The Xeromorphic Reaction: Permanent Effects of Short Dry Spells on CropProduction; the Use of Foliar Water Spray to Reduce their Damage

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ABSTRACT

Aiming to analyze the effects of mild and short dry spells on crop production, several experiments were conducted on Chichi-jima Island and Ishigaki Island, in Japan's subtropical zone, and in Xinjian, western China.

Coarse-clod soil decelerated tomato growth and decreased yield in the first half of the harvesting period, and increased leaf thickness, leaf water content and soil water content. Plowed hardpan decelerated sugarcane growth and decreased yield. Sugarcane in undisrupted hardpan plots had 71% of the leaf area of that in disrupted plots. However, transpiration in undisrupted plots in the month following the end of the dry spell was only 46% of that in disrupted plots. Poor transpiration in undisrupted plots did not recover during the subsequent month. Leaf water content was higher in undisrupted plots than in disrupted plots. These results show that mild water stress due to coarse-clod soil and plowed hardpan during a short dry spell had irreversible aftereffects on the stomata. We have named this course of plant behavior the 'xeromorphic reaction'.

Foliar water spray at 15:00 daily for nine days accelerated root growth in tomato; however, spraying at 9:00 and 12:00 did not. Foliar water spray in the late evening also accelerated papaya and sweet potato root growth but decelerated cabbage and melon root growth. Papaya receiving foliar water spray at 16:00 daily for 14 days showed increased stomatal conductance before noon, and increased photosynthesis and transpiration around 13:00. The results show foliar water spray to increase stomatal conductance first; this leads to increased photosynthesis and transpiration. Tomato plants receiving foliar water spray daily for nine days after transplantation showed increased yield. Their yield was not significantly different from the yield of plants supplied with 2.5 times as much water.

To analyze the difference in foliar water spray effects, the relation between leaf water loss and xylem pressure potential in tomato, papaya and melon cut leaves were compared. Leaf water loss significantly decreased xylem pressure potential in tomato and papaya, but less in melon. Our results show leaf water loss to significantly increase physical water uptake ability in tomato and papaya, but to a lesser degree in melon. In tomato and papaya, foliar water spray increases stomatal conductance. It enhances photosynthesis and reduces plant water stress. Water stress increases water uptake to compensate for loss of leaf water decreases. For these plants, foliar water spray is therefore beneficial. However, in melons, foliar water spray resulted in excess water loss, since leaf water loss in this species acts as a weaker signal to increase water uptake. For these plants, therefore, foliar water spray is harmful.

Keywords: foliar water spray, stomatal conductance, short dry spell, xeromorphic reaction

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Introduction

The main targets of research into crop water stress are the problems experienced in arid and semi-arid regions. Generally, water stress problems in humid and semi-humid regions are thought to be mild and short. Actually, even mild and short dry spells that last several months sometimes cause serious damage to crops in humid and semi-humid regions. The reason is due to previous conditions. Because a humid climate forces plants to develop poor quality, shallow roots, water uptake ability is less than potential transpiration, especially early on in a sudden dry spell after a period of sufficient rainfall. However, the aftereffects of short dry spells on plant productivity have not been sufficiently analyzed. Giorio *et al.* [5)] reported that decreased stomatal conductance (Cs) did not recover in olive trees, even after leaf water increased again in late summer. Their result supports the hypothesis that the aftereffects must be related to Cs. In this study, focusing on Cs, we analyzed the plant production-limiting aftereffects of a mild and short dry spell. We also analyzed the effects of foliar water spray on reducing the damage caused by these dry spells, since Kimura *et al.* have shown that leaf wetness due to rain increases Cs [6, 7)].

2. Materials and methods

Experiments were conducted on Chichi-jima (Bonin) Island and Ishigaki Island in Japan's subtropical zone, and in Xinjiang in western China. The meridian transit times at Chichi-jima Island (located at 27.08° N, 142.18° E) and Ishigaki Island (located at 24.33° N, 124.16° E) are approximately 20 minutes earlier and 40 minutes later than 12:00 in Japanese Standard Time, respectively. Time in Xinjiang was shown as Xinjiang local time.

2.1 Effects of coarse-clod soil on tomato growth and yield

The experiment was conducted on Chichi-jima Island from 1982 to 1983. Although it receives an annual precipitation of 1050 mm, dry spells continue from early June to early December. Forty tomato transplants (cultivar Azuma) sown on August 25 were transplanted on October 27 in two lines in a row 10 m long and 2 m wide in an open field, with the coarse clod content in the soil higher on one side than the other. Plants were divided into ten groups per side, with each group containing four plants. Plowed soils were sampled from the center positions of the four plants in each group, after which the soils were air-dried. Soils were screened using 2 mm mesh. The weights of total soil and soil clods over 2 mm in size were then measured.

Soil water content was measured by tensiometers placed at 20 cm depth from November 23-27. The maximum leaflet of the second newly expanded leaves was sampled in each plant on November 25 for dry weight measurement. Twelve leaf disks, 0.5 cm^2 in area, were sampled from the third and fourth newly expanded leaves in each plant on November 9, after which specific leaf areas were calculated. Four leaflets in the third and fourth newly expanded leaves in each plant were sampled at 13:00 on November 9. Relative water content (RWC) was then calculated using the following equation.

. RWC = (Sampled weight - Oven dry weight) / (Water saturated weight - Oven dry weight)

The harvesting period was from early January to the end of April 1983. Yields up to the end of February and from the start of March were designated as former yield and the latter yield, respectively.

2.2 Effects of plowed hardpan on sugarcane growth and yield

The study was conducted on Ishigaki Island. Although it receives an annual precipitation of 2536 mm, dry spells continue from early June to early September. Sugarcane cuttings (cultivar Ni 8) as stems with two nodes were planted at a distance of 35 cm in rows 140 cm apart on December 24, 2000. The experimental area was a 12 x 23 m rainfed open field, consisting of 8 rows. The field was divided into 4 plots, including two non-neighboring plots consisting of undisrupted and disrupted hardpan. The hardpan layer, identified as being present 30-40 cm deep and having a penetration resistance of 58 kg/cm^2, consisted of sandy clay loam soil with a massive structure$^{4)}$. In the disrupted hardpan plot, hardpan was broken up using a machine fork by inserting it vertically into soil, and then moving up it with soil. Hardpan disruption did not affect the distribution of penetration resistance; however, it made cracks in the soil below the hardpan.

2.2.1 Transpiration measurement

Transpiration (Tr) measurements were conducted on September 2001 using sap flow gauges. These gauges measure sap flow through the heat energy balance method as outlined by Sakuratani$^{10)}$ and Baker and Van Bavel$^{2)}$. There were two sap flow gauges installed in each plot stem. These gauges were changed between stems of disrupted and undisrupted plots on September 21.

2.2.2 Growth characteristics and yield

Crop growth characteristics were analyzed by obtaining 4 representative stems from each plot on September 25 and measuring leaf area, fresh weight and dry weight. Root development was determined on September 27 using the trench profile method$^{3)}$ of root distribution mapping. Crop yield was measured on the last week of December 2001.

2.3 Effects of foliar water spray on plant growth and yield

2.3.1. Root growth of tomato and papaya receiving foliar water spray

Tomato seeds (cultivar Kyôryoku Sasuga) were sown on August 1 in 1987 on Chichi-jima Island. Sixth foliar-stage transplants were planted on September 2 individually in sixteen plastic containers at a spacing of 30 cm x 15 cm and 60 cm depth. The soil in the containers was composed of 50% fine redsol, 25% alluvial soil and 25% palm leaf compost by volume. Each container had a transparent front root observatory. Each plant was supplied with two liters of water immediately after transplantation. Containers received four treatments: no spraying, and water spray at 9:00, 12:00 or 15:00. Four containers were used for each treatment. Plants received foliar water spray daily from September 3. Water (0.6 ml), to which had been added a surface-active agent, was sprayed using a hand spraygun on the leaf surfaces of each plant fifteen minutes before and after the treatment times. Leaf wetness remained about four minutes after spraying. Photographs of roots were taken though the transparent sides at 6:00 on September 11 and 12. The lengths of all roots were measured on the photographs using a curve length meter.

Papaya cutting transplants (cultivar Wonder Flare) were grown in 0.3-liter pots on Ishigaki Island in 2000. Perlite was placed in two large 80-liter pots in a greenhouse. Seven two-month-old transplants were transplanted to each pot and spaced at 20 cm on June 20, and enough water was applied to the perlite surface every day after transplantation. One pot was for no spraying, and the other pot was for foliar water spray on the upper and lower leaf surfaces, as in the above-described experiments. Plants received foliar water spray at 16:00 daily for 10 days after transplantation. On June 20 and 30, the leaf area of the largest leaves of individual plants was estimated from leaf length. On June 30, the plant roots were dug up. Roots that had developed in the primary pot soil were sampled for dry weight measurement.

2.3.2 Effect of foliar water spray in an arid region in western China

The experiment was conducted in Fukang, in the southern border of the Kurbantonkut Desert in Xinjiang, western China, which receives annual precipitation of 140 mm. The major aim of the experiment was to analyze the effects of foliar water spray on sweet potato and cabbage in an arid region.

Sweet potato and cabbage transplants were planted in an open field on June 14, 1997. The transplants received four treatments of combined spray or no spraying with or without watering. Six sweet potato and cabbage plants were used for each treatment. Ten days before transplantation, flood irrigation was supplied to the soil for all treatments. In the treatment including watering, a depth of 20 mm water was supplied to the plants by flood irrigation immediately after transplantation, according to local convention. In the no-watering treatment plots, two liters of water were supplied to the soil surrounding each plant immediately after transplantation. In treatments including spraying, plants received foliar water spray on their leaf surfaces four times per hour around 17:00 from June 15-20, except on the 18th, when it was supplied by a hand spraygun. Sweet potato and cabbage plants were sampled for dry weight measurement on June 28.

2.3.3 Leaf and root growth and water use of melon plants receiving foliar water spray at different times

The experiment was conducted on Chichi-jima Island. Melon seeds (cultivar Prince Melon PF6) were sown on September 1, 1987. Third foliar stage transplants were planted individually in sixteen plastic containers, following the procedure of the above-described experiment, on September 21. Each plant was supplied with 5.4 liters of water immediately after transplantation. Containers received four treatments: no spraying and spray at 9:00, 12:00, or 15:00. Four containers were used for each treatment. Plants in treatments including spraying received foliar water spray from September 22 as the same manner as in the above-described experiment. On September 28, leaf area was estimated from leaf lengths. Photographs of roots were taken though the transparent sides at 6:00 on September 29 and 30. Lengths of roots were measured in the same manner as in the above-described experiment. Differences in root container weights, equivalent to evapotranspiration, were calculated from weights at 6:00 on September 25 and 30.

2.3.4 Cs, photosynthesis (Pn) and Tr of papaya receiving foliar water spray

Cutting transplants of papaya (cultivar Wonder Flare) were planted in 80-liter pots and placed 3 m apart in a greenhouse in summer 1999 on Ishigaki Island. The pot soil was composed of 75% redsol and 25% compost by volume. A culture solution of 0.05% Polyfeed was supplied every day. Plants received two treatments: no spraying or spraying. Three plants were used for each treatment. Plants undergoing the spray treatment received foliar water spray on the leaf undersides using a watering tube at 16:00 daily from June 19, 2000. Diurnal variations in Cs, Pn, and Tr of upper sun-exposed and fully-expanded leaves were measured five times a day: around 8:00, 10:00, 13:00, 16:00 and 19:00 on July 3 using a Portable Photosynthesis and Transpiration Measurement System (Shimadzu SPB-H4A). On the measurement days, culture solution was supplied at 9:00, 12:00 and 15:00.

2.3.5 Yield of tomato plants receiving foliar water spray at different times and given copious watering

Tomato seeds (cultivar Azuma) were sown on August 25 in 1982 on Chichi-jima Island. On October 27, one hundred transplants in the sixth foliar stage were transplanted to an open field at a planting distance of 50 cm in rows that were 100 cm apart. The five treatments comprised no spraying, and spraying at 9:00, 12:00 or 15:00; and copious watering was carried out twice. Plants in treatments including spraying received foliar water spray for nine days daily from October 29 in the same manner as in the above-described experiments. Five liters of water were supplied to the soil surrounding each plant immediately after transplantation. By November 9, 14.4 and 5.7 liters, respectively, of water had been supplied to each plant in the copious watering plot and the other treatment plots. Total precipitation by the end of foliar water spraying was 0.5 mm. Total precipitation before the beginning of the rainy season on December 11 was 13.5 mm. Yields from the first to sixth clusters were recorded.

2.3.6 Relationship between water loss from cut leaves and xylem pressure potential

Expanded leaves of tomato and melon grown in the open field, and those of three-month-old papaya plants grown in pots were sampled on October 11, 2001 and on June 27, 2004, respectively and placed individually in a pressure chamber. Weights of exuded water from the cut stems were measured when the chamber pressure had been decreased to 0.1 MPa. Leaf areas were also determined.

3. Results

3.1 Effects of coarse-clod soil on tomato growth and yield

As shown in Fig. 1, soil water suction, specific leaf area, maximum leaflet area and former-half yield were higher in the fine soil. RWC was higher in the coarse soil. No difference between coarse and fine soils was found in the latter-half yield.

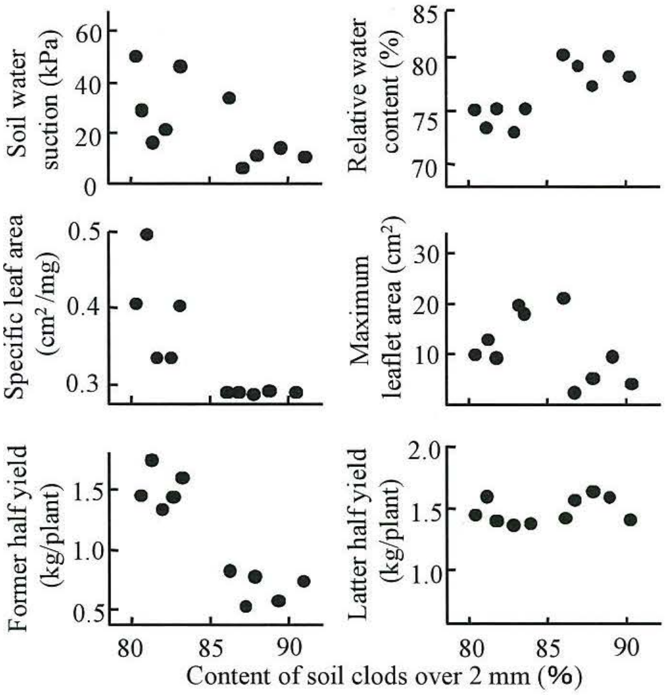

Fig. 1. Effects of coarse clods content on tomato growth and yield

3.2 Effects of plowed hardpan on sugarcane growth and yield

3.2.1 Daily transpiration

Figure 2 shows the daily behavior of Tr obtained from both the disrupted and undisrupted hardpan plots and daily precipitation during September. Total amount of precipitation during September was 888 mm, 3.5 times greater than in a normal year. The average daily Tr in the disrupted hardpan plot ranged from 2.5-9.1 mm/day for a monthly average of 6.3 mm/day. On the other hand, the Tr in the undisrupted hardpan plot ranged from 1.2-4.1 mm/day, with a monthly average of 2.9 mm/day.

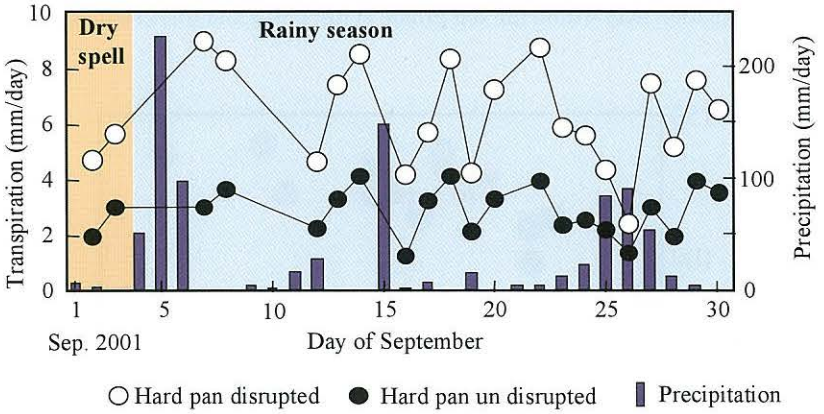

Fig. 2. Hardpan even decrease transpiration after the end of dry spell

3.2 Growth characteristics and yield

Table 1 shows plant growth characteristics obtained from measurements of representative stems. Leaf area index in the undisrupted hardpan plot was 71% of that in the disrupted plot. Plant water content in stem and leaf blades was higher in the undisrupted hardpan plot. There were no significant differences in fresh and dry weight or leaf sheath water content between the disrupted and the undisrupted hardpan plots.

Roots in the disrupted hardpan plot developed deeper into the subsoil, as shown in Figure 3. However, their development into the shallow soil above the hardpan was less than in the undisrupted hardpan plot.

As shown in Fig. 4, the number of sugarcane stems available for yield was more in the disrupted hardpan plot. This also indicated that disrupting the hardpan facilitated higher yield per stem.

Table. 1. Characteristics of plant growth in two plots

Plot	Leaf area index	Fresh weight (ton/ha)	Dry weight (t/ha)	% Water			
				Plant upper part	Stem	Leaf blade	Leaf sheath
Disrupted	5.21 ±0.93	158±17	46.1±5.1	70.9±0.1	70.5±0.0	78.0±1.0	67.4±2.7
Undisrupted	3.68 ±0.25	151 ±13	39.9±4.8	73.6±0.9	73.4±0.8	81.5±1.3	67.0±1.6

Mean ±SE

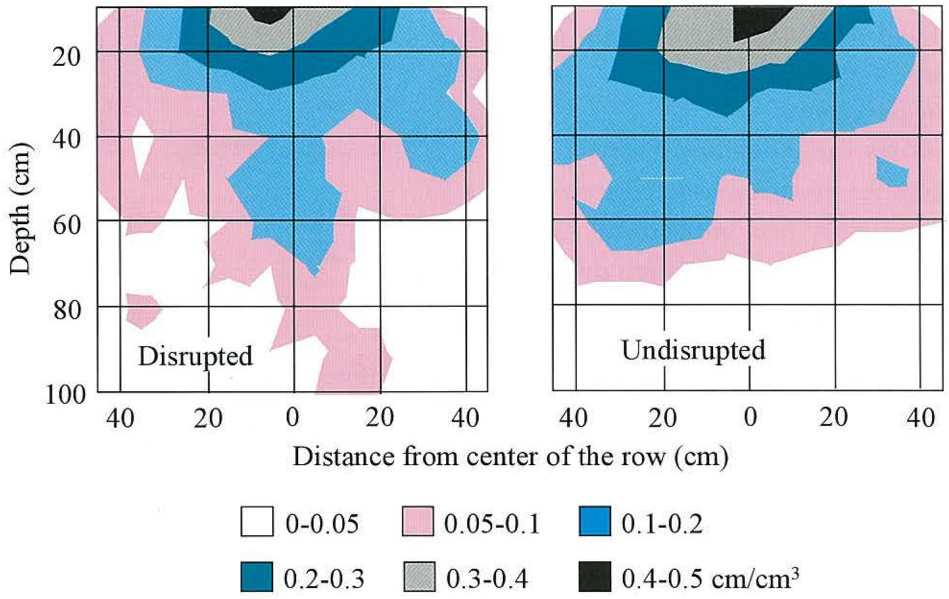

Fig. 3. Root distribution map within the soil profile of disrupted and undisrupted hardpan plots.

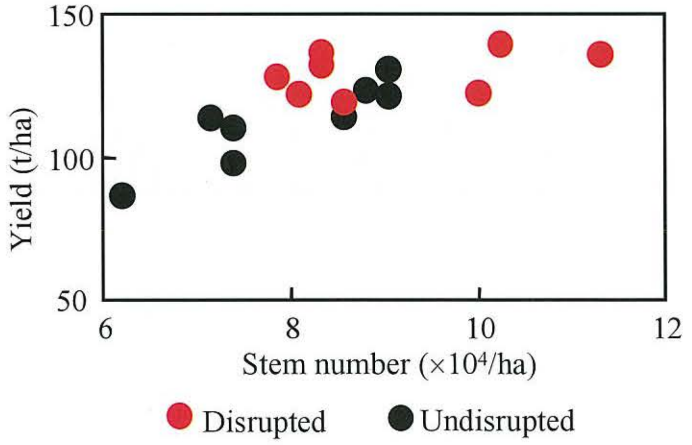

Fig. 4. Relation of stem number and yield in disrupted and undisrupted hardpan pots.

3.3 Effects of foliar water spray on plant growth and yield

3.3.1 Root growth of tomato and papaya receiving foliar water spray

As shown in Table 2, spraying at 15:00 accelerated tomato root growth during the day. As shown in Table 3, foliar water spray at 16:00 did not result in any significant differences in melon leaf area. However, spraying increased the dry weight of newly developed melon root.

Table. 2. Effect of foliar water spray time on one day tomato root growth

Treat	Root growth
	(cm/day)
Un-treated	5.2±2.7
Spray at 9	8.2±2.2
Spray at 12	11.5±7.3
Spray at 15	14.2±6.1

Mean±SE

Table. 3. Effect of foliar water spray on papaya leaf area increase and root growth

Treat	Leaf area increase of the largest leaf	Root dry weight
	(cm^2)	(g)
Un-treat	14.9±5.9	0.35±0.03
Spray	12.6±7.3	0.43±0.02

Mean±SE

3.3.2 Effect of foliar water spray in an arid region in western China

As shown in Table 4 and Fig. 5, sweet potato root weight in the spray treatment was superior to that in the other treatments. However, cabbage root weight in the spray treatment plots was inferior to that in the watered plots.

Table. 4. Effect of foliar water spray and watering on root fresh weights of sweet potato and cabbage transplants

Crop	Treat	Root fresh weight
		(g/plant)
Sweet potato	Un-treat	35±8
	Spray	60±7
	Watering	40±10
	Spray plus watering	23±11
Cabbage	Un-treat	107±30
	Spray	87±25
	Watering	150±25
	Spray plus watering	113±32

Mean ±SE

Fig. 5. Sweet potato transplants with and without foliar water spray continuous 5 days at 16:00

3.3.3 Leaf and root growth and water use of melon receiving foliar water spray at different times

As shown in Table 4, none of the spray treatments accelerated daily root growth. While the plant leaf area did not show any significant differences among treatments, daily water use (evapotranspiration) was lower in plants sprayed at 12:00 than in non-sprayed plants.

Table. 4. Effect of foliar water spray time on leaf area, root growth and water use of melon plants

Treat	Leaf area	Root growth	Water use
	(cm^2)	(cm/day)	(g/day)
Un - treat	348±25	28.2±7.3	303±21
Spray at 9	358±26	28.2±7.1	279±19
Spray at 12	356±27	29.1±6.9	253±20
Spray at 15	383±15	25.3±6.2	291±16

3.3.4 Leaf water, Cs, Pn and Tr of papaya receiving foliar water spray

Figure 6 shows diurnal variations in Cs, Pn and Tr. The spray increased Cs at 8:00, 10:00 and 13:00, and Pn and Tr at 13:00. No significant differences were found at 16:00 and 19:00 in Cs, or at 8:00, 10:00, 16:00 and 19:00 in Pn and Tr.

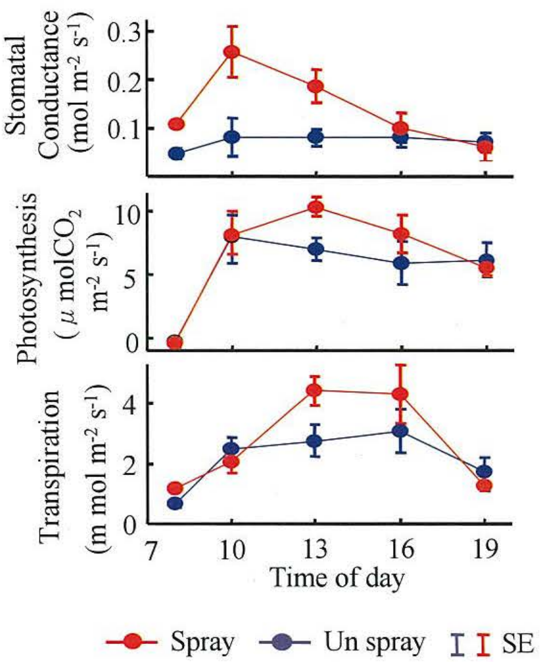

Fig. 6. Effect of foliar water spray on stomatal conductance, photosynthesis and transpiration of papaya plants

3.3.5 Yield of tomatoes receiving foliar water spray at different times and copious watering

As shown in Table 5, the yield of plants receiving spray at 15:00 was superior to that of non-sprayed plants. Spraying at 15:00 plus copious watering did not result in any significant differences in yield.

3.3.6 Relation between water loss from the cut leaves and xylem pressure potential

Figure 7 shows the relationship between accumulated leaf water loss, indicated leaf areas as denominators, and xylem pressure potential (XPP) of tomato, melon and papaya leaves. XPP of tomato and papaya leaves significantly decreased as accumulated leaf water loss increased. Similarly, XPP of melon leaves also significantly decreased as accumulated leaf water loss increased in the range of XPP above -0.9 MPa. However, the decrease in XPP of melon leaves was decelerated in the range of XPP below -0.9 MPa.

Table. 5. Effect of foliar water spray time and much watering on tomato yield

Treatment	Yield (g/plant)
Un -treat	2438 ± 371
Spray at 9	2454 ± 455
Spray at 12	2823 ± 220
Spray at 15	3202 ± 297
Much watering	3061 ± 303

Mean ±SE

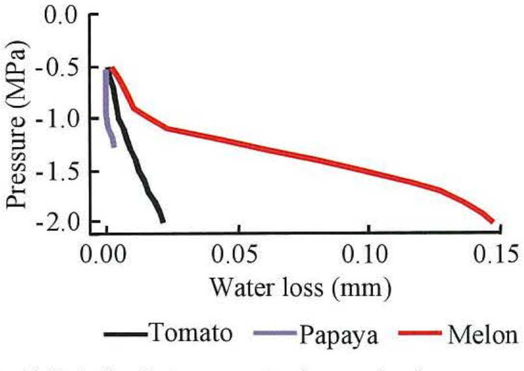

Fig. 7. Relation between water loss and xylem pressure potential in tomato, melon and papaya cut leaves

4. Discussion

Coarse soil decreased leaf growth and the former-half yield, and increased leaf thickness, leaf water content and soil water content (Fig. 1). Any increase in both leaf water and soil water content must result from increased resistance to increased transpiration, i.e., a loss of Cs. A similar result was obtained in melon[8]. The most notable result was that coarse-clod soil increased leaf thickness. This plant response results in xeromorphism, seen universally in CAM plants.

The measuring period of Tr was generally wet, as shown in Fig. 2, and therefore it can be assumed that there was enough soil water in the root zone for plant roots to absorb and plant leaves to transpire to their full potential. Because the estimated Tr, calculated using the FAO Penman-Montaith method[1] closely agreed with Tr in the disrupted hardpan plot[4], Tr under the undisrupted hardpan was below normal. In 2001, the dry spell continued from June 1 to September 4. Precipitation during the period was 151 mm. The result that Tr in the undisrupted hardpan plot did not increase during September suggests that *hardpan does not only limit the effective soil water reservoir available to plant roots. Hardpan had several irreversible effects on plants during the rainy and/or dry seasons before the period of Tr measured. Glimpses of these effects can be seen in the crop growth and yield results.

Leaf area index in the undisrupted hardpan plot was 71% of that in the disrupted plot (Table 1). Although the smaller leaf area in the undisrupted hardpan plot is a factor in decreasing growth and yield, the more remarkable factor is that the 71% leaf area transpired only 46% of the disrupted hardpan plot level during September (Fig. 2). This indicates that Cs in the undisrupted hardpan plot was markedly lower. The fresh weight in both plots was almost equal in the middle cropping stage. However, the plant water content of the undisrupted hardpan plot was higher than that in the disrupted plot (Table 1). This phenomenon is similar to that in tomatoes grown in coarse-clod soil, normally observed under continuous mild water-stressed conditions, resulting from decreasing Cs[8].

The Cs decreases both Tr and Pn. Lower Pn decreases both growth and yield (Fig. 4). The Tr in the undisrupted hardpan plot did not recover to its normal level, even during a month of rain. We named this form of plant behavior the 'xeromorphic reaction'.

Water uptake through the deeper developed roots in the disrupted hardpan plot (Fig. 3) probably prevented Cs from falling into an irreversible decline. These results suggest that growth and yield in the undisrupted hardpan plot might be improved by using cultural practices that prevent Cs from decreasing.

Kimura reported that wetness caused by rain increases the Cs of kidney bean and sweet potato[6]. However, his shortest rain treatment in his experiments was an hour. The fact that a few minutes wetness increased Cs in our experiments is a new observation.

Water spray at 15:00 accelerated tomato root growth after the spray time[9]. It also contributed to one day of root growth acceleration (Table 2). Similarly, spraying in the evening also accelerated the root growth of papaya and sweet potato (Table 3, Table 4 and Fig. 5). Water uptake increased (Fig. 6) because of root growth, which automatically increases growth and yield (Table 5).

Initial plant response to water spraying in the evening appears to be to accelerate the translocation of accumulated carbohydrates to the roots[11], leading to increased water uptake by the root growth within few days. The hypothesis further explains that water spray was not found effective for root growth at 9:00, when the carbohydrate accumulation in the leaves was lower (Table 4). It also clarifies the reason why root growth in more highly water-stressed plants sprayed at 12:00 was inferior to the lower water-stressed plants sprayed at 15:00[9].

Water spraying increased papaya Cs first. This was followed by an increase in Pn and Tr (Fig. 6), showing that increased Cs leads to increased Pn and Tr.

When plants can grow in good conditions, Pn, water and fertilizer absorption increase in parallel with higher Cs. The fact that foliar water spray, which increases Cs, improved growth and yield indicates that the direct reason for growth and yield reduction was not water stress: it was Pn shortage due to the lower Cs resulting from water stress. Sala *et al.* also reported that the aftereffects of drought are attributable to low Pn in a shortgrass steppe[13]. Xeromorphism is a plant protection mechanism for surviving under water-stressed conditions. Therefore, increasing the Cs does not always improve the growth of water-stressed plants. Foliar water spray was not effective in melon and cabbage root growth (Table 4 and Table 5).

Leaf water loss reduced xylem pressure potential in melon to a lesser degree than in tomato and papaya leaves (Fig. 7), indicating that increased Cs that results from foliar water spray increases physical water uptake ability to a lesser extent in melon than in tomato and papaya. The disadvantages of water loss due to increased Cs are greater than the advantages due to increased water uptake in melon, especially in plants sprayed at 12:00 (Table 5).

5. Conclusions

Based on the foregoing results, the following can be concluded:

1) Mild water stress due to coarse-clod soil and plowed hardpan during a dry spell resulted in permanent and irreversible effects on the stomata. Even after the end of the dry spell, plant Tr, equivalent to Cs, cannot recover to the normal level. The result is decreased growth and yield.

2) Foliar water spray can increase Cs. The spray in the late evening accelerates Pn and Tr, leading to increased yield. This technique can be used in tomato, sweet potato and papaya. However, it is harmful in melon and cabbage.

3) Foliar water spray increases Cs. A higher Cs increases water stress and accelerates gas exchange between the leaves and the atmosphere. In tomato and papaya, water stress accelerates water uptake. Its acceleration increases Pn accompanied by increased gas exchange. Increase in water uptake and Pn increases root growth first, followed by increases in growth and yield. However, water stress leading to increased Cs reduces growth and yield in melon since increased Cs triggers lower water uptake by the plant.

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