Irrigation Timing: Effect on Plant Growth, Photosynthesis, Water-Use Efficiency and Substrate Temperature

Stuart L. Warren and Ted E. Bilderback
Department of Horticultural Science
North Carolina State University
Raleigh, NC 27695-7609
USA

Keywords: irrigation volume, irrigation management, *Cotoneaster dammeri* 'Skogholm', leaching fraction.

Abstract

Pine bark based container substrates, common in the southeastern United States, have low moisture retention properties; therefore, daily irrigations during the growing season are required to maximize plant growth. Current guidelines state that irrigation should occur during the early morning hours (before 1000 HR) to reduce potential of wind blowing the irrigation water from the targeted area and to reduce evaporation of irrigation water. However, limited research indicated that multiple application of water each day resulted in more growth compared to early morning application. The objective of these studies were to evaluate the effects of irrigation timing on plant growth and photosynthesis, water-use efficiency, and substrate temperature. In experiment 1, the daily total volume of irrigation to maintain 0.40 leaching fraction (LF) in the predawn application (0300, 0500, and 0700 HR) was divided into three equal parts and applied at the following times: 0300, 0500, and 0700 HR; 1200, 1500, and 1800 HR; 0900, 1200, and 1500 HR; and 0500, 1200, and 1900 HR. In experiment 2, the daily total volume of irrigation to maintain 0.15 LF within each treatment was divided into three equal parts and applied at the following times: 0200, 0400, and 0600 HR; 0600, 0900, and 1200 HR; 1200, 1500, and 1800 HR; and 0600, 1200, and 1800 HR. Irrigation applied at 1200, 1500, and 1800 HR produced 57% and 69% greater plant dry weight in experiment 1 and 2, respectively compared to irrigation applied following current guidelines (predawn). Root : top ratio was unaffected by irrigation timing. In both experiments 1 and 2, irrigation applied at 1200, 1500, and 1800 HR had higher water use efficiency compared to irrigation applied at 0300, 0500, and 0700 HR; and 0600, 0900, and 1200 HR. In experiment 2, plants irrigated at 1200, 1500, and 1800 HR maintained higher rates of net CO_2 assimilation and had lower substrate temperatures from 1800 to 2200 HR compared to plants irrigated at 0300, 0500, and 0700 HR; and 0600, 0900, and 1200 HR.

INTRODUCTION

To produce a high quality plant requires proper irrigation management. Pine bark based container substrates, common in the southeastern United States, have low moisture retention properties; therefore, daily irrigations during the growing season are required to maximize plant growth. However, concerns with water-use have forced many nurseries to search for “best management practices” (BMPs) to improve irrigation application and water-use efficiency (Urbano, 1989). Current BMPs for determining irrigation volume state that it should be based on the amount of water lost since the last irrigation (Yeager et al., 1997). In addition, BMPs state that irrigation should occur during the early morning hours (before 1000) to reduce potential of wind blowing the irrigation water from the targeted area and to reduce evaporation of irrigation water (Yeager et al., 1997). A recent survey of Alabama nurseries suggests that most nurseries (> 60%) are following this recommendation (Fain et al., 2000). However, limited previous research indicate that multiple applications of water each day resulted in more growth compared to early morning application (Beeson, 1992; Keever and Cobb, 1985).

Much research has focused on increasing irrigation application efficiency. Cyclic irrigation, where the daily water allotment is applied in a series of cycles comprised of an irrigation and a resting interval (Karam, 1993), can improve irrigation application efficiency [(irrigation volume applied - volume leached) ÷ volume applied] by 25% to 38% (Fare et al., 1993; Lamack and Niemiera, 1993; Tyler et al., 1996a). Tyler et al. (1996a) reported the number of cycles (2, 3, or 6) did not differ in irrigation application efficiency.

Research examining irrigation volume has not received as much attention (Groves et al. 1998, Tyler et al. 1996b). A survey of growers in the southeastern United States revealed that the average daily amount of water applied ranged from 0.8 to 3.3 cm (Fare et al., 1993). Volume of irrigation would be dependent upon container size, substrate, plant, and environment. Leaching fractions (LF = irrigation water leached ÷ irrigation water applied) provide a more comparable number. Tyler et al. (1996b) reported a LF of 0.4 maximized growth of *Cotoneaster dammeri* 'Skogholm'. However, Groves et al. (1998) reported a LF of 0.15 maximized growth of 'Skogholm' contoneaster whereas, it required a LF of 0.3 to maximize growth of *Rudbeckia fulgida* 'Goldsturm'. Growers need additional techniques for irrigation and water-use efficiency to continue improvement. One technique may be irrigation timing.

Irrigation scheduling is defined as the process of determining how much to apply (irrigation volume) and timing (when to apply). The goal of irrigation scheduling is to control the water status of the crop to achieve a targeted level of plant performance. The performance level can vary from optimizing irrigation input to maximize water-use efficiency for optimum plant growth. Since the commercial value of woody landscape plants is generally based on size and aesthetics, most growers are focused on maximizing plant growth. Irrigation scheduling for field grown agronomic crops has been extensively studied all over the United States (Hill and Allen, 1996; Wanjura et al., 1995); however, the acreage where a systematic procedure is utilized for irrigation scheduling decisions is small. Past research and practical experience has shown that irrigation management practices must be simplistic, useable, flexible within the existing system design and maintenance constraints, and understandable by growers in order for them to be adopted. Therefore, it is not surprising, that the predominate irrigation scheduling method is decision making by the agricultural producer based on experience.

In field production, timing refers to determining the day that irrigation should be applied. Containerized nursery crop production is unique, in that, it most often requires daily irrigation. A better question regarding timing for nursery crop production might be not what day are you going to irrigate, but when during the 24 hours should you irrigate. There are techniques that might aid in determining irrigation timing: water content of the plant can be determined via changes in stem or trunk diameter (Riviere and Chasseriaux, 1999), leaf water potential (Riviere and Chasseriaux, 1999), and sap flux measurement (Sakuratani, 1981; Valancogne and Nasr, 1989). However, while these techniques may be good research tools, the current complexity of the systems combined with equipment requirements may preclude current grower use (Riviere and Chasseriaux, 1999). In addition, the plant is already under stress before the signal is given to irrigate. The use of tensiometers to monitor substrate water levels has been examined (Raviv et al., 1993; Testezlaf et al., 1999). They are relatively inexpensive, but have a limited operating range (0 to 80 kPa of suction), a response lag time, require continuous maintenance, and must maintain good contact with the substrate. Previous experience has shown that methods that require field measurements are not readily adopted by growers (Hill and Allen, 1996). A simple system based on applying water on time of day may offer the opportunity to improve irrigation application and water-use efficiency with minimal measurements and changes in their current system. This may increase the possibility of adoptation by growers.

Irrigation timing based on canopy temperature has also been examined in field crops. Decision criteria were based upon temperature thresholds and the cumulative time beyond these thresholds (Wanjura et al., 1995). While this approach has potential for

containerized nursery crops, it has not been studied with container grown plants. However, Keever and Cobb (1985) reported irrigation during the day (1300 HR or split application at 1000 and 1500 HR) reduced substrate and canopy temperature which they claimed enhanced top and root growth of *Rhododendron* x 'Hershey's Red' compared to irrigation at 2000 HR. Although, Keever and Cobb stated that the timing of irrigation to achieve maximum growth is not known, their results suggested that a single application applied 2 to 4 hr before maximum air temperature or split application at 1000 and 1500 HR was beneficial. Beeson (1992) working with four woody ornamentals also reported increased growth when irrigation was applied during the day in contrast to predawn (0600 HR) irrigation. However, he attributed the increased growth to lower daily accumulated water stress. Unfortunately, the times of irrigation during the day were not reported. Thus, irrigating during the day may increase growth by reducing heat load and minimizing water stress in the later part of the day. No studies have determined if irrigation timing affects water usage and water-use efficiency.

Since many growers in the United States traditionally irrigate during predawn or early morning hours, these data suggest that simple changes in current irrigation timing recommendations should be considered. Unlike the lack of adoptation of irrigation scheduling in field grown crops due to complexity of the systems and the measurements required, simple changes in irrigation timing could be readily adopted with minimal changes in the current growers' system. Therefore, our objective was to evaluate the effects of irrigation timing on plant growth, photosynthesis, water-use efficiency, and substrate temperature.

MATERIAL AND METHODS

Experimental Design and Cultural Practices

The study consisted of two experiments conducted in 1999 and 2000. Both experiments were in a randomized complete block design with 4 replications and were conducted for 100 days at the North Carolina State University Horticulture Field Laboratory, Raleigh. Rooted cuttings of *Cotoneaster dammeri* 'Skogholm' were potted into 3.8 L containers in an 8 composted pine bark : 1 sand (by vol) substrate amended with 0.9 kg m^{-3} dolomitic limestone. Each plant was fertilized at potting with 5.0 g N from 15-2.2-8.2 (17-5-10, 5-6 month, Pursell Technology, Sylacauga, AL). Nitrogen was supplied by polymer-coated ammonium nitrate. Plants were grown on a gravel bed subdivided into 16 separate plots that allowed for collection of all irrigation water leaving each plot. Plots were 8 x 2 m with a 2% slope. Twenty containers were placed in each plot for a total of 80 containers in each treatment.

Irrigation Volume and Timing

In experiment 1, the volume of irrigation to maintain 0.40 ±0.05 LF in the predawn application (treatment A below) was applied to all treatments (Table 1). The total daily volume of water was divided into three equal parts and applied at the following times: A. 0300, 0500, and 0700 HR (predawn); B. 1200, 1500, and 1800 HR (PM); C. 0900, 1200, and 1500 HR (midday); D. 0500, 1200, and 1900 HR (all day).

Predawn (treatment A) is similar to current grower practices. Leaching fraction was monitored daily to maintain 0.40 LF in the predawn treatment (0300, 0500, and 0700 HR).

In experiment 2, the daily total volume of irrigation to maintain a 0.15 ±0.05 LF within each treatment was divided into three equal parts and applied at the following times: A. 0200, 0400, and 0600 HR (predawn); B. 0600, 0900, and 1200 HR (AM); C. 1200, 1500, and 1800 HR (PM); D. 0600, 1200, and 1800 HR (all day).

Leaching fraction was monitored daily. In both studies, irrigation was applied via pressure compensated spray stakes [Acu-Spray Stick; Wade Mfg. Co., Fresno, CA (200 ml min^{-1})].

Physical Properties of Growing Substrate

Physical properties of the substrate (percent volume at drainage) were total porosity 78%, air space 16%, container capacity 62%, unavailable water 31%, and available water 30%. Physical properties were determined as described in Tyler et al. (1993).

Data collected

1. Substrate Temperature. Substrate temperatures were measured in two locations in one container in every replication (total of 8 thermocouples per treatment) for the entire study. One copper-constantan thermocouple was positioned in the substrate half-way down the container profile on the southern exposure, 2.5 cm from the container wall; the other thermocouple was positioned in the substrate half-way down the container profile on the northern exposure, 2.5 cm from the container wall. The thermocouples were connected to a 21X micrologger with AM-32 multiplexer (Campbell Scientific, Logan, Utah). Temperature data were recorded every 5 min and averaged over each 60-min interval. Maximum, minimum, and average temperature along with time of maximum, and time of minimum were recorded every 60 min.

2. Plant Response. For both studies, at harvest, tops (aerial tissue) from five randomly chosen containers per plot (total of 20 containers / treatment) were removed. Roots were placed over a screen and washed with a high pressure water stream to remove substrate. Shoots and roots were dried at 65 °C for 5 days and weighed. In experiment 2, diurnal measurements of net CO_2 assimilation (A) and stomatal conductance (gs) were made on 20 July and 17 August 2000 on one plant from each replication (4 plant treatment^{-1}), using a portable photosynthesis system containing a LI-6200 computer and LI-6250 gas analyzer (LI-COR, Lincoln, Nebraska). A diurnal measurement event consisted of measurements during late morning from 1030 to 1130 HR, at midday from 1300 to 1400 HR and late afternoon from 1600 to 1700 HR. The same plants were selected on both dates. Readings were made on the terminal 8 cm of growth. A 0.25-L curvette was used for measurements. PPF values average 1250±143, 1655 ±75, and 1134 ±45 µmol s^{-1} m^{-2} for morning, midday, and late afternoon measurement periods, respectively.

3. Statistical Analysis Data were subjected to analysis of variance procedures (ANOVA) (SAS, 1985). Treatments means were separated by LSD, P = 0.05. The following variables were determined: total plant dry weight = top + root dry weight; water use efficiency = irrigation volume retained in substrate / total plant dry weight (L of water required to produce 1 g plant dry weight); and root : top ratio (R:T) = root dry weigh ÷ top dry weight.

RESULTS AND DISCUSSION

Plant response

1. Experiment 1. All treatments received a total of 39.6 L of irrigation water resulting in LFs of 0.38, 0.19, 0.25, and 0.25, for predawn, midday, PM and all day treatments, respectively for the 100 days. Irrigation applied in PM and all day produced 56% and 46% greater top dry weight, respectively compared to predawn irrigation (Table 1). Plants irrigated with PM also had greater top dry weight compared to all day application (0500, 1200, and 1900 HR). Keever and Cobb (1984) reported that irrigation applications during the day (1300 HR, or 1000 and 1500 HR) increased top and root growth compared to irrigation applied at 2000 HR. Root dry weight increased 65% when irrigated with PM (1200, 1300, and 1600 HR) compared to predawn. Plants irrigated with midday, PM, and all day irrigation had similar root dry weights. Total plant dry weight had the same results as top growth. R:T ratio was unaffected by irrigation timing illustrating that top and root dry weight responded similarly to irrigation timing.

2. Experiment 2. A total of 18.7 L, 26.4 L, 27.5 L, and 26.4 L of irrigation water was applied to predawn, AM, PM, and all day, respectively resulting in LFs of 0.19, 0.15, 0.13, and 0.13, for predawn, AM, PM, and all day, respectively for the 100 days.

Irrigation applied PM had significantly greater top dry weight compared to all other irrigation timings (predawn, AM, and all day) (Table 2). Top dry weight was 71% heavier when irrigated with PM compared to predawn. Adjusting irrigation volume to maintain similar LFs for each treatment may account for the additional growth. Root growth results were similar to experiment 1, i.e., AM, PM, and all day had similar root dry weights. In addition, R:T ratio was unaffected by irrigation timing. These data combined with results from Keever and Cobb (1984) and Beeson (1992) support the hypothesis that plant growth can be increased significantly if irrigation is applied during the day. In general, plants irrigated with PM produced the best results which is in contrast to the current recommendation of irrigating in the early morning hours. These studies suggest that if presumable sufficient daily irrigation is restricted to predawn, growth will be significantly reduced compared to plants grown with irrigation applied during the day.

Water Use Efficiency

In experiments 1 and 2, PM had higher water use efficiency requiring 0.6 L and 0.3 L (g plant dry weight)$^{-1}$ compared to 0.7 L and 0.4 L (g plant dry weight)$^{-1}$ for predawn irrigation (Table 3). This is an increase of 17% and 33%, respectively. Even though it required more water to maintain the LF for PM and Midday treatments compared to predawn, PM and midday produced a gram of plant dry weight with less water.

Photosyntesis and Stomatal Conductance

Results from 20 July and 17 August were similar, so only data from 17 August are presented. At 1100 HR, plants irrigated with PM and all day had 48% higher rates of A compared to predawn and AM (Table 4). Compared to 1100 HR measurements, A of all treatments decreased at 1330 HR. This is probably due to increased canopy and substrate temperature. Martin et al. (1991) working with containerized *Magnolia grandiflora* 'St. Mary' in Florida reported a similar decline in midday A levels. They attributed the decline to increasing container and air temperature. Only plants irrigated all day had significantly greater A than predawn and AM at 1330 HR. This may reflect the two irrigation cycles all day (0600 and 1200 HR) had by 1330 HR compared to the one cycle for PM irrigation (1200 HR). Plants irrigated PM may have had reduced A due to limited water availability. At 1630 HR, A levels of plants irrigated predawn, AM, and all day decreased compared to 1330 HR suggesting increasing water and temperature stress. However, plants irrigated with PM had increased A measurements compared to 1330 measurements. At 1630 HR, plants irrigated with PM had 86% higher rates of A compared to predawn and AM. Both AM and all day had water applied at 1200 but this does not appear to be sufficient to maintain A levels through 1630 HR. Plants irrigated PM received additional water at 1500 HR which appeared to maintain A. Beeson (1992) reported the greatest differences in shoot water potential between plants irrigated predawn and plants irrigated throughout the day occurred in mid- to late afternoon. Generally by 1300 HR plants irrigated predawn had lower water potential with the difference becoming more pronounced by 1600 HR.

Compared to A, gs produced similar differences suggesting that differences in stomatal conductance were regulating A (data not presented). At low to moderate levels of water stress, most reductions in CO_2 assimilation are due to stomatal closure (Chaves, 1992). At 1100 HR, plants irrigated with PM and all day had significantly higher gs levels compared to predawn and AM. At 1330 HR, all day was still significantly higher that predawn and AM whereas, by 1630 HR only PM was significantly higher than predawn and AM.

Substrate Temperature

Substrate temperatures recorded on 16-17 August 2000 are presented as typical temperatures with sunny to partly cloudy sky conditions (Fig. 1). With the exception of time of daily maximum temperature, containers irrigated with predawn and AM

treatments had similar temperature profiles. The time of daily maximum for containers irrigated predawn occurred at 1630 HR (43.8 °C) whereas, the daily maximum for AM was 1730 HR (42.8 °C). Thus, data for AM is not presented. Time of daily maximum and maximum temperature for containers irrigated PM and all day was similar (1530 HR, 40.2 °C). Martin et al. (1991) working with a 3 pine bark : 1 peat : 1 sand substrate in Florida reported maximum container temperatures of 45 °C from 1715 to 1745 HR. Containers irrigated predawn had significantly lower temperatures at 0600, 0700, and 0800 HR compared to PM however, the differences were small. Container temperatures irrigated with PM and all day had significantly lower temperatures from 1800 to 2200 compared to predawn for most days. Compared to predawn, daily maximum temperatures for PM were usually significantly lower by 2 °C to 3 °C. This difference in temperature in combination with available water could have a significant impact on A (Ruter and Ingram, 1990). Martin et al. (1991) reported a 50% increase in caliper growth of *Magnolia grandiflora* 'St. Mary' when maximum temperature was reduced by 3 °C (48 °C to 45°C).

CONCLUSIONS

Irrigation timing had a significant affect on plant growth, container temperature, A, gs, and water use efficiency. Plants that were irrigated with PM significantly outperformed plants grown with current irrigation timing guidelines. From the data herein it is not possible to determine whether the reduction in substrate temperature or the increase in available water increased A. In either case, decreases in plant growth appear to be related to increases in diurnal water stress over the course of the growing season. Similarly, moderate water stress over long periods was more detrimental to dry matter accumulation than severe stress for short periods in eucalyptus (Myers and Landsberg, 1989). This strongly suggests that further investigations with irrigation timing with other nursery crops in other environments should be conducted.

Literature Cited

Beeson, R.C. 1992. Restricting overhead irrigation to dawn limits growth in container grown woody ornamentals. Hort. Science 27:996-999.

Chaves, M.M. 1992. Effects of water deficits on carbon assimilation. J. Expt. Bot. 42:1-16.

Fain, G.B., Gilliam, C.H., Tilt, K.M., Olive, J.W. and Wallace, B. 2000. Survey of best management practices in container production nurseries. J. Environ. Hort. 18:142-144.

Fare, D.C., Gilliam, C.G. and Keever, G.J. 1993. Monitoring irrigation at container nurseries. Hort. Technology 2:75-78.

Groves, K.M., Warren, S.L. and Bilderback. T.E. 1998. Irrigation volume, application and controlled-release fertilizers: I. Effect on plant growth and mineral nutrient content in containerized plant production. J. Environ. Hort. 16:176-181.

Hill, R.W. and Allen, R.G. 1996. Simple irrigation scheduling calendars. J. Irrig. Drain. Eng. 122:107-111.

Karam, N.S. 1993. Overhead sprinkle strategies to reduce water and nitrogen loss from container-grown plants. Ph.D. Dissertation. Virginia Polytechnic Institute and State University. Blacksburg.

Keever, G.J. and Cobb, G.S. 1985. Irrigation scheduling effects on container media and canopy temperature and growth of 'Hershey's Red' azalea. Hort. Science 20:921-923.

Lamack, W.F. and Niemiera, A.X. 1993. Application method affects water application efficiency of spray stake-irrigated containers. Hort. Science 28:625-627.

Martin, C.A., Ingram, D.L. and Nell, T.A. 1991. Growth and photosynthesis of *Magnolia grandiflora* 'St. Mary' in response to constant and increased container volume. J. Amer. Soc. Hort. Sci. 116:439-445.

Myers, B.J. and Landsberg, J.J. 1989. Water stress and seedling growth of two eucalyptus species from contrasting habitats. Tree Physiol. 5:207-218.

Raviv, M., Medina, S., Shamir, Y., Ben Ner, Z. and Tattine, M. 1993. Very low medium

moisture tension - a feasible criterion for irrigation control of container-grown plants. Acta Hort. 342:111-119.
Riviere, L.M and Chasseriaux, G. 1999. Different ways of monitoring the irrigation of container and pot plants. Acta Hort. 481:353-360.
Ruter, J.M. and Ingram, D.L. 1990. ^{14}Carbon-labelled photosynthesis partitioning in *Ilex crenata* 'Rotundifolia' as supraoptimal root-zone temperatures J. Amer. Soc. Hort. Sci. 115:1008-1013.
Sakuratani, T. 1981. A heat balance method for measuring water flow in the stem of intact plant. J. Agric. Meteorology 37:9-17.
SAS Institute, Inc. 1985. SAS User's Guide: Statistics. Version 6.09. SAS Institute, Inc. Cary, NC.
Testezlaf, R., Larsen, C.A., Yeager, T.H. and Zazueta, F.S. 1999. Tensiometric monitoring of container substrate moisture status. Hort. Technology 9:105-109.
Tyler, H.H., Warren, S.L., Bilderback, T.E. and Fonteno, W.C. 1993. Composted turkey litter: I. Effect on chemical and physical properties of a pine bark substrate. J. Environ. Hort. 11:131-136.
Tyler, H.H., Warren, S.L. and Bilderback, T.E. 1996a. Cyclic irrigation increases irrigation application efficiency and decreases ammonium losses. J. Environ. Hort. 14: 194-198.
Tyler, H.H., Warren, S.L. and Bilderback, T.E. 1996b. Reduced leaching fractions improve irrigation use efficiency and nutrient efficacy. J. Environ. Hort. 14:199-204.
Urbano, C.C. 1989. The environmental debate: An industry issue. Amer. Nurs. 169:69-73, 83, 85.
Valancogne, C. and Nasr, Z. 1989. Measuring sap flow in stem of small trees by a heat balanced method. Hort. Science 24:383-385.
Wanjura, D.F, Upchurch, D.R. and Mahan, J.R. 1995. Control of irrigation scheduling using temperature-time thresholds. Transactions ASAE 38:403-409.
Yeager, T.H., Gilliam, C.H., Bilderback, T.E., Fare, D.C., Niemiera, A.X. and Tilt, K.M. 1997. Best Management Practices Guide for Producing Container-Grown Plants. Southern Nurs. Assoc., Marietta, GA.

Tables

Table 1. Effect of irrigation timing on dry weight and root : top ratio of *Cotoneaster dammeri* 'Skogholm', experiment 1.

Irrigation Timing	Dry Weight (g)			
	Top	Rot	Total	Root:Top[z]
Predawn	31.9 c[y]	4.6 b	36.6 c	0.14 a
Midday	46.6 b	6.2 ab	52.8 ab	0.15 a
PM	49.9	7.6 a	57.5 a	0.13 a
All day	42.6 b	6.4 a	50.0 b	0.15 a

[z]Root : top = root dry weight ÷ top dry weight.
[y]Means within columns separated by LSD, P = 0.05.

Table 2. Effect of irrigation timing on dry weight and root : top ratio of *Cotoneaster dammeri* 'Skogholm', experiment 2.

Irrigation Timing	Dry Weight (g)			
	Top	Rot	Total	Root:Top[z]
Predawn	60.7 d[y]	12.8 b	73.5 c	0.21 a
Midday	80.3 c	18.0 a	98.3 b	0.22 a
PM	103.5 a	20.7 a	124.2 a	0.20 a
All day	91.0 b	19.7 a	110.7 b	0.22 a

[z]Root : top = root dry weight ÷ top dry weight.
[y]Means within columns separated by LSD, P = 0.05.

Table 3. Effect of irrigation timing on water use efficiency[z].

Irrigation Timing	Experiment	
	1	2
Predawn	0.7 a[y]	0.4 a
Midday	0.7 a	0.4 a
PM	0.6 b	0.3 b
All day	0.6 b	0.3 b

[z]Water use efficiency = liters water ÷ g dry weight
[y]Means within columns separated by LSD, P = 0.05.

Table 4. Effect of irrigation timing on net CO_2 assimilation of *Cotoneaster dammeri* Skogholm', experiment 2.

Irrigation Timing	CO_2 assimilation (µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)		
	1100	1330	1630
Predawn	5.9 b[y]	5.4 b	4.0 c
Midday	5.5 b	4.6 b	4.2 bc
PM	8. 7 a	6.5 ab	7.6 a
All day	8.4 a	7.5 a	6.0 ab

[z]Means within columns separated by LSD, P=0.05

Figures

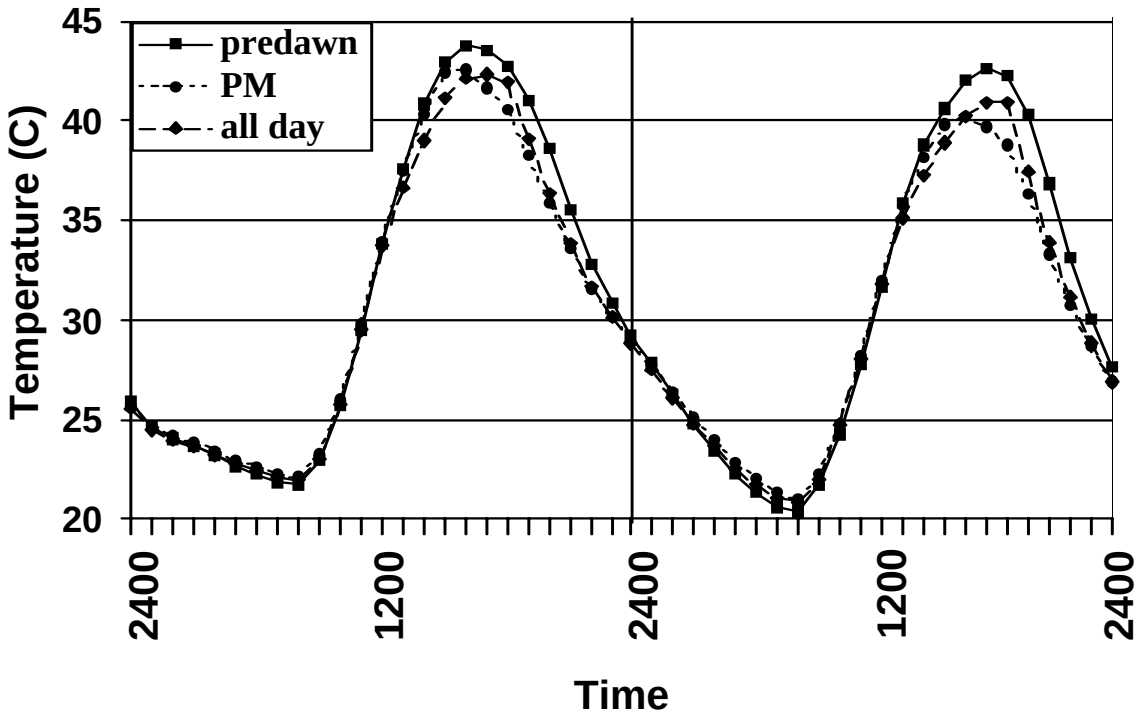

Fig. 1. Effect of irrigation timing on substrate temperature on 16 and 17 August 2000.