate change, particularly the increasing frequency of droughts and waterlogging, poses a serious threat to its production (Izzah et al., 2019). Drought stress can lead to reduced growth, poor yield, and increased susceptibility to diseases, while excessive rainfall and waterlogging can cause root rot and other waterborne diseases, negatively affecting plant health (Kaur et al., 2020). As these extreme conditions become more common due to climate change, it is crucial to study their impacts on the growth and development of black pepper to develop effective strategies for mitigating these challenges and ensuring sustainable cultivation.

Drought tolerance in plant varieties can fluctuate depending on growth stages and environmental factors (Farooq et al., 2012). Water shortages can reduce crop yields by up to 70%, with drought conditions varying across time and location (Dinar et al., 2019). Black pepper, typically grown in areas with abundant but uneven rainfall, often faces severe water shortages during dry seasons (Pallavi and Abida, 2018). Drought-tolerant black pepper varieties tend to have higher water retention and lower cell membrane permeability (George et al., 2017). Their drought resistance is linked to mechanisms such as stomatal regulation, water movement in leaves, and root penetration (Vasantha et al., 1990). Recent studies show black pepper adapts to drought by increasing water-use efficiency and intercellular CO2 while reducing stomatal conductance and photosynthesis. However, vegetative growth struggles to recover after rehydration, suggesting limitations in long-term drought resilience (Ferreira et al., 2024). Further research on black pepper's root system under drought stress is needed.

In waterlogged conditions, dissolved oxygen levels rapidly decline due to root respiration and microbial activity (Parent et al., 2008), leading to hypoxia that limits the aerobic respiration of submerged tissues (Blom and Voesenek, 1996; Bailey-Serres and Voesenek, 2008). Under hypoxia, roots shift to anaerobic respiration, relying on enzymes that primarily metabolize sugars and produce fermentation by-products like ethanol and acetaldehyde, which inhibit root growth in susceptible plants (Drew, 1997; Yin et al., 2013). To adapt, plants exhibit morphological changes such as root elongation, increased branching, and the development of adventitious roots (Daniel and Hartman, 2024), adaptations mainly observed in upland crops (Singh et al., 2018). Anatomical changes, such as the formation of gas-filled tissues, also facilitate oxygen transport from the stem to the roots (Justin and Armstrong, 1987; Seago et al., 2005; Ejiri et al., 2021). However, black pepper roots are particularly sensitive to waterlogging and lack significant resistance, as reported by Ton et al. (2008). Moreover, Kandianan et al. (2014) found that waterlogging significantly reduces photosynthetic pigment content, net photosynthetic rate, and stomatal conductance, while increasing proline content and water-use efficiency. Despite these findings, the waterlogging tolerance of black pepper remains understudied, particularly regarding root morphological traits. Therefore, further research is essential to evaluate root development as a key indicator of waterlogging tolerance, especially for crops like black pepper, which are highly susceptible to hypoxia.

This study aims to investigate the root morphology, physiology, and dry matter accumulation in black pepper under drought and waterlogged conditions. It addresses gaps in understanding how the root system responds to these stressors, focusing on root development as a key factor in the plant's ability to tolerate drought and waterlogging.

MATERIALS AND METHODS

Plant material and experimental design

The Vinh Linh black pepper variety was collected in Central Highlands of Vietnam (Dak Lak, Dak Nong, Lam Dong, and Gia Lai provinces).

Before conducting the experiments, the sandy clay-loam soil (composed of 56 % sand, 23 % silt, 20 % clay, and 1% humus) which was sieved through a 10-mm mesh screen. Afterward, the styrofoam box with a length of 70 cm, width of 50 cm, and height of 44 cm, containing full of soil, was prepared. The uniform commercial standard of pepper cuttings with the standard of 30 cm in shoot length were grown in a styrofoam box. After 21 days of planting, three water regimes, including well-irrigated (control), waterlogging, and drought treatment, were applied for 10 days. Briefly, control pepper plants were grown in soil with 30% moisture content, while waterlogged plants were subjected to wet soil conditions, and drought-stressed plants received no water. The experiment was laid out in a with three replicates. Six pepper plants were grown in a box and considered one replicate.

Mesurements

The morphological parameters of the root system, including total root length (RL), total root area (RSA), and root diameter (ARD), were evaluated at the end of treatments using the WinRhizo (Régent Instruments Inc.) root system. Plant height (PH), number of leaves (NoL), number of branches (NoB) stem diameter (SD), leaf area (LA), and chrophyll content (through SPAD value) were measured at the end of the experiment. PH measures from root to peak growth. SD uses a measuring micrometer caliper at a position 2 cm away from the ceramic. NoL is defined as the total number of complete leaves. NoB is determined when lateral shoots reach a length of about 1 cm. LA was calculated using a leaf area meter (Li-3100, Lin Coln Nebraska USA). SPAD value was recorded using SPAD502 meter (Konica-Minolta 502, Japan). Monitoring photosynthesis indicators such as photosynthetic intensity (A), stomatal sensitivity (GSW), and intracellular CO_2 concentration (Ci) were conducted using the LI-6800 (Lin Coln Nebraska USA) photosynthesis system at the final day of experimental treatment. The assessments took place between 8:00

and 12:00 h, with measurements taken from fully expanded leaves situated on the second or third node of main stem. Dry weight of shoot and root was determined after drying samples at 80 °C for three days in a drying chamber (Binder, USA) until a constant weight was achieved. Dry samples were weighted by the electronic balance (Ohaus STX-223, USA).

Data analysis

Analysis of variance (ANOVA) was performed to analyze the effects of water regimes using R (R Core Team, 2021). Means compared using LSD at a 5% significance level in the case of the significance of the impact of water regime on the measured variable.

RESULT

Effects of water regimes on root morphological traits of black pepper

Under drought and waterlogging conditions, black pepper plants significantly reduced RL and RSA compared to the control. A significant reduction was observed in total RL under both drought and waterlogging conditions (Table 1). The RL of black pepper under control reached 5,136.60 mm, while under drought conditions, RL was only 3,725.84 mm, which was 1,410.76 mm (27.47%) less than that under control. The RL under the waterlogging condition was the lowest, at 3,047.14 mm, which was 2,089.46 mm (40.7%) less than that under the control. Black pepper's total RSA under drought and waterlogging conditions was also lower than in the control. RSA in the control condition was the highest, reaching 19,032.13 mm². In contrast, under drought conditions, RSA was 12,284.09 mm², which was 6,748.04 mm² (35.46%) less than that under the control. The lowest RSA was observed in the waterlogging condition, reaching 11,481.62 mm², which was 7,550.51 mm² (39.66%) less than that under the control. Especially, the average root diameter (RD) in the waterlogging condition was higher than in the control. After 14 days of drought treatment, the average RD under the control was 1.18 mm, while under drought conditions, RD decreased by 0.13 mm (11.02%) compared to the control. Conversely, under the waterlogging condition, showed the highest RD, reaching 1.20 mm, which was 0.02 mm (1.69%) higher than that under the control.

Effects of water regimes on growth traits of black pepper

A significant reduction in plant height (PH), number of leaves (NoL), number of branches (NoB), stem diameter (SD), leaf area (LA), and SPAD values were detected under both drought and waterlogging conditions (Table 2). PH under drought conditions is lower than control. Particularly, PH reached 55.63 cm under control, while PH was 53.58 cm, a decrease of 2.05 cm (3.68%). The waterlogging treatment also reduces the height of pepper plants compared to the control. Under normal conditions, the height is 55.63 cm; under waterlogging, it is 52.91 cm, a 2.72 cm (4.89%) decrease. The PH of black pepper were lower under waterlogging conditions than that under drought conditions.

Additionally, NoB under drought conditions is consistently lower than in the control treatment. Under normal conditions, the NoL was 9.01; under drought, it was 8.70, reducing 0.31 leaves (3.44%). The waterlogging treatment generates fewer leaves than the control. Under normal conditions, the NoL was 9.01; under waterlogging conditions, it was 9.00, a 0.01 leaf reduction (0.11%). Following treatment, the number of leaves declined more under drought conditions than under waterlogging, with waterlogging at 9.00 and drought at 8.70, resulting in a 0.30 leaf decrease (3.33%).

The NoB during drought treatment is equivalent to normal conditions. The NoB was 2.00 under normal conditions and remains unchanged under drought conditions. However, there were greater branches in the waterlogging treatment than in the control. Under normal conditions, the NoB was 2.00; under waterlogging conditions, it was 2.11, up 0.11 branches (5.50%). Following treatment, the number of branches declined more under drought conditions than under waterlogging, with waterlogging at 2.11 branches and drought at 2.00 branches, for a total decrease of 0.11 branches (5.50%).

Waterlogging treatment also reduces the SD compared to the control. Under normal conditions, the SD was 5.94 mm; under waterlogging conditions, it was 5.33 mm, a 0.61 mm drop (10.30%). Following treatment, the SD declined more under waterlogging conditions than drought,

Table 1. Effects of water regimes on root morphological traits of black pepper

Parametr	RL (mm)	RSA (mm^2)	RD (mm)
Drought	3725.84 ± 15.63	12284.09 ± 28.60	1.05 ± 0.007
Control	5136.60 ± 19.48	19032.13 ± 18.46	1.18 ± 0.006
Waterlogging	3047.14 ± 35.52	11481.62 ± 17.43	1.20 ± 0.001
$LSD_{0.05}$	63.15	164.67	0.01

with drought at 5.72 mm and waterlogging at 5.33 mm, a difference of 0.39 mm (6.81%). The LA following drought treatment is lower than the control. During drought, the LA was decreased by 4.26 cm^2 (4.29%) to 95.01 cm^2, compared to 99.27 cm^2 during normal conditions. The waterlogging treatment results in the lowest LA (94.91 cm^2), representing a 4.39% reduction.

Finally, the SPAD index reduces with water scarcity, suggesting that the SPAD value was lower in drought conditions than in the control. Under normal conditions, the highest SPAD value is 45.96; under drought conditions, it was 44.47, a 1.49 (3.24%) decrease. In the waterlogging condition, the SPAD value is the lowest at 44.43, a 1.53 (3.33%) decrease.

Effects of water regimes on gas exchange parameters of black pepper

After 10 days of drought treatment, the photosynthetic intensity index in plants under normal conditions reached a maximum of 5.45 $\mu CO_2\ m^{-2}\ s^{-1}$, while in drought-stressed plants, it was 2.45 $\mu CO_2\ m^{-2}\ s^{-1}$. In waterlogged conditions, it was the lowest at 2.19 $\mu CO_2\ m^{-2}\ s^{-1}$, which is 0.26 $\mu CO_2\ m^{-2}\ s^{-1}$ lower than the control (Figure 1). Additionally, our results revealed a significant difference in stomatal sensitivity between the drought and waterlogged treatments compared to the control in pepper plants. Among them, stomatal sensitivity in plants under normal conditions reached the

Table 2. Effects of water regimes on growth traits of black pepper

Parameter	PH (cm)	NoL	NB	SD (mm)	LA (cm^2)	SPAD
Drought	53.58 ± 0.26	8.70 ± 0.09	2.00 ± 0.04	5.72 ± 0.06	95.01 ± 0.58	44.47 ± 0.46
Control	55.63 ± 0.45	9.01 ± 0.01	2.00 ± 0.08	5.94 ± 0.14	99.27 ± 1.34	45.96 ± 0.50
Waterlogging	52.91 ± 0.36	8.00 ± 0.09	2.11 ± 0.03	5.33 ± 0.04	94.91 ± 2.43	44.43 ± 0.31
$LSD_{0.05}$	1.32	0.25	0.12	0.31	3.82	1.42

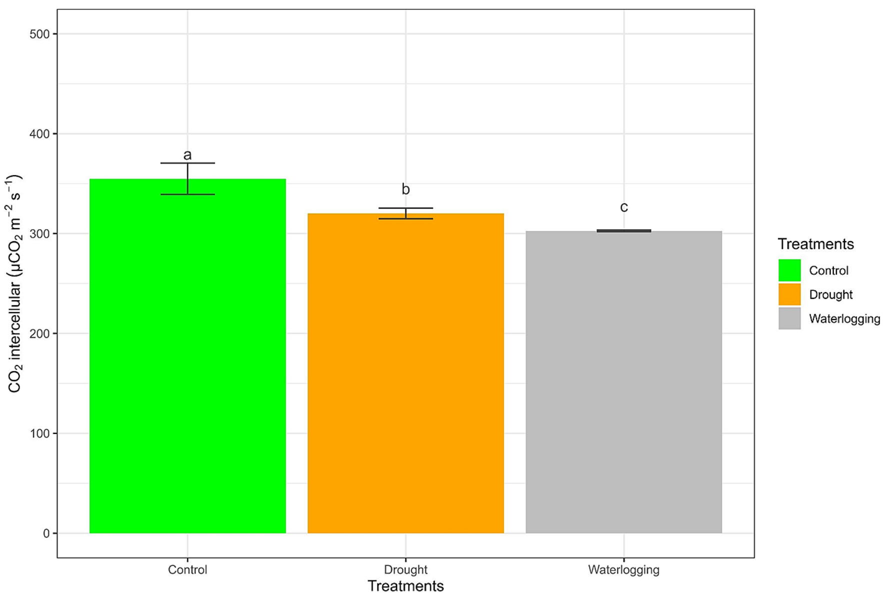

Figure 1. Effects of water regimes on photosynthetic intensity of black pepper plants. The treatment with different letters are significantly different at $p < 0.05$

highest value of 0.14 mol H_2O m^{-2} s^{-1}, whereas, in drought-stressed and waterlogged plants, it was 0.02 mol H_2O m^{-2} s^{-1}, showing a reduction of 0.12 mol H_2O m^{-2} s^{-1} (Figure 2). The internal CO_2 levels in Figure 3 showed that the control treatment had higher internal CO_2 levels compared to the drought treatment. After 14 days of drought treatment, plants under normal conditions achieved a maximum of 354.84 μCO_2 m^{-2} s^{-1}, whereas drought-stressed plants had a reduction of 34.68 μCO_2 m^{-2} s^{-1}. The lowest result was obtained in plants under waterlogged conditions, with 302.70 μCO_2 m^{-2} s^{-1}, which is 52.14 μCO_2 m^{-2} s^{-1} less than the control.

Effects of water regimes on dry weight accumulation of black pepper

The shoot dry weight of the black pepper plants in control was 3.3426 g, whereas, in the drought treatment, it was only 3.0076 g, a 0.335

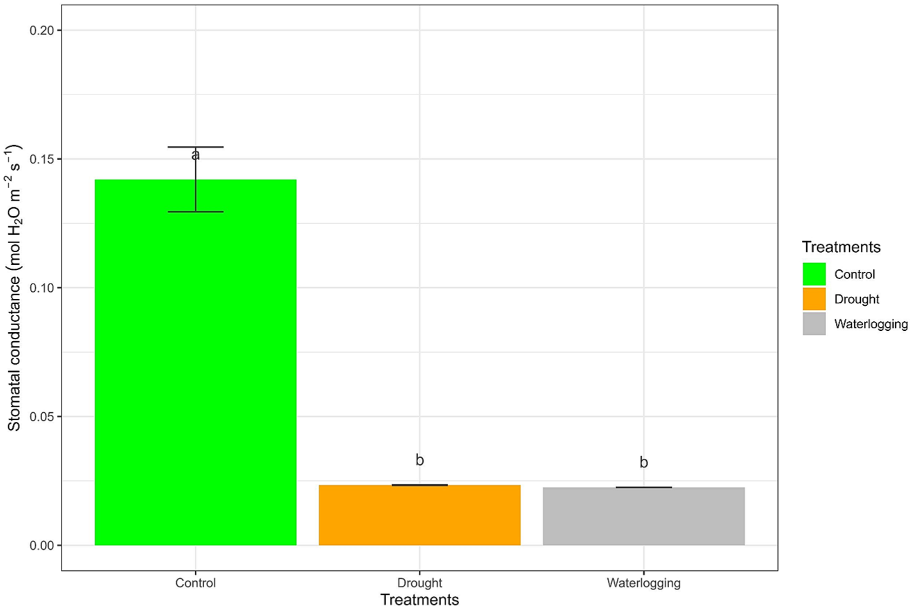

Figure 2. Effects of water regimes on the stomatal conductance of black pepper plants. The treatment with different letters are significantly different at $p < 0.05$

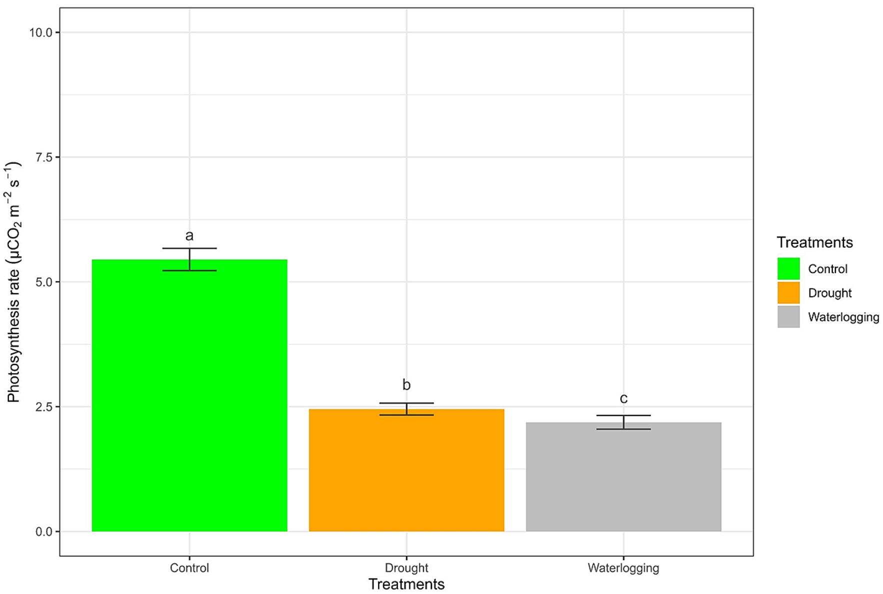

Figure 3. Effects of water regimes on the CO_2 Intracellular of black pepper plants. The treatment with different letters are significantly different at $p < 0.05$

g decrease. The lowest value was obtained under waterlogged conditions, with a dry weight of 2.8309 g, which was 0.1767 g less than in drought conditions. Similarly, the root dry weight following treatment revealed that the average root dry weight was the highest at 0.3811 g in normal conditions. Under drought conditions, the dry weight of the roots fell by 0.0444 g to 0.3367 g. The lowest value was obtained under waterlogged conditions, with a root dry weight of 0.3244 g and a drop of 0.0123 g from the drought condition (Table 3).

DISCUSSION

Plant roots adapt to variations in soil water regimes through morphological, anatomical, and physiological changes, which help them cope with environmental fluctuations. The root system is crucial for water and mineral absorption and synthesizing essential compounds for shoot growth (Fageria et al., 2011). Roots exhibit high plasticity, allowing them to adjust to environmental changes (Yetgin, 2024). Under waterlogged conditions, hypoxia results from a rapid reduction in soil oxygen levels due to root respiration and microbial activity (Blom and Voesenek, 1996; Bailey-Serres and Voesenek, 2008). Hypoxia dramatically inhibits root development, especially root elongation, while root diameter tends to increase (Sánchez-Bermúdez et al., 2022). Conversely, during drought conditions, plants typically expand their root systems deeper into the soil to access water from lower layers. This adaptation involves increased root length density and a higher root-to-shoot ratio, which enhances the plant's ability to absorb water in arid environments. For upland crops such as bread wheat (Ehdaie et al., 2012), cassava (Kengkanna et al., 2019), maize (Nakamoto, 1993; Gao and Lynch, 2016), millet (Rostamza et al., 2013), soybean (Ye et al., 2018), and tomato (Ekanayake and Midmore, 1992), deep rooting plasticity under progressive drought is particularly advantageous for maintaining growth and yield. However, the root traits of black pepper under drought and waterlogging conditions remain largely unexplored, highlighting a significant gap in understanding how this crop adapts to such environmental stresses. This study reports a new findings that under drought and waterlogging conditions, black pepper plants exhibited a significant reduction in RL and RSA compared to the control. The average RD was slightly higher under waterlogging conditions compared to the control, but decreased under drought conditions (Table 1).

New growth in pepper plants under water stress is very limited, with both plant height and leaf area being significantly affected, particularly the latter. During moisture stress, the leaf expansion rate decreases even before soil moisture reaches critical levels, indicating that screening cultivars based on leaf expansion rate may not be effective for black pepper (Ramadasan and Vasantha, 1994). Additionally, severe water stress leads to a decrease in chlorophyll a, chlorophyll b, and total chlorophyll content (Vasantha et al., 1989). The results of our study further corroborate these findings. Plant height (PH) was reduced under drought and waterlogging conditions, with waterlogging causing a more significant decrease than drought. Leaf area also decreased under both stress conditions, with the most substantial reduction observed under waterlogging, highlighting the heightened sensitivity of pepper plants to excess water (Table 2). These changes are consistent with the decrease in chlorophyll content under severe water stress, as observed in prior studies, further indicating that both drought and waterlogging negatively impact the photosynthetic capacity and overall growth of pepper plants

Gas exchange parameters, including photosynthetic rate (A), stomatal conductance (gs), and transpiration rate (E), were studied in both irrigated and water-stressed pepper plants (Delfine et al., 2002; Kabir et al., 2021). It was observed that A, gs, and E decreased drastically after just 6 days of stress induction of drought stress (Krishnamurthy et al., 2016). However, information on waterlogging stress was limited. In this study, we

Table 3. Effects of water regimes on dry weight accumulation of black pepper

Parameter	Shoot dry weight (g plant^{-1})	Root dry matter (g plant^{-1})
Drought	3.0076 ± 0.0532	0.3367 ± 0.0136
Control	3.3426 ± 0.0887	0.3811 ± 0.01876
Waterlogging	2.8309 ± 0.0941	0.3244 ± 0.0131
$LSD_{0.05}$	0.1468	0.0268

also found that A (Figure 1), gs (Figure 2), and E (Figure 3) continued to decrease after 10 days of drought. A new finding we detected was that waterlogging caused a greater reduction in A and E compared to drought conditions.

The results of this study, which showed that both drought and waterlogging significantly reduced root and shoot dry weight in pepper plants, align with findings from research on black pepper. Studies have shown that black pepper is highly sensitive to waterlogging, with reduced root growth and biomass under hypoxic conditions (Ton et al., 2008). Similar to the observations in this study, waterlogging has been found to have a more pronounced negative effect on black pepper compared to drought, as it disrupts root function and leads to decreased overall plant growth (Kandianan et al., 2014). These findings reinforce the vulnerability of black pepper to waterlogging and the critical role of root development in its tolerance to adverse conditions.

CONCLUSION

This study highlights the significant impact of drought and waterlogging on black pepper. The root traits of black pepper, such as root length and root surface area, showed considerable reductions under both stress conditions, with more severe impacts observed under waterlogging

These changes were accompanied by significant reductions in plant height, leaf area, and SPAD values, indicating compromised photosynthetic capacity and shoot growth. Gas exchange parameters also decreased markedly under drought stress, with waterlogging causing an even greater reduction. Both drought and waterlogging conditions significantly reduced both root and shoot dry weight in pepper plants. Further studies on root traits need to be conducted to better understand and manage the impacts of environmental fluctuations on black pepper plant.

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