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Physiological and Morphological Characteristics of Hevea *Rootstock in Response to Water Stress*

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The influence of rootstock and scion clones on physiological response of polybag buddings of Hevea *to prolonged water stress was studied in glasshouse experiments. Stomatal response of scion clones to water stress could be influenced by monoclonal seedling rootstock that was grafted on. Clones grafted on RRIM 623 rootstock exhibited drought avoidance characteristics. This was indicated by rapid stomatal closure at the onset of water stress and the ability to maintain a high relative water content. The stomatal response of clone PM 10 grafted on PB 260 and RRIM 600 seedling rootstocks was less consistent.* Hevea *rootstocks also had distinct morphological development of the root system which was influenced by moisture availability. Differences in pre-dawn leaf water potential were also detected between rootstocks indicating differences in quantity of feeder roots, hence capacity for water uptake. The importance of root morphological development and stomatal responses to soil water deficit, as affected by rootstocks in influencing rootstock field performance, are discussed.*

Key words: polybag buddings; water stress; RRIM 623; PB 260; RRIM 600: root system; stomatal responses; physiological responses; morphological characteristics

Monoclonal seedling rootstock is known to improve performance of *Hevea* clones. However, not much is known about the rooting characteristics of these rootstocks and whether these characteristics are related to rootstock influence on tree productivity. Early researchers had long thought that differences in vigour between *Hevea* clonal seedling families might be attributed to differences in their rooting characteristics[1]. A previous glasshouse study on young buddings has shown that although RRIM 623 and GT 1 monoclonal seedling rootstocks differed in their stomatal response to water stress, they had low pre-dawn leaf water potential and high root weight ratio, indicating a potential to develop extensive and/or deep rooting characteristics[2]. Among temperate forest species, deep rooting characteristics are paramount for survival: oak and hickory seedlings survive better than pine seedlings under forest stands because deep roots of the former seedlings ensure accessibility to deep soil water, where competition for water is less intense[3]. In citrus, differences in rootstock adaptability are related to root distribution and efficiency[4]. In these

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trees, rootstocks were shown to affect uptake and transport of water and nutrients to scion clones; these parameters were related to root quantity and hydraulic conductivities of the root system[4,5]. Fernandez and Perry[6] studying the root distribution patterns of clonal apple rootstock found that the number of roots/dm^2 soil and depth of rooting were affected by rootstock and soil type. They also reported positive correlation between number of roots and vigour and yield of scion. This is in agreement with reports by other researchers who found positive correlation between scion vigour and the intensity and extensiveness of the root system for many apple rootstocks[7,8]. This study evaluates the physiological responses of *Hevea* rootstock to water stress and moisture availability and how these responses are related to characteristics of the root system.

MATERIALS AND METHODS

In this study, monoclonal seedling rootstocks derived from seeds collected from the center of a block of a clone at least 20 m from the border was used. Three experiments: *Experiment WS 94*, *RS 98* and *GH*, were conducted in the glasshouse at the Experiment Station, Rubber Research Institute of Malaysia (RRIM), Sungai Buloh, Selangor.

Experiment WS 94

This experiment studied the physiological response of 2 scion clones, PM 10 and RRIM 901 grafted on RRIM 600, RRIM 623 and PB 260 rootstocks, to water stress. The experiment was arranged in a randomised complete block design with 10 replicates and 3 plants per plot. The buddings, grown in 17.8 cm × 38.1 cm layflat-polybags were watered daily and fertilised weekly with NPK mixture. Soil water deficits were imposed on the plants at the stage of three whorls of leaves, by withholding irrigation until the plants died.

On each day of soil drying cycle, leaf diffusive resistance (LDR), stomatal conductance (SC), relative water content (RWC), transpiration rate (TR) and leaf-water potential (LWP) were measured with determinations for each replicate being carried out on different days. Determination of LWP and RWC were carried out between 0800 and 0900 h, whilst measurements of other water relations parameters were carried out between 1100 and 1230 h, when light intensity was at least 1000 $\mu Em^{-2}s^{-1}$. These determinations were carried out on healthy, unshaded and recently fully-expanded leaves. Leaf diffusive resistance, SC and TR were measured using a steady state diffusion porometer (LI-1600, LICOR, Nebraska, USA).

Leaf-water potential was measured on one leaf per plant using a pressure chamber (PMS instrument Co., USA), according to the technique described by Ritchie and Hinckley[9]. Relative water content was determined using the method described by Turner[10]; for this determination, at least two leaf discs (1.9 cm diameter) per leaf were sampled from the same leaves used for the determination of LWP. Fresh weight of the discs were determined before and after floating them on distilled water, in Conviron growth chamber, for 4 h at a relative humidity of 90%, temperature of 25°C and under light compensation point of 160 $\mu Em^{-2}s^{-1}$. Scion height and diameter were measured on the 12th day of water stress before the experiment was terminated. The plants were harvested and dry weight of root components determined after oven drying at 80°C for 48 h. The relationship between LWP and other water relations parameters of scion leaves were determined to study the rootstock and clonal responses to soil water deficits. Data were fitted with polynomial equations.

Experiment RS 98

In this experiment, 3 rootstocks (GT 1, RRIM 712 and RRIM 937) were grafted with RRIM 712 and RRIM 937 clones. The buddings were grown in plastic containers (28 cm diameter × 60 cm height), containing a 1:1 mixture of Rengam series soil and sand incorporated with 120 g Christmas Island rock phosphate in the glasshouse. The experiment was arranged in a randomised block design, with four replicates and one plant per treatment combination per replicate. The plants were watered daily and fertilised with 'Kokei' slow release fertiliser every three months. About two months after transplanting into the plastic containers, cyclical water stress was applied to the plants by irrigating with 1 litre of water once in four days. Pre-dawn LWP (measured between 6.30 a.m. – 7.00 a.m. before daylight) were monitored before and at monthly intervals after imposition of water stress. The plants were harvested after 9 months of cyclical water stress and dry weight of various plant parts determined after oven drying at 80°C for at least 48 h. Green leaf area was determined immediately after harvesting using a LI-COR area meter (Model LI-3000). Specific leaf area was calculated as mean area of leaf per unit leaf dry weight[11].

Experiment GH

This experiment tested the response of rootstocks to moisture availability. Three rootstocks (GT 1, PB 260 and RRIM 623) grown in plastic containers were grafted with RRIM 901 scion clone at 3 months. The containers used in the experiment consisted of two 4-litre plastic buckets with one bucket placed on top of the other (*Figure 1*). Two treatments were tested: shallow water treatment with roots exposed to dry substrate at 26 cm from soil surface and control treatment with the root system having access to soil, adapting the method described by Callaway[12]. In each treatment, ten holes of 1 cm in diameter were drilled into the base of the top bucket which contained a mixture (80:20) of sand and Rengam series soil. Growing medium in bottom buckets consisted of either pea gravel (1–2 cm in diameter) for shallow water treatment or a 50:50 mixture of sand and pea gravel for control treatment. The bottom bucket of shallow water treatment was drained by 10 large holes of 1 cm in diameter, whilst that in control treatment was drained by 10 smaller holes (1.5 mm diameter). The experiment was arranged in a randomised complete block design with three plants per replicate per treatment. Before treatment application, the buddings were watered daily and fertilised with 'Kokei' slow release fertiliser. Water stress was imposed on the buddings when they had attained two whorls of fully expanded leaves by applying 300 mL water to field capacity every 4 days. Scion diameter and height were measured at monthly intervals. The plants were harvested six months after imposition of water stress and dry matter of various plant parts determined after oven drying at 80°C for at least 48 h.

RESULTS

Water Relation Parameters

Experiment WS 94. The influence of rootstock on water relation parameters of PM 10 and RRIM 901 clones is shown in

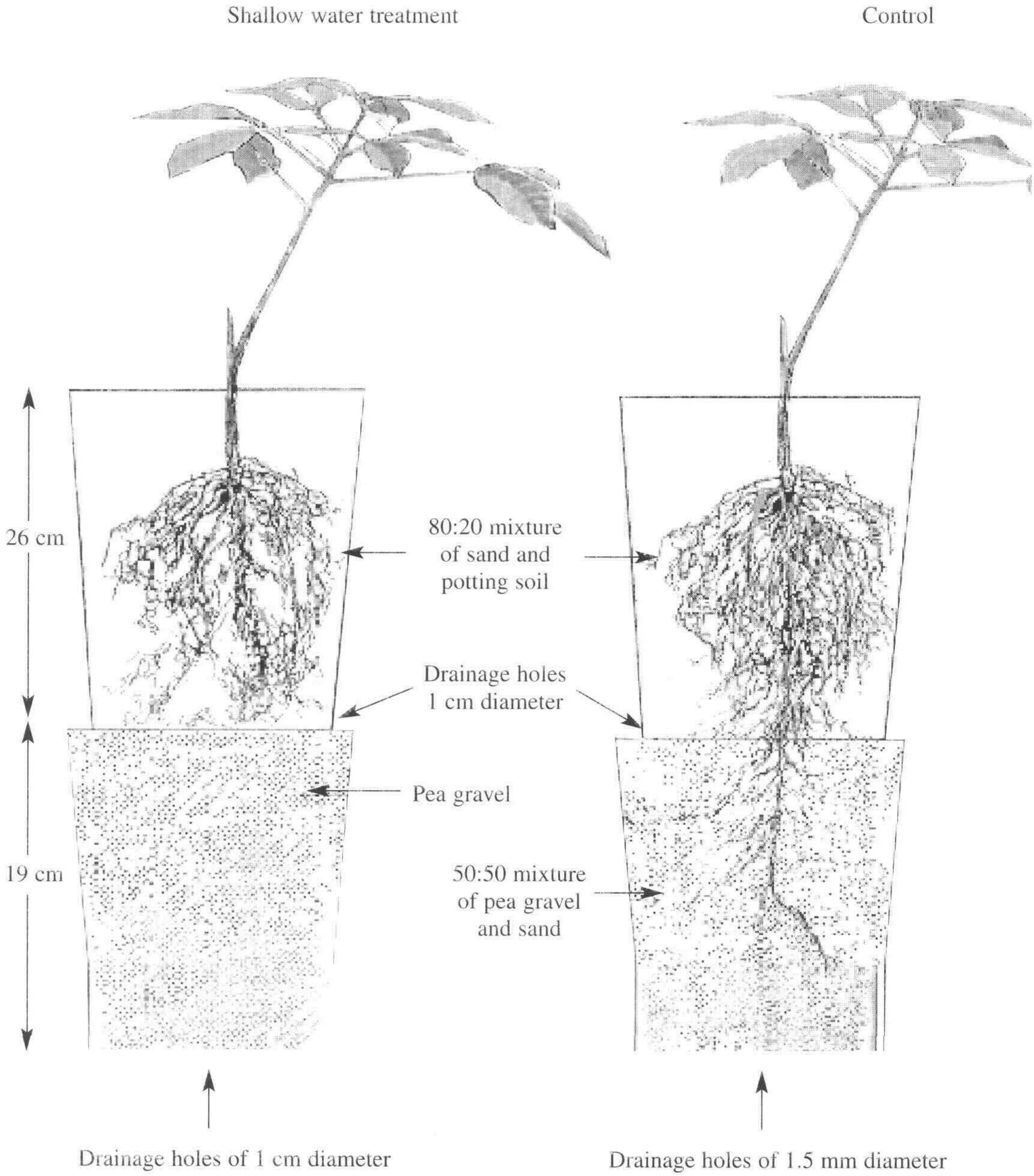


Figure 1. Hevea *buddings grown in containers with two types of soil water treatment.*

Figures 2–5. Generally, there were significant relationship between pre-dawn LWP and LDR, SC, TR and RWC (*Appendix I*). The relationship was improved using polynomial regression; r^2 ranged from 0.6326 to 0.9653. Both RRIM 901 and PM 10 clones became more sensitive to soil-water deficit when grafted on RRIM 623 rootstock, since the stomata tended to close earlier than with those on the other rootstocks, at the onset of water stress (at LWP of about –10 bars). This was evident by rapid increase in leaf diffusive resistance (which changed by 0.5 to 0.6 units per unit change in LWP) and rapid decline in SC and TR (*Figures 2–4*). As a result of rapid stomatal response to water stress, these plants were able to maintain relatively high RWC (*Figure 5*). PB 260 rootstock also tended to induce rapid stomatal closure in RRIM 901 clone on the onset of water stress as reflected by its LDR, SC and TR values. However, these plants could not maintain high RWC throughout the drying cycle, as did those on either RRIM 623 or RRIM 600 rootstocks. In contrast, RRIM 901 clone grafted on RRIM 600 rootstock tended to be less sensitive to water stress. This was evident by a gradual increase in LDR (about 0.14 unit per unit change in LWP) and a gradual decline in SC with increasing soil water deficit indicating that more stomata of this clone remained open as LWP decreased beyond –10 bars whilst those on the other two rootstocks were virtually closed. However, the stomatal response of PM 10 grafted on RRIM 600 and PB 260 rootstocks was less consistent. For instance, the low stomatal sensitivity of these plants to water stress as indicated by gradual increase in LDR with decreasing LWP did not correspond to the rapid decline in SC and TR values. Additionally, there was hardly any difference in RWC of this clone due to the three rootstocks (*Figure 5*).

Experiment RS 98. Rootstocks had a marginal influence ($P<0.10$) on pre-dawn LWP before the imposition of water stress with RRIM 712 rootstock giving significantly lower values than RRIM 937 rootstock (*Table 1*). After the imposition of water stress, rootstock influence was only evident after four months with RRIM 937 and GT 1 rootstock producing significantly lower pre-dawn LWP than RRIM 712 rootstock. This trend was maintained at 9 months after imposition of water stress. Additionally, there was significant interaction between scion and rootstock, indicating that rootstock influence on pre-dawn LWP was dependent on scion clone (*Table 2*). The highest pre-dawn LWP was produced by both control plants (RRIM 712/RRIM 712 and RRIM 937/ RRIM 937 combinations) whilst scion/ rootstock combination of RRIM 712/ RRIM 937 gave the lowest pre-dawn LWP, followed by RRIM 712/GT 1 combination.

Growth

Experiment WS 94. *Table 3* shows growth and biomass of root components of plants in *Experiment WS 94*. Rootstock had a highly significant effect on scion growth as well as on dry matter production and distribution to root components. In contrast, scion clone only influenced scion diameter with PM 10 having significantly better diameter (6.25 +/– 0.87 cm) than RRIM 901 (5.58 +/– 1.35 cm). RRIM 623 rootstock gave the best scion growth in terms of diameter and height, whilst RRIM 600 rootstock gave the poorest scion growth. The root system of RRIM 623 rootstock, as reflected by dry weight of root components, also tended to be more vigorous than RRIM 600. Amongst the three rootstocks studied, RRIM 623 rootstock diverted most

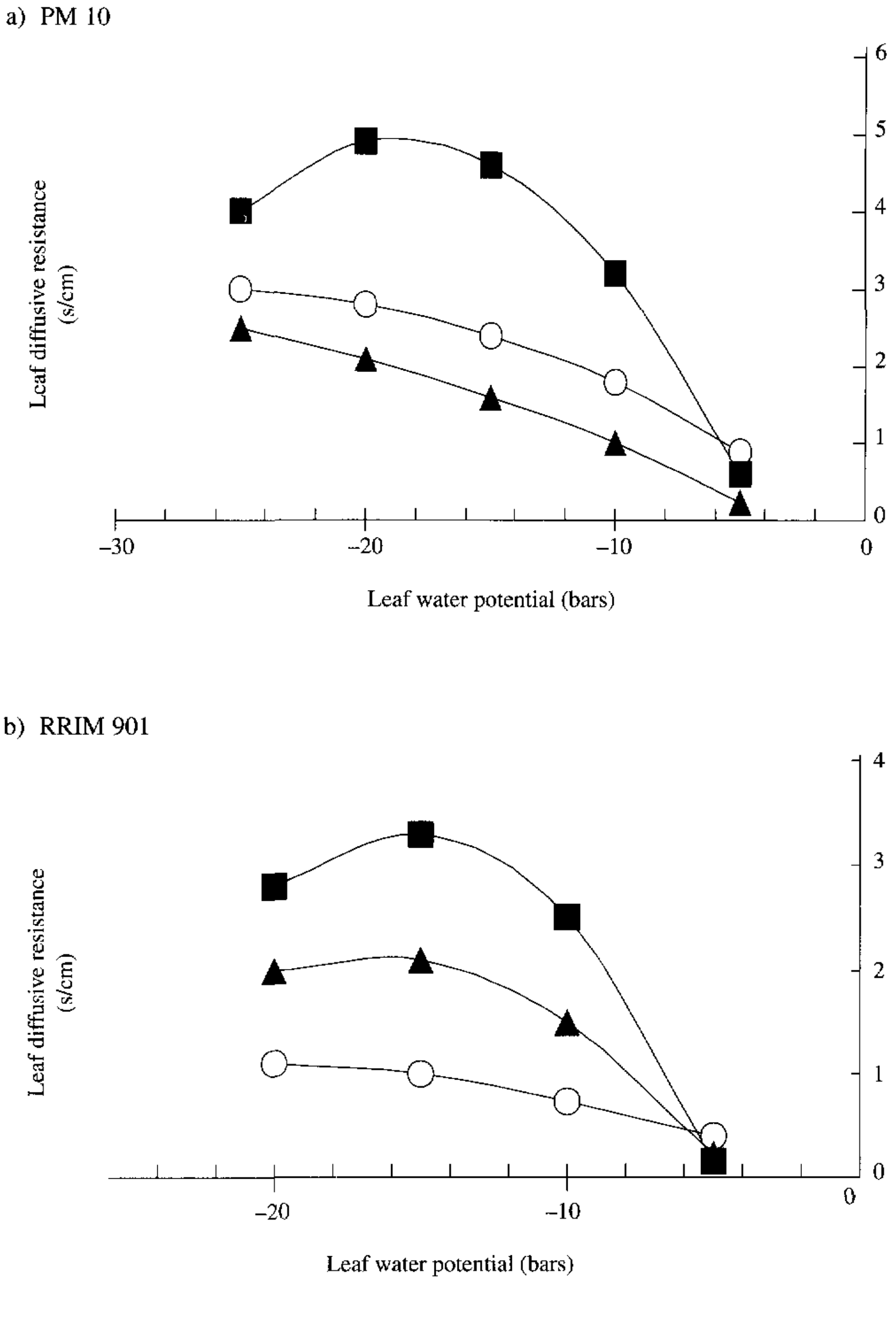
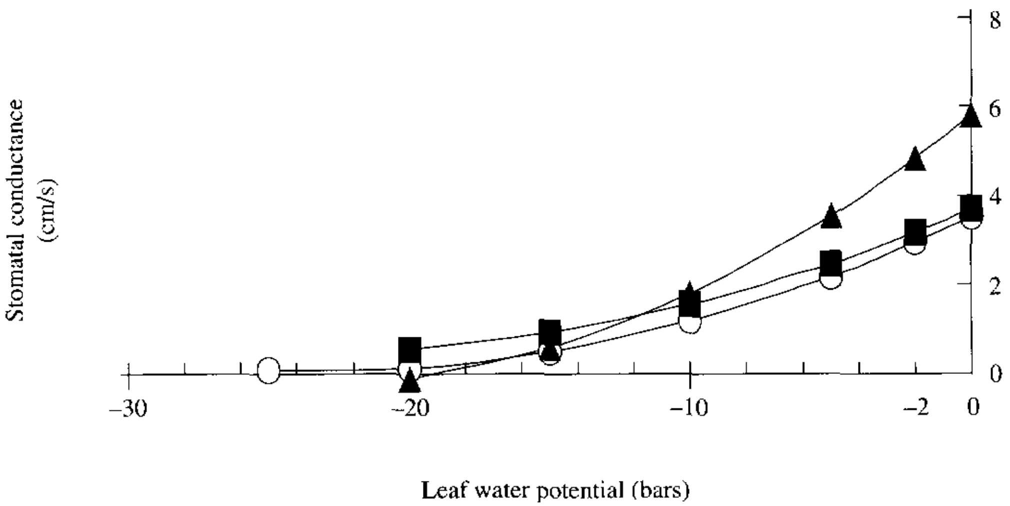


Figure 2. Effect of rootstock on leaf diffusive resistance of PM 10 and RRIM 901 scion clones during water stress. Monoclonal seedling rootstock: RRIM 600 (—○—); RRIM 623 (—■—); PB 260 (—▲—).

a) PM 10



b) RRIM 901

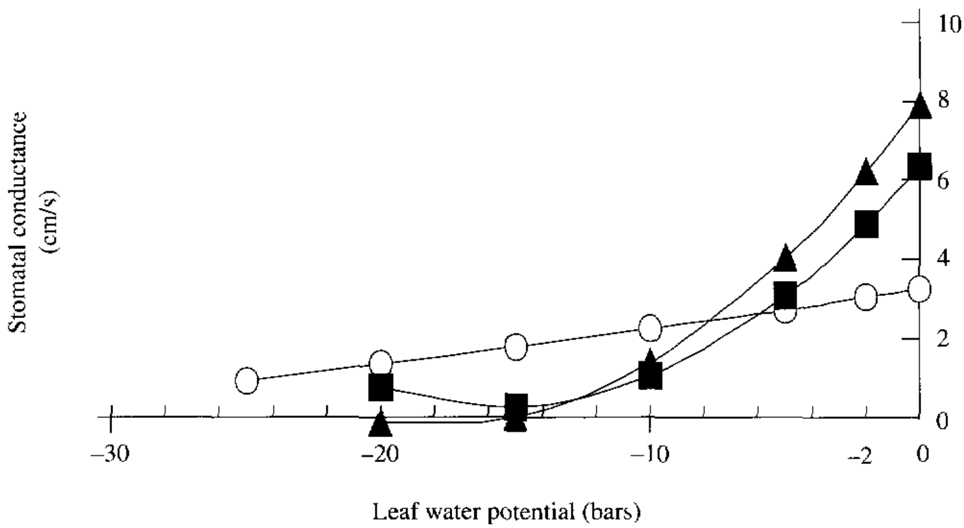


Figure 3. Effect of rootstock on stomatal conductance of PM 10 and RRIM 901 scion clones during water stress. Monoclonal seedling rootstock: RRIM 600 (—○—); RRIM 623 (—■—); PB 260 (—▲—).

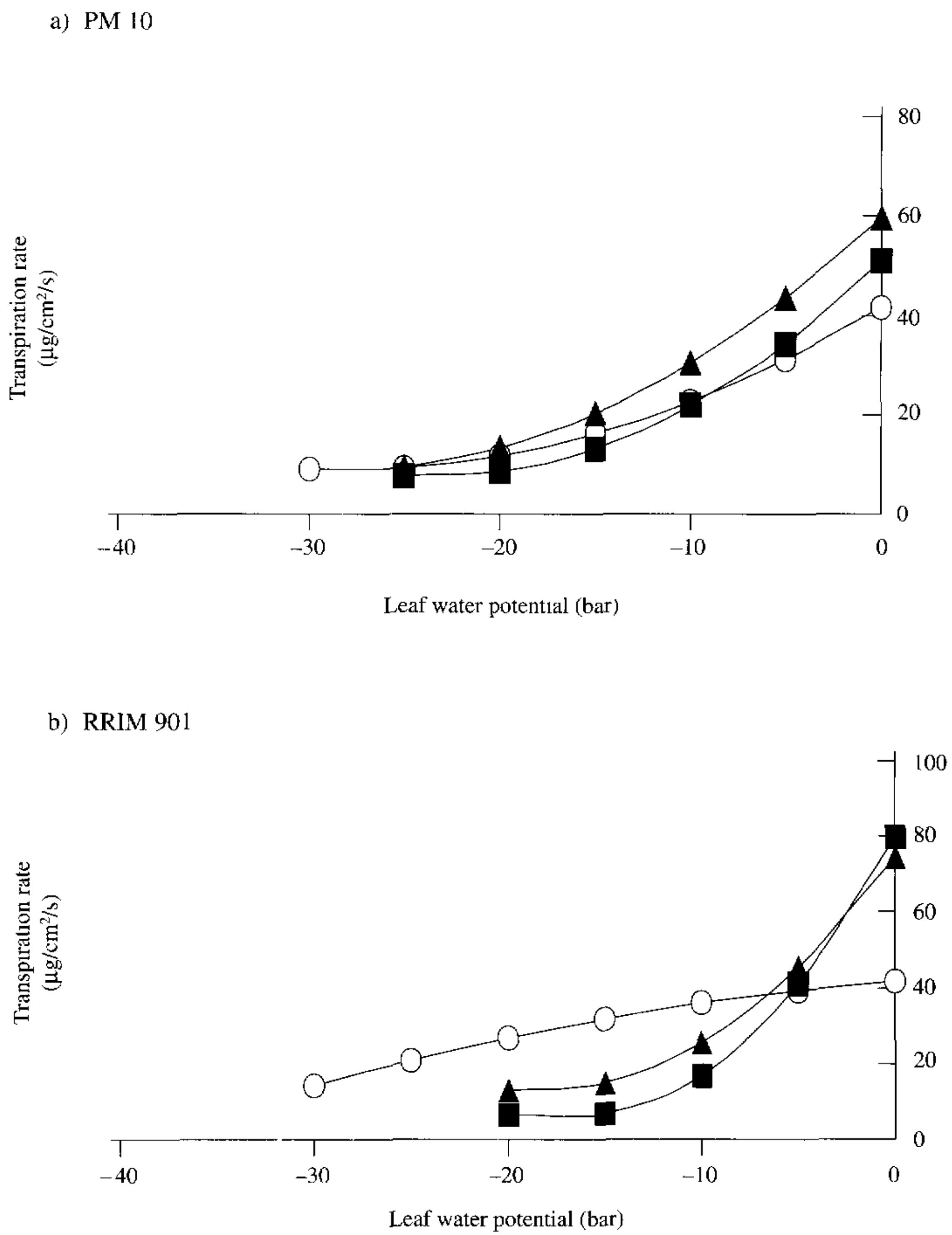


Figure 4. Effect of rootstock on transpiration rate of PM 10 and RRIM 901 scion during water stress. Monoclonal seedling rootstock: RRIM 600 (—○—); RRIM 623 (—■—); PB 260 (—▲—).

a) PM 10

b) RRIM 901

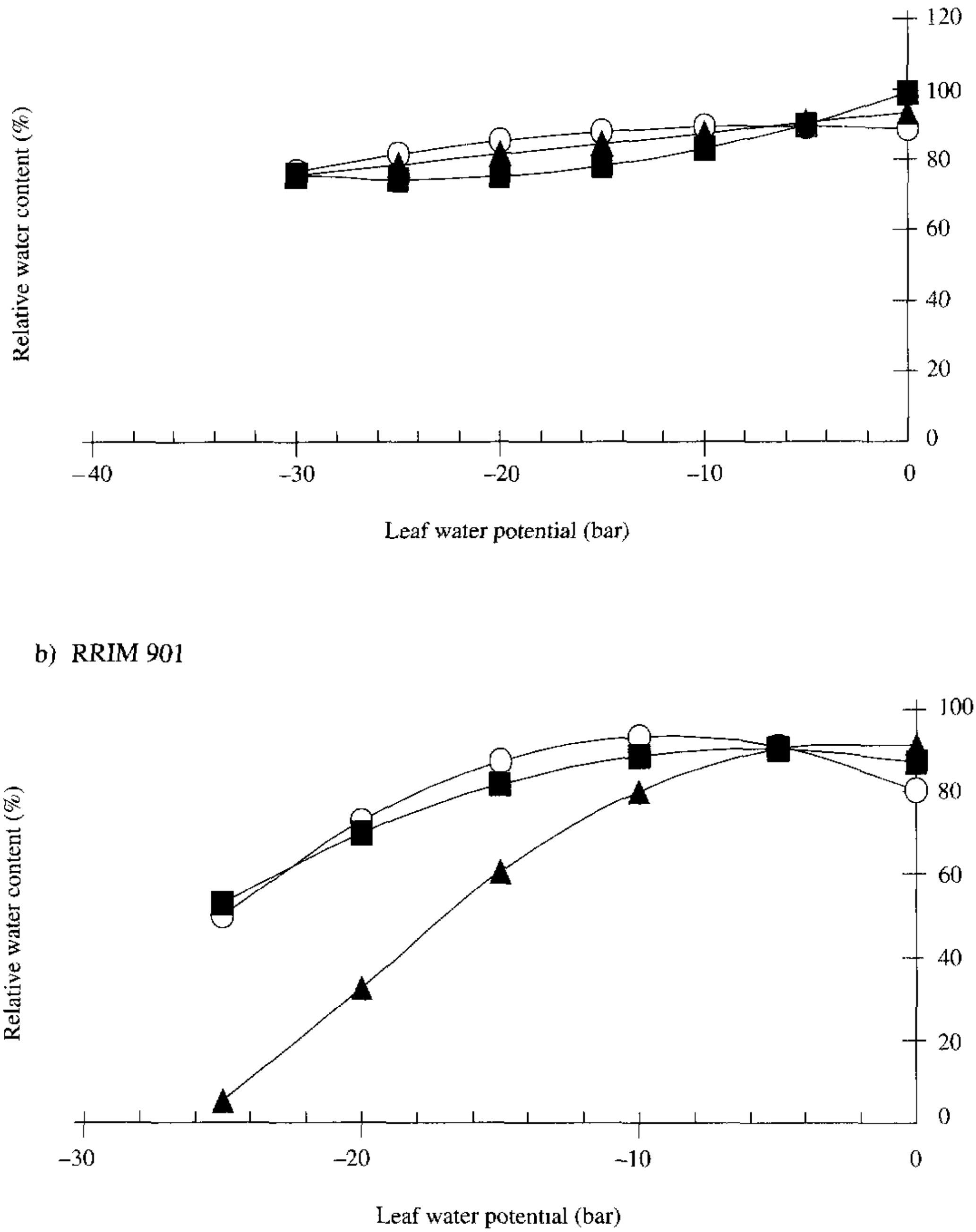


Figure 5. Effect of rootstock on relative water content of PM 10 and RRIM 901 scion during water stress. Monoclonal seedling rootstock: RRIM 600 (—○—); RRIM 623 (—■—); PB 260 (—▲—).

TABLE 1. EFFECT OF ROOTSTOCK ON PRE-DAWN LEAF WATER POTENTIAL DURING WATER STRESS[c]

Monoclonal seedling rootstock	Months after water stress					
	0	1	2	3	4	9
RRIM 712	–0.99 a	–1.0 a	–2.78 a	–2.45 a	–2.59 b	–3.57 b
GT 1–0.90 ab	–1.0 a	–2.58 a	–2.49 a	–2.88 a	–3.73 a	
RRIM 937	–0.86 b	–0.99 a	–2.68 a	–2.43 a	–2.94 a	–3.78 a
Probability level	#	NS	NS	NS	*	*

[c]Each value is an average of 2 scion clones
Means with the same letters within columns are not significantly different
NS,#,* : F-test. non-significant or significant at $P<0.10$ or 0.05, respectively.

TABLE 2. EFFECT OF ROOTSTOCK ON PRE-DAWN LEAF WATER POTENTIAL AT NINE MONTHS OF CYCLICAL WATER STRESS

Scion / rootstock combination	Pre-dawn leaf water potential (bars)
RRIM 712 / RRIM 937	–4.0 a
RRIM 712 / GT 1	–3.8 b
RRIM 937 / GT 1	–3.7 bc
RRIM 937 / RRIM 712	–3.7 bc
RRIM 937 / RRIM 937	–3.6 cd
RRIM 712 / RRIM 712	–3.5 d
Probability level	**
Coefficient of variation (%)	2.56

Means with the same letters within column are not significantly different
** : F-test significant at $P<0.01$

dry matter in the whole root system for production of tap-root (73%), but it diverted the least dry matter (27%) for lateral root production. In contrast, RRIM 600 rootstock diverted the least dry matter (69%) for tap-root production whilst its lateral roots received a greater percentage of dry matter compared to the other two rootstocks. PB 260 rootstock showed an intermediate trend between these two rootstocks, with respect to percentage dry weight of lateral and tap-root.

TABLE 3. EFFECT OF ROOTSTOCK ON SCION GROWT, BIOMASS AND DISTRIBUTION OF ROOT COMPONENTS IN *EXPERIMENT WS94*[d]

Monoclonal seedling rootstock	Scion height	Scion diameter	Dry weight (g) Tap-root	Lateral root	Whole root	g/g whole root % tap-root	% lateral root
RRIM 623	60.7 a	6.9 a	23.5 a	8.0 a	31.5 a	73.1 a	26.9 b
PB 260	47.3 b	5.7 b	18.4 b	7.3 a	25.7 b	70.8 ab	29.2 ab
RRIM 600	41.7 b	5.1 c	14.9 c	6.2 b	21.1 a	68.6 b	31.4 a
Rootstock effect	***	***	***	**	***	**	**
Scion effect	NS	**	NS	NS	NS	NS	NS

[d]Each value is an average of 10 samples and 2 scion clones
Means with the same letters within columns are not significantly different
NS,**,*** : F-test, non-significant or significant at P<0.01 or 0.001, respectively.

Experiment RS98. The influence of rootstock on leaf area and dry matter production after nine months of cyclical water stress are shown in *Tables 4–6*. Rootstock influenced only dry weight of fibrous roots (*Table 4*) and percentage dry weight of fibrous and tap-roots in the root system (*Table 6*), whilst scion clone influenced dry weights of scion stem, whole shoot and consequently dry weight of whole plant. Between the two scion clones, RRIM 937 with stem dry weight of 62.7 +/–6.85 g had better shoot growth than RRIM 712 clone (stem dry weight of 41.5+/–12.96 g). Amongst the three rootstocks studied, GT 1 rootstock had the largest fibrous root dry weight. This rootstock also allocated more dry matter to fibrous roots than to tap-roots. In contrast, both RRIM 712 and RRIM 937 rootstocks allocated greater proportion of dry matter to the development of tap-root than to fibrous roots.

Experiment GH. The influence of rootstock and soil water treatment on dry matter production and distribution to various plant parts are shown in *Tables 7–9*. With the exception of percentage dry weight of scion stem, both rootstock and soil water treatment did not have any significant influence on dry matter production and distribution to other above-ground plant parts. However, both of these variables had substantial influence on growth and development of the root system. Rootstock did not have a significant influence on mean dry weight of yellow feeder roots, tap-root and roots growing below 26 cm depth (*Table 7*). However, rootstock influence was evident for dry weight of brown lateral roots, whole lateral roots, roots in top bucket and whole root (*Table 8*). The apparent rootstock differences with respect to root biomass that were not accompanied by differences in shoot growth contributed to the differences in root/shoot ratio, the ratio being significantly higher for plants on GT 1 than those on PB 260 rootstock (*Table 7*). Across soil water treatment, GT 1 rootstock had the largest biomass of whole lateral roots, roots in top bucket and consequently whole root biomass. In contrast, RRIM 623 rootstock had the lowest dry weight of these root components whilst PB 260 rootstock gave intermediate values.

TABLE 4. EFFECT OF ROOTSTOCK ON LEAF AREA AND BIOMASS OF PLANT PARTS OF RRIM 937 AND RRIM 712 SCION CLONES

Monoclonal seedling rootstock	Dry weight (g)[d]							Leaf area (cm^2)[d]
	Fibrous root	Tap-root	Whole root	Leaf	Scion stem	Whole shoot	Whole plant	
GT 1	76.29 a	77.1 a	144.7 a	24.8 a	62.1 a	88.6 a	233.2 a	6108 a
RRIM 712	41.83 b	74.8 a	116.7 a	18.0 a	48.4 a	70.2 a	187.0 a	5219 a
RRIM 937	31.56 b	77.5 a	109.0 a	23.2 a	45.8 a	67.2 a	176.3 a	6101 a
Probability level (R)	*	NS	NS	NS	NS	NS	NS	NS
Probability level (S)	NS	NS	NS	NS	*	*	*	NS
Probability level (SXR) interaction	NS	NS	NS	NS	NS	NS	NS	NS

[d]Each value is an average of 4 replicates and 2 scion clones
Means with the same letters within columns are not significantly different : R = rootstock; S = scion
NS,* : F-test, non-significant or significant at $P<0.05$.

TABLE 5. EFFECT OF ROOTSTOCK ON PERCENTAGE DRY WEIGHT OF PLANT PARTS AND SPECIFIC LEAF AREA OF RRIM 937 AND RRIM 712 SCION CLONES

Monoclonal seedling rootstock	Percentage dry weight (g/g whole plant)[d]			Leaf area (cm^2)	Specific leaf area (cm^2/g)[d]
	Whole stem	Whole shoot	Whole root		
GT 1	0.26 a	0.38 a	0.59 a	27.2 a	264.2 a
RRIM 712	0.26 a	0.41 a	0.63 a	35.6 a	292.1 a
RRIM 937	0.27 a	0.36 a	0.64 a	30.4 a	288.6 a
Probability level (R)	NS	NS	NS	NS	NS
Probability level (S)	NS	#	#	NS	NS
Probability level (RXS) interaction	NS	NS	NS	NS	NS

[d]Each value is an average of 4 replicates and 2 scion clones
Means with the same letters within columns are not significantly different; R = rootstock, S = scion
NS, # : F-test, non-significant or significant at $P<0.10$, respectively.

TABLE 6. EFFECT OF ROOTSTOCK ON PERCENTAGE DRY WEIGHT OF ROOT COMPONENTS

Monoclonal seedling rootstock	Percentage dry weight (g/g whole root)[c]		Root : shoot ratio[c]
	Tap-root	Fibrous root	
GT 1	0.54 b	0.46 a	1.70 a
RRIM 712	0.67 a	0.33 b	1.48 a
RRIM 937	0.67 a	0.33 b	1.91 a
Probability level (R)	*	*	NS
Probability level (S)	#	#	#
Probability level (RXS) interaction	NS	NS	NS

[c]Each value is an average of 4 replicates and 2 scion clones
Means with the same letters within columns are not significantly different; R = rootstock, S = scion
NS, #, * : F-test, non-significant or significant at $P<0.05$ or 0.10, respectively.

The distribution of dry matter in scion stem and root components as affected by rootstock and soil water treatment is shown in (*Table 9*). There was a tendency for plants on PB 260 rootstock to allocate about 30% more dry matter to scion stem than those on either GT 1 or RRIM 623 rootstock. Rootstock had significant influence on the proportion of whole lateral-roots and tap-root in the root system; however, its influence on percentage dry weight of whole root, brown lateral roots and roots in bottom bucket was only marginal ($P<0.10$).

Despite the marginal rootstock differences in the allocation of dry matter to whole roots, it is apparent that both RRIM 623 and GT1 rootstock partitioned about 17%–28%, respectively more dry matter into whole root system than did PB 260 rootstock (*Table 9*); this is in agreement with data on root/shoot ratio (*Table 7*). RRIM 623 rootstock had significantly higher percentage (57%) dry weight of tap-root in the whole root system than PB 260 rootstock (41%) whilst the reverse is true for percentage dry weight of whole lateral roots. GT 1 rootstock had intermediate values for these parameters since tap-root and lateral root form about 45% and 51% respectively, of whole root dry weight.

Soil water treatment affected dry weight of whole roots, roots in top and bottom bucket and percentage dry weight of brown lateral roots, roots in bottom and top bucket in the whole root system (*Tables 8–9*); but it did not influence root:shoot ratio. Extremely low amount of root was found in the gravel of shallow water treatment since root found there weighed only about 14% to 36% of the control (*Table 8*). Shallow water treatment also reduced root dry weight in the upper 26 cm of the root system by about 11%; this contributed to a reduction in biomass of whole roots in the shallow water treatment by about 15% of the control. Compared to the control, shallow water treatment reduced the allocation of dry matter to roots in bottom bucket by about 64%–83%

TABLE 7. EFFECT OF ROOTSTOCK ON DRY WEIGHTS OF VARIOUS ROOT COMPONENTS AND ROOT: SHOOT RATIO AT SIX MONTHS AFTER CYCLICAL WATER STRESS[c]

Monoclonal seedling rootstock	Dry weight (g)			Root: shoot ratio (%)
	Yellow feeder root	Tap-root	Roots in bottom bucket	
PB 260	4.31 a	6.66 a	0.70 a	40.6 b
GT 1	3.04 a	8.19 a	0.60 a	93.94 a
RRIM 623	2.33 a	7.74 a	0.87 a	61.69 ab
Probability level	NS	NS	NS	*

[c]Each value is an average of 4 replicates
Means with the same letters within columns are not significantly different
NS, * : F-test, non-significant or significant at P<0.05.

TABLE 8. EFFECT OF ROOTSTOCK AND SOIL WATER TREATMENT ON DRY WEIGHT OF PLANT PARTS AND ROOT COMPONENTS AFTER SIX MONTHS OF TREATMENT APPLICATION[a]

Dry weight (g)	Monoclonal seedling rootstock						R	SWT	RXSWT
	PB 260		GT 1		RRIM 623				
	SWT	Control	SWT	Control	SWT	Control			
Scion stem	18.3	20.71	11.11	14.63	11.91	11.16	#	NS	NS
Laminae	5.16	6.49	6.23	5.86	5.87	6.3	NS	NS	NS
Petiole	1.28	1.65	0.97	1.81	1.62	1.25	NS	NS	#
Brown lateral roots	6.21	3.98	6.23	5.21	2.97	3.62	*	NS	NS
Whole lateral roots	7.68	8.96	9.52	8.08	5.46	5.78	*	NS	NS
Roots in top bucket	12.57	16.69	17.02	16.73	12.91	13.8	**	*	#
Roots in bottom bucket	0.25	1	0.13	0.91	0.42	1.18	NS	**	NS
Tap-root	4.89	7.83	7.5	8.66	7.46	8.02	NS	#	NS
Whole root	12.81	17.69	17.13	17.65	13.2	14.9	*	**	NS
Whole plant	37.58	46.55	35.43	39.95	32.6	33.61	NS	NS	NS

[a]Each value is an average of 4 replicates
NS, #, *, ** : F-test, non-significant or significant at P<0.10, 0.05 or 0.01, respectively
R = rootstock; SWT = soilwater treatment

TABLE 9. EFFECT OF ROOTSTOCK AND SOIL WATER TREATMENT ON PERCENTAGE DRY WEIGHT OF STEM AND ROOT COMPONENTS AFTER SIX MONTHS OF TREATMENT APPLICATION[c]

% Dry weight	Monoclonal seedling rootstock PB 260		GT 1		RRIM 623		R	SWT	RXSWT
	SWT	Control	SWT	Control	SWT	Control			
Scion stem[a]	48.2	42.7	31.4	36.6	36.4	33.9	*	NS	NS
Laminae[a]	14.15	14.03	17.0	13.37	17.7	16.1	NS	NS	NS
Petiole[a]	3.42	3.57	2.7	4.4	4.9	3.67	NS	NS	*
Brown lateral roots[b]	48.37	22.1	38.18	31.67	23.36	25.43	#	*	*
Yellow lateral roots[b]	12.23	27.32	17.16	16.33	17.57	11.01	NS	NS	NS
Whole lateral roots[b]	60.60	49.46	55.33	48.01	40.93	36.45	*	NS	NS
Roots in top bucket[b]	98.14	94.38	99.15	94.87	98.2	93.95	NS	**	NS
Roots in bottom bucket[b]	2.02	5.62	0.85	5.13	2.7	6.68	#	***	NS
Tap-root[b]	37.39	44.93	43.82	46.87	57.27	57.51	*	NS	NS
Whole root[a]	34.2	39.7	48.9	45.6	41.0	46.4	#	NS	NS

NS, #, *, **, *** : F-test, non-significant or significant at $P<0.10$, 0.05, 0.01 or 0.001, respectively
R = rootstock; SWT = soil water treatment
[a]per g whole plant dry weight
[b]per g whole root dry weight
[c]Each value is an average of 4 replicates

(*Table 9*). However, this loss was compensated by an increase in the allocation of dry matter to roots in the top bucket by about 5%, the increase being attributed mainly to brown lateral roots. There was significant interaction effect between rootstock and soil water treatment with respect to percentage dry weight of brown lateral root. This parameter was not affected by rootstocks under control treatment; however, under shallow water treatment, PB 260 rootstock produced the highest percentage dry weight of brown lateral roots followed by GT 1 rootstock whilst RRIM 623 rootstock recorded the least value.

Among the three rootstocks studied , PB 260 rootstock was the most severely affected when moisture was not available to the growing root tips since its whole root dry weight in the shallow water treatment was only about 72% of the control (*Table 8*). The growth reduction was mainly attributed to a decrease in growth of tap-root (by about 38%). In contrast, overall root growth of RRIM 623 rootstock was only slightly reduced (by about 11%) when moisture was not available to the root tips. Shallow water treatment reduced dry weight of tap-root of GT 1 rootstock by about 13%; however, this was compensated by an increase in lateral root growth in the top bucket, so that there was little difference in biomass of whole root in this treatment compared to the control.

DISCUSSION

Effect of Moisture Availability on *Hevea* Root System

Dry substrate (gravel) in the bottom bucket of soil water treatment in *Experiment GH* acts as a mechanical resistance to further root growth since root tips mostly died upon entry into the dry substrate (*Table 8*). In contrast, root growth was promoted in the wetter soil in the bottom bucket of control treatment because the mechanical resistance was low rather than because of high soil water potential. Greacen and Oh[13] showed that root growth of peas was more sensitive to mechanical impedance than to changes in soil water potential, presumably because growth rate of a plant cell is determined by the extensibility of the cell wall material and wall pressure. The obstruction to root growth in the dry substrate of the present experiment not only reduced root growth in the substrate but it also has a deleterious effect on root growth in the upper bucket and consequently overall root growth (*Table 8*). The three *Hevea* rootstocks generally responded to obstruction to root growth in the bottom bucket by increasing the proportion of dry matter allocated to root growth in the top bucket indicating increased capacity to generate roots in this region (*Table 9*). Similarly, many crops such as oak, apple and lupin responded to either obstruction to root growth or water stress by stimulating lateral root growth or by increasing the percentage of fibrous roots near the soil surface[6,12,14] presumably due to increase in levels of endogenous abscissic acid[15].

Morphological and Physiological Responses of Rootstocks to Water Stress

RRIM 623 rootstock. Based on the classification of dehydration tolerance of some tropical crops and pasture species by Levitt[16], results obtained in *Experiment WS94* indicate that RRIM 623 rootstock can be classified as having drought avoidance strategy, since it exhibited many characteristics which tend to postpone desiccation during water stress[17]. Both PM 10 and RRIM 901 scion grafted on this rootstock had effective stomatal control as shown by early stomatal closure on the onset of water stress (*Figures 2–4*). This behaviour would enable the plants to maintain high RWC, thus avoiding severe tissue water deficit (*Figure 5*) and probably explains the ability of RRIM 623 rootstock to maintain root growth when moisture was not available to the growing roots in shallow water treatment of *Experiment GH* (*Table 9*).

RRIM 623 rootstock studied in *Experiments WS 94* and *GH* had high dry weight and percentage dry weight of tap-root (*Tables 8 and 9*) indicating that it is a fast growing rootstock with a high potential to develop into strong deeply penetrating tap-root, a finding in agreement with results of previous study[2]. This is yet another drought avoidance strategy developed by RRIM 623 rootstock by which it maximizes water uptake and postpones desiccation during drought. Studies in *Populus* clones and eucalyptus species have also shown the importance of extensive early root system for plant growth and survival during drought[18,19].

Several researchers[4,15] have shown that pre-dawn LWP which is a good estimate of soil water potential with which plants have come into equilibrium during the night[20], would also indicate differences in the capacity of the root system to absorb water attributed mainly to quantity of feeder roots. In our previous report, RRIM 623 rootstock was shown to have relatively low predawn LWP[2] indicating abundance of feeder roots in its root system[4,14]. However, there was no significant difference in dry weight of feeder roots amongst the three rootstocks studied in *Experiment GH*; this is probably explained by failure to recover fully all the feeder roots during washing due to their fine structure as attested to by the large coefficient of variation (68%) value obtained for this parameter. Since RRIM 623 rootstock did not increase the proportion of brown lateral roots when root growth was obstructed in the gravel of soil water treatment (*Table 9*), it can be concluded that its root system lacks plasticity and may be dependent only on deep soil water.

PB 260 rootstock. With the exception of LDR, other water relations parameters of the two-scion clones grafted on PB 260 rootstock did not show any consistent response to water stress (*Figures 2–5*). There was a tendency for plants grafted on PB 260 rootstock to exhibit both drought tolerance (shown by gradual decline in LDR of the two scion clones and rapid decline in RWC of RRIM 901 clone) and drought avoidance features[17] (shown by the ability of PM 10 clone to maintain relatively high RWC throughout the dehydration period). The inconsistent physiological responses to water stress shown by these plants is not surprising since it has been reported that not all perennials can fit in closely into either drought avoidance or tolerance categories[21].

PB 260 rootstock is characterised by extensive shallow lateral root system since the lateral roots formed a major proportion (more than 50%) of the root system (*Table 9*). Data on dry weight and percentage dry weight of tap-root indicate that PB 260 rootstock has low inherent capacity to develop into deep tap-root systems (*Tables 8 and 9*). Growth of the tap-root was substantially curtailed when growing into dry substrate of soil water treatment; consequently this led to substantial reduction in overall growth of the root system (*Table 8*). The more pronounced effect of moisture unavailability on growth of PB 260 rootstock compared to the other two rootstocks, probably indicates that PB 260 rootstock has low tolerance to soil water deficit and is more dependent on water near the soil surface. The higher percentage dry weight of brown lateral roots of this rootstock in shallow water treatment compared to other rootstocks is consistent with these assumptions. Coile[22] reported that under drought conditions, soil dries from the surface downward because of evaporation and high concentration of roots near the soil surface. As a result , shallow-rooted plants tend to suffer severe water deficit long before deeper rooted plants However, despite the substantial reduction in root growth, plants on PB 260 rootstock were able to maintain growth since there was no difference in growth of scion stem and whole plant between the two soil water treatments (*Tables 8 and 9*). This suggests that the plants in soil water treatment were able to meet the water requirement by promoting more growth of lateral roots as evident by increased allocation of dry matter to brown lateral roots (*Table 9*). Thus, it can be inferred that PB 260 rootstock with extensive shallow lateral root system could adapt morphologically to dry substrate since lateral root growth was stimulated when root growth was obstructed in the gravel of shallow water treatment to exploit the soil surface moisture.

RRIM 600 rootstock. Like PB 260 rootstock, RRIM 600 rootstock also did not appear to elicit consistent stomatal response to water stress on the two-scion clones (*Figures 2–5*).

This could probably be attributed to the general lack of significant relationship between most of these water relation parameters with LWP for this rootstock (*Appendix 1*), an observation quite similar to our earlier report[2]. Apart from results obtained in *Experiment 94* which showed relatively shallow root system of RRIM 600 rootstock (*Table 3*), we do not have other information on the morphological response of this rootstock to water stress. However, limited information available indicate a tendency for field-grown RRIM 600 rootstock to have inherently lower amount of feeder root in the first 10 cm soil depth than invigorating PB 5/51 rootstock (Bastiah Ahmad)[23] (*Appendix 2*). Similarly in apples, less invigorating rootstocks were also reported to have less efficient root system on account of their smaller quantity of roots, less extensive root spread and slower hydraulic conductivity than vigorous rootstocks[24,25].

GT 1 rootstock. Physiological responses of GT 1 rootstock were not studied in *Experiment WS 94*. However, our previous report[2] had shown that this rootstock induced drought resistance response to RRIM 901 scion under water stress as indicated by gradual stomatal closure with increase in soil water deficits. In *Experiment GH*, GT 1 rootstock with moderately deep tap-root and extensive lateral-root system, was the most vigorous among the three rootstocks studied (*Table 8*); this seems to confirm a previous study[2]. Although not statistically different, GT 1 rootstock in *Experiment RS 98*, also had vigorous root system even though it was only moderately deep rooting compared to RRIM 937 and RRIM 712 rootstock (*Tables 4 and 6*). However, data on pre-dawn LWP implied the presence of larger quantity of feeder roots[14] for both GT 1 and RRIM 937 rootstock compared to RRIM 712 rootstock (*Table 1*). A corollary to this observation is that rootstocks having a potential to develop into deep root systems such as RRIM 712 rootstock may not necessarily be endowed with abundant feeder roots.

The behaviour of GT 1 rootstock appears to be quite similar to PB 260 rootstock since it responded to the obstruction to root growth in the dry substrate of *Experiment GH* by increasing the proportion of dry matter allocated to brown lateral roots (*Table 9*). This characteristic, together with its potential to develop into moderately deep root systems, seems to suggest that GT 1 rootstock is morphologically adaptable as it can utilise either surface or deep soil water in response to moisture availability. This is quite similar to the behaviour of *Quercus lobata* (valley oak) species described by Callaway[12].

In *Experiment RS 98*, plants with unlike scion/rootstock combinations tended to have lower pre-dawn LWP (*Table 1*) indicating presence of larger quantity of feeder roots and consequently, better capacity for water uptake than those with similar combinations. This is especially true for combinations grafted with RRIM 712 clone but less so for those grafted with RRIM 937 clone. These observations tend to indicate the invigorating effect of scion clone on rootstock growth particularly feeder roots: this influence may not necessarily be proportional to scion vigour as amply shown in many crops[26]. Soong[27] working on *Hevea* has reported the influence of scion clones on quantity of feeder roots of Tjir-1 rootstock with vigorous clones producing substantially more feeder roots than slow growing clones.

CONCLUSION

Data from the present study indicate that dry matter production and distribution of the root system of *Hevea* monoclonal seedling rootstocks may give indications of their later growth characteristics in the field. In forest tree seedlings, early growth characteristics such as root growth capacity determined at early stage were found to be correlated to field performance[28]. It may therefore be possible, albeit after more research, to estimate relative field performance of *Hevea* monoclonal seedling rootstocks with respect to influence on clonal growth and yield, based on the quantity and distribution of their root systems.

In the present study, successful rootstocks appear to establish extensive root systems during early growth in the form of either deep penetrating tap-root as in RRIM 623 rootstock or a combination of moderately deep tap-root and extensive lateral roots as in GT 1 rootstock. Early rapid growth builds up a reserve that will help plants to survive severe drought and contribute to yield irrespective of whether the plants are resistant to drought[29]. These superior rootstocks are also ensured of better survival and establishment success on account of their accessibility to deep soil water and their capacity to generate feeder roots. Besides having a deep root system, RRIM 623 rootstock also has effective stomatal regulation of water loss, enabling it to sustain growth and productivity, even under severe drought. The dual survival mechanism exhibited by RRIM 623 rootstock that minimises water loss through effective stomatal control and maximises water uptake through a deep rooting system, probably explains for the good performance of clones grafted on this rootstock in Malaysia.

Besides having vigorous root system, the success of GT 1 rootstock may also be attributed to the morphological flexibility of its root system as well as to its drought tolerant response to water stress. These factors probably contribute to the hardy nature of this rootstock and explains its good field performance since it is currently one of a few rootstocks that is known to improve rubber growth and yield[30]. The behaviour of GT 1 rootstock in this investigation is consistent with field observation that GT 1 seedling rootstocks are more tolerant to drought than most other *Hevea* rootstocks[31].

In contrast, the root systems of PB 260 and RRIM 600 rootstock which are known to have poor field performance[30] tend to lack deep tap-root systems; these rootstocks also did not seem to give any consistent stomatal response to soil water deficit.

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APPENDIX 1.

REGRESSION COEFFICIENTS OF POLYNOMIAL EQUATIONS BETWEEN PREDAWN LEAF WATER POTENTIAL AND WATER RELATIONS PARAMETERS IN *EXPERIMENT WS 94*

Parameter	Scion: PM 10			RRIM 901		
	Monoclonal seedling rootstock					
	PB 260	RRIM 600	RRIM 623	PB 260	RRIM 600	RRIM 623
Leaf diffusive resistance	0.9735***	0.4081 NS	0.7798 *	0.6507 #	0.6326 *[a]	0.9379 **
Stomatal conductance	0.7322 *	0.7574 *	0.7268 #	0.6202 #	0.6326 *[a]	0.6772 #
Transpiration rate	0.7991 *	0.7015 #	0.7501 #	0.6228 #	0.2914 NS	0.7537 #
Relative water content	0.81 *	0.5378 #[a]	0.8009 *	0.9246 **	0.3694 NS	0.9653 **

NS, #, *, **, ***: F-test, non-significant or significant at P<0.10, 0.05, 0.01 or 0.001, respectively.
[a]Regression coefficient for linear relationship

APPENDIX 2.

EFFECT OF ROOTSTOCK ON FEEDER ROOT DENSITIES[a] WITHIN 30 CM OF SOIL SURFACE

Soil depth (cm)	Monoclonal seedling rootstock	Mean root density +/– SD cc/1000 cc of soil	mg/1000 cc of soil
0 – 10	PB 5/51	625.0 +/– 31.7	457.9 +/– 54.9
	Mixed seedlings	551.4 +/– 113.3	442.2 +/– 117.6
	RRIM 600	356.4 +/– 152.7	300.5 +/– 99.7
10 – 20	PB 5/51	117.8 +/– 35.9	122.8 +/– 24.0
	Mixed seedlings	70.3 +/– 36.5	78.0 +/– 42.7
	RRIM 600	87.9 +/– 41.2	92.1 +/– 40.9
20 – 30	PB 5/51	63.5 +/– 25.6	60.8 +/– 22.6
	Mixed seedlings	37.3 +/– 30.3	42.1 +/– 33.6
	RRIM 600	29.1 +/– 14.9	25.9 +/– 13.9

[a]Feeder root densities of three rootstocks grafted with RRIM 600 clone were determined from 9-year-old composite trees grown in RRIES. The determinations were carried out between May to June 1993 using auger as described by Soong[27]. Feeder roots were sampled from 3 trees per replicate from a total of 3 replicates. Feeder roots (<2 mm diameter) were washed and root length measured by a line intersect method using Delta-T root length meter. Root dry weights were determined after oven drying at 80°C for 48 h.

SD = standard deviation.