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Physiological responses of mycorrhizal and uninoculated seedlings of mangosteen (*Garcinia mangostana* L.) to water depletion and subsequent rewatering

[Tindak balas fisiologi anak benih manggis (*Garcinia mangostana* L.) yang bermikoriza dan tanpa mikoriza terhadap pengurangan dan pemberian semula air]

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Key words: mycorrhiza, physiological processes, water stress, recovery, mangosteen

Abstrak

Kajian awal mendapati bahawa inokulasi mikoriza meningkatkan pertumbuhan dan mutu keseluruhan anak benih manggis. Oleh itu, pengetahuan tentang ketahanan anak benih ini semasa tegasan air sangat penting. Dalam percubaan yang dijalankan di rumah kaca, anak benih manggis berumur 15 bulan yang diinokulatkan dan tanpa inokulasi digunakan. Pengairan anak benih ini diberhentikan selama 10 hari diikuti dengan pengairan semula pada hari yang ke-11. Tindak balas anak benih terhadap keadaan tegasan air dan pemulihan diukur melalui perubahan potensi air daun (Ψ_L), konduktans stomata (g_s) dan fotosintesis (Pn). Hasil daripada percubaan menunjukkan bahawa Ψ_L anak benih yang mengalami tegasan air jatuh sehingga mencecah –1.5 MPa 10 hari selepas pengairan diberhentikan. Akan tetapi anak benih yang cukup pengairannya Ψ_L kekal antara –0.2 hingga –0.4 MPa. Perbezaan yang ketara antara nilai Ψ_L kedua-duanya sudah bermula sejak hari yang keempat lagi. Anak benih yang bermikoriza boleh mengekalkan Ψ_L yang lebih tinggi berbanding dengan pokok tanpa mikoriza. Bagi setiap unit kejatuhan Ψ_L, g_s dan Pn masing-masing menyusut sebanyak 1.38–1.44 cm/saat dan 1.64–1.89 µmol/m^2/saat berbanding dengan kejatuhan yang lebih teruk sebanyak 1.94 cm/saat (g_s) dan 2.08 µmol/m^2/saat (Pn) yang dialami oleh anak benih tanpa jangkitan mikoriza. Setelah pengairan semula, Ψ_L , g_s dan Pn anak benih bermikoriza pulih kepada nilai yang sama dengan anak benih yang diberikan pengairan dengan lebih cepat. Untuk seunit pemulihan Ψ_L, proses fisiologi anak benih bermikoriza pulih dengan kadar 0.34–0.42 cm/saat (g_s) dan 1.78–2.50 µmol/m^2/saat (Pn) berbanding dengan pemulihan sebanyak 0.18 cm/saat dan 1.45 µmol/m^2/saat bagi anak benih tanpa mikoriza. Kesimpulannya inokulasi mikoriza arbuskel membaiki hubungan air anak benih manggis baik semasa tegasan mahupun pemulihan. Oleh yang demikian, inokulasi ini penting untuk meningkatkan kemandirian mereka selepas dialih ke ladang.

Abstract

Earlier reports have shown that mycorrhizal inoculation enhanced growth and overall quality of mangosteen seedlings. It is therefore imperative to evaluate the performance of these seedlings under the rigours of transplanting conditions. A glasshouse experiment was conducted by subjecting 15-month-old pre-inoculated

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mangosteen seedlings to non-irrigated conditions for 10 days followed by recovery irrigation from the 11th day onwards. Response of these seedlings to both water stress and recovery conditions was evaluated by comparing changes in leaf water potential (Ψ_L), stomatal conductance (g_s) and photosynthesis (Pn) with those of uninoculated seedlings. Results showed that as Ψ_L of irrigated seedlings remained between –0.2 and –0.4 MPa, the Ψ_L of stressed plants decreased progressively and reached –1.5 MPa after 10 days of withholding water. These Ψ_L values were significantly different from those of irrigated treatments as early as the fourth day. Mycorrhizal seedlings were able to maintain a relatively higher Ψ_L than the uninoculated ones. For every unit drop in Ψ_L, g_s in mycorrhizal seedlings decreased by 1.38–1.44 cm/s while Pn by 1.64–1.89 µmol/m^2/s. The corresponding decreases for g_s and Pn of uninoculated seedlings were 1.94 cm/s and 2.08 µmol/m^2/s respectively. On any given day, g_s and Pn of mycorrhizal seedlings were consistently higher than that of uninoculated seedlings. Upon rewatering, Ψ_L, g_s and Pn of mycorrhizal seedlings recovered to values not significantly different from irrigated plants within a shorter time period. The recovery rate of these processes was relatively faster than in uninoculated seedlings. As per unit increase in Ψ_L, physiological processes of mycorrhizal seedlings recovered at 0.34–0.42 cm/s (g_s) and 1.78–2.50 µmol/m^2/s (Pn) as compared with 0.18 cm/s and 1.45 µmol/m^2/s respectively by uninoculated seedlings. In conclusion, arbuscular mycorrhizal inoculation improved water relations of mangosteen seedlings both during stress and recovery period that could be important for their survival after field planting.

Introduction

Water availability is one of the dominant factors influencing early growth of transplanted seedlings. Higgs et al. (1995) had shown that fluctuation in water supply during transplanting adversely affected survival and later performance of seedlings. Even a relatively short-term decrease in water availability may cause transient effects on seedling performance such as partial stomatal closure, change in nutrient accumulation or decline in enzyme activity (Talouizite and Champigny 1988). Furthermore, the loss of roots at lifting and slow root regeneration when transplanted make many plant species succumb to water stress conditions during establishment (Struve 1990).

Arbuscular mycorrhiza (AM) fungi are important because they have been shown to improve the water relations of host plant during water stress. Sieverding and Toro (1987) had shown that increased survival of mycorrhizal coffee and tea seedlings after transplanting resulted from improved water relations. Similarly, pre-inoculated seedlings of two native forbs grew significantly larger than non-inoculated seedlings under drought conditions (Zajicek et al. 1987). In addition, more rapid recovery from water stress and higher soil water extraction have been observed in mycorrhizal plants (Hardie and Leyton 1981).

A report by Masri et al. (1998) has shown that inoculation with arbuscular mycorrhiza fungi enhanced growth and improved the overall quality of mangosteen seedlings. The improvements were mostly due to positive alterations of root system characteristics by the fungi (Masri and Azizah 1998). Since one of the common problems in the cultivation of mangosteen is the high mortality rate after transplanting, it is therefore important to evaluate the performance of these seedlings under the rigours of transplanting conditions. The implications of these responses may be vital for a successful seedling establishment in the field. This experiment therefore aims to evaluate the response of arbuscular mycorrhizal-inoculated mangosteen seedlings to water stress and recovery conditions.

Materials and methods

Inoculation and plant preparation

Both inoculated as well as uninoculated mangosteen seedlings were prepared prior to conducting the experiment. Seeds were sown in sand-beds and 2 weeks after full germination, uniform-sized seedlings were randomly selected and transferred into 30 cm x 36 cm polyethylene bags filled with 10 kg of potting mixture comprising sand, soil and cowdung in the ratio of 3:2:1 by volume. Seedlings of the two mycorrhizal treatments were inoculated with *Glomus mosseae,* and a mixture of *G. mosseae* and *Scuttelospora calospora*. Uninoculated seedlings were regarded as controls. They were respectively designated as GM for *Glomus mosseae*, MS for the mixed species and –M for the uninoculated controls. A full description on the inoculation process was given by Masri et al. (1998).

On completion of the inoculation, seedlings were all grown and maintained under a 50% shade nursery for 15 months. They were irrigated daily and regularly maintained free from pests and weeds. After 15 months, the seedlings had attained a suitable size and were ready for the water stress treatments.

Water stress experiment

The experiment was conducted in a glasshouse at Universiti Putra Malaysia, Serdang. Prior to imposition of treatments, some roots were sampled, cut into 1-cm length, cleared and stained using chlorazol black-E (Brundrett et al. 1984). The root segments mounted on glass slides were later scanned under microscope and mycorrhizal infection in inoculated seedlings was determined adopting the method of Bethlenfalvay et al. (1981). Water stress treatment comprised two levels of soil moisture regimes, namely daily irrigation of 500 mL of water per polyethylene bag and water withholding for 10 days followed by rewatering from the 11th day onwards, were imposed on both inoculated as well as uninoculated seedlings.

Measurements of parameters

Measurements of parameters were made on every alternate day. Leaf water potential (Ψ_L) was estimated on different plants for each sampling occasion using a pressure chamber (Scholander et al. 1965). Leaf petioles were cut with a sharp razor and immediately inserted through a small hole in the lid of the chamber. The pressure of the chamber was increased until the sap from the xylem started to ooze out. This is visible with the help of a hand lens. The pressure at this point was assumed to be equal to the $\Psi_{L.}$

Stomatal conductance (g_s) and photosynthesis (Pn) of fully matured leaves were measured using the LCA3 Portable Photosynthesis System (ADC-Hoddesdon, UK). A total of 8–10 measurements were made for each plant replicate. Measurements were made at midday from 1100 h to 1500 h. The photosynthetic active radiation (PAR), relative humidity and glasshouse temperatures during these measurement hours ranged from 200 to 500 µmol/m^2/s, 65.5% to 72.1% and 28.9 °C to 33.2 °C respectively.

From the 11th day onwards, the stressed seedlings were rewatered with 500 mL of water daily. Changes in the Ψ_L, g_s and Pn were measured again on every alternate days of the recovery period. The experiment was terminated when these parameters resumed to similar levels at par with the well-watered seedlings.

On the 10th day after treatments were imposed, matured leaves located one node below the most recent flush were randomly selected from each plant replicate and oven dried at 80 °C for 48 h. Dried leaves were subsequently ground using a hammer mill. Plant potassium concentration was measured by inductively coupled plasma emission spectrometric analysis using wet-ashing procedures (Ahmad 1993).

Design and statistical analysis

Treatment combinations were arranged in a randomized complete block design with four replications. Analyses of variance were performed using the procedures of SAS (SAS Institute Inc. 1985). For significant water x mycorrhizal interaction effects *(Table 1)*, the Least Significant Difference (LSD) method was used to compare the means of mycorrhizal treatments under stress conditions.

Results

Leaf water potential

Leaf water potential (Ψ_L) was used as the indicator of plant water status. Midday Ψ_L of irrigated seedlings remained between –0.2 and –0.4 MPa throughout the drying period *(Figure 1)*. However, the midday Ψ_L of stressed seedlings decreased rapidly as the water withholding period increased. By the fourth day, Ψ_L of stressed seedlings had dropped to about –0.6 MPa that was significantly lower than the Ψ_L of irrigated plants. The decreasing trend of Ψ_L in stressed plants continued progressively and reached the lowest value of about –1.5 MPa on the 10th day after water was withheld.

Response to water stress

Water stress had little effect on stomatal conductance (g_s) of irrigated seedlings *(Figure 2)*. The g_s of irrigated seedlings remained relatively constant and ranged from 0.5 to 1.0 cm/s throughout the drying period. However, g_s of stressed plants decreased tremendously as duration of water withholding increased. By the fourth day after water was withheld, g_s of seedlings began to drop progressively. Although their values were not statistically significant, there was a trend of lower conductance in uninoculated compared with mycorrhizal seedlings beginning on the fourth day.

Photosynthetic rates of mycorrhizal and uninoculated seedlings as affected by water stress are shown in *Figure 3*. The average photosynthesis (Pn) of irrigated mangosteen seedlings fluctuated between 2.9 and 3.8 μmol/m^2/s for the 10-day period. In contrast, Pn of stressed plants decreased as water stress became progressively more severe and reached significantly lower values by the sixth day after water withholding. By the 10th day, Pn of stressed plants dropped to less than 0.1 μmol/m^2/s, indicating almost complete closure of stomata. Similar to g_s, the drop in Pn seemed more severe in the uninoculated seedlings. On any day, uninoculated seedlings had lower Pn than the mycorrhizal seedlings.

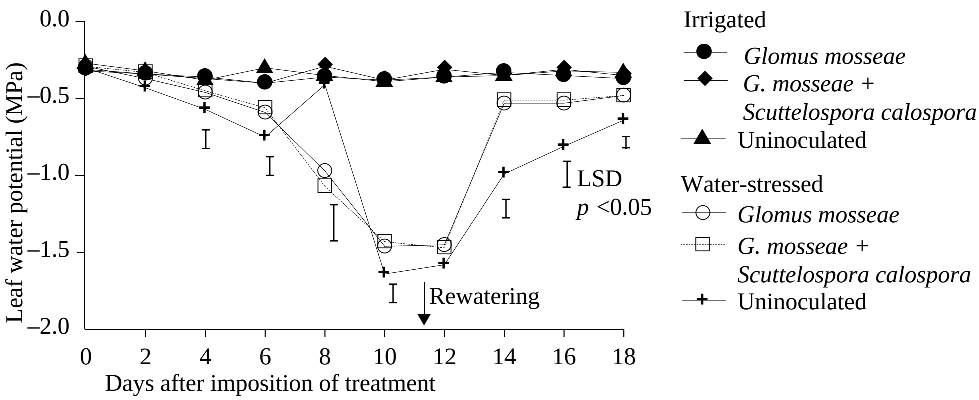

Figure 1. Changes in leaf water potential of irrigated and water-stressed seedlings after imposition of treatments

Table 1. Mean squares of the ANOVA for leaf water potential, stomatal conductance and photosynthesis at different days after imposition of treatments

Source	df	Mean squares after imposition of treatments								
		Day 2	Day 4	Day 6	Day 8	Day 10	Day 12	Day 14	Day 16	Day 18
Leaf water potential										
Replicate	3	0.059	0.144	0.615	1.402	0.459	6.434	0.178	0.342	0.251
Water (W)	1	2.042	9.127**	53.701**	404.261**	763.802**	86.940	66.667**	54.300**	21.094**
Mycorrhiza (M)	2	0.128	1.042*	1.100	11.682**	3.072**	0.895	14.884**	5.540**	1.095*
W x M	2	0.365	0.672*	4.480*	10.121**	3.282**	0.555	13.730**	5.807**	2.375**
Error	15	0.079	0.163	0.500	0.575	0.279	5.265	0.394	0.839	0.189
Total	23									
Stomatal conductance										
Replicate	3	0.651	0.012	0.118	0.002	0.130	0.180	0.139	0.092	0.085
Water (W)	1	0.021	0.170	0.753	1.058	2.576	4.076	3.278	1.576	0.152
Mycorrhiza (M)	2	0.090	0.005	0.001	0.004	0.008	0.002	0.007	0.030	0.326*
W x M	2	0.002	0.005	0.016	0.015	0.008	0.007	0.026	0.073	0.244*
Error	15	0.043	0.027	0.020	0.015	0.035	0.047	0.072	0.049	0.057
Total	23									
Photosynthesis										
Replicate	3	1.686	0.451	1.959	0.212	0.487	0.186	0.244	0.343	0.302
Water (W)	1	0.796	0.810	18.550	16.023	41.712	47.969	25.810**	9.601**	1.131*
Mycorrhiza (M)	2	0.697	0.260	0.139	0.165	0.228	0.009	1.471**	1.748*	0.715*
W x M	2	0.343	0.178	0.042	0.119	0.004	0.288	0.981*	1.648*	0.951*
Error	15	0.372	0.509	0.330	0.086	0.337	0.107	0.205	0.348	0.211
Total	23									

**significant at $p < 0.01$
*significant at $p < 0.05$

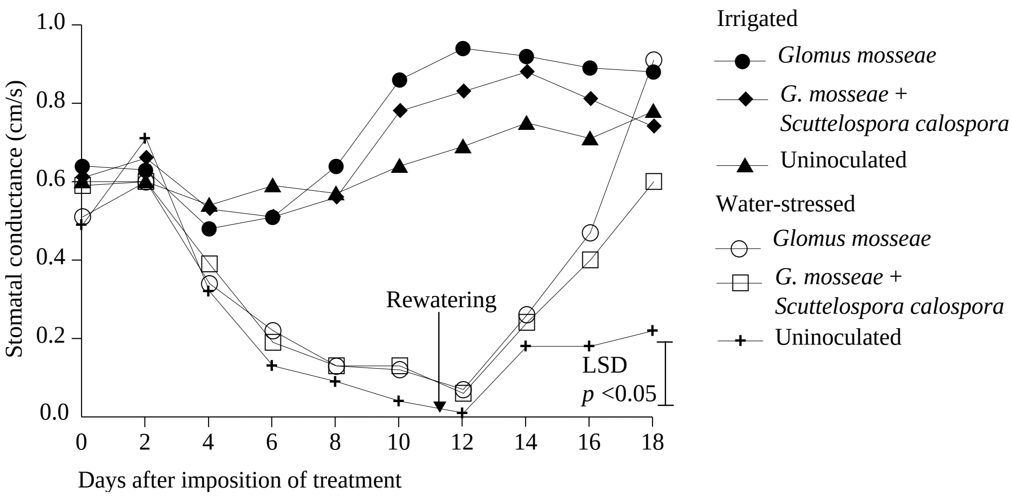

Figure 2. Changes in stomatal conductance of irrigated and water-stressed seedlings during period of water withholding and after rewatering

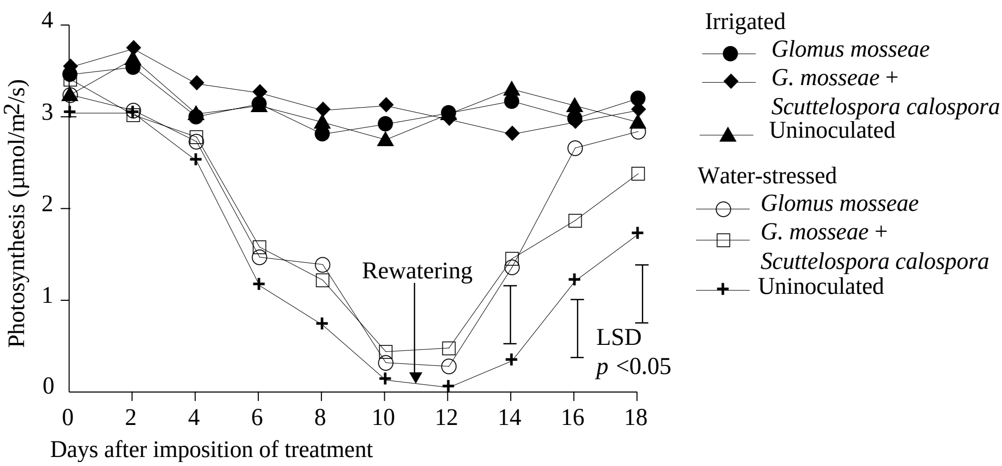

Figure 3. Photosynthesis of irrigated and water-stressed seedlings during period of water withholding and after rewatering

Leaf potassium (K) concentrations of mycorrhizal and uninoculated seedlings measured at the end of the stress period are shown in *Table 2*. Seedlings inoculated with mycorrhiza accumulated significantly higher percentage of K than uninoculated seedlings.

Response to rewatering

Upon rewatering, Ψ_L of stressed plants showed a one-day lag phase during which no recovery of Ψ_L took place *(Figure 1)*. After this lag phase, recovery of Ψ_L commenced and proceeded rapidly. However, Ψ_L of mycorrhizal plants recovered faster and resumed to values not significantly different from their respective controls 3 days after rewatering. In contrast, Ψ_L values of the uninoculated seedlings remained significantly lower than that of the irrigated seedlings even after 7 days of rewatering indicating they did not fully recover.

Parallel to this, the recovery of g_s and Pn also showed a one-day lag period. Their rapid recovery only commenced after 3 days of rewatering. It was observed that the recovery of g_s and Pn of inoculated seedlings completed after 7 days of rewatering. In contrast, the g_s of uninoculated seedlings did not fully recover within the same period. The g_s of GM and MS-treated seedlings recovered at the rate of 0.20 and 0.13 cm/s/day respectively, compared with only 0.05 cm/s day for the uninoculated seedlings. Similarly, the Pn of these seedlings recovered at 0.80 and 0.66 $\mu mol/m^2/s$ per day compared with 0.43 $\mu mol/m^2/s$ per day for the uninoculated controls.

In terms of per unit Ψ_L, g_s of inoculated seedlings recovered at 0.42 cm/s (GM) and 0.34 cm/s (MS) as opposed to 0.18 cm/s per unit increase in Ψ_L in the uninoculated seedlings *(Table 3)*. Similarly, Pn recovered at 2.50 and 1.78 $\mu mol/m^2/s$ respectively for every unit recovery of Ψ_L for GM and MS-treated seedlings compared with only 1.45 $\mu mol/m^2/s$ for the uninoculated seedlings.

Table 2. Accumulation of potassium by mycorrhizal and uninoculated seedlings during water stress

Treatment	Concentration (%)
Inoculated	
Glomus mosseae	1.58a
G. mosseae + S. calospora	1.58a
Uninoculated	1.22b

Mean values with the same letter are not significantly different at $p < 0.05$

Discussion

Midday Ψ_L of irrigated plants remained between –0.2 and –0.4 MPa indicating that the plants were not under stress conditions. However, withholding water for 10 days had successfully induced the required water stress. This was clearly indicated by the significantly lower values of Ψ_L in stressed treatments beginning on the fourth day after water was withheld. The lowest Ψ_L of –1.5 was recorded on the 10th day. Visual symptoms of water stress such as midday leaf drooping and shrinking of the petiole were observed in these plants as early as 8 days after water withholding. Responses of mycorrhizal and uninoculated seedlings to water stress showed some differences, although water stress significantly reduced Ψ_L of both seedlings. Results showed that mycorrhizal plants could maintain relatively higher Ψ_L during the stress period. This could be due to greater water extraction capabilities of the mycorrhizal plants compared with the uninoculated controls. Greater water extraction by mycorrhizal plants was basically due to their greater root

Table 3. Linear equations of the relationship between stomatal conductance (g_s) and photosynthesis (Pn) with leaf water potential (Ψ_L) during the stress and recovery period

Treatment	Condition	Equation	r^2
Glomus mosseae (GM)	Stress	Ln $g_s = -0.37 + 1.38\Psi_L$	0.81
		Ln Pn = $1.78 + 1.89\Psi_L$	0.93
	Recovery	$g_s = 0.65 + 0.42\Psi_L$	0.67
		Pn = $3.64 + 2.50\Psi_L$	0.74
G. mosseae + *Scuttelospora calospora* (MS)	Stress	Ln $g_s = -0.28 + 1.44\Psi_L$	0.78
		Ln Pn = $1.67+1.64\Psi_L$	0.94
	Recovery	$g_s = 0.54 + 0.34\Psi_L$	0.67
		Pn = $3.02 + 1.78\Psi_L$	0.72
Uninoculated (–M)	Stress	Ln $g_s = 0.05 + 1.94\Psi_L$	0.89
		Ln Pn = $1.92 + 2.08\Psi_L$	0.88
	Recovery	$g_s = 0.34 + 0.18\Psi_L$	0.98
		Pn = $2.33 + 1.45\Psi_L$	0.80

growth and functions (Masri and Azizah 1998). Several earlier studies have also shown the ability of mycorrhizal plants to absorb water more efficiently during drought than non-mycorrhizal plants (Dixon et al. 1980; Levy et al. 1983; Kothari et al. 1991). Bethlenfalvay et al. (1988) had shown that increased length and biomass of fungal hyphae under drought stress could be another factor for increased water extraction by mycorrhizal plants. The ability to maintain higher Ψ_L had strong impact in increasing drought tolerance of these plants.

As expected, water stress had significantly reduced critical physiological processes such as g_s and Pn of mangosteen seedlings. These effects were also observed in other fruit trees exposed to water stress such as starfruit (Mohd. Razi et al. 1992; Masri 1995), durian (Mohd. Razi et al. 1994) and *Lansium* spp. (Mohd. Razi et al. 1993).

It was observed that stomatal regulated processes such as g_s and Pn correlated strongly with plant water status. Mycorrhizal mangosteen seedlings seemed to have somewhat higher g_s and Pn at the same level of Ψ_L as compared with uninoculated seedlings. These results clearly indicate that the Ψ_L at which the stomata close was much lower in mycorrhizal plants. As such, they were more tolerant to water stress because they could maintain reasonably higher g_s and Pn. Several studies have been reported on similar stomatal regulation by mycorrhiza under water stress conditions. Allen (1982) found water stress mycorrhizal *Boutaloua gracilis* plants had lower stomatal resistance and higher transpiration rate than non-mycorrhizal plants. Similarly, Huang et al. (1984) demonstrated that mycorrhizal plants had relatively higher g_s that apparently resulted in more carbon assimilation. In fact, Levy and Krikun (1980) had earlier concluded that most of the effect of AM association under water stressed condition was on stomatal regulation.

The substantially higher g_s and Pn in mycorrhizal plants proved that they were more tolerant to water stress. This can be considered as their strategy for stress tolerance. This strategy is very useful for their quick establishment after field planting. Auge and Duan (1991) reported that changes in g_s were in fact the mechanism by which mycorrhizal plants increased their resistance to drought. Ludlow et al. (1985) had earlier put forth the concept of stomatal adjustment as an acclimation process that occurs in many plants subjected to water deficits. They defined stomatal adjustment as a progressive reduction in stomatal sensitivity to changes in Ψ_L.

In this study, the improved performance of mycorrhizal seedlings under water stress conditions was partly due to better K nutrition. Mycorrhizal seedlings subjected to water stress had significantly higher leaf K content. Potassium plays a cationic solute that is responsible for stomatal movement in response to the changes in leaf water status (Ruiz-Lozano et al. 1995). Lehto (1992) and Berry et al. (1992) also found improved stomatal behaviour of mycorrhizal seedlings due to better P and K nutrition. Higher uptake of K by mycorrhizal plants therefore allows maintenance of high g_s and Pn at low Ψ_L.

Upon rewatering, recovery of Ψ_L, g_s and Pn in stressed plants occurred in two separate stages. The first stage was characterised by a one-day lag phase, during which no recovery took place. After this lag phase, Ψ_L, g_s and Pn recovered progressively and rapidly. Kirschbaum (1988) also observed a distinct bi-phasic pattern of recovery in water stressed *Eucalyptus pauciflora*. Stomatal conductance recovered at 0.42 cm/s (GM) and 0.34 cm/s (MS) as opposed to only 0.18 cm/s per unit increase in Ψ_L in the uninoculated seedlings. Similarly, Pn recovered at 2.50 and 1.78 $\mu mol/m^2/s$ respectively for every unit recovery of Ψ_L for GM and MS-treated plants compared with only 1.45 $\mu mol/m^2/s$ for the uninoculated seedlings.

The existence of lag phase indicated that recovery is only possible above a certain threshold level of Ψ_L. Once the levels had been attained, recovery commenced and proceeded rapidly. The results also showed that recovery of mycorrhizal plants was more rapid than the uninoculated controls. The complete and rapid recovery of the inoculated seedlings was related to their ability to absorb more water and therefore make maximum use of the available water after the relief from water stress. Mycorrhizal infections have been shown to increase root hydraulic conductivity and hence water uptake (Kothari et al. 1990; Cui and Nobel 1992). Faster recovery from water stress by mycorrhizal mangosteen plants strongly indicated that they could survive better under the rigours of transplanting conditions.

Conclusion

The present results show that mycorrhizal inoculation increased the tolerance of mangosteen seedlings to water stress. They had greater water extraction ability and could maintain higher g_s and Pn at lower levels of Ψ_L. In addition, more rapid and complete recovery from water stress was evidently observed in inoculated seedlings. Mycorrhizal inoculation therefore significantly improved water relations of mangosteen seedlings during water stress and recovery. As such, the serious problems of water stress which mangosteen seedlings are usually exposed to during transplanting may be effectively alleviated by mycorrhizal inoculation. This in turn could result in greater seedling survival rate during early establishment stage.

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