

The Exploitation of Root-sourced Signals to Reduce Irrigation and to Regulate Leaf Growth of Pepper Plants *Capsicum annuum* L.

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ABSTRAK

Pengaruh pengeringan separa akar (PSA) terhadap pertumbuhan dan proses fisiologi tanaman cili, *Capsicum annuum*. L kultivar MC12 telah dikaji dalam keadaan suhu dan kelembapan tinggi di iklim tropika. Potensi air daun, kadar fotosintesis, konduksi stomata dan kadar transpirasi *Capsicum* yang diberi rawatan PSA dalam jangka masa 10 hari adalah rendah dibandingkan dengan pokok yang diberikan air yang berterusan. Pembuangan akar yang terdedah kepada tegasan air menghasilkan pemulihan semula kesemua parameter pertukaran gas mengesahkan kehadiran signal dihasilkan terus dari akar yang mengalami tegasan air. Pertumbuhan daun dipengaruhi secara negatif melalui teknik PSA, juga menyebabkan pengurangan luas daun sepokok. Penghasilan pokok yang ditanam dalam keadaan PSA adalah 73% dari jumlah hasil pokok yang diberikan air berterusan manakala jumlah air yang diberikan kepada pokok PSA adalah separuh dari jumlah yang diberikan kepada pokok kawalan.

ABSTRACT

The effect of partial root drying (PRD) on growth and physiological responses of pepper plants *Capsicum annuum* L. cultivar MC12 was investigated under high temperatures and a humid tropical climate. The leaf water potential, photosynthetic rate, stomatal conductance and transpiration rate of *Capsicum* plants grown under PRD over a period of 10 days were lower than those grown under well watered conditions. Removal of the droughted roots resulted in resumption of all leaf gas exchange parameters confirming the presence of signals coming directly from the droughted roots. Leaf growth rate was negatively affected by PRD techniques; as a consequence leaf area per plant was reduced. Total fruit yield of PRD plants was about 73% of the control plants' fruit yield while the amount of water added to the PRD plants was half the quantity added to the controls.

INTRODUCTION

The control of the stomatal aperture is often paramount in the regulation of water balance and it represents the first defence line against adverse environmental stimuli such as water stress (Raschke 1975). A fall in water potential and turgor of the leaf tissue can result in stomatal closure (Begg and Turner 1976). It is still not fully understood to what extent this closure is due to a direct hydraulic effect on the guard cells or whether a signal within the leaf plays a role. Ample evidence indicates that shoot processes such as growth rate and stomatal closure are controlled by signals from the root and that the root is capable of conveying this information

to the shoot in the form of a positive chemical signal such as an increase in ABA (Davies and Zhang 1991; Davies *et al.* 2000; Loveys *et al.* 2000). This suggests that the shoot growth and functioning may be modified as a function of the chemical signals synthesized in the root after contact with drying soil (Loveys *et al.* 1984; 1991; 1998; 2000).

Loveys and colleagues, who first exploited the use of PRD which generated from the split root of Gowing (1990), successfully reduced the need for grapevine pruning without altering the balance between leaf production and fruit yield while the quality of the fruit produced was greatly increased. This experiment was designed

to study the effects of root to shoot signaling of Capsicum plants when half of the root system is exposed to drying soil. It also attempts to determine to what extent the technique of partial root drying can be used to reduce the irrigation and to regulate containerized Capsicum plant growth under protective environmental agriculture.

MATERIALS AND METHODS

Experimental Treatment and Design

The experimental materials used were pepper plants *Capsicum annuum* L., cultivar MC12. This cultivar was produced by Malaysian Agricultural Research Development Institute (MARDI). Pepper plants were raised from seeds sown in peat-based compost under a shade house. Seedlings were potted into seedling pots when their first true leaf pair emerged and sown for a further 15 days at 28-32°C daily temperatures without supplementary light. The seedlings were irrigated daily to drip point with tap water and twice per week with half strength Cooper solution (Cooper 1976). Seedlings of similar size and vigor were then selected and transferred to the shade house with their root system washed free of peat. The root system was separated into approximately two equal parts and the plants were re-potted into 2-liter pots which were refilled with a soil mixture of 3:2:3 (soil: sand: peat respectively). A compound fertilizer (NPK) was added to the plants at a rate of 5 g per pot after transplanting. Plants were allowed 25 days to establish their root system in the new containers under well-watered conditions before treatments were applied. The two pots were raised from the ground to prevent drained water from well-watered pots reaching the un-watered ones. The daily temperature of the shade house was 28-32°C without supplementary light. The relative humidity was about 65% and 80% day and night. After seedlings established their roots in the new containers, the seedlings were divided into two groups: 1) control plants where the two pots received watering to drip point and 2) stressed plants in which both pots received watering to drip point at the beginning of the experiment and then roots in one pot remained without irrigation and allowed to dry the soil to about 40% of the soil moisture content (*Fig. 1*). After 10 days the previously dry pots (10 pots out of 20) were watered to drip point and the previously watered pots were allowed to dry the soil

moisture to about 40%. The cycle of the drying period was 10 days. As for the other 10 plants, after the first partial root drying regime (10 days), their roots in drying soil were severed and cut off the plants to investigate the physiological responses of the plants. The rest of the plants continued the partial root drying cycle until harvest. The experiment was arranged in a completely randomized design and each treatment was replicated 20 times. Stomatal conductance of fully expanded leaves was recorded with a diffusion prometer (AP-4, Delta-T Devices Ltd., Cambridge). Leaf water potential was measured daily on fully expanded leaves with a pressure chamber. Photosynthetic and transpiration rates of plants' leaves were monitored using an LCA-3 portable infrared gas analyzer (It is an open system used with a Parkinson broad leaf cuvette with leaf area of 6.2 cm²). The airflow rate was 400 cm³min⁻¹. Measurements were carried out on the same matured fully expanded leaves used for stomatal conductance. The expansion rate of newly expanding leaves was measured daily throughout the experimental period on both the well watered and PRD plants. A number of the flowers opened and flower abscise was recorded daily. Abscission was confirmed when flowers fell down or fell after a gentle touch. Mature fruits were harvested every 3 days and at each harvest, the number of fruit, total yield of fruit per plant and length of the fruit were determined.

RESULTS

Midday Leaf Water Potential

Midday leaf water potential was determined daily in the 2 youngest fully expanded leaves of 5 plants randomly selected from each treatment from the onset of the PRD regime. *Fig. 2* displays the results of measurements over two weeks from the onset of the treatments in control and stressed plants (PRD) and after the removal of the droughted roots. The leaf water potential of control plants remained high throughout the period as compared to that of the PRD plants. The leaf water potential of PRD plants started to decline from the onset of the experimental treatment but no significant differences were observed during the first 5 days. The statistically significant differences between the leaf water potential of the controls and the PRDs were clearly observed from Day 6 to Day 10 of the treatments. PRD plants exhibited a lower leaf

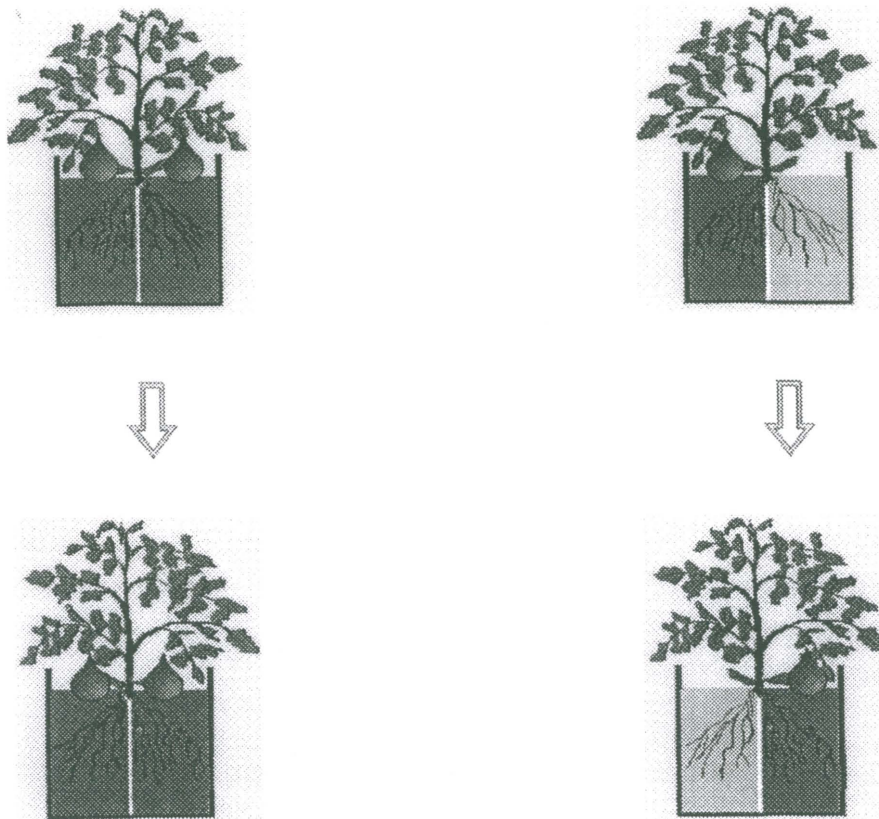


Fig. 1: Schematic representation of partial root drying technique. droplets represent watering. Dark color represents well watered and light color represents drying treatment

water potential compared to that of controls. This suggests that the PRD plants had undergone a water deficit compared to the controls. After the removal of the roots growing in the drying soil, the leaf water potential of PRD plants increased progressively and reached the values of the controls. Two days after the removal of the roots the leaf water potential of PRD exceeded that of the controls.

Stomatal Conductance

The stomatal conductance of well-watered plants and those of PRDs are presented in Fig. 3. The stomatal conductance of well-watered controls remained high throughout the experimental period. The stomatal conductance of PRDs started to decline from day 4 of the treatment. On day 10 the value of the stomatal conductance of PRD plants was about 44% of the controls. After the removal of the roots, stomatal conductance of the PRD plants increased and

reached a value of 84% of the control plants 2 days later, but never reached the value of the control plants.

Transpiration Rate

Transpiration rates of the *Capsicum annuum* L cv. MC12 plants grown under control or PRD are presented in (Fig. 4). The transpiration rate of the control plants fluctuated during the period of the measurement but remained high throughout the period as compared to that of the PRD plants. Three days after the onset of the treatment, the rate of transpiration started to decline progressively and reached a value of about 37% of the control value on Day 9. After the removal of the droughted roots transpiration rates of the PRD plants started to increase but did not reach the value of the control plants. The trend of the transpiration rate follows that of the stomatal conductance (Fig. 3).

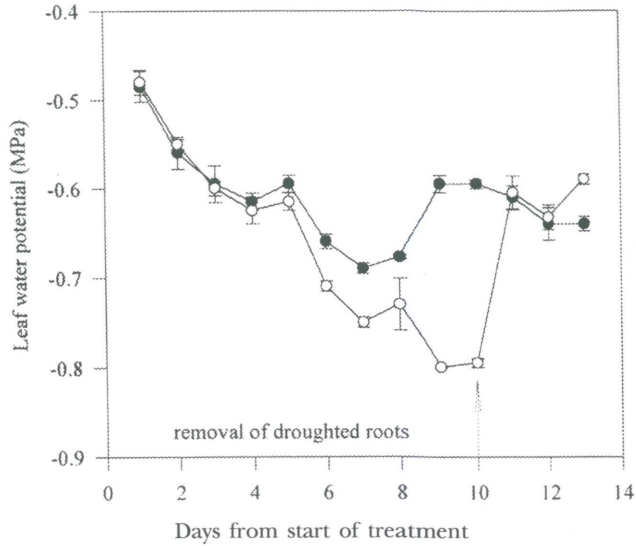


Fig. 2: Midday leaf water potential of *Capsicum* plants cv. MC12 grown under well-watered conditions (Control, closed circle) or half of the root system grown under well-watered conditions and the other half allowed to deplete soil moisture over weeks (PRD, open circle). Bars represent standard error of the means

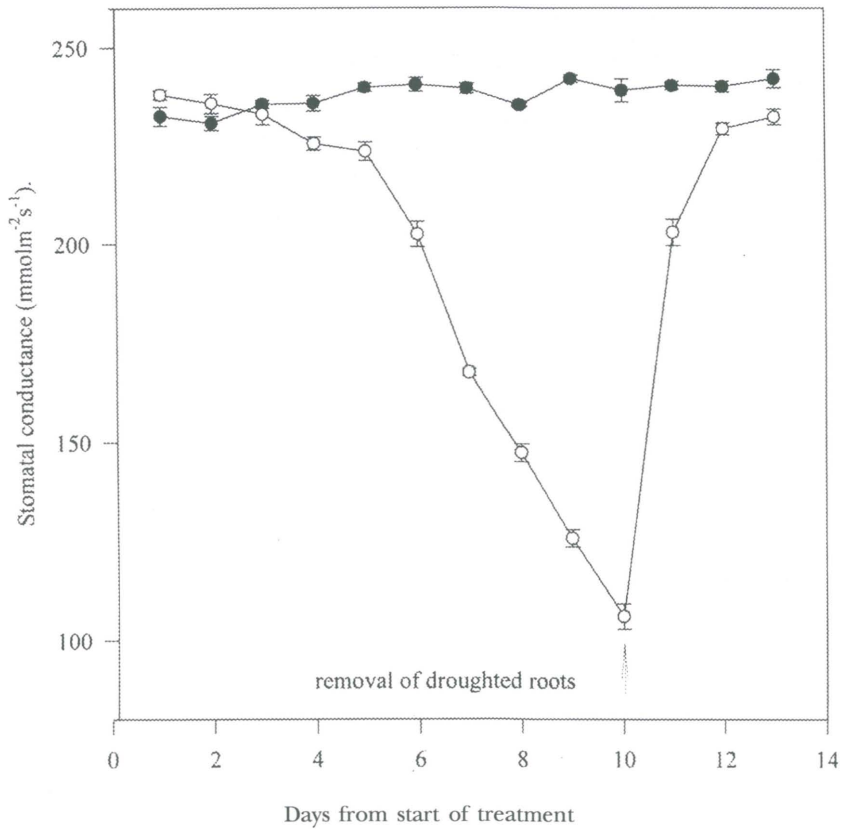


Fig. 3: Stomatal conductance of *Capsicum* cultivars MC12 with both halves of the root system grown under well-watered conditions. Control plants (closed circle) or plants grown with half of the root system in drying soil and the other half in well-watered conditions. PRD (open circle). Bars represent standard error of the means

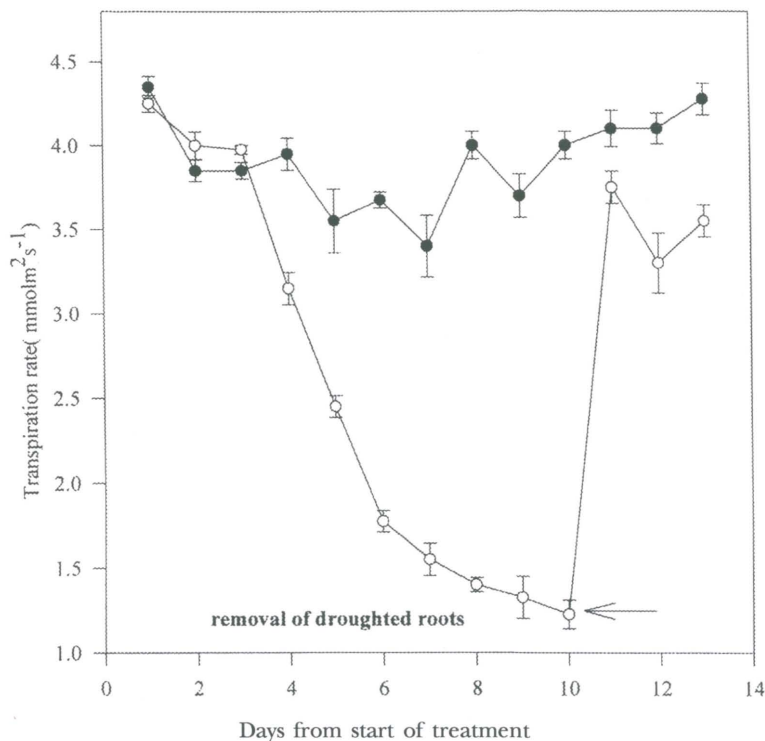


Fig. 4: Transpiration rate of *Capsicum* cultivar MC12 grown under well-watered conditions (Control plants closed circle) or plants grown with half of the root system in drying soil and the other half in well watered conditions (PRD plants open circle). Bars represent standard error

Photosynthetic Rate

The photosynthetic rate of the PRD plants remained similar to that of the controls up to Day 5 of the treatment (Fig. 5). After Day 6 the photosynthetic rate of the plants started to decline until it reached about 40% of the controls on Day 10. After the removal of the droughted roots, the photosynthetic rate of the PRD plants increased successively but did not reach that of the controls.

Leaf Length Increment

The daily leaf length increment of control plants and PRD plants are presented in Fig. 6. The control plants' daily increment in leaf growth is statistically higher than that of the PRD plants on Day 5. Leaf length expansion rate of the PRD plants started to decline from Day 3, but the statistically significant difference was observed on Day 5. The reduction in length growth rate of the PRD plants' leaves amounted to 12% of that of the control plants' leaves. The control plants' leaves reached the highest growth rate on Day 7, after which the elongation rate started to decline progressively, and reached a level of

growth plateauing between Day 12 and 13 from the start of treatments. On the other hand, the expansion rate of the PRD plants' leaves started to decline from Day 3 compared to that of the controls. On Days 8 and 9 no length increment was observed on the PRD plants' leaves. After the removal of droughted roots of PRD plants, the leaves resumed the expansion growth and it was significantly higher than that of the control plants on Day 13.

Growth and Reproductive Responses

Table 1 represents the responses of *Capsicum annuum* L. cv. MC12 grown under well-watered conditions and under partial root cyclic drying. Controls exhibited a higher total plant leaf area as compared to those grown under PRD and the difference between them after the final harvest was statistically significant at a 0.05 level. Total plant leaf area of the PRD plants was about 74% of the control plants suggesting that the PRD technique significantly affects the leaf area of the plants or that leaf growth of the PRD plants is reduced which is reflected in the resultant leaf area.

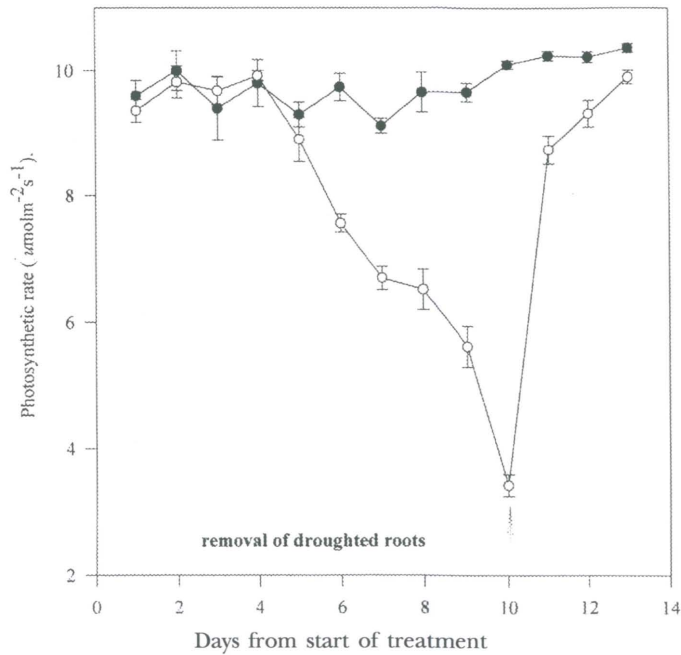


Fig. 5: Photosynthetic rate of *Capsicum* cultivar MC12 grown either under well-watered conditions (control) closed symbols or plants grown with half of their root system in drying soil and the other half in well-watered conditions (open symbols). Bars represent standard error

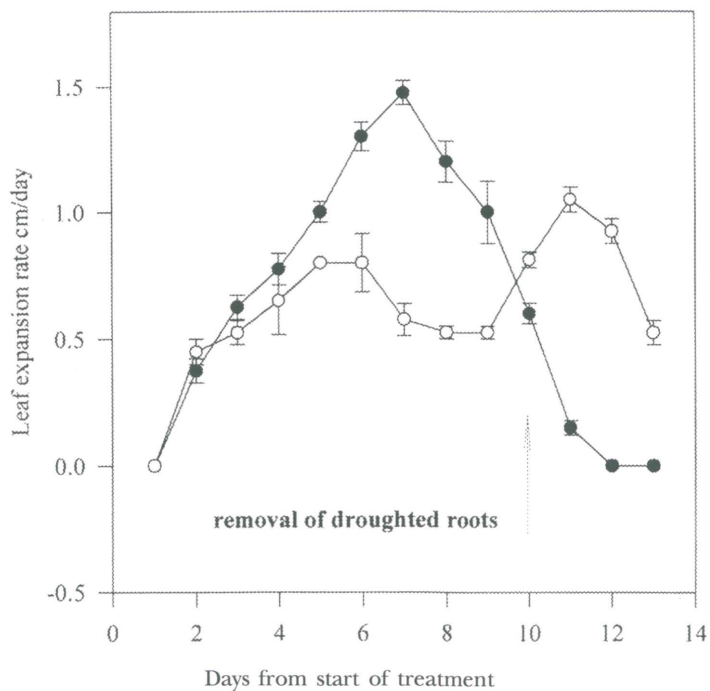


Fig. 6: Leaf elongation rate of *Capsicum* cultivar MC12 grown under well-watered conditions (control) closed symbols or half of the root system grown under soil drying and the other half under well-watered conditions (open symbols). Bars represent standard error

TABLE 1

Growth responses of *Capsicum annum* L. cultivar. MC12 plants grown under well-watered (control) or half of the root system under well-watered conditions and the other half allowed to dry soil moisture over 10 days

Treatment	Leaf area (cm ² /plant)	Plant height (cm)	No. of flowers / plant	No. of flow- ers abscised/ plant	No. of fruits per plant	Total fruit yield g/plant	Fruit length cm	Fruit set (%)
Control	5350.45a (150)	83.70a (4.2, D.S)	165.4a (16)	68.1a (8)	46.1a (3.2)	143.9a (11.2)	9.84a (0.5)	27.87a (3.2)
PRD	4359.78b (138)	76.52b (3.1)	166.6a (13)	89.7b (6)	37.0b (2.6)	104.9b (8.7)	8.94b (0.2)	22.20b (4.1)

Data are means \pm standard error which are between two bracts (n=20).

Means in the same column followed by similar letter are not significantly different at $P < 0.05$ by least significant difference (Lsd).

The higher total flower count produced per plant was produced by the PRD plants as compared to that of the controls but the difference between them was not significantly different at a 0.05 level.

DISCUSSION

Shoot water status can regulate leaf expansion during light periods, particularly when a low soil water potential is coupled with a high evaporative demand. The most likely control of leaf expansion in water-stressed plants would be exerted by signals arising from root or mature leaves. However, the regulation is complex and is not likely to be due to the action of a single hormone alone (Stoll *et al.* 2000). The results obtained in this experiment revealed that PRD caused a significant reduction in the leaf expansion rate which started to decline early after the application of the partial root drying technique, without any appreciable decline in leaf water potential. This is probably due to the signals coming from the dried roots via the transpirational stream. Those signals affect many physiological and biochemical processes in the shoot system (Awad *et al.* 2000) which associates peroxidase activity together with the elevated values of pH in the xylem sap of stressed pepper plants and plays a role in reducing the rate of leaf expansion during the time course of a water deficit. Similar findings were reported (Bacon *et al.* 1997; Wilkinson *et al.* 1997, 1998; Davies *et al.* 2000). The plant function that is most likely to be affected by a water deficit is stomatal closure which can lead to a decrease in transpiration, leaf gas exchange and probably an increase in water use efficiency, that is the dry matter produced per unit of water transpired (During *et al.*

1997). This may explain the reduced values of photosynthetic rates and transpiration of the PRD plants as compared to those of the controls. These results are in agreement with the findings observed by Hussain *et al.* (1999) and Mullholland *et al.* (1999) who suggested that a rise in xylem sap pH plays a role on ABA which in turn has a central role in the regulation of gas exchange of transgenics and mutant plants.

The concept of using PRD as a technique to control water deficit responses originated from the observation that root-derived abscisic acid was an important factor in regulating grapevine stomatal conductance (Loveys 1984; Gowing *et al.* 1990) and in regulating shoot growth under circumstances where vigour may be a disadvantage (Loveys 1991). The results obtained in this experiment showed that the shoot growth of the PRD plants could be significantly reduced by PRD. The reduction in leaf area of PRD plants amounted to 20% of that of controls. Similar reductions were observed with the PRD plants (Davies *et al.* 2000).

In this experiment the number of flowers produced per plant in both controls and PRD was similar, which means the flowering process was sustained, but there were significant differences in the total fruit yield per plant as PRD caused a significant increment of abscised flowers. The PRD plants yield was 73% of that of the controls. When looking to the yield as a mere figure the differences are significant, but if we relate the yield obtained to the amount of water added during the growing season until harvest, the significant differences between the two treatments would diminish.

Large differences between leaf water potential values of control plants and PRD plants were

observed in this experiment after 6 days. This reduction is probably attributed to the availability of water in the growing media; therefore the differences in the amount of irrigation water led to the differences of media moisture which consequently altered leaf water status. As a result of an increase in the water deficit intensity in the drying part, the leaf water potential of the PRD plants experiencing a water deficit was lower at midday on Day 6 than during the first 5 days. After Day 6, the severity of the reduction in media water content of the PRD treatment plants container was significantly higher compared to that of control plants as PRD plants received half the amount of water added to the control plant. Similar variations of leaf water potential were reported in field-grown sunflowers subjected to mild or severe water deficits (Dry *et al.* 1996; Tardieu *et al.* 1996; Davies *et al.* 2000) and pepper plants grown under partial root drying techniques (Gowing *et al.* 1990).

The PRD technique resulted in a gradual reduction in stomatal conductance values of stressed plants during the first 4 days. This reduction was increased during the following days until the dried roots were severed from the plants. The detachment of the dried roots resulted in an appreciable increment of the stomatal conductance values of the PRD plants, which confirmed the existence of a chemical signal coming from the root system which altered the stomatal behaviour of the PRD plants. Similar findings were found to exist in previous results (Dry *et al.* 1996, 1999; Loveys *et al.* 2000; Stoll *et al.* 2000). This reduction may be attributed to the ABA coming from the dried parts of the root system via the stream of the xylem sap (Gowing *et al.* 1990; Dry and Loveys 2000). Although the stomatal conductance of the PRD plants after the removal of the dried roots did not reach that of the control plants, this was probably due to the persistence of the signals' effects at the site of action. This reduction in the stomatal conductance value may give a good explanation for the rise in leaf water potential following the removal of the dried roots; that stomatal conductance effectively governs the leaf water potential of the plants since it resulted in significantly higher values of leaf water potential of the PRD plants on Days 12, 13 and 14 compared to that measured in control plants. The present results confirm previous observations which demonstrate that the photosynthetic rate

is reduced by water stress (Hsiao 1973). The relationship between the photosynthetic rate and midday leaf water potential is presented in Fig. 7. It shows a considerable scatter in the photosynthetic rate- midday leaf water potential. High photosynthetic rates ($6.7 \text{ mmol m}^{-2} \text{ s}^{-1}$) were recorded at -0.75 MPa in the PRD plants before removing roots from contact with drying soil, but it can be observed that even high – at relatively low water potential (-0.8 MPa) photosynthetic rate can be reduced by as much as 67% from the maximum value recorded. The decrease in the photosynthetic rate observed in water-stressed plants has long been explained by the reduction in the flow of CO_2 from the external atmosphere, which results from partial or complete stomatal closure (Munns and Cramer 1996). The close relationship obtained when plotting photosynthetic rate against stomatal conductance (Fig. 7) is in agreement with the explanation and suggests that stomatal regulation effectively controls the water balance of the leaf at the expense of a lower photosynthetic rate. Differences in photosynthetic rates between control and PRD plants' leaves were associated with differences in leaf water potential suggesting that leaf water potential can be used as a parameter of plant water status in photosynthetic studies of pepper leaves. However, the pattern of scatters observed when plotting photosynthetic rates against water potential suggest that spot measurement of water potential and photosynthetic rates should be handled with care. Since stomata are the way by which carbon dioxide enters the leaf and water vapour transpires, changes that a water deficit induces on stomatal opening affect CO_2 and assimilation, and therefore plant growth. Under water deficit conditions, internal CO_2 drops in the stomatal chamber thereby decreasing CO_2 assimilation, Mansfield *et al.* (1990). The partial closure of the stomata of PRD plants may be attributed to the transient nature of ABA accumulation together with pH gradients in the leaf tissues which control the ABA distribution in the leaf, and the ABA concentration at the primary site(s) of action at guard cell complexes, which then influences stomatal aperture and transpirational water loss (Bacon *et al.* 1997; Dry and Loveys 1996; Loveys *et al.* 2000). ABA carriers at epidermal plasma membranes, and the metabolism of ABA in the cytosol of mesophyll and epidermal cells are important for keeping the apoplastic

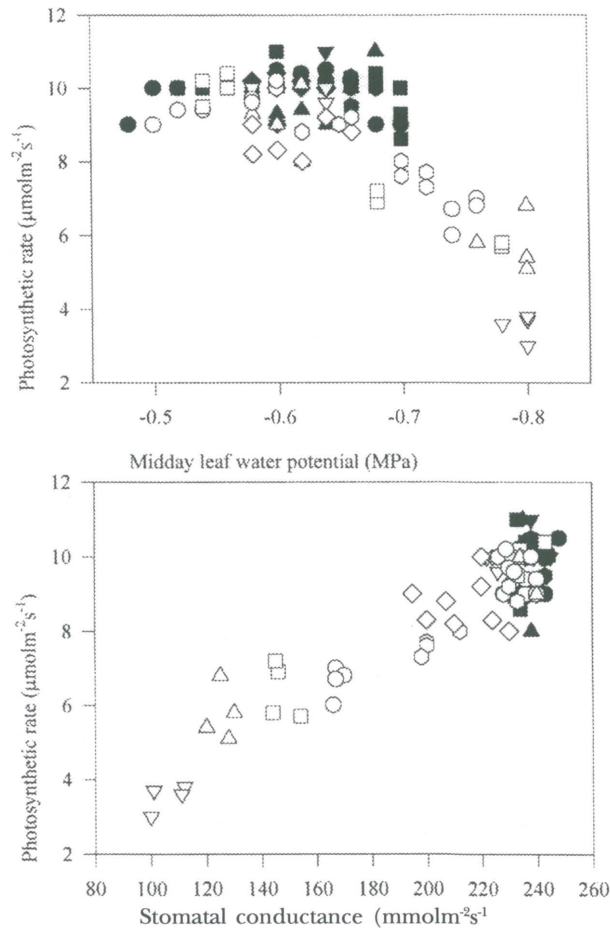


Fig. 7: Relationship between photosynthesis, leaf water potential and stomatal conductance for young fully expanded leaves of *Capsicum* plants. Points represent measurements on different days over stress period. Closed symbols represent control plants and Open symbols represent PRD plants.

ABA concentration in unstressed leaves low, and for speeding up ABA redistribution under stress. As a result stomatal conductance value reduced and the transpiration rates of the plants undergoing water deficit conditions declined. This can probably explain the low values of stomatal conductance and transpiration observed in the PRD plants. It is worth stating that ABA is not the unique candidate that can bring about this action, it is probable that other factors such as reduction in cytokinin concentration may also play a role. Auer (1996) and Medford *et al.* (1989) found that the ratio of ABA to cytokinin that occurs in roots of grape vine during the PRD cycle is altered and the cytokinin derived from dried roots have great impact on stomatal conductance (Stoll *et al.* 2000).

CONCLUSION

We concluded from this experiment that partial root drying resulted in the transference of a signal from the root to the shoot system. As a consequence, this signal modifies shoot growth and reduces stomatal conductance and transpiration rate. The amount of irrigation water added to the partial root drying was half of that added to the control plants, and this resulted in a reduction in total yield obtained. The partial root technique could be used in areas where water is a limited factor in yield production.

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