

## Effect of Soil Moisture Stress at Selected Stages of Growth on the Net Photosynthetic Rate and Stomatal Resistance and their Impact on the Yield of Chilli (*Capsicum annuum* L.)

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**ABSTRACT.** *A study was conducted to evaluate the effects of soil moisture stress on the net photosynthetic rate (Ps) and stomatal resistance (Rs) of Chilli var. 'Arunalu'. Two moisture stress cycles, each of 15 days duration were imposed as the treatments at various stages of growth. A re-watering at every 5<sup>th</sup> day for a period of 15 days in between the stress cycles was practised. The 1<sup>st</sup> stress cycle was imposed during the late vegetative, flowering and podding stages belonging to different treatments of the crop. A vast increase in the Rs and a considerable reduction in the Ps were noticed on account of stress in plants irrespective of the stages of growth. The Ps and Rs were not completely recovered soon after the removal of stress. Repeated stress cycles had pronounced effects on Ps and Rs than a single stress cycle. Moisture stress at the late vegetative stage showed highest yield reduction compared to the other stages of growth. An increase in Rs followed by a decline in CO<sub>2</sub> fixation are the physiological reasons for the yield reduction. The sensitivity of stomatal resistance to stress did not vary much despite the age of the crop. The relationship between Ps and Rs in the stressed, control and re-watered plants was assessed on the 10<sup>th</sup> day from the commencement of each stress cycle. A large variation in Ps to a narrow range of low Rs in the control plants indicated the stress avoidance characteristics of chilli. Persistence of a fairly high Ps to a wide range of high Rs in the water stressed plants showed the presence of stress tolerance characteristics in chilli.*

### INTRODUCTION

Most agricultural crops obtain water periodically during the growing season, either by natural rainfall or by irrigation. In between periods of water availability soil moisture stress some times becomes severe and limits plant growth and development. This is particularly true in rain-fed agricultural areas where the amount of rainfall is insufficient for the plant to complete growth, and also in irrigated agricultural areas where the available water is limited. Even brief water shortage is likely to interfere with the normal function of vital processes of plants (Techawongstien *et al.*, 1992).

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Timing of water stress during crop growth and development is an important factor in determining the magnitude of the effect of stress. In indeterminate and perennial crops, in which vegetative growth and reproductive processes overlap, the situation is not very clear (Begg and Turner, 1976). In chilli, after a period of vegetative development, reproductive growth including flower opening and fruit development, and vegetative growth occur concurrently.

The reaction of stomata to the development of plant water deficits, and its influences on CO<sub>2</sub> assimilation is an important factor in the evolution of vascular plants (Hall and Schulze, 1980). Assmann (1988) demonstrated that the environmental stresses can decrease photosynthesis by a direct effect on photosynthetic capacity of the mesophyll or by a CO<sub>2</sub> limitation resulting from stomatal closure. Boyer (1971) revealed that the water stress may reduce assimilation partially through a CO<sub>2</sub> limitation resulting from stress-induced stomatal closure and partially by a direct effect of the stress on mesophyll photosynthetic properties.

Water stress leads to wilting after-effects and the physiological processes fail to return to normal immediately (Mansfield and Davies, 1981). There are numerous reports showing that water deficit limit yield while irrigation increases yield. The degree of yield reduction by water deficit depends on the degree, duration and timing of the deficit (Begg and Turner, 1976). It is the physiological parameters such as Ps and Rs which ultimately affect the yield during stress periods.

This study was conducted to investigate the physiological responses of chilli var. 'Arunalu' to moisture stress when subjected at three different stages of the crop growth and to make recommendations regarding the most critical stages to water deficit stress.

## MATERIALS AND METHODS

This research was carried out at the Field Crops Research and Development Institute, Maha Illuppallama which is located at an elevation of 138 m above mean sea level and at a latitude of 8°5' North located in the North Central Province of Sri Lanka. Here the climate is warm (33–35°C) with an average annual rainfall of 1500 mm. Chilli var. 'Arunalu' (4–4½ months duration) was sown on nursery beds in the Yala 1998. The seedlings (35 days) were transplanted in a Reddish Brown Earth field.

### Land preparation and cultural practices

The land was cleared, ploughed and levelled. Twenty four plots each of 6×4:05 m were established. The ridges and furrows were made within each plot. A distance of 2 m was maintained between the plots in order to reduce the seepage of water from one plot to the other during irrigation. Polyethylene sheets (500 gauge) were inserted into the soil to a depth of 50 cm surrounding each plot to prevent the lateral movement of water.

Rain shelters were constructed to prevent the entry of rain water into the experimental plots during the rainy season. The seedlings were transplanted on the ridges

at a spacing of 60×45 cm. The ridge and furrow method of irrigation was practised. The experiment was managed in accordance with the recommended cultural practices.

### Fertilizer application

The fertilizer mixture containing 240 g triple super phosphate and 120 g muriate of potash was added as basal to each plot. The 1<sup>st</sup> application of urea (156 g plot<sup>-1</sup>) as top dressing was done at the 2<sup>nd</sup> week after transplanting. The subsequent applications of urea (204 g plot<sup>-1</sup>) were made during the 4<sup>th</sup>, 8<sup>th</sup>, 12<sup>th</sup> and 14<sup>th</sup> week after transplanting. Muriate of potash (120 g plot<sup>-1</sup>) was applied for the 2<sup>nd</sup> time during the 8<sup>th</sup> week after transplanting.

Gypsum blocks were inserted into the soil to a depth of 10, 20 and 30 cm in all plots in order to quantify the soil moisture content. The meter readings were recorded on the 3<sup>rd</sup>, 5<sup>th</sup>, 7<sup>th</sup> and 9<sup>th</sup> day from the commencement of each stress cycle using the soil moisture meter (Model # 5910, Soil Moisture Equipment Corp.).

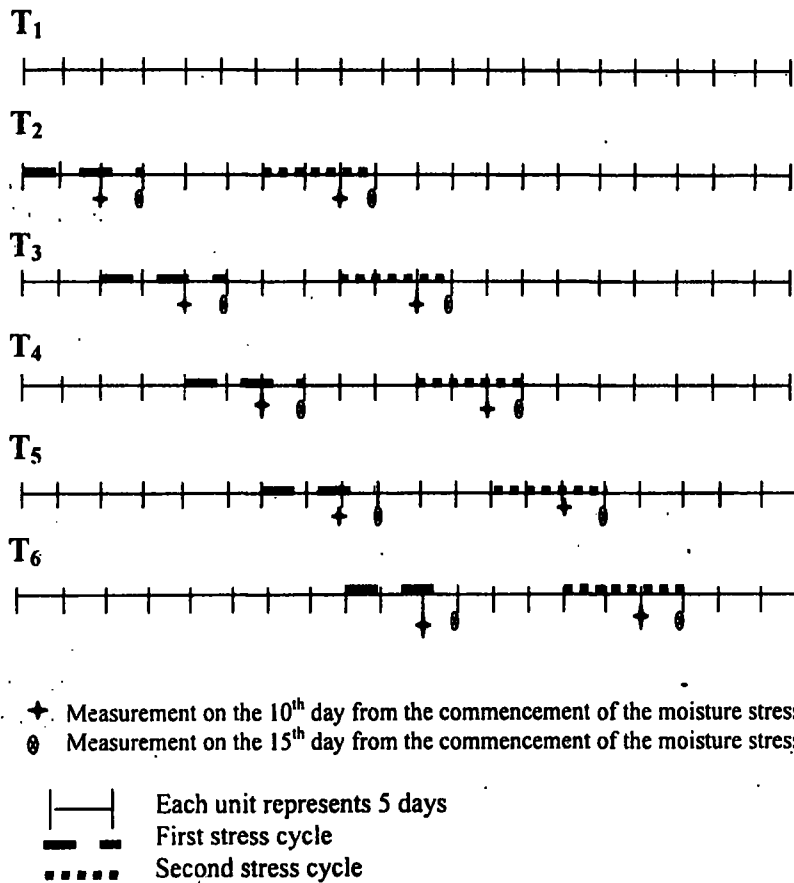
The experiment was arranged in a Randomized Complete Block Design with 6 treatments and 4 replications. Moisture stress treatment was induced by withholding water completely. The treatment structure is shown in Fig. 1.

The leaves which matured most recently, *i.e.*, 4<sup>th</sup> or 5<sup>th</sup> leaves from the apex in the stressed, control and re-watered plants were selected for the determination of the physiological characteristics. The net photosynthetic rate ( $P_n$ ) and stomatal resistance ( $R_s$ ) were measured with a portable Photosynthetic System (Model LI-6200, LICOR Inc.) from 9–11 am on the 10<sup>th</sup> day from the commencement of each stress cycle. The area of leaves used to measure the  $P_n$  was determined by a leaf area meter ( $\delta T$  Devices Ltd., UK). The same leaf area meter was used to measure the leaf area of chilli. Measurements were made when the Photosynthetically Active Radiation (PAR) was higher than the saturation PAR of 1480  $\mu E s^{-1} m^{-2}$  for chilli. The average PAR during the measurement period was 1900  $\mu E s^{-1} m^{-2}$ . The average leaf temperatures of the control and stressed plants during the crop growth period were 31.3±1.2°C and 35.1±1.4°C respectively.

The ripened fruits were harvested in 6 pickings from 20 plants plot<sup>-1</sup> at 2–3 weeks interval. The plants selected for harvesting the fruits were located at a site away from the border plants in order to overcome the border effects.

## RESULTS AND DISCUSSION

The average maximum and minimum temperatures during the cropping period were 33.4±1.3°C and 24.5±0.81°C respectively with an average rainfall of 68.3 mm. The average soil moisture contents of the water stressed plots at a depth of 10, 20 and 30 cm from the surface of the soil were 8.1%, 9.8% and 10.4% respectively, when measured on the 10<sup>th</sup> day from the commencement of each stress cycle. The control plots were irrigated to field capacity.



**Fig. 1.** Diagrammatic representation of the stress treatments were at various stages of growth.

[Note: T<sub>1</sub> = Control-Regular watering to field capacity at 5 days interval, T<sub>2</sub> = 15 days stress at late vegetative and podding stages, T<sub>3</sub> = 15 days stress at flowering and pod maturing stages, T<sub>4</sub> = 15 days stress at pod setting and pod maturing stages, T<sub>5</sub> = 15 days stress at podding and fruit ripening stages, T<sub>6</sub> = 15 days stress at pod maturing and fruit ripening stages].

There were significant differences between treatments in the net photosynthetic rate (Ps) and stomatal resistance (Rs) during the late vegetative, flowering and podding stages of the crop (Tables 1 and 2).

In the treatment where the 1<sup>st</sup> stress cycle was experienced by the plants during the late vegetative stage (T<sub>2</sub>), the Ps on the 10<sup>th</sup> day of measurement from the commencement of the stress was significantly lower than the control. The Rs on the 10<sup>th</sup> day was significantly higher than the control. Plants belonging to treatment Nos. 3, 4, 5 and 6 were regularly watered and their Ps values were similar to those of the control ones. When the plants of the flowering stage (T<sub>3</sub>) were exposed to the 1<sup>st</sup> stress cycle, the Ps on the 10<sup>th</sup> day of measurement from the commencement of the stress was significantly lower

than the control. The Rs on the 10<sup>th</sup> day was significantly higher than the control. There was no complete recovery in the measured physiological parameters on the 5<sup>th</sup> day of re-watering the plants which previously experienced 15 days stress during the late vegetative stage. The Ps of 29.8  $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$  and Rs of 2.2  $\text{s cm}^{-1}$  were recorded on the 5<sup>th</sup> day of re-watering.

**Table 1.** The effect of soil moisture stress at selected stages of growth on the net photosynthetic rate (Ps) of chilli.

Treatments	Net photosynthetic rate ( $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ )		
	Late vegetative	Flowering	Podding
T <sub>1</sub>	35.5 a	36.2 a	36.1 a
T <sub>2</sub>	23.4 b	29.8 b	19.3 d
T <sub>3</sub>	36.7 a	22.1 c	35.4 a
T <sub>4</sub>	35.8 a	35.9 a	29.8 b
T <sub>5</sub>	36.9 a	35.8 a	23.1 c
T <sub>6</sub>	37.1 a	34.9 a	35.9 a

Values in the same column followed by the same letter do not differ significantly ( $P<0.05$ ). Values are the means of 120 plants in 4 replicates.

**Table 2.** The effect of soil moisture stress at selected stages of growth on the stomatal resistance (Rs) of chilli.

Treatments	Stomatal resistance ( $\text{s cm}^{-1}$ )		
	Late vegetative	Flowering	Podding
T <sub>1</sub>	0.97 b	0.93 c	0.91 d
T <sub>2</sub>	15.80 a	2.20 b	18.20 a
T <sub>3</sub>	0.86 b	16.30 a	0.89 d
T <sub>4</sub>	0.89 b	0.90 c	2.40 c
T <sub>5</sub>	0.94 b	0.89 c	16.10 b
T <sub>6</sub>	0.90 b	0.96 c	0.90 d

Values in the same column followed by the same letter do not differ significantly ( $P<0.05$ ). Values are the means of 120 plants in 4 replicates.

In the treatment where the plants experienced the 2<sup>nd</sup> stress cycle during the podding stage, the Ps when measured on the 10<sup>th</sup> day from the commencement of the 2<sup>nd</sup> stress cycle was significantly lower than the Ps of the plants that received the 1<sup>st</sup> stress cycle

during the podding stage ( $T_3$ ). Similarly, the  $R_s$  was significantly higher on the 10<sup>th</sup> day of the 2<sup>nd</sup> stress cycle than on the 10<sup>th</sup> day of the 1<sup>st</sup> stress cycle. The physiological parameters were completely recovered on the 15<sup>th</sup> day after re-watering the plants which previously underwent moisture stress during the flowering stage ( $T_3$ ). The physiological parameters were not completely recovered on the 5<sup>th</sup> day of re-watering the plants which previously received the 1<sup>st</sup> stress cycle during the pod setting stage ( $T_4$ ). The values of net photosynthetic rate and stomatal resistance of the control, stressed and re-watered plants did not vary much throughout the crop growth. The moisture stress during the late vegetative stage of the crop showed the highest pod yield reduction compared to the other stages (Fig. 2).

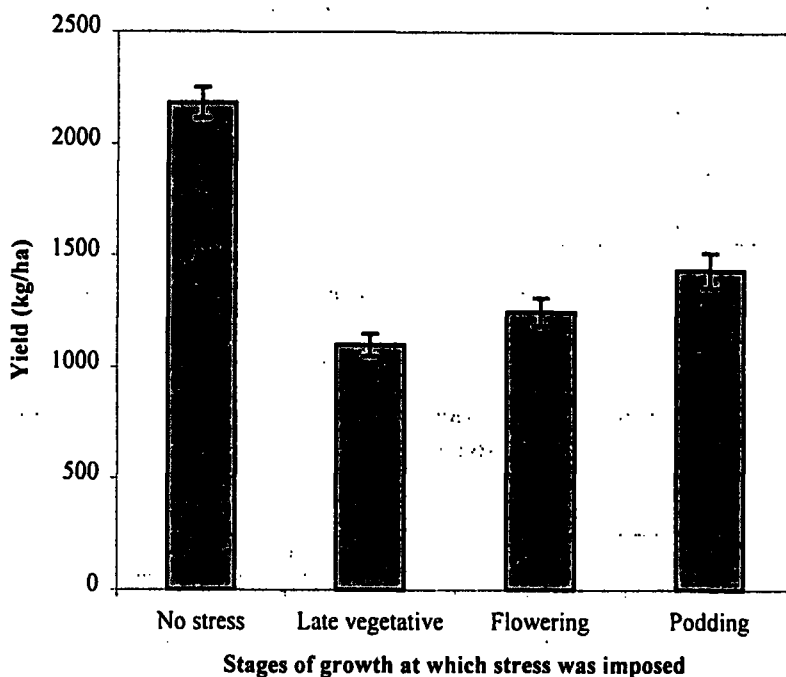


Fig. 2. Effect of soil moisture stress at selected stages on the yield of chilli var. 'Arunalu'.

Stomatal closure which results from soil water depletion is mediated by changes in root water status through effects on the flow of signal from root to shoot (Bates and Hall, 1981). As stated by Bradford and Yang (1981) stomatal closure was a consequence of a chemical signal moving between root and shoot. Abscisic acid (ABA) is thought to be the chemical involved in the signaling and strong evidence that ABA is synthesized in increased quantities in roots in drying soil was provided by Davies and Zhang (1991). ABA moves from roots to shoots primarily through the xylem stream and good correlative evidence is provided that drought induced restriction in stomatal conductance resulted from ABA accumulation in the xylem stream (Zhang and Davies, 1987).

Several studies suggest that the leaf conductance of some plant species is closely coupled to leaf water status so that with very slight increases in leaf water deficit cause decrease in conductance. Leaf conductance is, however, ultimately determined by turgor levels in the epidermis and may often be only slightly related to the water potential of the mesophyll cells (Davies *et al.*, 1981).

Stomatal closure leads to a decline in the CO<sub>2</sub> uptake and a consequent reduction in the Ps. Reduction in Ps results both from the stomatal and non-stomatal components of the leaf. As pointed out by Hale and Orcutt (1987) stomatal closure reduces CO<sub>2</sub> uptake and coincides with a decrease in carbon fixation. Redshaw and Meidner (1972) showed that changes in the stomatal resistance can account for only about 50% of the reduction in the rate of assimilation due to water stress. Cornic *et al.* (1983) indicated that the degree of inhibition of leaf photosynthetic gas exchange is caused by lowered stomatal conductance (which could change the internal CO<sub>2</sub> pressure, Pi) and the direct effect of the stress on the photosynthetic reaction.

According to Redshaw and Meidner (1972) an increase in the liquid-phase resistance ( $\Psi_m$ ) to the fixation of CO<sub>2</sub> within the leaf is also possible as the water content of the leaf falls. The causes of increased resistance to CO<sub>2</sub> uptake within the mesophyll cells (liquid-phase resistance) is a matter of speculation but some conclusions may be drawn with reference to other work. Translocation of assimilates has been shown to be reduced in leaves under water stress leading to accumulation of sugars within the leaf and this has been shown to reduce the rate of net photosynthesis.

The possible mechanisms by which the increased assimilate concentration could reduce the rate of CO<sub>2</sub> fixation are increased respiration, reduction in the quanta of light reaching the chloroplasts, reduction of NADPH<sub>2</sub> and ATP production, and an increase in the resistance to CO<sub>2</sub> diffusion within the mesophyll cells. Any of these mechanisms may cause the apparent increase in the liquid-phase resistance due to water stress.

In the treatment where the 1<sup>st</sup> stress cycle was experienced by the plants during the late vegetative stage, the stress was long and severe. Re-watering on the 5<sup>th</sup> day after this prolonged stress may not cause an immediate effect on the complete opening of stomata. As stated by Fischer *et al.* (1970) the delay in stomatal opening of tobacco and bean leaf discs placed on water to recover from stress was shown to be dependent on the degree and duration of the stress treatment. Bielora and Hopmans (1975) indicated that neither stomatal resistance nor transpiration fully returned to pre-stress conditions after irrigation, and even partial recovery required several days.

Allaway and Mansfield (1970) pointed out that the major after effect of stress clearly resided in the guard cells and subsequently showed to be due to the persistence of abscisic acid which has a direct effect on guard cells. Amount of ABA produced by the plant was related to leaf water potential (Wright, 1977). The delayed recovery of photosynthetic rate after re-watering may be due to delayed stomatal opening. An after-effect of stress on photosynthetic rate is actually caused by the after-effect on stomatal opening (Fischer, 1970).

The plants which were exposed to the 1<sup>st</sup> and the 2<sup>nd</sup> stress cycles had different experience with regard to soil moisture deficit. When the plants of the late vegetative stage were exposed to the 1<sup>st</sup> stress cycle, the closure of stomata would have been associated with the ABA in the xylem vessels and its release in the guard cells. The released ABA would have been compartmentalized on complete recovery of Rs on the 15<sup>th</sup> day after re-watering. As pointed out by Cummins (1973), ABA released could be compartmentalized away from its site of action on re-watering. ABA would have been newly synthesized in the drying roots during the 2<sup>nd</sup> stress cycle and accumulated in the xylem vessels. Hence, during the 2<sup>nd</sup> stress cycle both, a release from the compartmentalized ABA and newly synthesized ABA would have contributed to the observed reduction in stomata compared to that of plants which experienced the 1<sup>st</sup> stress cycle. The above phenomenon would have lead to more stomatal reduction in the plants during the 2<sup>nd</sup> stress cycle than the 1<sup>st</sup> stress cycle. As a result, lesser amount of CO<sub>2</sub> would have been fixed in the plants that experienced the 2<sup>nd</sup> stress cycle than the 1<sup>st</sup> stress cycle.

A complete recovery of Rs in the plants on the 15<sup>th</sup> day of re-watering which previously experienced moisture stress at the flowering stage suggests that the ABA produced on account of the 1<sup>st</sup> stress cycle would have been compartmentalized away from the place of action and had no effects on the subsequent stomatal opening. A complete recovery of photosynthetic rate in these plants on the 15<sup>th</sup> day of re-watering may be due to one or more of the following reasons: a) complete regain in the stomatal opening, b) reduction in the hydraulic resistance of mesophyll cells, c) increase in the translocation of assimilates and d) the repair of the damaged enzyme systems.

The relationship between Ps and Rs was assessed in the stressed, control and re-watered plants by plotting graphs using the values of Ps and Rs collected from the experimental plants belonging to all the treatments on the 10<sup>th</sup> day from the commencement of each stress cycle. The above data were collected during the late vegetative, flowering and podding stages of the crop.

The Ps of the control plants are very sensitive to a narrow range of low Rs in the above 3 stages of the crop (Figs. 3a, 3b and 3c). This indicates the stress avoidance characteristics of chilli under well watered condition. The Ps of water stressed plants are less sensitive to a range of high Rs which shows that chilli can maintain Ps at a fairly high value under water limited situations. This is a stress tolerance characteristic of chilli under water deficit condition.

From the above observations it appears that the chilli variety 'Arunalu' shows stress avoidance and stress tolerance features based on the moisture status of the soil. The stress tolerance characteristics could be used in crop improvement programmes. The Ps which was less sensitive to a range of high Rs during the water deficit period has become highly sensitive to a narrow range of low Rs on the 5<sup>th</sup> day of re-watering during the flowering and podding stages (Figs. 3b and 3c). The sensitivity of Ps to Rs however, is lesser than that of the control plants. Less sensitivity may be due to the delayed recovery of the physiological parameters on the 5<sup>th</sup> day of re-watering. The acclimatization for the stress treatment with respect to Ps and Rs was not observed in the plants despite the previous stress experience (Fig. 3c). The plants underwent a period of long and rapid



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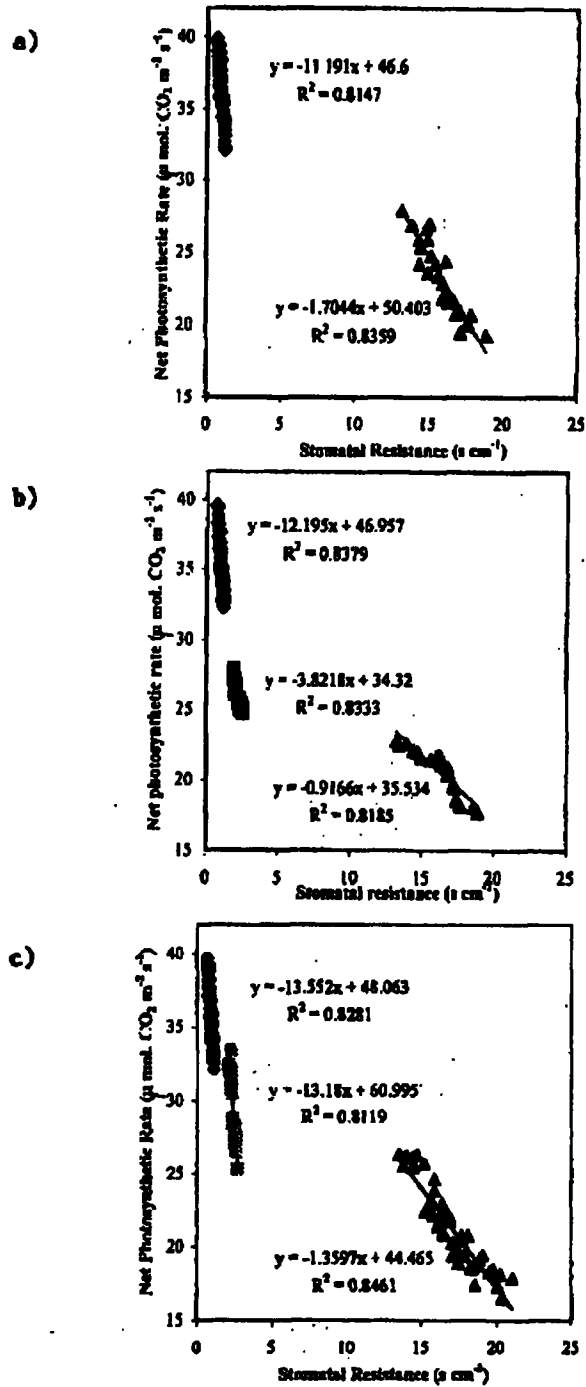


Fig. 3. The relationship between net photosynthetic rate (Ps) and stomatal resistance (Rs) of chilli during a) late vegetative, b) flowering and c) podding stages of the crop.

[Note: ◆ - control, ■ - re-watered, ▲ - stressed plants].

(water withheld completely at once) stress. Hence, a damaging rather than a hardening effect would have occurred to these plants.

Increased  $R_s$  followed by reduced  $P_s$  during the periods of moisture stress are the physiological causes for the yield reduction in chilli. Highest reduction in the yield of chilli during the time, which the crop experienced moisture stress at the late vegetative stage indicates the critical stage of the crop. As pointed out by Techawongstien *et al.* (1992) plant growth and yield were more appreciably affected by stress at the vegetative stage than at the mature stages in chilli. The prolonged water stress at the late vegetative stage would have considerably affected flower bud formation and development in chilli presumably due to the poor development of the vegetative parts in the treated plants at this stage.

The plants which experienced the soil moisture stress during the vegetative stage were stunted in appearance with an average height of 23 cm. The leaves were severely wilted and showed wrinkled appearance. The surface of the leaves was thin, soft and leathery. The canopy size of 17.6 cm length and 17 cm breadth was noticed when the stress was imposed during the vegetative stage. The canopy size of the well watered plants was 33.4 cm length and 30.6 cm breadth during the vegetative stage. When the plants were exposed to moisture stress at the flowering stage, a severe drop in flowering (an average of 1.8 g dry weight of flowers plant<sup>-1</sup>) was noticed. The flowers of the stressed plants were smaller (an average of 0.7 cm in length) than those of the control (an average of 1.6 cm in length) ones.

The number of fruits formed were  $4.5 \times 10^6$  ha<sup>-1</sup> when the stress was imposed during the late vegetative stage compared to the control value of  $9.3 \times 10^6$  ha<sup>-1</sup>. The average length and width of the pods from the above treated plants were 6 and 0.5 cm compared to the control values of 10 and 0.9 cm respectively. The yield reduction in the plants treated at the late vegetative stage would have been caused by the decrease in the fruit number. Moisture stress reduces cell division and thereby affects leaf area development. The leaf area of 302.2 cm<sup>2</sup> plant<sup>-1</sup> was obtained when the stress was imposed during the late vegetative stage compared to the control value of 703.7 cm<sup>2</sup> plant<sup>-1</sup>. The leaf area of the plants which were exposed to stress during the flowering and podding stages was 382.4 and 558.8 cm<sup>2</sup> plant<sup>-1</sup> compared to the control values of 793.6 and 996.6 cm<sup>2</sup> plant<sup>-1</sup>, respectively. Reduction in leaf area reduces the photosynthetic capacity of the leaves. This results in low carbohydrate production for the future pod formation in chilli.

## CONCLUSIONS

The above experiment determined the extent to which the photosynthetic rate and stomatal resistance were affected when chilli experiences a severe water shortage. The recovery of the above parameters is as important as the water deficit itself, especially when the crop is exposed to a severe and prolonged moisture stress. Long term moisture deficits such as those experienced above further delays the recovery of the physiological characteristics and subsequently affect the yield. Whether other varieties of chilli experience quicker recovery from a stress of this nature needs investigation. This study revealed the prevalence of two types of stress resistance characteristics in chilli; stress avoidance and stress tolerance. The stress tolerance characteristics of chilli under water

deficit condition are important criteria for crop improvement programmes in the dry zone of Sri Lanka where severe water deficit occurs frequently for a substantial period of time. From this study it was found that the late vegetative stage is the most critical stage to water deficit among the other tested stages of crop growth for an indeterminate crop such as chilli. The timing of irrigation thus could be adjusted so that no water deficit is experienced by the plants during the late vegetative stage in order to sustain the yield.

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