J. Trop. Agric. and Fd. Sc. 34(1)(2006): 27–36

Effects of root restriction on growth, flowering and water uptake of starfruit

(Kesan pembatasan akar terhadap tumbesaran, pembungaan dan pengambilan air belimbing besi)

M. Zainudin*

Key words: root restriction, growth, flowering, sap flow velocity, starfruit (*Averrhoa carambola* L.)

Abstract

Starfruit plants cv. B17 were subjected to four different container sizes namely 3, 6, 12 and 24 litres to determine the effects of root restriction on growth, flowering and water uptake. The experiment was carried out using randomised complete block design with three replications. Each experimental unit consisted of three plants. At the sixth month, a sensor was installed into the plant stem of each treatment for three consecutive weeks to measure the sap flow. The entire experiment was carried out under a glasshouse for eight months. Irrigation and fertilization were given accordingly to schedule.

The growth was linearly increased with container volumes suggesting that plant growth was retarded under root restricted conditions. Similar trend response was observed in dry matter percentage distribution. However, root dry matter percentage (DRMP) did not follow the same manner whereby DRMP increased by 38% in 3- or 6-litre compared to 26.5% in 24-litre containers. The 'day to flowering' was 60 days earlier with respect to decrease in similar container volume. But, sap flow velocity reduced from 22.3 to 9.5 cm/h and leaf water potential increased from –1.2 to 2.2 MPa when container volume reduced by eight folds. The physiological changes of the plant were due to the root restriction resulting from different container sizes.

Introduction

Plants growing in adversely confined container or soil volumes will change their plant growth, physiology, water and nutrient uptake. Reduced soil volumes influence water availability of the plants, which in turn induces stress (Van Iersel 1997). Water uptake via sap flow studies carried out by Gavloski et al. (1992) showed that plant stress in maize due to restricted watering of the root system reduces water uptake from root to shoot. Restricting half of the root system in sectional root boxes resulted in decreased stem sap flow. Branch sap flow and leaf water potential in pecan has been shown to have a linear relationship (Steinberg et al. 1990). In another study, Lightbody et al. (1994) showed that lateral root sap flow exhibits a similar sap flow pattern to the stems.

Root restriction has been related to induce flowering in temperate tree fruit crops such as apple and peach (Bukovac 1984; Williamson and Coston 1990), and in

*Horticulture Research Centre, MARDI Headquarters, Serdang, P.O. Box 12301, 50774 Kuala Lumpur, Malaysia
Author's full name: Zainudin Haji Meon
E-mail: zmeon@mardi.my

tropical fruits such as mango and starfruit (Ghani and Malik 1993; Ismail and Mohd Noor 1996). Induction of flowering in apple was suggested due to low nutrient and moisture levels (Bukovac 1984) but the exact effect of internal stress of root restriction on flowering remain unknown.

Quantification of water uptake passing through the stems of individual plants was pioneered by Bloodworth et al. (1955) and further developed by Baker and Van Bavel (1987) and later by others (Heilman and Ham 1990; Steinberg et al. 1990; Gavloski et al. 1992). Measurements of sap flow in the xylem of plants were based on a heat pulse technique. This technique involves measuring the time required for a discrete heat input to travel from its source to a sensor further up the stem. Recent work used this technique in kiwifruit (Green and Clothier 1995) and mango (Lu and Chacko 1998).

The aim of this study was to determine the effects of root restriction on growth and flowering of starfruit.

Materials and methods

A total of 36 grafted starfruit plants cv. B17 were planted in four container volumes of 3, 6, 12 and 24 litres. The study was carried out in a glasshouse at MARDI, Serdang on 24 September 1997 for eight months. The experiment was conducted in a completely randomised block design with three replications and each experimental plot contained three plants. The experimental plants were watered at 1,000 ml per plant daily and fertilised as scheduled. A hand-held automatic pressure transducer tensiometer was used to monitor soil moisture regimes at every second day at depths of 15 and 30 cm in the pots. Rewatering commenced whenever soil water potential dropped below –0.5 MPa.

Leaf water potential was measured with a pressure bomb of Scholander type using two or three abaxial leaf surfaces of new and fully expanded leaves. The leaf petiole was cut with a sharp razor and quickly inserted through a small hole of the chamber with a cut-end of the petiole protruding from the hole. The hole was sealed airtight with modelling clay (Blutack). The pressure was then increased at a constant rate using compressed gas until the sap from the xylem oozed out of the petiole. It was recorded and assumed to be equal to the leaf water potential. The measurements were made between 1100–1300 h.

Plants were harvested at eighth month and fresh leaves, roots and stems were separated. The shoots were then oven-dried at 60 °C for 72 h and total shoot dry weight was calculated for biomass. Root size was categorised into two sections: i) root diameter less than 10 mm, and ii) root diameter less than 2 mm. Root density was obtained by dividing total root dry weight by container volume (mg/cm). Soil moisture content was determined by gravimetric method and soil bulk density of the potting media was obtained from every treatment before harvest according to methods by Brady (1974).

Flowering

Flowering and flower intensity were recorded, including the number of plants which flowered on different dates in each treatment. This value was converted to the percentage of flowers based on the total number of plants. Flower intensity was based on flower count per inflorescence. Flower number at different stages (anthesis and full bloom), and swollen bud number were also recorded at various dates based on three branches of equal diameter and length.

Sap flow measurements in the stem

Four miniprobes, SF200 were installed at a height of 15 cm on the stems of four treated plants; each plant represented a treatment *(Figure 1)*. The surface of each implant was drilled into the sapwood for about 5 mm in depth. Each miniprobe was inserted into the hole ensuring the sensor (Greenspan sapflow sensor) was within the stem *(Plate 1)*. Once

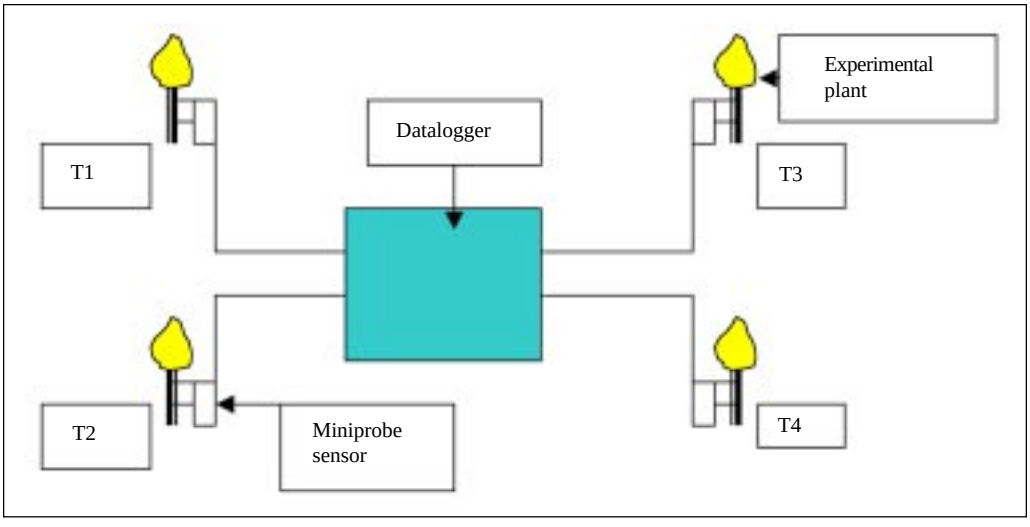

Figure 1. Schematic diagram of sap flow mini sensor probes inserted on stems of experimental plants with respect to different container volumes

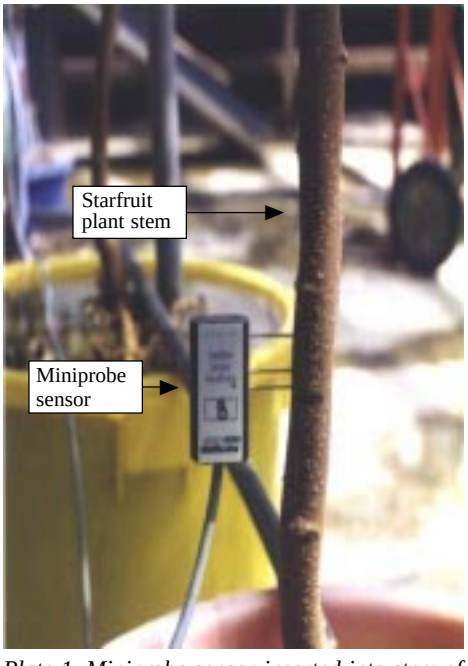

Plate 1. Miniprobe sensor inserted into stem of starfruit plant

all the probesets were implanted, the implanted portion of the trunk was wrapped entirely with aluminium foil to protect it from solar radiation. The four probes were then connected to a data logger *(Figure 1).* Data logging took place for three consecutive weeks. The sap flow velocity (*S*) was recorded every 30 min for 21 days. Since four miniprobes could be operated at one time, sap flow was measured in only one plant from each treatment. Sap flux (SF) in the stem was calculated using the weighted average technique of Hatton et al. (1990). The sap flux was calculated as follows:

SF = Sap flow velocity *(S)* * Sapwood Area (SA);
SA = TCSA * FAS, where TCSA is trunk cross-sectional area and FAS is fractional area of sapwood.

This technique requires only the depths at which *S* was measured and the depths to the cambium and the heartwood (e.g. the sapwood boundaries).

Experimental design and statistical analysis

The experiment consisted of four volumes container arranged in completely randomised block design with three replications. Sampling of three plants was taken from each treatment per replicate and only mean values were used. The data were analysed using SAS procedures (SAS Inst. 1985). Least Significant Differences (LSD) was used to test significant differences

among treatments. Simple linear regression model $y = a + b^x$ was fitted using SAS PROC REG procedures between number of flowering plants and days to flowering and between stem girth (trunk cross sectional area) and sap flux.

For sap flow measurements, T-test analysis was performed to compare between the container sizes at each period namely; 0000; 0400; 0800 1200; 1600 and 2000 h.

Results

Flowering

The percentage of flowering plants and flower intensity are shown in *Figure 2.* The time to flowering decreased with increasing container volume. Earliness in flowering was detected in the container volumes of 3 litres and 6 litres at the 80th day. The percentage of flowering plants was 44% in the 3-litre containers compared to 10% in the 6-litre containers and none were observed in the 12 and 24-litre containers. By the 100th day, the percentage of flowering plants in 3-litre containers was almost double 44% in both 6 and 12-litre containers and all plants flowered in all treatments by the 160th day. Flowering intensity was influenced by the treatments at the 100th day. The container volumes of 3 and 6 litres had about 5 flowers per plant at the 100th day compared to none in the 24-litre containers. At the 140th day, flower intensity had increased; however, there was inconsistency between treatments at 160 and 180 days *(Figure 3).*

During anthesis, full bloom and swollen bud formation, the number of flowers was not affected by the container volumes until the eighth month. However, two weeks later at full bloom, flower numbers were significantly reduced when container volumes were reduced from 24 to 3 litres. There was a similar decrease in flower fresh weight *(Table 1).*

This data showed that flowering was enhanced in small containers, but flower numbers at both anthesis and full bloom stage were not affected by the container

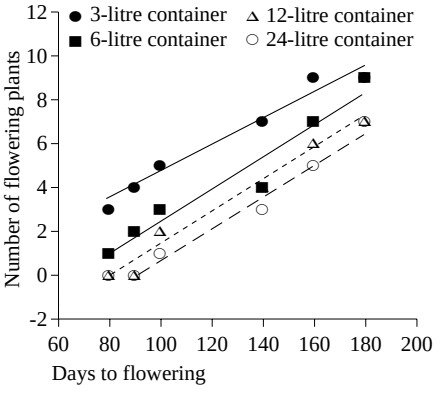

Figure 2. Relationship between number of flowering plants and days to flowering in different container volumes

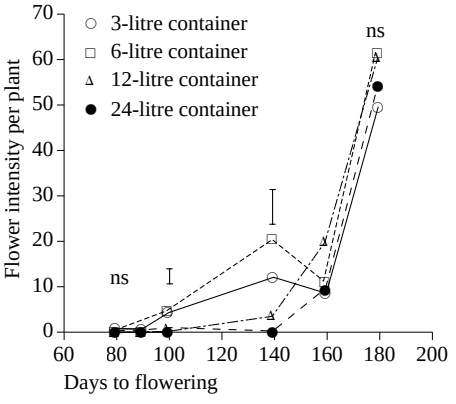

Figure 3. Flowering intensity and days to flowering in different container volumes

volumes. This could mean that increased root growth in the limited containers experienced high water potential that triggered flowering, although flower numbers and development per inflorescence varied widely. Returning bloom however, was affected by container size treatments.

Sap flow velocity and sap flux

The size of the container significantly affected sap flow velocity between 0000 h and 2000 h *(Figure 4).* Reduction in container volumes resulted in decreased sap flow velocity. Sap flow velocity fluctuated during the day, with maximum oscillation of 30 cm/h at midday. The diurnal course sap flow velocity for each treatment started at

Table 1. Number of flowers per branch at anthesis (AT), full bloom (FB), swollen bud (SB) and flower fresh weight (FFW) at 8th month

Treatment (litres)	11 March 1998			25 March 1998			FFW[a] (g/plant)
	AT	FB	SB	AT	FB	SB	
3	3.8ab	10.8a	39.7a	0.3a	4.1a	22.3a	4.0a
6	2.9a	19.8a	51.8a	0.6a	3.7a	23.9a	8.7ab
12	6.3b	14.0a	46.2a	1.3a	7.9ab	24.2a	11.2b
24	2.2a	17.0a	47.9a	0.9a	13.0b	21.1a	10.8b

[a]sampling at harvest

Mean values in the same column with similar letters are not significantly different at $p < 0.05$

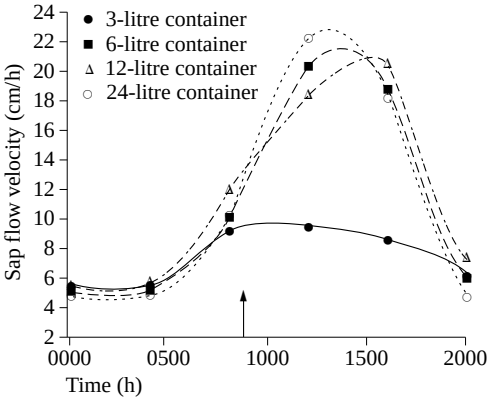

Figure 4. Sap flow velocity and time in different container volumes. Arrow denotes irrigation time

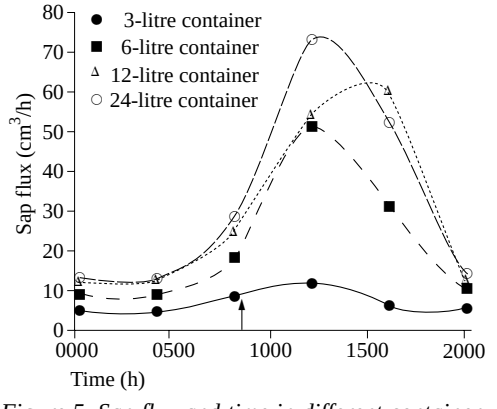

Figure 5. Sap flux and time in different container volumes. Arrow denotes irrigation time

dawn (0000 h) until morning (0500 h); average sap flow was 5.0 cm/h. The actual consumption of water started at 0900 h in the morning and gradually increased to 10 cm/h. When irrigation was applied at 0900 h, sap flow velocity increased instantly from 10 to 25 cm/h in 6, 12 and 24-litre containers but the 3-litre container sap flow was only 12 cm/h. Sap flow rates increased by three-fold by midday, particularly between 3-litre and 24-litre containers. In the late afternoon, sap flow rate progressed to low values (7 cm/h) in the 3-litre containers. There was rapid sap flow decrease in all treatments at 1530 h and sap flow velocity remained low (5 cm/h) at dawn *(Figure 4)*.

Apparently, large volume corresponded to high sap flux. The diurnal sap flux was affected by the treatments. Sap flux was significantly influenced by the container volume. In the 24-litre containers, sap flux was 73 cm/h at noon compared to 11.42 cm/h in 3-litre containers. This demonstrated that increase in container volume from 3 litres to 24 litres increased water uptake by as much as six times *(Figure 5)*.

These results imply that water uptake corresponded with the amount of root growth in the container, which had been affected by transpiration rate of the plants that fluctuated with time.

Leaf water potential

Leaf water potential in all treatments is shown in *Table 2*. Leaf water potential was influenced by the container volumes; the smallest container volume had significantly higher leaf water potential. Leaf water potential in the 3-litre container was 62% higher than in the 24-litre containers, while partial differences were detected in the 12-litre containers at the 170th day. An increase

Table 2. Leaf water potential, soil moisture content (%) and bulk density (g/cm^3)

Treatment (litres)	Leaf water potential (-MPa)[x]		Soil moisture content		Bulk density	
	11 Mar. '98 (170th day)	25 Mar. '98 (185th day)	1 Apr. '98 (190th day)	10 Apr. '98 (200th day)	1 Apr. '98 (190th day)	10 Apr. '98 (200th day)
3	1.3a	2.2b	13.9a	14.9a	1.6a	1.7a
6	1.3a	2.1b	13.9a	14.1a	1.6a	1.7a
12	1.3a	1.9b	15.4a	14.5a	1.6a	1.7a
24	1.2a	1.2a	11.1a	13.9a	1.8b	1.8a

[x]Data taken during sap flow measurement
Mean values in the same column with similar letters are not significantly different at p <0.05

in leaf water potential from –1.8 to –2.16 MPa occurred within the 3-litre containers, compared to the increase from –1.21 to –1.25 MPa in the 24-litre containers between the 170th and the 185th day. This indicated that plants in the small containers experienced moisture stress when leaf water potential exceeded –2.0 MPa, even though regular rewatering was provided.

However, soil moisture content did not differ among the treatments, indicating that there was adequate water in the containers. Bulk density of the treatment is shown in *Table 2*. The 24-litre containers had 1.79 g/cm^3 compared to 1.63 g/cm^3 in 3-litre containers at the 190th day, and increased to 1.81 g/cm^3 in the former and 1.75 g/cm^3 in the latter treatment.

This indicated that high root water usage despite rewatering, even in small and medium size containers, increased leaf water potential in plants which seemed to coincide with sap flux. Increase in root growth was attributed to a corresponding increase in water absorption from the growth medium that caused an increase in soil bulk density. Reduced sink demand induced by restricted root growth has been shown to lead early flowering.

Partitioning of dry matter

The partitioning of dry matter in leaf, stem and roots is shown in *Figure 6.* Leaf dry weight was significantly higher in the largest 24-litre containers (33.20%) compared to 3-, 6- and 12-litre containers. In contrast, root dry matter partitioning was lowest in the

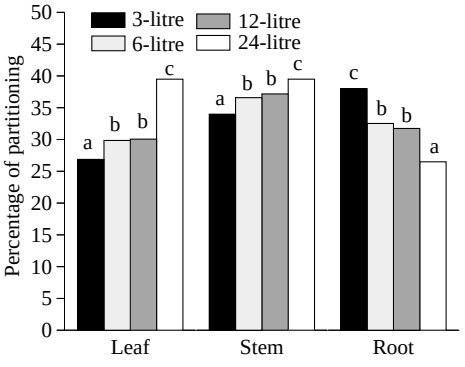

Figure 6. Partitioning percentage in leaf, stem and roots of different container volumes

24-litre containers (26.5%) followed by the 6-litre and 12-litre containers, while the highest was obtained in the 3-litre containers (38.0%).

Biomass and total root dry weight were affected by the container volumes. Increase in container volumes led to a significant increase in biomass and total root dry weight *(Table 3)*. Increase in container volumes from 3 to 24 litres showed 4.6 and 3.2 times increase in biomass and total root dry weight, respectively. However, root:shoot ratio decreased significantly with increase in container volumes. Root:shoot ratio decreased from 0.62 to 0.37 when container volume was increased by eight times even though there was a high partitioning percentage of dry matter to roots.

As far as root dry weight (RDW) is concerned, roots in the smallest containers were denser and compact than in large container volumes. Container size

Table 3. Biomass, total root dry weight (TRDW), root:shoot ratio, root dry weight (RDW) and root weight density

Treatment (litres)	Biomass (g/plant)	TRDW (g/plant)	Root:Shoot ratio	RDW (g/plant)		Root weight density (mg/cm^3)
				<10 mm	<2 mm	
3	106.3a	41.4a	0.6c	20.4a	14.1a	0.013d
6	209.4b	67.9 b	0.4b	38.2b	19.0b	0.011c
12	308.0c	104.1c	0.4b	54.4c	34.9b	0.008b
24	489.8d	132.3d	0.3a	65.0c	42.7b	0.006a

Mean values in the same column with similar letters are not significantly different at $p < 0.05$

significantly affected root distribution in two categories, including thick roots (<10 mm) and fine roots (<2 mm) at $p < 0.05$. Increase in container size from 3 to 24 litres increased root dry weight by more than three times in both root categories *(Table 3)*, but root weight density was negatively influenced by the container volumes. Increase in container volumes led to a reduction in root weight density. Increase from 3 to 6 litres, 12 litres and 24 litres reduced root weight density to 0.011, 0.008 and 0.006 mg/cm^3, respectively *(Table 3)*.

These results indicated that although root dry weight at both root diameters increased accordingly with increase in container volumes, root weight density decreased. Increase in root weight density probably resulted in greater decline in leaf water potential, particularly in limited containers, due to progressively increased water uptake.

Discussion

By using different container volumes, roots of starfruit were significantly restricted especially in small container volumes. Root restriction hastened flowering by 60 days earlier when container volumes decreased by three folds. Carmi (1995) suggested that flowering during root restriction and adequate water supply are attributed to the development of internal stress. Earlier studies by Ismail and Mohd Noor (1996) also confirmed that root restriction hastens flowering in starfruit. However, similar treatment delays flowering of tomato (Ruff et al. 1987).

Plants in reduced container volumes experienced water stress (>–2.0 MPa) due to highly compact root growth that caused high soil bulk density. Masle and Passioura (1987) pointed out that hard, dry soil might affect shoot development through limitation of water supply and mechanical impedance of root growth. Bulk densities greater than 1.2 g/cm^3 would restrict root growth (Alberty et al. 1984). Aeration of the growing medium may also affect cell growth (Dubik et al. 1990). The high root density in restricted containers might have reduced the amount of air space in the growing medium, thus restricting diffusion of O_2 and CO_2 from the containers. This may lead to anaerobic conditions in the root zone and reduced root activity (Van Iersel 1997).

Root restriction resulted in stress to the plants. In this context, more dry matter was partitioned to the roots, causing root:shoot to increase. Smucker (1993) suggested that the stress environment caused more C to be used for the development of additional structural tissues, maintenance of membrane integrity, production of toxic anaerobic metabolites, exudation losses and the reallocation of C to other parts of the plant. The energy cost of developing and maintaining a functional root system subjected to adverse environments is much greater than in non-stress environments.

Plants under adverse root restriction condition showed maximum decrease in leaf water potential indicating they were under stress. This was followed by decreased in sap flow velocity. Sap flow velocity was lower (9 cm/h) and leaf water potential was

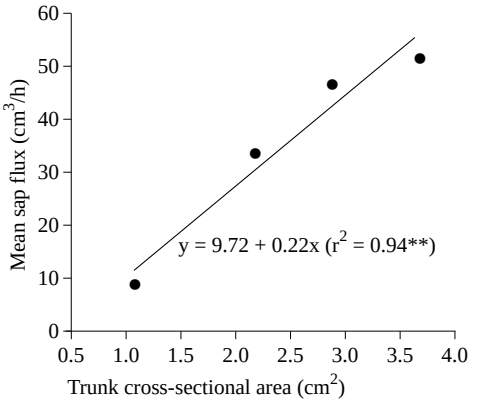

Figure 7. Relationship between mean sap flux and trunk cross sectional area

–2.16 MPa in the limited container size, while in the largest container (24-litre) sap flow velocity was 25 cm/h and leaf water potential was –1.25 MPa. Studies by Steinberg et al. (1990) provided evidence that in pecan, leaf water potential decreased with decreasing sap flow in a linear fashion.

In this study, the stem sap flux showed a high relationship with trunk cross-sectional area ($r^2 = 0.94$) *(Figure 7).* Heilman and Ham (1990) pointed out that stem sap flux could represent transpiration measurement in plants; studies in ligustrum *(Ligustrum japonicum)* showed that sap flux was very closely related to transpiration in both growth chamber and field environment. Studies by Vertessy et al. (1995) also showed that stem diameter accounted for 88% of transpiration in young mountain ash *(Eucalyptus regnans)*. Therefore, restricting the roots in the present study reduced stem diameter, which in turn reduced transpiration.

Conclusion

Root restriction resulted in decrease in sap flow velocity, and led to the hastening of changes from vegetative to reproductive development in starfruit. Although flower intensity was inconsistent, there was indication that root restriction could sustain flowering percentage. Prolonged root restriction not only resulted in stress plants (more negative leaf water potential), but increased soil bulk density and more partitioning of dry matter to roots. The stress could enhance flowering and precocity; and efficient plants are of benefit to growers.

Acknowledgement

The author would like to thank Mr Mohd. Nasir Abdullah, Ms Zaharah Talib and Dr Izham Ahmad for their field assistance, statistical analysis and technical comments, respectively. The project has been funded by IRPA (Research Grant No. 01-01-03-0371).

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Abstrak

Kajian pembatasan akar terhadap pokok belimbing besi (B17) telah dijalankan dengan menggunakan empat bekas pembatasan akar yang berlainan isi padu iaitu 3, 6, 12 dan 24 liter bertujuan untuk mengetahui tindak balas terhadap tumbesaran, pembungaan dan pengambilan air. Kajian ini telah dijalankan dengan menggunakan reka bentuk rawak lengkap dengan tiga replikat. Setiap replikat diulang sebanyak tiga kali. Pada bulan keenam setiap perlakuan dipasang alat pengesan untuk memantau pengambilan air melalui 'sap flow' selama tiga minggu berturut-turut. Keseluruhan kajian mengambil masa selama lapan bulan dan dijalankan di dalam rumah kaca. Pengairan dan pembajaan terhadap tanaman yang dikaji telah dilaksanakan mengikut jadual.

Pertambahan tumbesaran tanaman adalah seiringan mengikut bekas isi padu; manakala peratusan taburan bahan kering didapati mengikuti aliran yang sama. Walau bagaimanapun, peratusan taburan bahan kering akar meningkat sebanyak 38% apabila tanaman berada di dalam bekas 3 atau 6 liter berbanding dengan hanya 26.5% bagi tanaman di dalam 24 liter. Masa untuk pembungaan pula didapati 60 hari lebih cepat apabila tanaman berada di dalam bekas 3 liter berbanding dengan 24 liter. Sementara itu, kelajuan 'sap flow' juga berkurangan daripada 22.3 kepada 9.5 cm sejam dan ketegasan air di dalam daun meningkat kepada lebih negatif daripada –1.2 kepada –2.2 MPa apabila isi padu bekas bekurangan sebanyak lapan kali. Perubahan fisiologi tanaman belimbing adalah disebabkan oleh pembatasan akar di dalam bekas dengan isi padu yang berbeza.

Accepted for publication on 2 June 2005