

Shoot and Root Growth in Common Bean (*Phaseolus vulgaris* L.) Exposed to Gradual Drought Stress

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ABSTRACT

Drought condition during the dry season is a major constraint for intensifying agricultural activities at riparian wetlands in Indonesia, particularly for annual vegetables, including common bean (*Phaseolus vulgaris* L.). Besides inhibiting growth and reducing yield, drought also causes alteration of the shoot and root growth and development. The objective of this study was to evaluate responses of common bean to three durations of drought stress and the bean ability to recover after termination of the stress treatments. Gradual drought stress treatments were imposed by withholding all water sources to the treated plants. Three durations of drought stress imposed were 4, 8, and 12 days. The ability of the stress-treated plants to recover was evaluated at 7 days after termination of each treatment. The result of this study revealed that common bean was able to tolerate and recover from gradual water deficit for up to 8 days; however, prolonged water deficit for 12 days inhibited the growth of above-ground organs in common bean. Despite root regrowth during the recovery period, plants previously treated with 12 days of drought were unable to recover but those treated with shorter drought stress period were able to recover.

Keywords: drought stress; growth analysis; riparian wetland; stress recovery; water deficit

INTRODUCTION

Despite the advancement of technology and instruments for monitoring climate changes, predicting climate behavior has not become easier during last few decades. Incidences of climate extreme have been more frequently reported, including extreme and prolonged drought. Drought stress or water deficit for agricultural activities also occur during the dry season in riparian wetlands in Indonesia. Drought condition in wetlands was considered as one of the biophysical factors that influenced farmer's choice in planting vegetable crops during the dry season (Taiwo, 2013). Drought condition causes the negative effect to the farming operation and plant production. Garssen, Verhoeven, & Soons (2014) reported the long duration of drought for more than 30 days strongly decreased total plant biomass at riparian wetlands. The highest risk of growth reduction and harvest losses caused by drought stress led to the serious constraint in agricultural activity, especially in vegetable production.

Most of the annual vegetables, unfortunately, are sensitive to drought, including common bean (*Phaseolus vulgaris* L.). Thus, drought stress may extremely decrease quantity, quality, and economic value of vegetables. The previous study revealed that drought stress inhibited the growth of vegetative organs and development of reproductive organs in the bean, i.e. decreased the number of trifoliate leaves, decreased number of main branches, affected both flowering and pod-filling stages, and finally caused serious impact on grain production in dry bean (Mathobo, Marais, & Steyn, 2017). Inadequate water supply also induced alteration of leaf morphological parameters such as total leaf area, fresh weight, and dry weight (Sankar, Gopinathan, Karthishwaran, & Somasundaram, 2014). Under drought stress condition, leaf area was reduced during acclimation stage in three species of tomatoes and accompanied by the reduction of leaf dry weight and stem diameter (Tapia, Méndez, & Inostroza, 2016).

Drought does not only inhibit growth and reduce yield but also alter shoot to root ratio. Ammar et al. (2015) stated that drought stress decreased shoot and root length. Moreover, it increased dry matter

allocation to the roots. Dynamic of the shoot and root changes are considered as an important parameter in analyzing plant adaptation mechanism (avoidance or tolerance) in response to water deficit condition.

Plants exhibit different mechanisms in dealing with water deficit condition. Farooq, Wahid, Kobayashi, Fujita, & Basra (2009) reported that the main mechanisms included enhancing diffusive resistance, increasing water acquisition, developing deep root systems, and reducing transpiration loss by inducing smaller and succulent leaves. The plant also displayed physiological and biochemical responses to drought stress. Plants adjust hormonal and biochemical processes through relocation of metabolites from shoots to roots or by modifying biochemical regulation of root development including increment of ABA (Sankar, Gopinathan, Karthishwaran, & Somasundaram, 2014), proline accumulation (Ammar et al., 2015), ethylene synthesis, auxin and cytokinin alteration, and production of reactive oxygen species (ROS).

Each plant organ might have different sensitivity level to drought stress. Leaves in many crops display earlier and visible sign of stress due to their direct interaction with the surrounding environment (Chitwood & Sinha, 2016). Larger leaves imposed to drought stress expectedly lead to greater water loss through transpiration. Under deficit water condition, plants displayed leaf morphology alteration like leaf rolling and leaf wilting as an effort to preserve turgor. The inability of a plant to maintain turgor directly inhibited growth, as indicated by the decrease in stomatal conductance, decline of photosynthetic rate, and reduction of leaf area (Riboldi, Oliveira, & Angelocci, 2016). Widuri et al. (2017) found that relative leaf expansion rate (RLER) was a promising indicator for early detection drought stress in chili pepper. Furthermore, at the early stage of drought stress, specific leaf fresh weight (SLFW) and specific leaf water content (SLWC) showed no significant change in response to the stress. Total leaf area (TLA), however, exhibited an interesting finding as an indicator for drought stress in chili pepper due to its ability to compensate imbalance of water uptake and loss during stress.

Root growth may behave differently under drought stress since there is direct interaction between root and moisture deficit in the soil. Alteration of root development occurs as result of an osmotic adjustment in response to limited soil moisture condition (Blum, 2017; Borgo, Marur, & Vieira, 2015). Each plant has been reported to have different mechanism during water shortage conditions including root elongation. Reduction of water content in plant organs is directly associated with the imbalance of water uptake by roots and water loss through leaves. Absorption of water less than the loss due to transpiration leads to decrement cell turgor and water volume in the cell, thus cell lost osmotic and water potential.

Competition for water among plant organs occurs during water deficit condition. Water redistribution within plant organ occurs due to differences in osmotic and water potential. To compensate for the loss of water content during drought caused by transpiration, the plant should increase water uptake by roots. If roots cannot supply sufficient water to shoot, the entire metabolic processes could be disturbed which directly affected plant growth. However, this is a reversible process up to a certain level of drought stress (Feller, 2016). Plants have the ability to recover from drought stress. Yet, this recoverability is different amongst plants.

The objective of this study was to evaluate common bean responses to three durations of gradual drought stress and its ability to recover after the stress treatments were terminated.

MATERIALS AND METHODS

The research was conducted from November 2016 to February 2017, in a constructed plastic house for preventing common bean plants received rainwater during drought treatment. The research facility was located in Jakabaring (104°46'44"E; 3°01'35"S), Palembang, Sumatera Selatan. Common bean seeds of PV072 cultivar were soaked in water for five hours and then wrapped with a damp cloth for four days. Two healthy and vigorous germinated seeds transferred into black polyethylene bags filled with mixed substrate consisted of soil, manure, and compost at the ratio of 1:1:1 (v/v/v). More vigorous seedling of the two seedlings per bag was kept and less vigorous one was cut. The main stem of each plant was cut at position 1 cm above petiole base of the third trifoliate leaf to induce development of lateral branches.

NPK fertilizers were applied at 7, 14, and 48 days after planting (DAP). Both insects and diseases were controlled by applying bio-pesticide. In addition, plants were daily watered and bio-fertilizer was

applied to maintain optimal plant growth until late of the vegetative stage, prior to drought stress treatments. Substrate water status was monitored daily using soil moisture meter (Lutron PMS-714).

Drought stress treatments were imposed gradually during late vegetative phase by withholding all water sources to the treated plants. Three durations of drought stress were applied, i.e. 4, 8, and 12 days. Drought treatments were terminated by rewatering the plants; thus, allowing the stressed plants to recover. The ability of the stress-treated plants to recover was evaluated based on crop ability to regrow during 7 day period after termination of each drought stress treatment.

Destructive measurements of growth parameters were done on daily basis starting at the day of treatment was started (D0) and during stress treatments (4 DAT, 8 DAT, and 12 days after treatment (DAT)), then, continued for 7 days of recovery period (4 DAT + 7 R, 8 DAT + 7 R, and 12 DAT + 7 R). Common bean leaves were collected to obtained growth analysis data including leaf area. Leaf area estimated based on linear measurements of leaf length and width using a model developed by Lakitan, Widuri, & Meihana (2017).

Shoot and root components were harvested and measured to collect fresh and dry weight data. Dry matter of each plant organ was obtained by keeping samples in the oven at temperature 80 to for 2 days. Weighting was conducted using an analytical scale. Evaluation of dynamic shoot and root during drought stress treatment was calculated based on growth analysis variables, including total leaf area (TLA), leaf weight ratio (LWR), and root weight ratio (RWR).

Statistical analyses for evaluating treatment's effect on measured variables were carried out using the Analysis of Variance (ANOVA) based on the Completely Randomized Design. Differences between means were tested using the Least Significant Difference (LSD) at $p < 0.05$. Data analysis was done using statistical software of the SAS® University Edition. Average and standard deviation values were calculated for the shoot to root ratio (SRR), crop water content, and plant biomass (total and partitioned).

RESULTS AND DISCUSSION

Common Bean Growth during Gradual Drought Stress and Recovery Period

Drought stress treatment in common bean did not completely halt leaf growth as indicated by the increase in TLA (Table 1). In contrary, drought stress led to the decrease of TLA in *Jatropha curcas* (Sapeta et al., 2013), leaf size in corn (Olawuyi, Bello, Ntube, & Akanmu, 2015), and leaf area in *Anthocephalus cadamba* (Sudrajat, Siregar, Khumaida, Siregar, & Mansur, 2015). TLA in kidney bean plant in optimal condition showed significant increment until 8 weeks after planting throughout growing season but slowly declined after 10 weeks after planting (Nassar, Ahmed, & Boghdady, 2010). In this study, TLA increased gradually during drought stress treatments and recovery periods as plant continued to grow.

Table 1. Effect of imposing drought stress for 4 to 12 days and allowing 7 days of recovery on total leaf area (TLA), leaf weight ratio (LWR), and root weight ratio (RWR)

Treatment	TLA (cm ² per plant)	LWR (g g ⁻¹)	RWR (g g ⁻¹)
D 0	778.69 ± 35.297 c *	0.556 ± 0.024 a	0.055 ± 0.005 ab
4 DAT	1283.21 ± 38.869 Bc	0.508 ± 0.023 b	0.047 ± 0.014 ab
4 DAT + 7 R	1357.14 ± 38.873 Bc	0.469 ± 0.036 bc	0.060 ± 0.006 a
8 DAT	1434.99 ± 41.727 Ab	0.460 ± 0.054 c	0.042 ± 0.009 bc
8 DAT + 7 R	1871.54 ± 44.095 Ab	0.431 ± 0.019 c	0.050 ± 0.017 ab
12 DAT	1513.86 ± 45.306 Ab	0.425 ± 0.021 c	0.048 ± 0.002 ab
12 DAT + 7 R	2027.68 ± 48.229 A	0.334 ± 0.031 d	0.030 ± 0.005 c

Remarks: * = Mean values within a column followed by the same letters are not significantly different at $p < 0.05$ according to LSD.05

Based on data in Table 1, the relative increase of TLA for the first 4 days of drought stress treatment was 64.7 %, decreased by 11.8 % for the next additional 4 days period of stress, and further decreased by 5.5 % for the last 4 days of treatment. It implied that common bean plants experienced severe stress only after the treatment was applied beyond 4 days. The result of LSD test at $p < 0.05$ indicated that there was no significant difference in TLA amongst plants treated for 8 days and 12 days, even after each of them was allowed to recover for 7 days. These two facts lead to the conclusion that the

critical duration of drought stress in common bean is between 4 to 8 days, at time of sharp decline of TLA occurs.

It is interesting to note that despite TLA still increased (although at slower rates) during stress treatments and recovery period, yet LWR consistently decreased (Table 1). The similar result also reported by Erice, Louahlia, Irigoyen, Sanchez-Diaz, & Avice (2010) that drought stress decreased LWR in alfalfa. This might be an adaptive mechanism of the plant to drought. Decreasing of LWR in common bean was observed during each day of treatment and after recovery stage. Significant decrement was found in common bean after 8 days exposed to stress. Stress treatment for 12 days caused sharp decline of LWR not only during the stressed period but also during the recovery period.

Increase in TLA may or may not followed by increase total assimilates produced in leaves, depending on net assimilation rate (NAR). In either case, the only explanation on the decrease in LWR despite the increase in TLA was associated with the fact that assimilates synthesized in leaves were mostly transported out of leaves into other plant organs, most likely to the stems since RWR was also declined. Increasing dry matter partitioning from leaves to roots is considered as an adaptive strategy of the plant to cope drought condition.

Dry matter translocation to roots enhances root growth and subsequently increases water uptake ability of the plants. Decreasing of LWR involved biochemical signaling between root and shoot to adjust the shoot growth during water-limited condition. Hormonal and signaling process are produced in roots due to drought condition and these signals trigger alteration of the shoot and root growth. Rowe, Topping, Liu, & Lindsey (2016) reported that root growth under water-related stress was regulated by abscisic acid interacted with other hormones. Zhao et al. (2015) added that mycorrhiza also influenced crop growth under soil water deficit.

Inhibition of leaf, stem, and root growth was observed during drought stress treatment (Díaz-López et al., 2012) but water stress triggered bigger impact on shoot growth than in root growth. Reduction in shoot growth exposed to drought stress may be caused by loss of turgor which leads to limited cell enlargement and subsequently also leaf expansion. Inhibition of leaf growth also reduced photosynthetic activity due to stomatal closure (Tombesi et al., 2015) since the closure directly restricted gas exchange (García-Castro, Volder, Restrepo-Díaz, Starman, & Lombardini, 2017). Moreover, disturbance to photosynthesis caused some enzymatic and hormonal changes (Neves et al., 2017).

In addition, proline also considered as important osmoregulation to reduce negative impact under drought stress. Proline accumulation in leaves controlled stability of photosynthesis and plant growth during drought condition (Nazar, Umar, Khan, & Sareer, 2015). Earlier studies stated that proline accumulation increased in leaves during water deficit (Ammar et al., 2015). Another study also reported that increment of proline accumulation in relation to severity of drought stress detected in shoot tissue. The increment of proline accumulation correlated with the decrement of relative water content in leaves (Kavas, Baloğlu, Akça, Köse, & Gökçay, 2013). Proline plays multiple roles, including as osmoprotectant and osmoregulation to relieve stress in the plant. Enhancement of proline synthesis was a strategy for most of the plants to survive and continued to grow under water deficiency.

Drought stress decreased root weight ratio (RWR) after 4 DAT and 8 DAT (Table 1). The gradual reduction in RWR showed at 4 DAT and 8 DAT indicated that roots were also sensitive to water deficit. Performance of roots under drought stress determines the ability of the plant to survive in water-limited condition (Rowe, Topping, Liu, & Lindsey, 2016). After exposed to water stress, root cell experienced dehydration.

RWR increased particularly at 4 DAT + 7 R and 8 DAT + 7 R treatments. Interestingly, plants were able to recover in each level of drought stress treatments, except at 12 DAT of stress as indicated by the increase of RWR. Chemical signaling from the root was transferred to shoot via xylem to suppress shoot growth. It caused RWR value in 12 DAT + 7 R did not increase as much as 4 DAT and 12 DAT treatments. Common bean might display mechanism to cope stress condition by transferring more assimilate to root.

Mechanism of assimilates partitioning from shoot to root under drought stress condition reported by Farooq, Wahid, Kobayashi, Fujita, & Basra (2009). Translocation of assimilating to roots could inhibit the accumulation of starch and dry matter to reproductive organ. Low photosynthetic rate under drought stress caused the low export of sucrose out of the leaves. Consequently, it affected the development of

the reproductive organ. For common bean, the low export rate of assimilating could inhibit pod filling and lead to the decrease of pod yield.

Roots in drying soil enhanced root respiration and triggered more carbon consumption. Carbons produced from photosynthesis were utilized by root for growth and maintenance. Franco, Banon, Vicente, Miralles, & Martinez-Sanchez (2011) reported main changes in the characteristic of root systems subjected to drought stress, including extensive and deeper root system; also changing density and diameter of root xylem vessels. In this study, larger common bean root system was observed under drought stress condition.

Shoot-Roots Interaction during Gradual Drought Stress and Recovery Period

The gradual increment in the shoot-root ratio (SRR) shown at 4 DAT and 8 DAT indicated the greater development of shoot than root growth (Fig. 1). Greater development of shoot did not indicate rapid growth of shoot, especially in producing new leaves. Mutual shading of leaves induced thinner leaf blades. In addition, shading declined light interception for photosynthesis. The low photosynthetic process leads to the reduction of assimilates production and growth. As consequence, development of new leaf declined (Mathobo, Marais, & Steyn, 2017).

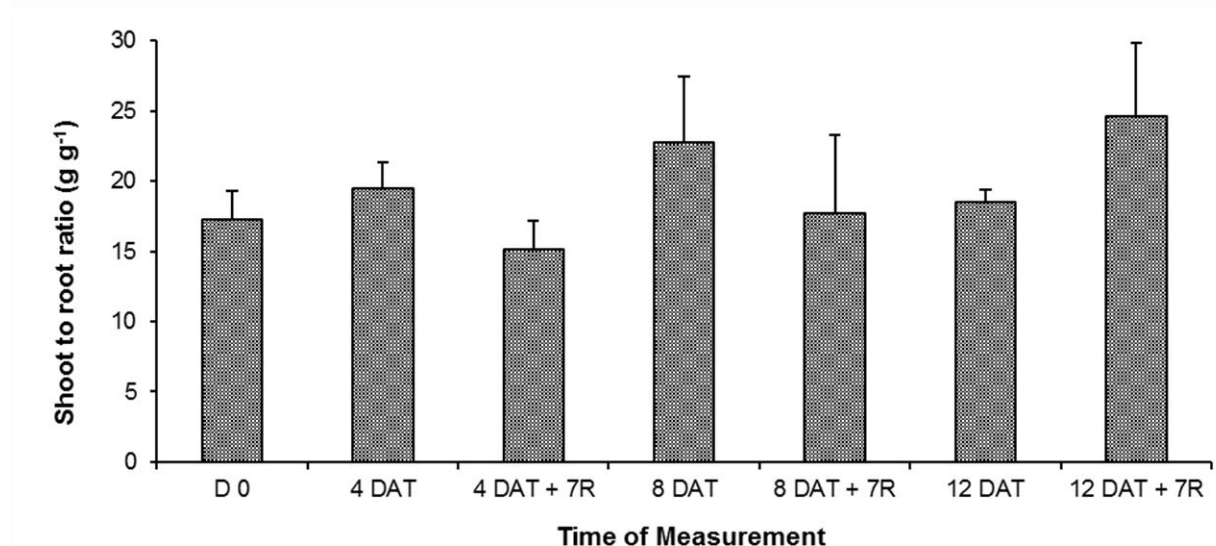


Fig. 1. Shoot to root ratio (SRR) of common bean under gradual drought stress conditions. DO = measured at day of treatment was started; 4 DAT, 8 DAT, and 12 DAT = 4, 8, 12 days after initiation of the stress treatment; 4 DAT + 7 R, 8 DAT + 7 R, and 12 DAT + 7 R = 7 days after each of specified treatment was terminated

Roots were less sensitive compared to shoot exposed to drought stress (Avramova et al., 2016), as also indicated by the increase in root to shoot ratio (Ahmad, Malagoli, Wirtz, & Hell, 2016). After termination of treatments, RWR recovered gradually as water was replenished. Accumulation of dry weights in leaf, stem, and root was significantly restricted during water stress treatments. Furthermore, variability in growth was more pronounced during the recovery period (Fig. 2).

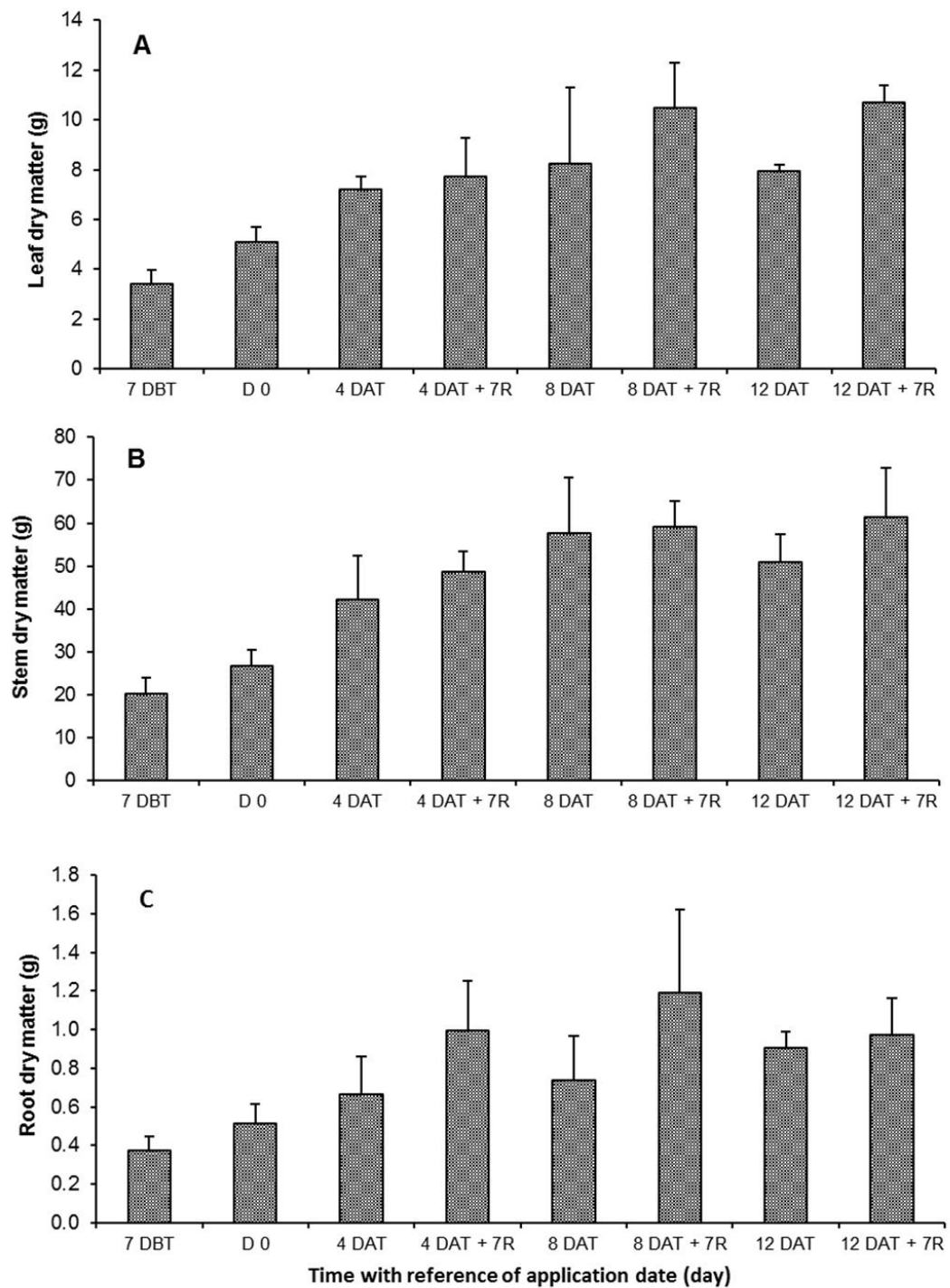


Fig. 2. Leaf dry matter (A) stem dry matter (B) and root dry matter (C) of common bean under drought stress treatment. 7 DBT = at 7 days before treatment; D 0 = at day of treatment was started; 4 DAT, 8 DAT, and 12 DAT = 4, 8, 12 day after treatment; 4 DAT + 7 R, 8 DAT + 7 R, and 12 DAT + 7 R = at 7 days after each specified treatment was terminated.

The early sign of water content decreases in leaves was visible after 4 days without water. After 8 days stress, water transport to the leaf was more restricted than water transport to stem. The longer duration of stress at 12 days further reduced leaves and stem water contents but the decrease was less noticeable in roots (Fig. 3).

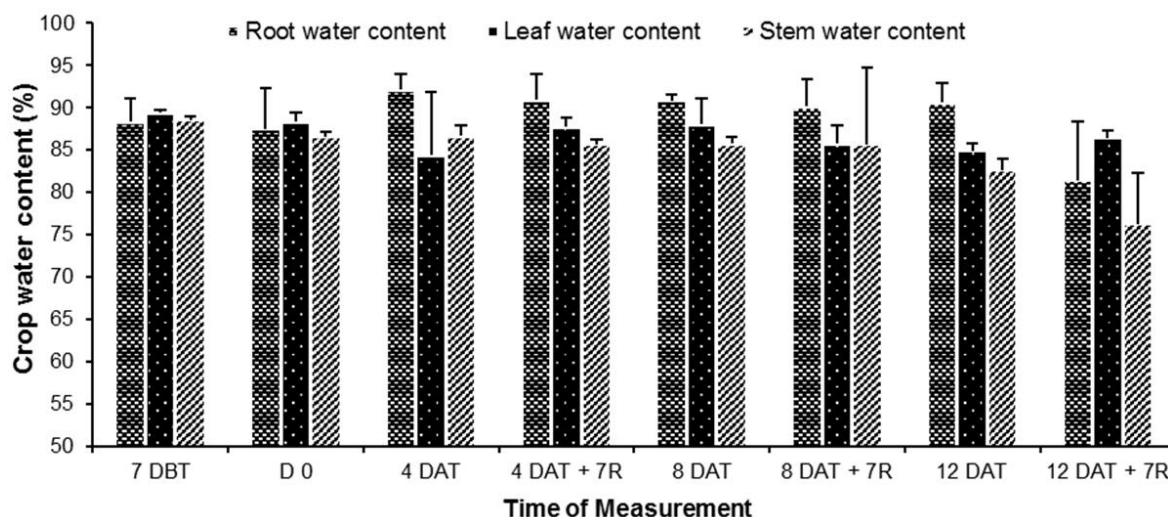


Fig. 3. Crop water content of common bean under gradually drought stress treatment. 7 DBT = at 7 days before treatment; D0 = at day of treatment was started; 4 DAT, 8 DAT, and 12 DAT = 4, 8, 12 day after treatment; 4 DAT+7R, 8 DAT+7R, and 12 DAT+7R = at 7 days after each specified treatment was terminated

Water availability in plant biomass was analyzed in leaf, stem, and root. Wide differences in water content have been studied in various plant parts. It depends on species and different stages of plant development. Plant tissues compete for water among organ. It depends on the different stage of plant growth and level of exposure to unfavorable environmental conditions. In normal condition, the highest water content of common bean was observed in leaf organ. The high water content in the leaf is beneficial for the plant since water will be used for maintaining leaf temperature through transpiration (Xiong et al., 2015).

Redistribution of water within plants was influenced by internal resistance to water flow. It depends on the exposure of the plant to an unfavorable environment. After being exposed to water stress, fluctuation of water content in plant organs was changed inconsistently. At the critical level of water stress, the competition of water transport occurred between shoot and root. At shoot level, competition among leaves occurred between young and old leaves, which young leaves often inhibited to develop or die early under water stress condition. It was associated with leaves function in transpiration for maintaining cell turgidity and controlling stomata closure.

Plant ability to recover is depending on the level of damages due to the stress. Severe water stress causes serious injury in common bean. There was a possibility that common bean needs longer time to recover, i.e. more than 7 days. The inability of a plant to recover after experiencing drought stress might be related to the severe disturbance on the physiological and biochemical mechanism (Rivas et al., 2016). More specifically, Sapeta et al. (2013) argued that restricted photosynthetic activity caused failure of plants to regrow during the recovery period. Drought stress could cause permanent damage to plant tissue, especially in leaf photochemical system.

The sharp drop in shoot water content was observed after common bean plants were exposed to water deficit condition. In contrast, root water content did not distinctly decrease (Table 2). In general, root water content did not significantly affect water limiting condition up to 12 days period. Assuming that

stomatal closure has occurred at leaf due to low leaf water content; therefore, there might be the water tensile strength within xylem vessel has been broken causing failure of water transport from root to leaf. It indicated that plant improved ability of roots to uptake more water and to reduce water loss through transpiration from its leaves (Avramova et al., 2016).

Hormonal metabolism also involved in plant strategy to cope water deficit. The important phytohormones are ABA, ethylene, and cytokinin (Pozo, López - Ráez, Azcón - Aguilar, & García - Garrido, 2015). ABA synthesized in drought stress induced plant abscission, growth inhibition, increased production of trichomes and spines, and increased root/shoot ratio. The most important role of ABA production is to control stomatal closure (Albert et al., 2017; Eisenach et al., 2017). Regulation of ABA involved signal transduction via root system and then transport to the shoot via xylem. High accumulation of ABA in roots plays a role as chemical agent to induce stomatal closure.

Interestingly, another phytohormone like cytokinin has opposite interaction with ABA production during drought stress (Li, Herrera-Estrella, & Tran, 2016). Limited water status leads to increase ABA production and reduce Cytokinin level. Cytokinin plays important role in opening stomata but in the drought condition, phytohormone induces stomatal closure and maintains water loss by transpiration. Ethylene produced by stressed plant induces leaf abscission and accelerates senescence in plant tissue. Regulation of hormonal mechanism in the plant under drought stress can also be considered as another indicator to describe plant response in biochemical level.

Plant Water Relations and Plant Survival Mechanisms Under Drought Stress

In common bean, resistance strategy to cope drought stress condition was developed by constructing root architecture system and osmotic adjustment. In drying soil, roots begin to trigger signaling mechanism to uptake more water by enhancing root growth and/or developing the deeper root system. Optimizing root function to uptake water was triggered by remobilization of assimilates from shoot to root. Less branching and deep primary root were commonly found at stress plants.

Common bean could survive during drought stress for 4 DAT and 8 DAT indicated that plant could preserve water within plant tissue (Table 2). Alteration of leaves water content also related to stomatal behavior. Stomatal closure during water stress treatment was induced by early signaling process between shoot and root system (Golldack, Li, Mohan, & Probst, 2014).

Table 2. Shoot water content and root water content of common bean under drought stress treatment

Treatment	Shoot water content (%)	Root water content (%)
7 DBT	89.056 ± 0.267 a *	88.369 ± 2.720 a
D 0	87.677 ± 0.799 ab	87.538 ± 4.803 a
4 DAT	87.713 ± 0.766 ab	92.162 ± 1.892 a
4 DAT + 7 R	86.912 ± 0.435 b	90.883 ± 3.174 a
8 DAT	87.022 ± 1.894 b	90.838 ± 0.760 a
8 DAT + 7 R	85.228 ± 1.081 c	90.176 ± 3.174 a
12 DAT	83.810 ± 1.017 d	90.631 ± 2.302 a
12 DAT + 7R	83.748 ± 0.476 d	81.456 ± 6.945 b

Remarks: * = Mean values followed by the same letters within each column are not significantly different according to LSD test at $p < 0.05$

The osmotic adjustment also involved in survival strategy to minimize water loss from leaves tissue by accumulating solute content in the cell to control turgor under low water potential condition. This mechanism has been considered as the main physiological parameter associated with water deficit. Osmotic adjustment played important roles to preserve turgor potential and other processes, including stomatal opening, photosynthesis, shoot growth, and continuous root growth (Bahadur, Chatterjee, Kumar, Singh, & Naik, 2011).

Sensitive genotypes have the different water conservation strategy than resistant genotypes do. Resistant genotypes have the ability to maintain osmotic adjustment and increased cell wall elasticity. These abilities are essential in extending the duration of survival period under drought stress. The ability of a plant to maintain osmotic adjustment could reduce the serious damaging impact in plant cells during stress. In other hands, sensitive genotypes are less able due to inability to maintain membrane stability.

The osmotic adjustment was the more effective mechanism for the common bean to cope water stress condition by promoting stomatal closure and preserving high relative water content (Lanna, Mitsuzono, Terra, Vianello, & de Figueiredo Carvalho, 2016). But, in the low osmotic adjustment, plant maintains the loss of water by restricting transpiration rate.

Plants also have a morphological strategy to survive under drought. Farooq, Wahid, Kobayashi, Fujita, & Basra (2009) called it phenotypic flexibility mechanism. Survival strategy is not only at the shoot and root components but also at the whole plant level. Leaf characteristic supported plant adjustment to environment condition such as developing smaller leaf and hairy leaves. Hairy leaf characteristic has advantages in maintaining water loss by transpiration, increasing light reflectance, and reducing leaf temperature. Other plant leaves also have boundary layer to control water loss during transpiration. Characteristics of trifoliate leaf surface in common bean supported plant for survival under water deficit. Waterproof layer in the outer leaf surface which covered by thick layers of epidermal hairs considered as a way to minimize the negative impact of drought stress in common bean.

Several biochemical adaptations by the plant in response to drought stress were already described by Bahadur, Chatterjee, Kumar, Singh, & Naik (2011). Under stress condition, the plant produced many secondary metabolites for the defense mechanism. The importance of these metabolite compounds was to protect plant tissue from oxidative damage. Secondary metabolites were produced by stressed plant including glycine-betaine and myo-inositol. Accumulation of glycine-betaine plays important role in the enzymatic process. Myo-inositol play role in membrane and protein stabilization during stress condition (Díaz-López et al., 2012).

CONCLUSION AND SUGGESTION

Common bean was able to tolerate and recover from gradual water deficit condition for up to 8 days; however, prolonged water deficit for 12 days inhibited the growth of above-ground organs. Plants previously treated with 12 days of drought were unable to recovery meanwhile those treated with shorter drought stress period did. This study evaluated common bean responses to drought stress and recovery using pot experiment. Further, field experiments are needed to fully understand the plant response to drought stress at tropical riparian wetland ecosystem.

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REFERENCES

- Ahmad, N., Malagoli, M., Wirtz, M., & Hell, R. (2016). Drought stress in maize causes differential acclimation responses of glutathione and sulfur metabolism in leaves and roots. *BMC Plant Biology*, 16, 247. <http://doi.org/10.1186/s12870-016-0940-z>
- Albert, R., Acharya, B. R., Jeon, B. W., Zañudo, J. G. T., Zhu, M., Osman, K., & Assmann, S. M. (2017). A new discrete dynamic model of ABA-induced stomatal closure predicts key feedback loops. *PLoS Biology*, 15(9), e2003451. <http://doi.org/10.1371/journal.pbio.2003451>
- Ammar, M. H., Anwar, F., El-Harty, E. H., Migdadi, H. M., Abdel-Khalik, S. M., Al-Faifi, S. A., ... Alghamdi, S. S. (2015). Physiological and yield responses of faba bean (*Vicia faba* L.) to drought stress in managed and open field environments. *Journal of Agronomy and Crop Science*, 201(4), 280–287. <http://doi.org/10.1111/jac.12112>
- Avramova, V., Nagel, K. A., Abdelgawad, H., Bustos, D., Duplessis, M., Fiorani, F., & Beemster, G. T. S. (2016). Screening for drought tolerance of maize hybrids by multi-scale analysis of root and shoot traits at the seedling stage. *Journal of Experimental Botany*, 67(8), 2453–2466. <http://doi.org/10.1093/jxb/erw055>
- Bahadur, A., Chatterjee, A., Kumar, R., Singh, M., & Naik, P. (2011). Physiological and biochemical basis of drought tolerance in vegetables. *International Journal of Vegetable Science*, 38(1), 1–16.

- Retrieved from https://www.researchgate.net/profile/A_Chatterjee/publication/278784748_Physiological_and_biochemical_basis_of_drought_tolerance_in_vegetables/links/5585abec08aeb0cdaddf6821.pdf
- Blum, A. (2017). Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant Cell and Environment*, 40(1), 4–10. <http://doi.org/10.1111/pce.12800>
- Borgo, L., Marur, C. J., & Vieira, L. G. E. (2015). Effects of high proline accumulation on chloroplast and mitochondrial ultrastructure and on osmotic adjustment in tobacco plants. *Acta Scientiarum. Agronomy*, 37(2), 191–199. <http://doi.org/10.4025/actasciagron.v37i2.19097>
- Chitwood, D. H., & Sinha, N. R. (2016). Evolutionary and environmental forces sculpting leaf development. *Current Biology*, 26(7), R297–R306. <http://doi.org/10.1016/j.cub.2016.02.033>
- Díaz-López, L., Gimeno, V., Simón, I., Martínez, V., Rodríguez-Ortega, W. M., & García-Sánchez, F. (2012). *Jatropha curcas* seedlings show a water conservation strategy under drought conditions based on decreasing leaf growth and stomatal conductance. *Agricultural Water Management*, 105, 48–56. <http://doi.org/10.1016/j.agwat.2012.01.001>
- Eisenach, C., Baetz, U., Huck, N. V., Zhang, J., De Angeli, A., Beckers, G., & Martinoia, E. (2017). ABA-induced stomatal closure involves ALMT4, a phosphorylation-dependent vacuolar anion channel of arabidopsis. *Plant Cell*, 29(10), 2552–2569. <http://doi.org/10.1105/tpc.17.00452>
- Erice, G., Louahli, S., Irigoyen, J. J., Sanchez-Diaz, M., & Avice, J. C. (2010). Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. *Journal of Plant Physiology*, 167(2), 114–120. <http://doi.org/10.1016/j.jplph.2009.07.016>
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development*, 29(1), 185–212. <http://doi.org/10.1051/agro:2008021>
- Feller, U. (2016). Drought stress and carbon assimilation in a warming climate: Reversible and irreversible impacts. *Journal of Plant Physiology*, 203, 84–94. <http://doi.org/10.1016/j.jplph.2016.04.002>
- Franco, J., Banon, S., Vicente, M. J., Miralles, J., & Martinez-Sanchez, J. (2011). Root development in horticultural plants grown under abiotic stress conditions – a review. *Journal of Horticultural Science & Biotechnology*, 86(6), 543–556. <http://doi.org/10.1080/14620316.2011.11512802>
- García-Castro, A., Volder, A., Restrepo-Díaz, H., Starman, T. W., & Lombardini, L. (2017). Evaluation of different drought stress regimens on growth, leaf gas exchange properties, and carboxylation activity in purple passionflower plants. *Journal of the American Society for Horticultural Science*, 142(1), 57–64. <http://doi.org/10.21273/JASHS03961-16>
- Garssen, A. G., Verhoeven, J. T. A., & Soons, M. B. (2014). Effects of climate-induced increases in summer drought on riparian plant species: A meta-analysis. *Freshwater Biology*, 59(5), 1052–1063. <http://doi.org/10.1111/fwb.12328>
- Golldack, D., Li, C., Mohan, H., & Probst, N. (2014). Tolerance to drought and salt stress in plants: Unraveling the signaling networks. *Frontiers in Plant Science*, 5, 151. <http://doi.org/10.3389/fpls.2014.00151>
- Kavas, M., Baloğlu, M. C., Akça, O., Köse, F. S., & Gökçay, D. (2013). Effect of drought stress on oxidative damage and antioxidant enzyme activity in melon seedlings. *Turkish Journal of Biology*, 37, 491–498. <http://doi.org/10.3906/biy-1210-55>
- Lakitan, B., Widuri, L. I., & Meihana, M. (2017). Simplifying procedure for a non-destructive, inexpensive, yet accurate trifoliate leaf area estimation in snap bean (*Phaseolus vulgaris*). *Journal of Applied Horticulture*, 19(1), 15–21. Retrieved from https://www.researchgate.net/publication/316600834_Simplifying_procedure_for_a_non-destructive_inexpensive_yet_accurate_trifoliate_leaf_area_estimation_in_snap_bean_Phaseolus_vulgaris
- Lanna, A. C., Mitsuzono, S. T., Terra, T. G. R., Vianello, R. P., & de Figueiredo Carvalho, M. A. (2016). Physiological characterization of common bean (*Phaseolus vulgaris* L.) genotypes, water- stress induced with contrasting response towards drought. *Australian Journal of Crop Science*, 10(1), 1–6. Retrieved from <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/139430/1/CNPAF-2016->

- Li, W., Herrera-Estrella, L., & Tran, L. S. P. (2016). The yin-yang of cytokinin homeostasis and drought acclimation/adaptation. *Trends in Plant Science*, 21(7), 548–550. <http://doi.org/10.1016/j.tplants.2016.05.006>
- Mathobo, R., Marais, D., & Steyn, J. M. (2017). The effect of drought stress on yield, leaf gaseous exchange and chlorophyll fluorescence of dry beans (*Phaseolus vulgaris* L.). *Agricultural Water Management*, 180(Part A), 118–125. <http://doi.org/10.1016/j.agwat.2016.11.005>
- Nassar, R. M. A., Ahmed, Y. M., & Boghdady, M. S. (2010). Botanical studies on *Phaseolus vulgaris* L. I-morphology of vegetative and reproductive growth. *International Journal of Botany*, 6(3), 323–333. <http://doi.org/10.3923/ijb.2010.323.333>
- Nazar, R., Umar, S., Khan, N. A., & Sareer, O. (2015). Salicylic acid supplementation improves photosynthesis and growth in mustard through changes in proline accumulation and ethylene formation under drought stress. *South African Journal of Botany*, 98, 84–94. <http://doi.org/10.1016/j.sajb.2015.02.005>
- Neves, D. M., Almeida, L. A. D. H., Santana-Vieira, D. D. S., Freschi, L., Ferreira, C. F., Soares Filho, W. D. S., ... Gesteira, A. D. S. (2017). Recurrent water deficit causes epigenetic and hormonal changes in citrus plants. *Scientific Reports*, 7(13684), 1–11. <http://doi.org/10.1038/s41598-017-14161-x>
- Olawuyi, O. J., Bello, O. B., Ntube, C. V., & Akanmu, A. O. (2015). Progress from selection of some maize cultivars' response to drought in the derived Savanna of Nigeria. *AGRIVITA Journal of Agricultural Science*, 37(1), 8–17. <http://doi.org/10.17503/Agrivita-2015-37-1-p008-017>
- Pozo, M. J., López-Ráez, J. A., Azcón-Aguilar, C., & García-Garrido, J. M. (2015). Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. *New Phytologist*, 205(4), 1431–1436. <http://doi.org/10.1111/nph.13252>
- Riboldi, L. B., Oliveira, R. F., & Angelocci, L. R. (2016). Leaf turgor pressure in maize plants under water stress. *Australian Journal of Crop Science*, 10(6), 878–886. <http://doi.org/10.21475/ajcs.2016.10.06.p7602>
- Rivas, R., Falcão, H. M., Ribeiro, R. V., Machado, E. C., Pimentel, C., & Santos, M. G. (2016). Drought tolerance in cowpea species is driven by less sensitivity of leaf gas exchange to water deficit and rapid recovery of photosynthesis after rehydration. *South African Journal of Botany*, 103, 101–107. <http://doi.org/10.1016/j.sajb.2015.08.008>
- Rowe, J. H., Topping, J. F., Liu, J., & Lindsey, K. (2016). Absciscic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. *New Phytologist*, 211(1), 225–239. <http://doi.org/10.1111/nph.13882>
- Sankar, B., Gopinathan, P., Karthiashwaran, K., & Somasundaram, R. (2014). Variation in growth of peanut plants under drought stress condition and in combination with paclobutrazol and abscisic acid. *Current Botany*, 5, 14–21. Retrieved from <http://updatepublishing.com/journal/index.php/cb/article/view/2945/2911>
- Sapeta, H., Costa, J. M., Lourenço, T., Maroco, J., van der Linde, P., & Oliveira, M. M. (2013). Drought stress response in *Jatropha curcas*: Growth and physiology. *Environmental and Experimental Botany*, 85, 76–84. <http://doi.org/10.1016/j.envexpbot.2012.08.012>
- Sudrajat, D. J., Siregar, I. Z., Khumaida, N., Siregar, U. J., & Mansur, I. (2015). Adaptability of white jabon (*Anthocephalus cadamba* MIQ.) seedling from 12 populations to drought and waterlogging. *AGRIVITA Journal of Agricultural Science*, 37(2), 130–143. <http://doi.org/10.17503/Agrivita-2015-37-2-p130-143>
- Taiwo, O. J. (2013). Farmers' choice of wetland agriculture: Checking wetland loss and degradation in Lagos State, Nigeria. *GeoJournal*, 78(1), 103–115. <http://doi.org/10.1007/s10708-011-9434-6>
- Tapia, G., Méndez, J., & Inostroza, L. (2016). Different combinations of morpho-physiological traits are responsible for tolerance to drought in wild tomatoes *Solanum chilense* and *Solanum peruvianum*. *Plant Biology*, 18(3), 406–416. <http://doi.org/10.1111/plb.12409>
- Tombesi, S., Nardini, A., Frioni, T., Soccolini, M., Zadra, C., Farinelli, D., ... Palliotti, A. (2015). Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. *Scientific Reports*, 5(12449), 1–12. <http://doi.org/10.1038/srep12449>

- Widuri, L. I., Lakitan, B., Hasmeda, M., Sodikin, E., Wijaya, A., Meihana, M., ... Siaga, E. (2017). Relative leaf expansion rate and other leaf-related indicators for detection of drought stress in chili pepper (*Capsicum annuum* L.). *Australian Journal of Crop Science*, 11(12), 1617–1625. <http://doi.org/10.21475/ajcs.17.11.12.pne800>
- Xiong, D., Yu, T., Ling, X., Fahad, S., Peng, S., Li, Y., & Huang, J. (2015). Sufficient leaf transpiration and nonstructural carbohydrates are beneficial for high-temperature tolerance in three rice (*Oryza sativa*) cultivars and two nitrogen treatments. *Functional Plant Biology*, 42(4), 347–356. <http://doi.org/10.1071/FP14166>
- Zhao, R., Guo, W., Bi, N., Guo, J., Wang, L., Zhao, J., & Zhang, J. (2015). Arbuscular mycorrhizal fungi affect the growth, nutrient uptake and water status of maize (*Zea mays* L.) grown in two types of coal mine spoils under drought stress. *Applied Soil Ecology*, 88, 41–49. <http://doi.org/10.1016/j.apsoil.2014.11.016>