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Water Relations, Stomatal Responses and Physiological Changes of *Lansium domesticum*

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ABSTRAK

Pengaruh tegasan air terhadap pertumbuhan, kaitan air dan perubahan fisiologi pokok Lansium domesticum *muda telah dikaji. Terdapat pengurangan yang signifikan terhadap jisim kering daun, batang dan akar apabila berlaku tegasan air. Kandungan air relatif telah didapati menurun tetapi densiti stomata dan kandungan klorofil meningkat dengan tegasan air. Peningkatan densiti stomata walaubagaimanapun tidak memperbaiki respons stomata oleh kerana rintangan stomata didapati meningkat apabila berlaku tegasan air. Peningkatan rintangan stomata menyebabkan pengurangan kadar fotosintesis. Rintangan stomata bagi pokok yang diberi tegasan yang ketara tidak pulih ke nilai yang sama dengan pokok yang diberi pengairan berterusan selepas air dibekalkan semula. Rintangan stomata juga didapati rendah pada jenis langsat dibandingkan dengan dokong menunjukkan langsat mempunyai mekanisma kawalan stomata yang baik sewaktu tegasan air.*

ABSTRACT

The effects of water stress on growth, water relations and physiological changes of young Lansium domesticum *plants were investigated. There was a significant reduction in leaf, stem and root dry weight with increasing water stress. Relative water content was reduced but stomatal density and chlorophyll content were increased with water stress. An increase in stomatal density of plants subjected to water stress did not improve stomatal functioning as stomatal resistance was greater in these plants. This contributed to the reduction in leaf photosynthesis rate. Stomatal resistance of severely stressed plants did not reach a similar level as plants watered continuously after rewatering. Stomatal resistance of langsat was lower than dokong plants indicating that langsat exhibited a better stomatal control than dokong plants.*

Keywords: ***Lansium domesticum*, growth, relative water content, stomatal resistance, stomatal density, photosynthesis rate**

INTRODUCTION

Lansium domesticum Jack is native to the Malay Peninsula, the Philippines and Java where it is widely distributed and grown. The plant is classified under the order Meliales in the Family Meliaceae. The tree has been well described (Ochse *et al.* 1961; Bamroongrungsa and Yaacob 1990). There are three different types of *Lansium* which are commonly grown in Malaysia, namely langsat, duku and dokong (subtype of duku-langsat). In Malaysia, there is an increasing interest among government agencies and the private sector in large-scale production of duku and dokong especially. Although *Lansium* only contributes 0.1% of export value for tropical fruits in Malaysia, there is a tendency for production to rise in the future due to increasing demand from local and international markets. (Malaysian Fruit Industry Directory 1989/1990). Data on the cultivated area of dokong in Peninsula Malaysia (Table 1) show that the crop has yet to be exploited. Further information on agroclimatic requirements needs to be gathered.

Loam or sandy soil with sufficient organic matter content, good but moist drainage, is suitable for growing the crop. It has been estimated that 150-200 days of rain per annum are required for the crop (Bamroongrungsa and Yaacob 1990). There is no physiological basis for this recommendation. In most crops, favourable microclimatic conditions from the nursery phase to establishment in the field are vital for growth and plant development. It is generally acknowledged that water is of utmost importance to sustain a high percentage of survival at transplanting. It is a well-known fact that water deficiency will affect plant growth and development. There is a lack of information on the impact of water availability on growth and other plant processes in *Lansium*. These studies have been conducted to understand the physiological processes of *Lansium* plants in response to water stress. A comparative study on the stomatal resistance of dokong and langsat was also conducted.

TABLE 1
Cultivated area of *Lansium domesticum*

Lansium type	Area (ha)
Dokong	186
Langsat	2803
Duku	68

Source: Ministry of Agriculture Malaysia (1988)

MATERIALS AND METHODS

The experiments were conducted in the Greenhouse Unit, Faculty of Agriculture, Universiti Pertanian Malaysia, Serdang, Selangor. The mean daily air temperature ranged between 24.6°C and 33.6°C. The relative humidity ranged between 42% to 78% RH. The plants were grown in pots containing 17 kg mixture of top soil: organic matter: sand in the ratio 3:2:1.

A cyclical water stress was imposed on five-month-old dokong plants for 3, 6, 12 and 24 days. After each drying cycle was completed, plants were watered to field capacity. Soil was maintained at the field capacity for the control plants (by gravimetric method). The experiment was conducted in a completely randomized design with 4 replicates, 2 plants assigned for each replicate.

In another experiment, the stomatal response during recovery phase was determined. Plants were stressed by withholding water for 6 and 24 days and then rewatered. Five plants were used for each of the treatments in this study. Variations in air temperature, vapour pressure deficit (VPD) and intercepted radiation were monitored when the measurements of stomatal resistance were made. Another set of dokong and langsat plants consisting of 10 plants each were planted in pots containing the same soil mixture of 3:2:1, as mentioned above. These plants were used to compare the stomatal response when exposed to water stress. Five plants from each group were stressed for 6 and 24 days, and another five plants were watered to field capacity.

For vegetative growth measurements, stem diameter (7 cm from the base) was recorded using a Vernier caliper. Plant height was recorded fortnightly and the data presented as the cumulative increment of height. Leaf area index (LAI) was recorded using a plant canopy analyser (Model LAI-2000 LiCor, Nebraska, USA) at intervals of two weeks. Leaf area was determined using a leaf area meter (Delta-T Cambridge, UK) at final harvest. Root volume was recorded by the displacement method. Dry weight of leaf, stem and root was determined at final harvest, i.e. 68 days after commencement of the treatments. Plant tissues were oven-dried at 105°C for 16 hours.

Relative water content was determined according to the method by Weatherley (1950). Ten leaf discs of 10 cm^2 from each replicate were weighed for fresh weight and floated on distilled water for 14 hours to determine their turgid weight. Leaf discs were oven-dried for 6 hours at 85°C for dry weight determination. Relative water content was calculated from the following equation:

$$\text{Relative water content (RWC)} = \frac{\text{Fresh wt - Dry wt}}{\text{Turgid wt - Dry wt}} \times 100$$

Ten leaf discs were also sampled for chlorophyll determination. Chlorophyll was extracted using 95% ethanol, and the determination was done according to the procedure by Nose (1987).

Stomatal density was recorded using the methods described by Stoddard (1965). Nail varnish was used to obtain imprints from the abaxial surface of leaves. The calculation of stomatal density was done from the nail varnish peels which were placed on a haemocytometer slide and viewed through a compound microscope (Model Leitz SM-LUX).

Leaf photosynthesis rate, stomatal conductance and internal CO_2 concentration were recorded using an infrared gas analyser (LCA2- ADC Hoddesdon, UK). The above measurements were determined when plants were 48 days into the treatments. For diurnal determinations of stomatal resistance, a transit time porometer (MK-3 Delta -T Devices, UK) was used. In one of the studies, the changes in stomatal resistance were followed in sequence with the cumulative radiant energy recorded by a solarimeter attached to a microvolt integrator. Measurements were made at two-hour intervals.

RESULTS

Stem Diameter and Plant Height Increment

There was a significant reduction (P<0.05) in stem diameter after the plants had been exposed to a cyclical stress regime of more than 6 days (*Fig. 1* and Table 2). After 12 and 24 days of cyclical stress, stem diameter of stressed plants was 50% and 70% lower respectively, compared to the non-stressed plants in the control and to plants subjected to 3 days of water stress (Table 2).

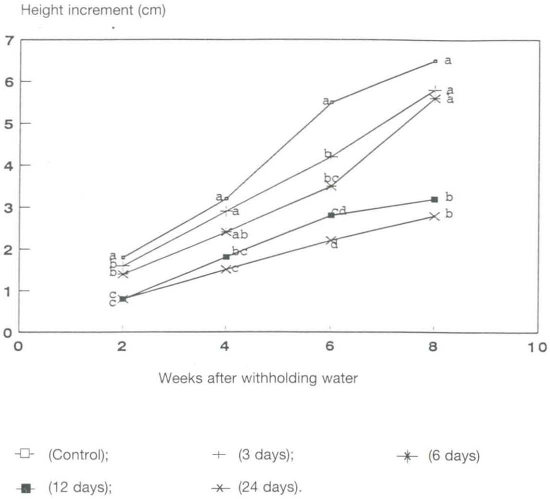


Fig. 1. Height increment as influenced by duration of water stress.

TABLE 2
Effects of water stress on leaf area, stem diameter, leaf elongation and root volume

Treatment (day)	Leaf area (cm^2)	Stem diameter (cm)	Leaf elongation (cm)	Root volume (cm^3)
Control	2111.0a	0.47a	18.73a	33.5a
3	1870.0b	0.39ab	18.20b	32.5a
6	1276.0c	0.37b	15.97c	25.5b
12	937.5d	0.27c	12.97d	18.5c
24	430.0e	0.09d	10.70e	13.0c

Mean separation by DMRT at 5% level

Leaf Area, Leaf Elongation and Root Volume

Leaf growth reduced significantly (P<0.05) with increasing water stress. There was a 11%, 40%, 55% and 80% reduction in leaf area with increasing stress for 3, 6, 12 and 24 days respectively. Similar reductions were observed in leaf elongation. Leaf elongation rate for control plants averaged 0.26 cm/day compared to only 0.14 cm/day for plants that were subject to cyclical stress for 24 days. Root volume also decreased with water stress after more than 3 days (Table 2).

LAI, Leaf, Stem and Root Dry Weight

Fig. 2 illustrates the dry weight of leaf, stem and root at final harvest. There was a significant reduction in leaf dry weight which related well with the decrease in leaf area as shown in Table 2. Root dry weight also decreased at higher water stress. There was a larger decline in leaf growth than root growth. Stem dry weight only affected plants undergoing cyclical water stress for more than 6 days. The results clearly demonstrated that LAI was significantly smaller at cyclical water stress after more than 3 days. The reduction in leaf size and the promotion of abscission of the leaves contributed to the lower LAI of stressed plants after the sixth week *(Fig. 3)*.

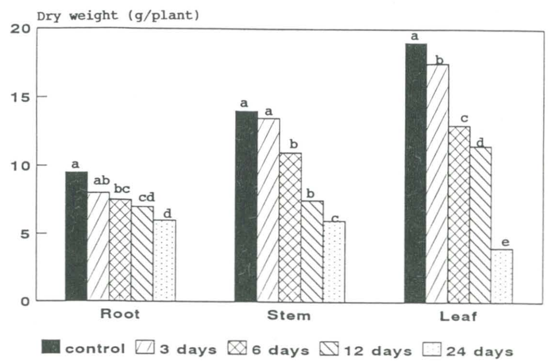


Fig. 2. Dry weight of root, stem and leaf as influenced by duration of water stress.

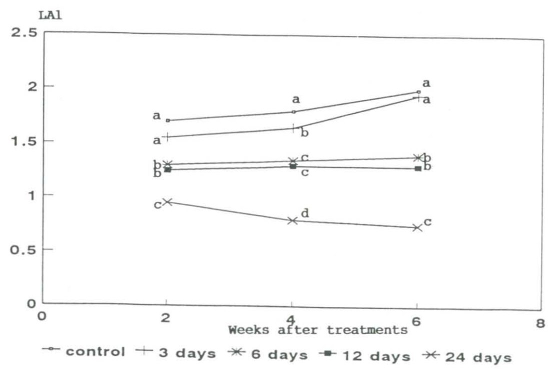


Fig. 3. Leaf area index as influenced by duration of water stress.

Relative Water Content, Stomatal Density, Stomatal Resistance, Chlorophyll Content and Photosynthesis Rate

Relative water content decreased with increasing water stress. At 12 and 24 days of water stress, relative water content was reduced by 8 and 30%, indicating a water deficiency in the leaves. Other stress treatments gave smaller decreases. The results also showed that stomatal density and chlorophyll content per unit area significantly increased with water stress. Increase in stomatal number, however, did not improve stomatal response as its resistance was greater than non-stressed controls in plants. This resulted in a significant fall ($P<0.05$) in photosynthesis rate to 2.05, 1.88 and 0.71 μmol $CO_2/m^2/s$ at 6, 12 and 24 days, respectively (Table 3).

TABLE 3

Stomatal density (sd), diffusive resistance (dr), photosynthesis rate (Pr), chlorophyll content (Chl) and relative water content (RWC) as influenced by water availability.

Treatment	sd Unit/ mm^2	dr $s\ cm^{-1}$	Pn (μmol/ m^2/s)	Chl (mg/ cm^2)	RWC (%)
Control	160b	1.86a	6.07a	3.31c	80.8a
3	173b	1.31a	–	3.35c	77.1ab
6	204a	7.69b	2.05b	3.60b	73.7ab
12	204a	13.50c	1.88b	3.64a	72.3b
24	218a	13.7c	0.71c	3.80a	50.9c

Fig. 4 shows the stomatal response to rewatering. In general, stomatal resistance of severely stressed plants did not revert to the control values when water was made available. For moderately stressed plants, the stomatal response indicates a recovery from water stress. The changes in the plant microclimatic variables such as air temperature and VPD may have prevented the resistance to attain values similar to those in the control since the measurements were not carried out under the controlled environment. As shown in *Fig. 5*, there were large variations in temperature, radiation and VPD in the greenhouse throughout the day.

The changes in stomatal resistance with cumulative radiant energy are illustrated in *Fig. 6*. Apart from the closure at late evening of all the leaves in the present experiment, the results showed that plants that were stressed for 12 and 24 days showed a midday stomatal closure approaching 17.2 and 32 sec cm^{-1} respectively. This could be attributed to the high VPD in the plant canopy.

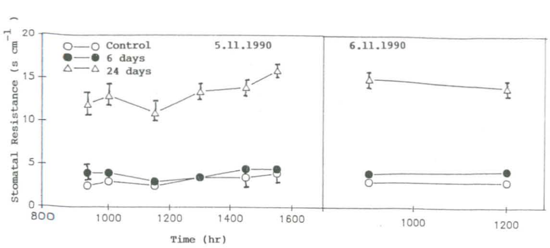


Fig. 4. Response of stomata upon rewatering. Arrows show plants were rewatered. The plants were exposed to one cycle of stress of 6 and 24 days.

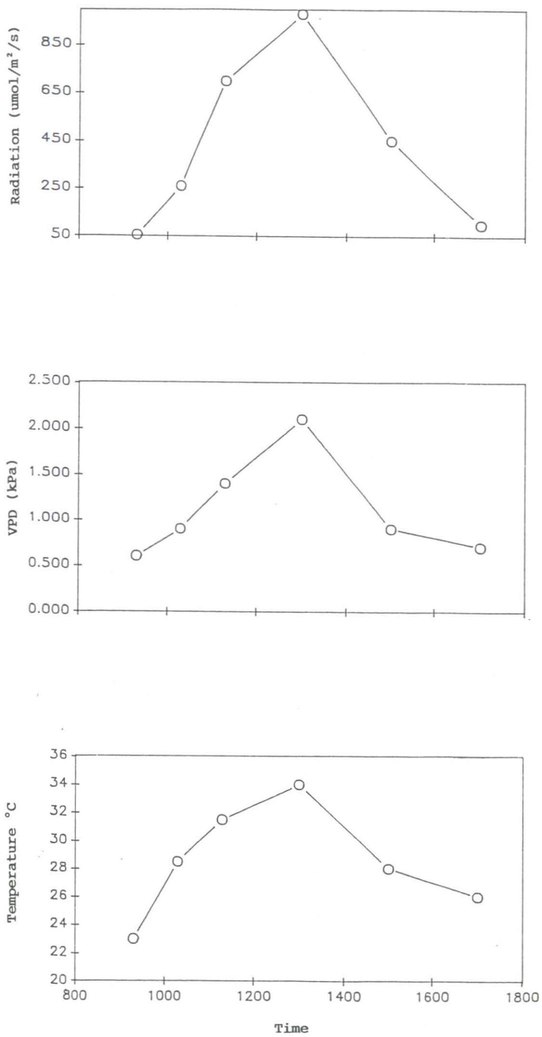


Fig. 5. Variation in air temperature, radiation and vapour pressure deficit (VPD) in the greenhouse

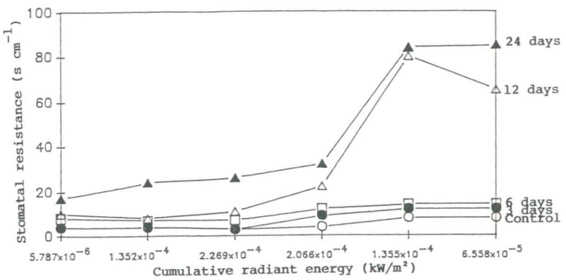
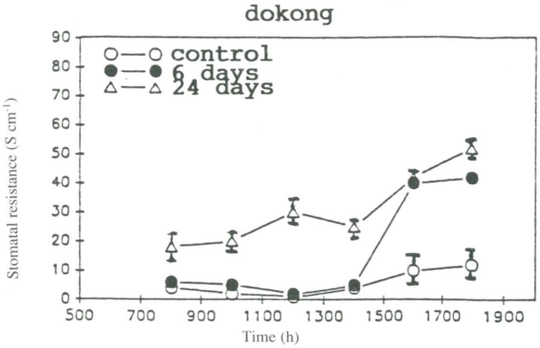


Fig. 6. Changes of stomatal resistance with cumulative radiant energy. The radiant energy values were obtained from the cumulative recorded throughout the day. The time of day is shown in brackets at the respective value for cumulative radiant energy.

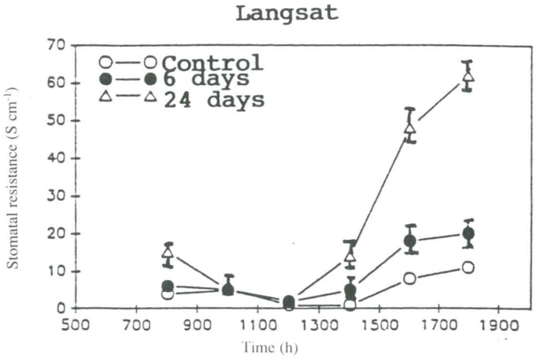
A comparative study on stomatal resistance between dokong and langsat showed a significant difference between the two types of *Lansium*. It is clearly demonstrated that stomatal resistance was lower in langsat than in dokong when plants were exposed to water stress at midday determinations. No significant differences were recorded for the early morning and late afternoon measurements of stomatal resistance between dokong and langsat. This could be due to the influence of radiation. Stomatal resistance was significantly higher ($P<0.05$) at severe water stress throughout the day on both langsat and dokong plants *(Fig. 7)*.

DISCUSSION

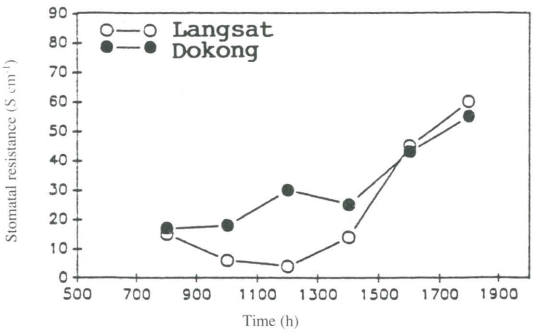
The present study shows that plant vegetative growth was sensitive to water availability. A small depletion in water content in the leaves as a result of the reduced water availability significantly decreased leaf growth. The reduction in leaf growth has been attributed to a disruption in cell expansion and elongation (Acevedo *et al.* 1971; Hsiao 1973; Bradford and Hsiao 1982). The smaller leaf area as well as reduced leaf photosynthesis per unit leaf area may have contributed to the lower accumulation in dry weight of leaves. The fall in LAI *(Fig. 3)* associated with water stress would indicate that there was a reduction in the radiation interception by the leaves, which could have resulted in the lower accumulation of dry weight by plants. Masri and Boote (1988) reported that LAI of maize and soyabean decreased with drought which caused a similar reduction in the accumulation of dry weight by plants. The other possible reason contributing to the lower LAI is that more leaves are shed under water stress. The inhibition of shoot development under water stress was also reported by Levy *et al*. (1978).



(A)



(B)



(C)

Fig. 7. Comparative data on stomatal resistance of two types of Lansium domesticum, *dokong and langsat. a = dokong, b = langsat, c = comparison of stomatal resistance at severe water stress.*

The effects of water stress on root growth *(Fig. 2)* were not as obvious as they were on the leaves and shoots; hence the observed increase in root: shoot ratio when water stress increased. Water stress which induces the adpative mechanism in plants has been reported elsewhere (Kramer 1983; Reid *et al.* 1991). The smaller root volume associated with water stress is also consistent with the results obtained by Raja and Bisnoi (1990).

Relative water content, stomatal response and photosynthesis rate are closely related in affecting growth (Table 3). Bennet *et al.* (1984) reported that stomatal closure of peanut occurred when water potential reduced to -1.6 MPa and relative water content reduced to 86%. The closure of stomata resulting in the inhibition of photosynthesis has been reported by other workers (Bunce 1978; Harder *et al.* 1982; Bradford and Hsiao 1987; Ismail and Awang 1992).

The results also demonstrate that a higher stomatal number in dokong leaves is not essential during periods of water stress. Although stomatal number in stressed plants increased relatively to those in the control plants, resistance was high, indicating that most of the stomata were fully or partially closed and that gas exchange in the leaves may have been inhibited. Manning *et al.* (1977) reported similar increases in stomatal number under water stress and suggested that higher stomatal resistance was associated with the reduced leaf size with stressed leaves. Stomatal closure at midday in plants that were stressed for 24 days could have limited water loss, and allowed the plants to continue growing for several days even when water was not made available.

A comparison of the changes of stomatal resistance between dokong and langsat *(Fig. 7)* revealed higher stomatal resistance in dokong leaves particularly at midday. This could be associated with avoidance mechanism in plants to water deficiency. Langsat, however, exhibits better stomatal control when subjected to water stress. Hence, a higher photosynthesis rate could be expected with langsat than dokong under severe water stress. Details of the osmoregulation in both types of *Lansium* need to be investigated to ascertain the nature of their drought-tolerance mechanisms.

CONCLUSION

Our studies reveal that reduced water availability inhibited growth and physiological processes of 5-month-old *Lansium* plants. The inhibitions are associated with the reduction in plant water status caused by the depletion of soil water. Recovery of stomatal response was influenced by the intensity of water stress; under severe water stress, stomata remained closed although water was available. The study demonstrates that langsat exhibited better stomatal response under water stress than dokong.

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