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Growth Dynamics of Young Avocado (*Persea americana* Mill) Plants under Drought Stress in Potted Condition

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Abstract

Drought stress significantly influences plant metabolic processes, including overall vegetative growth and the transition from the vegetative to the generative phase. Under changing environmental conditions, plants adapt through specific mechanisms to survive unfavorable circumstances, including a reduction in the juvenile phase. This study aimed to examine the effects of drought stress on the growth dynamics of young avocado plants. The experiment consisted of three treatment levels: routine watering as the control (P1), drought stress for 8 weeks (P2), and drought stress for 16 weeks (P3). The 8 week drought stress did not significantly reduce the number of leaves or increase the number of vegetative buds; however, one plant produced flowers at week 33. The drought stress for 16 weeks (P3) significantly reduced the number of leaves but did not affect branch length. Instead, it increased the number of vegetative buds per branch at 16 and 24 weeks after treatment (WAT). Drought-stressed plants exhibited a compensatory growth mechanism following rewatering, as demonstrated by an increase in the number of leaves and vegetative buds at 24 WAT.

Keywords: compensatory growth, flower induction, inflorescence, rewatering

Introduction

Avocado is a seasonal fruit with abundant availability during the primary harvest season and limited supply outside of this period. Avocados are typically harvested in West Java between October and February, whereas in North Sumatra, the harvest season occurs from June to August (Lestari et al., 2016). The high demand for avocados necessitates year-round production to meet market needs. However, the long juvenile phase of avocado plants presents a challenge for year-round production, necessitating efforts to synchronize flowering in young avocado trees.

In Indonesia, several avocado varieties have been widely cultivated, including "Wina", "Miki", "Hass", "Jambon", "Pluwang", "Murapi", "Kendil", and "Aligator" (Verti et al., 2021). However, many other avocado cultivars have the potential for large-scale production and further development. One such promising variety is the "Deana" avocado, originating from Gunung Pati, Semarang. This cultivar is particularly valued for its small fruit size (250–300 g), small seed, and vibrant yellow flesh. It is also known for its rich, creamy texture and balanced sweetness, making it highly desirable for both fresh consumption and commercial production. Given its unique characteristics and potential economic value, the "Deana" avocado presents an opportunity for further research on its growth dynamics and flowering induction techniques to enhance its productivity.

Avocado trees aged 1–4 years are classified as young, while those aged 8 years and older are considered mature and fully productive, with a productive lifespan that may extend beyond 20 to 25 years (Dorantes et al., 2004). Grafted avocado plants generally begin flowering at approximately 3-5 years after grafting, whereas seedling plants propagated generatively may take 10–15 years to flower (Bamba and Wall, 2018).

Under changing environmental conditions, plants adapt through specific mechanisms to survive unfavorable circumstances, including a reduction in the juvenile phase. Drought stress has been reported to induce various negative impacts, such as a reduction in photosynthetic rate (Wang et al., 2018), inhibition of vegetative growth (Acosta-Rangel et al.,

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2021) low temperature is known to induce flowering, but effects of other environmental factors remain equivocal. In addition, documentation of interactions among environmental factors, floral gene expression and subsequent flower development is limited. Thus, in this research, the effects of environmental factors on the temporal expression patterns of genes related to flowering time, floral meristem identity and floral organ identity were quantified in buds relative to inflorescence number. 'Hass' avocado trees were subjected to four different environmental conditions: optimal growth condition (OGC, and decreased fruit yield (Mira-García et al., 2023) two irrigation treatments were applied during stage II of fruit growth: control (well irrigated, automatically managed by soil water content sensors. However, under controlled stress conditions, plants can enhance photosynthetic rate (Luo et al., 2016), increase leaf number (Marron et al., 2003), and trigger early flowering due to compensatory growth mechanisms after rewatering (Chen et al., 2023).

Research on the effects of drought stress on flowering induction has been reported in various crops, including several citrus species (Azizah et al., 2022; Thammatha et al., 2021) including pummelo (Citrus grandis and starfruit (Wu et al., 2017). Flowering induced by stress conditions is now recognized as a third type of flowering response, alongside those influenced by low temperature and photoperiod treatments (Takeno, 2016).

Low-temperature treatments have been reported to induce flowering in avocado plants (Acosta-Rangel et al., 2021) low temperature is known to induce flowering, but effects of other environmental factors remain equivocal. In addition, documentation of interactions among environmental factors, floral gene expression and subsequent flower development is limited. Thus, in this research, the effects of environmental factors on the temporal expression patterns of genes related to flowering time, floral meristem identity and floral organ identity were quantified in buds relative to inflorescence number. 'Hass' avocado trees were subjected to four different environmental conditions: optimal growth condition (OGC). However, in tropical regions, drought stress, such as that experienced during the dry season, is commonly associated with the induction of flowering (Fauzi et al., 2017). Drought-induced flowering is a well-documented phenomenon in perennial plants. Despite this, studies on the regulatory mechanisms of drought stress in avocados remain limited, primarily due to the lengthy vegetative growth phase and the extended time required for such research (Chen et al., 2023).

Drought stress significantly influences plant metabolic processes, including overall vegetative growth and the transition from the vegetative to the generative phase. While flowering induction treatments are predominantly applied to mature plants, limited research has been conducted on their effects on younger plants. Plant age, environmental factors, nutrients, and the balance between source and sink influence vegetative and flowering time (Wang et al., 2020; Rankenberg et al., 2021). Plants require sufficient sugar availability to meet the energetic demands of flower and seed development, as these organs act as primary sinks during reproductive growth (Wingler, 2018). This study examines the effects of drought stress on the growth dynamics of 2.5-year-old "Deana" avocado plants. Examining young avocado plants' response to drought stress provides growth dynamics and preliminary insights into the potential flowering induction in young avocado plants.

Materials and Methods

Site Description

The research was conducted at Kebun Tabulampot Wa Reza, Cijeruk, Bogor (6.652° S, 106.800° E) from March to November 2024, at an altitude of 402 meters above sea level. The average temperature was 26°C, with a minimum of 21.9°C and a maximum of 34.3°C. The mean precipitation was 3,953 mm during the experiment period (BMKG, 2024). Laboratory analysis was conducted at the Integrated Laboratory of Bioproduct, National Research and Innovation Agency, and Postharvest and Biomass Laboratory, Department of Agronomy and Horticulture, IPB University.

Experimental Procedures

The planting material used in this study consisted of 2.5-year-old "Deana" grafted avocado plants with an average height of approximately 150-170 cm, stem diameter of 2.5-3 cm, and 90-120 cm canopy size of 90-120 cm. The plants were grown in 150 L planter bags (60 cm × 54 cm) containing a planting medium composed of a mixture of soil, rice husks, manure, and vermicompost in a ratio of 2:1:1:1 (v/v/v/v).

The experiment was conducted using a single-factor Randomized Complete Group Design comprising three treatment levels: routine watering (P1, control), drought stress for 8 weeks (P2), and drought stress for 16 weeks (P3, Figure 1). Each treatment was replicated 10 times, resulting in 30 experimental units. Each experimental unit consisted of a single plant,

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bringing the total number of plants observed to 30.

The moisture content of the planting media was standardized before the treatments were initiated. Water was gradually poured into the planting media until it drained out of the planter bags, and the volume of water applied was recorded to establish a baseline for subsequent watering. Soil moisture levels were monitored using a soil moisture meter (3-in-1 Soil Moisture Tester, B19002), which categorizes moisture levels on a scale of 1–3 (dry), 4–7 (moist), and 8–10 (wet). The routine watering treatment (P1, control) involved maintaining the planting media at field capacity and scale of 8-10 (wet) through regular watering. For the drought stress treatments (P2 and P3), the top of the planting media was covered with plastic to prevent rainwater infiltration. In these treatments, no watering was provided for 8 weeks (March 11 to May 6, 2024), during which the moisture level of the planting media decreased to a scale of 2–3 (dry).

In the P2 treatment, after 8 weeks of drought stress, the planting media were rehydrated to field capacity, and regular watering was resumed until the end of the observation period in week 24 (August 26, 2024). In the P3 treatment, after the planting media reached a scale of 2–3 (dry) at the end of week 8 (May 6, 2024), the plants were rehydrated to field capacity, and the media was subsequently covered with plastic again. Drought stress was reapplied for an additional 8 weeks until week 16 (July 1, 2024). At the end of week 16, when the moisture level of the planting media once again reached a scale of 2–3 (dry), the plants were watered to field capacity and maintained with routine watering until the end of the observation period (August 26, 2024). The illustration of the experiment procedures is presented in Figure 1.

Soil Physical Properties and Plant Growth Measurements

Soil moisture scale

Soil moisture was measured using a soil moisture meter (3 in 1 Soil Moisture Tester, B19002) by inserting the device at three points within each planter bag: the top, middle, and bottom. This device provides a simple and rapid real-time estimation of soil moisture levels, while laboratory-based soil moisture content analysis was also conducted to ensure data accuracy. Measurements were conducted every two days to capture the moisture dynamics while maintaining manageable data collection over the 24 week observation period.

Soil moisture content

Soil samples (10 g) were collected and oven-dried at 105°C for 24 hours. Observations were performed before treatment application, at the end of the drought stress period, and after routine watering was resumed. Soil moisture content was calculated using the following formula:

$$Soil\ moisture\ content\ (\%) = \frac{initial\ soil\ weight - dried\ soil\ weight}{initial\ soil\ weight}\ x\ 100\%$$

Relative water content (RWC)

The relative water content (RWC) of leaves was analyzed using the method described by Kirigwi and Saha (2022). Observations were done by determining leaf samples' fresh weight (FW). The leaves were then immersed in distilled water in a closed container at 22°C for 4 hours to reach full turgidity, after which the turgid weight (TW) was measured. The leaves

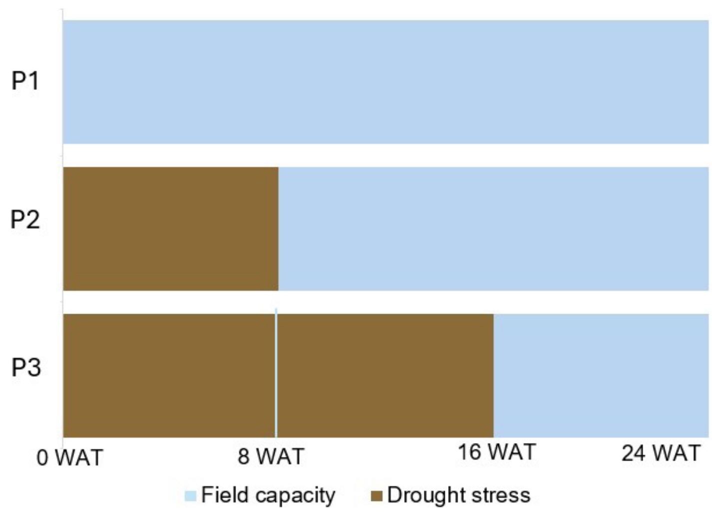

Figure 1. Experimental design and watering treatments in potted young avocado plants under drought stress. WAT: weeks after treatment.

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were oven-dried at 90°C for one hour to determine their dry weight (DW). Observations were conducted before the treatment, at the end of the drought stress period, and after the resumption of routine watering. The RWC was calculated using the formula:

$$RWC\ (\%) = \frac{(FW - DW)}{(TW - DW)}\ x\ 100\%$$

Leaf and soil water potential

Leaf and soil water potentials were measured as described by Rahayu et al., (2020) using a WP4 Dewpoint Potential Meter (Decagon Devices Inc., USA). Healthy, fully developed leaves were sampled for leaf water potential analysis. Soil samples (approximately 10 g) were collected from the root zone and placed in sample cups for measurement. Observations were conducted at the end of the drought stress period and after rewatering.

Chlorophyll analysis

Chlorophyll content in leaves was analyzed following the method described by Yudiansyah et al. (2024). Leaf samples were collected using a 10 mm punch tool and then weighed and homogenized. The homogenized sample was transferred into a 5 mL volumetric flask, and acetone was added to bring the volume to 5 mL. The resulting solution was transferred to a 15 mL centrifuge tube and centrifuged at 6000 rpm for 7 minutes using a Frontier™ 5000 Series Multi-Type FC5705 230V Ohaus centrifuge. The absorbance of the supernatant was measured using a Shimadzu UV-Vis Type 1280 spectrophotometer at wavelengths 470, 537, 647, and 663 nm.

Plant growth parameters, including the number of leaves, branch length, and the number of vegetative buds, were observed at 0, 8, 16, and 24 weeks after the treatment (WAT).

Flowering parameters

Flowering parameters evaluated in this study included the number of flowering plants, the time of first flower emergence, the number of flowers per inflorescence, the total number of flowers, and the inflorescence size.

Data Analysis

The data obtained were analyzed using analysis of variance (ANOVA) at the 5% significance level. Results showing significant differences were further analyzed using Duncan's Multiple Range Test (DMRT) at the 5% level, and statistical analysis was performed using SAS Studio.

Results and Discussion

Soil Moisture Scale

The planting media in the control treatment (no drought stress) was maintained at a moisture scale of 8–10 through regular watering. In contrast, the drought stress treatments (P2 and P3) gradually decreased moisture content, reaching nearly a scale 3 at 8 WAT, indicating that the planting media was almost dry (Figure 2). At 8 weeks, the P2 and P3 treatments showed average moisture scale values of 3.50 and 3.70, respectively. The planting media in the P2 treatment returned to moist conditions after routine watering was resumed, with moisture scale values ranging from 8 to 9. In contrast, the planting media in the P3 treatment continued to experience reduced moisture due to the ongoing drought stress until 16 WAT. At 16 WAT, the average moisture scale value of the planting media in the P3 treatment was 3.50.

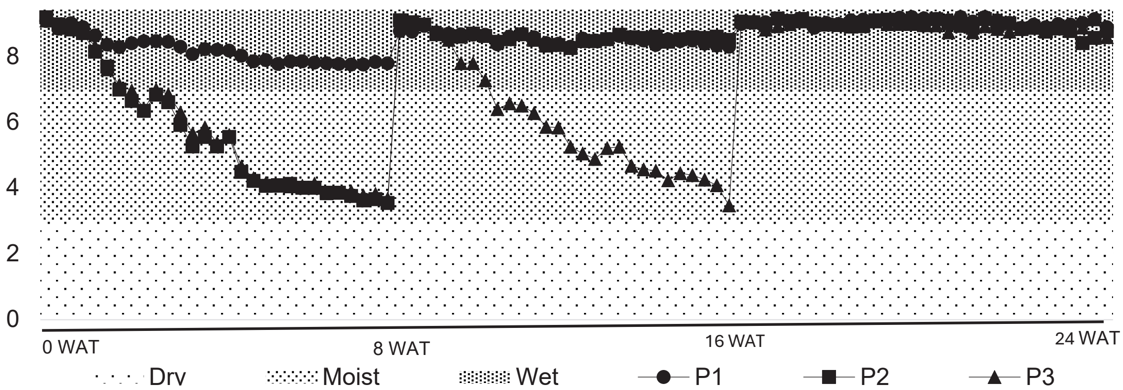

Figure 2. Soil moisture scale

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Soil Moisture Content

Observations indicated that at the beginning of the experiment, the soil moisture was uniform at field capacity, ranging from 32.02% to 32.89% (Table 1). After 8 weeks of drought stress, the soil moisture content in the P2 and P3 treatments decreased significantly by 54.40% and 55.30%, respectively, compared to the control. After 16 weeks of drought stress, the moisture content of the P3 planting media was reduced by 67.40% compared to the control. However, the moisture content of the planting media returned to field capacity at 16 WAT and 24 WAT, as indicated by the absence of significant differences between treatments after the plants were rewatered.

Relative Water Content

Before the treatment, the leaves' relative water content (RWC) was over 90%, indicating that the leaves were in a turgid state. After 8 weeks of drought stress, the RWC of the leaves decreased to 86.90% and 85.74% in the P2 and P3 treatments, respectively (Table 2). In the P2 treatment, RWC increased at 16 WAT due to the resumption of regular watering. In contrast, the RWC of P3 plants significantly decreased by 28.83% compared to the control plants at 16 WAT. Plants typically exhibit wilting when relative water content (RWC) values drop to approximately 60% (Mndela et al., 2023). After rewatering, all treatments showed improved relative water content values.

Leaf and Soil Water Potential

Drought stress treatments significantly reduced leaf and soil water potential, although no significant difference was observed between the 8 week and 16 week stress treatments (Table 3). Under drought stress conditions, plants regulate osmotic potential to survive by reducing water uptake, decreasing intracellular water content, and reducing cell volume while increasing cell solute content. These mechanisms lower the free energy of water within the cell, maintain the water potential gradient between the inside and outside, and enable the cell to absorb water under conditions of lower external water potential (Yang et al., 2021).

Soil water potential must be higher than cell water potential for water absorption. Table 3 indicates that soil water potential was lower under drought stress than leaf water potential, making it difficult for plants to absorb water. This limitation adversely affects various growth and physiological processes in plants. A study

Table 1. Soil moisture content under drought stress treatments

Treatment	Soil moisture content (%)			
	0 WAT	8 WAT	16 WAT	24 WAT
Routine watering (P1)	32.24	33.26a	33.99a	34.74
8 weeks of drought stress (P2)	32.02	15.15b	34.83a	35.04
16 weeks of drought stress (P3)	32.89	14.88b	11.07b	33.06

Note: values followed by different letters in the same column are significantly different in the DMRT test at α=0.05.

Table 2. Relative water content in avocado leaves

Treatment	Relative water content (%)			
	0 WAT	8 WAT	16 WAT	24 WAT
Routine watering (P1)	94.27	94.97a	93.89a	92.91
8 weeks of drought stress (P2)	95.68	86.90b	91.20a	91.85
16 weeks of drought stress (P3)	93.52	85.74b	66.82b	93.34

Note: values followed by different letters in the same column are significantly different in the DMRT test at α=0.05.

Table 3. Leaf and soil water potential under drought stress treatments

Treatment	Leaf water potential (MPa)	Soil water potential (MPa)
Routine watering (P1)	-2.60a	-0.09a
8 weeks of drought stress (P2)	-3.06b	-16.95b
16 weeks of drought stress (P3)	-3.25b	-19.09b

Note: values followed by different letters in the same column are significantly different in the DMRT test at α=0.05. Data were measured at the end of each drought period: P1 (routine watering, week 16), P2 (8 week drought, week 8), and P3 (16 week drought, week 16).

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by Rahayu et al. (2020) reported that drought stress for 72 days in 'Madura' orange plants resulted in a soil water potential of -18.32 MPa, causing severe drought stress symptoms and inhibiting flowering induction.

At the beginning of the experiment, all treatments exhibited a uniform number of leaves per branch. After 8 weeks of drought stress, there was no significant difference in the number of leaves among treatments, although a trend toward a reduction in leaf number was observed (Table 4). After 16 weeks of drought stress, the number of leaves decreased significantly, showing a 58.85% reduction compared to the control.

Under drought stress, plant roots receive environmental signals that trigger the synthesis of abscisic acid (ABA). These signals are transmitted to other tissues, prompting physiological responses to reduce water loss, such as stomatal closure, nutrient translocation from older to younger leaves, and leaf shedding (Chen et al., 2015; Yang et al., 2021). After rewatering, no significant differences were observed between treatments, suggesting that the leaves shed during the stress period were replaced. Notably, P3 exhibited a strong vegetative regrowth with leaf numbers increasing from 8.93 at 16 WAT to 27.35 at 24 WAT. While the difference was not statistically significant, P3 consistently showed a tendency toward higher leaf numbers compared to other treatments at 24 WAT.

The branch length showed no significant differences at any treatment level or observation time. However, there was a noticeable trend of increased branch length in the avocado plants subjected to regular watering after 8 and 16 weeks of drought stress, compared to the control plants, which exhibited stagnant branch growth throughout the observation periods (Table 5).

Drought stress for 8 weeks showed no significant difference in the number of vegetative buds compared to the control. In contrast, prolonged and repeated drought stress for 16 weeks significantly increased vegetative bud formation at 16 and 24 WAT (Table 6). This substantial growth can be attributed to a mechanism known as compensatory growth, which refers to the ability of plants to accumulate biomass through rapid growth once water becomes available again, compensating for the biomass loss caused by drought stress (Wang et al., 2020).

Table 4. The number of avocado leaves under drought stress treatments

Treatment	Number of leaves			
	0 WAT	8 WAT	16 WAT	24 WAT
Routine watering (P1)	20.10	21.05	21.70a	20.92
8 weeks of drought stress (P2)	21.13	17.58	24.55a	22.54
16 weeks of drought stress (P3)	21.28	18.50	8.93b	27.35

Note: values followed by different letters in the same column are significantly different in the DMRT test at α=0.05.

Table 5. Avocado branch length under drought stress treatments

Treatments	Branch length (cm)			
	0 WAT	8 WAT	16 WAT	24 WAT
Routine watering (P1)	34.76	35.98	38.28	41.38
8 weeks of drought stress (P2)	31.70	32.05	37.09	40.54
16 weeks of drought stress (P3)	33.40	33.70	34.33	39.23

Note: values followed by different letters in the same column are significantly different in the DMRT at α=0.05.

Table 6. The number of avocado vegetative buds number under drought stress treatments

Treatments	Number of vegetative buds			
	0 WAT	8 WAT	16 WAT	24 WAT
Routine watering (P1)	1.75	1.95	2.33b	2.13b
8 weeks of drought stress (P2)	2.00	2.03	3.30b	3.26b
16 weeks of drought stress (P3)	1.98	1.98	8.03a	5.73a

Note: values followed by different letters in the same column are significantly different in the DMRT at α=0.05.

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In cotton, Niu et al. (2018) reported that after rewatering, the levels of abscisic acid (ABA) and gibberellic acid (GA) in the roots decreased, which promoted root growth and repaired the damage caused by drought stress, thereby contributing to compensatory growth. Additionally, when drought-stressed plants are rewatered, their photosynthetic rate can match or even exceed that of non-stressed plants (Luo et al., 2016). This phenomenon likely explains why drought-stressed plants showed a similar number of leaves and branch lengths compared to the control but a greater number of buds after the rewatering period. The number of vegetative buds in P3 slightly decreased at 24 WAT (5.73 buds) compared to 16 WAT (8.03 buds), possibly due to a small portion of vegetative buds observed at 16 WAT failing to develop into shoots by 24 WAT (Table 6).

Leaf Pigment Analysis

The plant's response to drought stress is also reflected in physiological changes, such as alterations in leaf chlorophyll content. The results showed that drought stress significantly reduced chlorophyll levels in avocado leaves compared to the control. However, no significant difference was observed between the 8 week and 16 week stress treatments (Table 7).

Chlorophyll synthesis is strongly influenced by water availability. Drought stress reduces chlorophyll synthesis and chlorophyll degradation, leading to the yellowing of the leaves (Khodabin et al., 2020). The decrease in total chlorophyll under drought conditions is associated with the production of reactive oxygen species (ROS), which can degrade chloroplasts and reduce the efficiency of chlorophyll a and b in capturing light (Mafakheri et al., 2010; Qiao et al., 2024).

Flowering Response of Young Avocado Plants

One out of 10 plants subjected to 8 weeks of drought stress (P2) began to flower in the 33rd week of observation. In contrast, no flowering was observed in either 16 weeks of repeated drought stress (P3) or the control treatment with routine watering (P1). The absence of flowering in P3 may be attributed to the repeated drought stress cycles, where periods of stress were alternated with rewatering. This intermittent stress likely stimulated vegetative recovery rather than floral induction, as evidenced by the increased number of vegetative buds, as previously described. The compensatory growth observed after rewatering in P3 (Table 4 and Table 6) suggests that plants prioritized vegetative recovery over reproductive development. As shown in Table 8, a plant treated with 8 weeks of drought stress produced 19 inflorescences, totaling 509 flowers, with an average of 26.78 flowers per inflorescence. These results may have the potential for developing drought stress treatments to accelerate flowering in potted young avocado plants.

Adult avocado plants can produce thousands of inflorescences, each consisting of 100-500 flowers, and can generate millions of flowers in total (Hapuarachchi et al., 2022). However, the plants used in this study were still young and transitioning from the vegetative to the generative phase. This likely explains the low flowering response to the drought stress treatment, which has not yet reached the optimal productivity levels of mature avocado plants.

Table 7. Chlorophyll content under drought stress

Treatments	Chlorophyll a ($mg.g^{-1}$)	Chlorophyll b ($mg.g^{-1}$)	Total chlorophyll ($mg.g^{-1}$)
Routine watering (P1)	1.88 a	0.68a	2.56a
8 weeks of drought stress (P2)	1.16 b	0.42b	1.58b
16 weeks of drought stress (P3)	1.04 b	0.37b	1.42b

Note: values followed by different letters in the same column are significantly different in the DMRT test at α=0.05. Data were measured at the end of each drought period: P1 (routine watering, week 16), P2 (8 week drought, week 8), and P3 (16 week drought, week 16).

Table 8. Young avocado flowering under drought stress

Treatments	NF	TF (WAT)	NI	NFI	NFP
Routine watering (P1)	0/10	0	0	0.00	0
8 weeks of drought stress (P2)	1/10	33	19	26.78	509
16 weeks of drought stress (P3)	0/10	0	0	0.00	0

Note: NF: Number of flowering plants per total plants, FT: Time of first flower appearance, NI: Number of inflorescences, NFI: Number of flowers per inflorescence, NFP: Number of flowers. Data were recorded until week 37 (December 1, 2024), when all shoots in all observed plants had fully developed and no flowering responses were observed.

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Moreover, rainfall during the experiment period was high, reaching 3,953 mm from March to November, whereas the optimal annual rainfall for avocado cultivation ranges between 1,500 and 3,000 mm (Putri et al., 2016). Excessive rain during the flowering period may have further contributed to the reduced flower production. Further water stress experiments should be conducted outside the heavy rain season to enhance the reliability of stress induction and promote favorable physiological responses.

Conclusions

The 8 week drought stress did not significantly reduce the number of leaves, branch length, or the number of vegetative buds; however, flowering was observed in one out of ten plants. The 16 week drought stress significantly reduced the number of leaves but increased the number of vegetative buds at 16 and 24 weeks after treatment, but no flowers were produced. Upon the resumption of regular irrigation, the plants demonstrated compensatory growth mechanisms.

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