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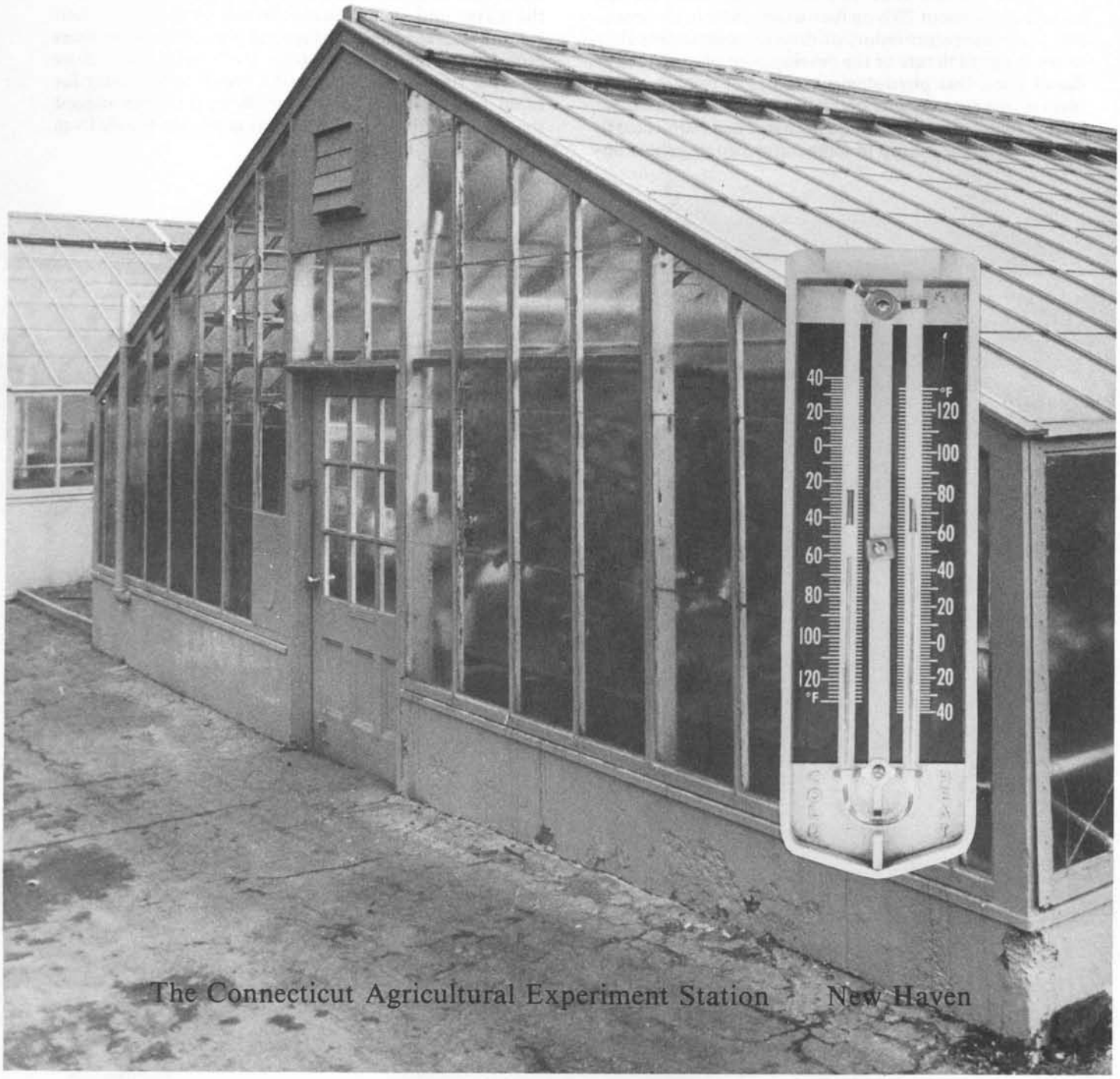
Split-night Temperatures in a Greenhouse:
The Effects on the Physiology and Growth of Plants

By Martin P. N. Gent, John H. Thorne, and Donald E. Aylor



The Connecticut Agricultural Experiment Station · New Haven

SUMMARY

The split-night regime refers to lowering the minimum temperature of a greenhouse from 60 F (15.5 C) to 45 F (7.2 C) for 8 hours after 10 pm. We calculate that this scheme saves about 20% on fuel in the winter in Connecticut. The temperature reduction does not appreciably slow either the growth rate or the development of tomatoes or Easter lilies. Our physiological studies of tomato plants suggest two reasons why plant growth is so little affected by this energy saving technique. First, plants subjected to a repeated nightly drop in temperature do not show lingering inhibition of photosynthesis, translocation, or carbohydrate metabolism the following morning. Second, to compensate for the inhibition of physiological processes during the cool part of the night, plants subjected to split-night temperatures move sugars more quickly out of the leaves and stems during the day by degrading their starch reserves faster. This second phenomenon becomes especially evident during fruit production when more efficient translocation from the leaves is necessary for rapid fruit growth. These physiological studies suggest that economic production of many crops will benefit from the split-night regime.

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During the winter in Connecticut, greenhouses are usually heated to 60 F or 65 F to insure proper plant development and timeliness of flowers or fruit. In 1978, about 25% of the cost of producing greenhouse crops was for heating fuel.

Although turning down the thermostats in greenhouses will save fuel, the plants may grow poorly when temperatures are kept low for an entire night. We reasoned however, that the limited amount of sugar produced in the dim sunlight of winter might not require an entire night to be translocated and metabolized. Therefore, we split the night into two parts for purposes of temperature control; starting at 10 pm (EST) we reduced the thermostat from 60 F (15.5 C) to 45 F (7.2 C) for 8 hours each night. We call this the split-night temperature regime and calculate that it would save about 20% of the fuel normally used to maintain a greenhouse in New Haven, CT at 60 F for the entire night (see Appendix 1).

In this report we compare the growth and physiology of tomato, lily, and tobacco grown in split-night temperatures, with plants grown at 60 F for the entire night. An understanding of the physiological response of plants to split-night temperatures should allow growers to choose a management scheme that will save fuel without sacrificing growth.

METHODS

Experimental design and temperature control

The experimental greenhouse, located in New Haven, CT, has single-pane clear glass and an east-west ridge line. The house is separated into an east and west half by a glass partition covered with translucent polyethylene for insulation. Each side was heated by a double row of steam radiators on the side walls which were controlled by a centrally-located thermostat. The top vents opened automatically when temperatures exceeded 80 F (27 C). In the east half, the temperature was lowered to 45 F (7.2 C) for part of each night, i.e., the night was split into two parts. The temperature in the west half was maintained at 60 F (15.5 C) throughout the night. Air temperature was measured by shaded hygrothermographs located in each half near the thermostats. Outdoor temperatures were recorded by a thermograph in a weather shelter located 40 feet north of the greenhouse. Although both halves of the greenhouse received almost equal amounts of sunlight, the split-night side tended to get more in the morning and less in the afternoon.

Fifteen Easter lily, 75 tomato, and 5 tobacco plants in individual pots were arrayed in blocks five rows deep on benches above the height of the radiators and near the south wall of the greenhouse. The lilies were closest and the tobacco farthest from the partition. Each week, the plants were randomly rearranged. Nellie White lilies were supplied (Long's Greenhouse, East Haven, CT) in 3 *l* pots in soil-peat-perlite mix (1:1:1), pH 5.9. Tomato seeds (Patio Hybrid, Comstock Co., Wethersfield, CT and Fireball 861, Harris Seed Co., Rochester, NY) were germinated on December 18, 1978 and grown at 80 F day and 65 F night in Promix until they were transplanted on January 7 into 3 *l* pots containing equal parts soil, sand, peat and vermiculite, at a pH of 6.5. Tobacco seedlings (var. Havana seed), supplied in the 4 or 5 leaf stage by Dr. I. Zelitch were grown in a similar soil mix.

The tomato and tobacco plants were watered daily at 7 am with 50 to 250 ml of water at 70 F (21 C) to raise the temperature of the soil. The lilies were watered once a week. The volume of water was adjusted to the size of the plants to prevent waterlogging and root rot. Fertilizer was applied once a week starting on February 1 as 100 ml per pot of "Miracle-Gro" (15-15-15) at $2.64\,g \cdot l^{-1}$. Starting April 1, fertilizer was increased by 50%. Soil temperatures were measured in three pots on each side of the greenhouse.

On January 8, 1979 the plants were divided into two groups. Half were put in one side and half in the other side

of the greenhouse. Growth dates are calculated from January 8, 1979 as day 1. Tomatoes were 21-days-old at the start of the experiment.

Growth

The individual growth and development of 20 indicator tomato plants (ten each, selected at random from the control and split-night environments) was monitored throughout the experiment. The growth of each tobacco and lily plant was measured. Plant height and number of leaves was recorded during the vegetative growth. The length and width of tobacco leaves were measured during the period of fastest growth.

To convert the height of the 20 indicator tomato plants to dry weights, we used the heights and dry weights of other plants that were harvested and dissected for sugar determination or radioactive translocation analysis.

Since the height of the main stem indicates the weight of tomato plants (Went, 1944), we obtained a second-order regression of plant height versus dry weight.

$$\text{Dry weight} = -1.2114 + 0.2511 \cdot \text{height} + 0.002618 \cdot \text{height}^2 \quad (1)$$

with a correlation coefficient of 0.949 and a 3.0 g standard error about the mean. This relationship fits the data well throughout the growth of the plants (see Fig. 1).

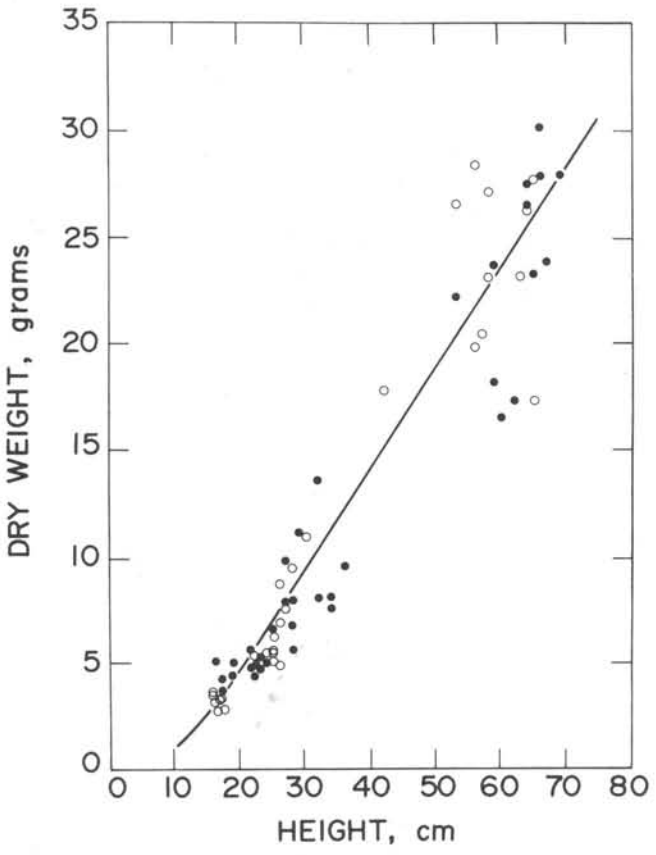

Fig. 1 The relationship between the dry weight and height of control (•) and split-night (o) tomato plants. The regression line calculated from equation 1 is shown by the solid line.

The number of flower buds and flowers on each Easter lily and tomato were recorded twice a week.

The same 20 tomato plants were observed during fruit growth to maturity. When a fruit grew larger than 1 cm in diameter it was identified with a tag, and its height and diameter were recorded twice a week. A fruit's volume was calculated using the geometric relationship for the volume of an oblate spheroid. The volumes were summed to give a growth curve for the total fruit of each plant which was fitted to a logarithmic growth function.

As fruits turned red, they were picked, weighed while fresh, then dried at 60 C for 2-3 days, and then reweighed. Fruit that were still green when the experiment was terminated on May 21 were weighed and included in the final harvest.

The rates of vegetative and fruit growth were analyzed separately for each of the 20 tomato plants measured throughout the experiment. For each plant, the growth curves were fitted to a logarithmic growth function:

$$G(t) = \frac{\text{Final Weight}}{1 + \exp\left[-\frac{(t \cdot \text{Mid-growth Date})}{\text{Duration}}\right]} \quad (2)$$

where $G(t)$ is the weight in grams at time t; Final Weight is the predicted harvest weight; Mid-growth Date is the time in days when $G(t)$ = half of the Final Weight; and Duration is the time required to reach the Final Weight if the growth were linear and equal to the fastest growth rate (given by Final Weight/Duration). This procedure gives four parameters (Final Weight, Mid-growth Date, Maximum Rate, and Duration) describing the growth of each tomato plant. The parameters were varied independently to minimize the mean squared difference between the ideal and actual growth curves. These growth parameters were subjected to an analysis of variance to find significant differences between the control and split-night populations.

Photosynthesis and transpiration

Usually starting at noon, a continuous, diurnal record of water vapor and carbon dioxide (CO_2) fluxes was obtained for individual plants isolated in a chamber adjacent to the bench. Different plants were measured on different days and plants from the split-night and control sides were sampled on alternate days. Gas exchange with the soil was prevented by a polyethylene bag surrounding the pot, which was tied about the stem. The chamber was a wooden frame 1 meter · 0.6 meter · 0.3 meter covered with Propafilm-C110 plastic (ICI, Wilmington, Del.); the door and the base were sealed with foam rubber. A fan and a baffle kept the air in the chamber well stirred.

Air was supplied to the chamber at 10 to 15 $l \cdot \text{min}^{-1}$ and sampled at 5 $l \cdot \text{min}^{-1}$ via 6 mm diameter tygon tubing. The air was drawn from outdoors to keep the CO_2 concentration relatively constant and the initial humidity low. After passing through the chamber, the water vapor in the air was measured with a dew point hygrometer. The air was then dried, and the CO_2 concentration was measured with

a differential infrared gas analyzer. These measurements, as well as temperature and photosynthetically active radiation, were recorded by a Fluke Datalogger every 15 minutes.

The net photosynthesis of tobacco was also measured on isolated leaf discs. At 9 am on one day, four leaf discs, 6 mm in diameter, were sampled from tobacco plants from both environments. They were allowed to photosynthetically assimilate $^{14}CO_2$ at 600 ppm, 30 C, and 450 μEinsteins $\cdot$ $m^{-2} \cdot sec^{-1}$ radiation for 5 minutes (Oliver and Zelitch, 1977), and were then digested in hydroxlyamine before the radioactivity was assayed by liquid scintillation.

Stomatal resistance of the lower leaf surface of the tobacco was measured directly on several days using an aspirated diffusion porometer (Turner et al., 1969; Turner and Parlange, 1970). The same three leaves on each of five plants were measured three or four times during the day. The time to measure all leaves in both halves of the greenhouse was about 20 minutes.

During early flowering (day 52) of the tomatoes and again during fruit development (day 86) diurnal trends of ^{14}C-labelled photosynthate distribution and carbohydrate levels were determined to evaluate the effects of night-time temperatures on the production, distribution, and metabolism of carbohydrates. Both day 52 and 86 were clear and sunny but were preceded by at least two cloudy, overcast days.

Translocation

Six plants randomly selected from the control and six from the split-night populations were allowed to assimilate radioactive CO_2. Plants were labelled at 11 am and at 5 pm inside a Propafilm chamber. During labelling, $^{14}CO_2$ (0.06 millicurie $\cdot$ l^{-1}, 290 ppm CO_2 in nitrogen) was supplied at a rate of 0.111 $\cdot$ min^{-1} for 5 minutes. The gas was stirred by a fan. The light intensity was 500 μEinstein $\cdot$ m^{-2} $\cdot$ sec^{-1} and the chamber remained lighted for 1 minute after the gas was turned off. Immediately after, the plants were returned to the greenhouse.

Six and 12 hours after labelling (5 pm, 11 pm, 5 am) three of the six plants from each treatment were immediately dissected. Leaves, stems, roots, and immature fruit were quickly frozen at –20 C and freeze dried. Roots were severed at the cotyledonary node and washed in cold water prior to freezing. The pericarp of immature fruit and stems were sliced to speed drying. The dried samples were weighed and ground. A subsample of 100 mg of the ground material from each plant part was digested in a solution of 0.5 ml 70% $HClO_4$ and 0.5 ml 30% H_2O_2 for 24 hours at 60 C; 5 ml water and 10 ml Aquasol II scintillation fluid were added, and radioactivity was measured by liquid scintillation spectroscopy using external standard correction for quenching.

Carbohydrate

Carbohydrate levels were also determined in these tissues to evaluate the effects of reduced night temperature on the production and distribution of photosynthate. Three plants from each regime were harvested at 5 pm, 11 pm, 5 am, and 11 am to provide samples just before and just after the cold period and correspond to harvests for the study of translocation. The plants were harvested, dissected, and frozen as described above. Dried tissues were weighed and ground to pass a Wiley 40-mesh screen. Subsamples of 50 mg fruit, 100 mg leaves or stems, and

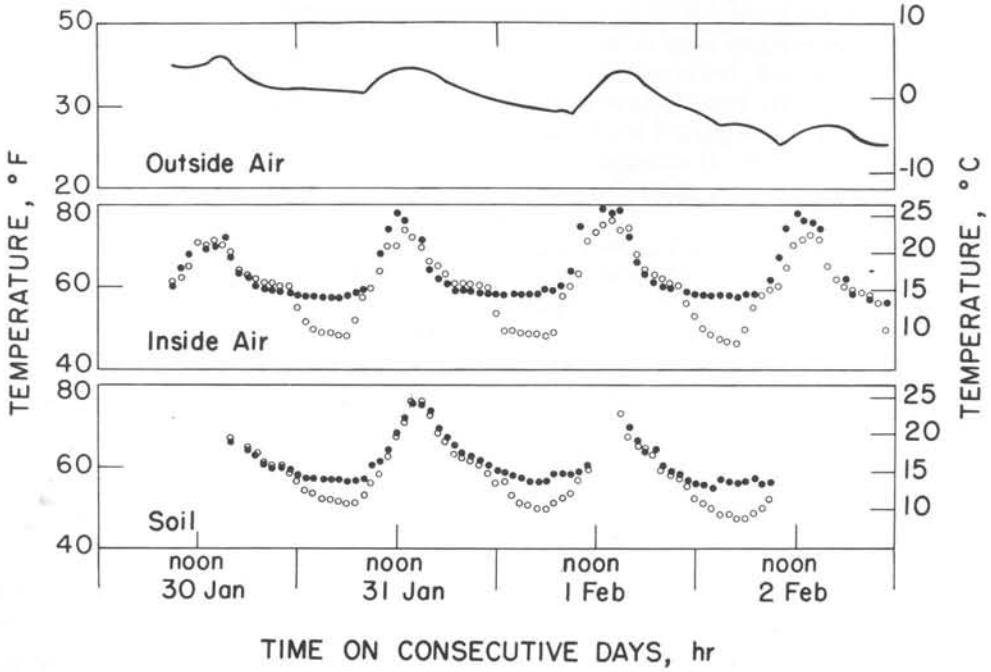

Fig. 2 Diurnal trend of the air and soil temperatures in the control (•) and split-night (o) greenhouse. The outside temperature is shown by the solid line.

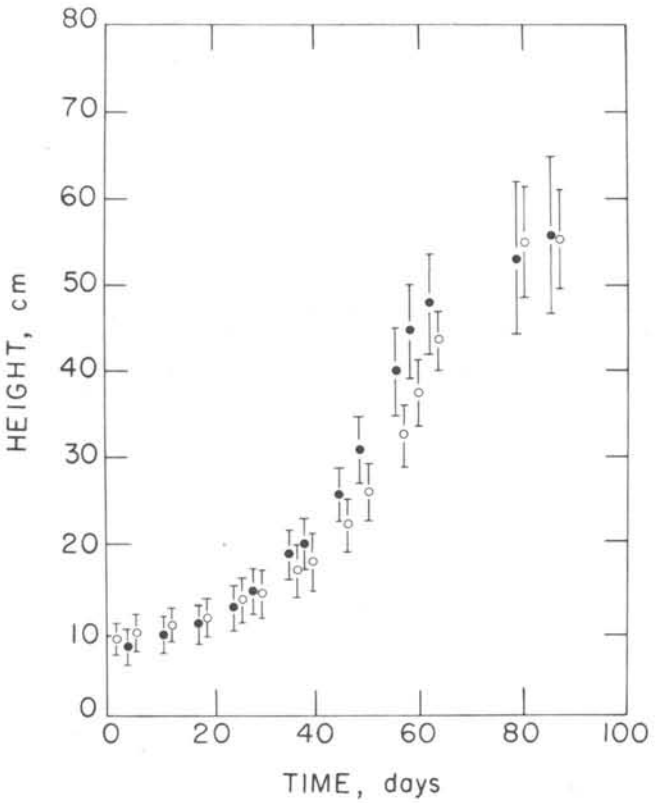

Fig. 3 The average height of control (•) and split-night (o) tomato plants. The I bar indicates the standard deviation from the sample mean.

200 mg root were repeatedly extracted with boiling 80%(v/v) ethanol. They were centrifuged, and the supernatants were combined to a final volume of 25 ml. The sucrose concentrations in the extracts were determined with a resorcinol procedure (Ashwell, 1957), which assays the fructose moiety of sucrose after free fructose is destroyed by NaOH(0.5 N final concentration). The concentrations of reducing sugars in extracts of immature fruit were found, using Clark's modification of Nelson's test (Clark, 1964).

Starch in the residue following ethanol extraction was solubilized in 15 ml of boiling water for 30 minutes. After cooling, starch was digested to glucose with 500 units of glucoamylase in 0.2 M sodium acetate buffer (pH 4.5) at 40 C . After 44 hours, samples were filtered and the filtrate brought to 100 ml with H_2O. The glucose concentration was determined colorimetrically (Clark, 1964), and the starch equivalent was found by multiplying the result by 0.9.

RESULTS

Diurnal Trends in Temperature

Since the temperature of the greenhouse was controlled by the minimum temperature settings of the thermostats, temperature control was not precise. Figure 2 illustrates the temperature variation over a 3-day period. On sunny days in January and February the control side was warmer than the split-night side by several degrees during the day. During March and April, however, this trend was reversed. After the thermostat was reduced to 45 F (7.2 C), the split-night greenhouse slowly cooled to a minimum temperature in 4 to 6 hours. Whenever the outside temperature was above 32 F (0 C), the split-night temperature never reached 45 F, but it usually went below 50 F. On very cold nights, the control greenhouse cooled below the set point to 55 F (12.8 C). The temperature differential of the two night environments was greater than 10 F (5.6 C) and less than 15 F (8.3 C) throughout the experiment.

Soil temperatures lagged behind the air temperatures about 2 hours. To speed the heating of roots in the morning, plants received 70 F (21.1 C) water at 7 am. Since the volume of warm water was limited to 50 to 250 ml per pot per day, the soil temperature was only raised 3.5 F (2 C). The soil temperatures of the split-night plants did not reach the temperatures of the controls until 10 am, but from then until nearly 12 pm the soil temperatures were the same for both sets of plants (Fig. 2).

Change in Growth

Vegetative growth of the split-night tomato plants was slower than the controls. Final height or weight, however, was similar because the split-night plants continued to grow longer. The time course of height of both populations are shown in Fig. 3. The slower growth of split-night plants was most obvious in the analyses of the Mid-growth Date parameter of the logarithmic growth curve where the delay of 5 days was significant at the 10% level of probability (Table 1A). The rate of growth of split-night plants given by the growth curve was about 15% slower than the controls. Since the duration of their growth was extended 3 days, they grew to the same final height when vegetative growth ended during fruit formation.

Table 1A Parameters describing the vegetative growth of Patio hybrid tomatoes.

Growth Parameter	Control	Split Night	Average
Final Weight (gm)	25.0 ±4.9	24.2 ±4.2	24.6 ±4.4
Mid-growth Date (da)	55.4 ±6.6	60.4 ±4.9	57.9 ±6.2
Rate* (gm/da)	0.96±0.16	0.83±0.14	0.89±0.16
Duration (da)	26.4 ±6.6	29.4 ±4.4	27.9 ±5.6

*Significantly different at the P>0.10 level of probability.

Table 1B Parameters describing the fruit growth of Patio hybrid tomatoes.

Growth Parameter	Control	Split Night	Average
Final Volume* (ml)	666 ±102	582 ±66	627 ±94
Mid-growth Date (da)	117 ± 6	115 ± 4	116 ± 5
Rate (ml/da)	32.3± 5.3	30.3± 3.6	31.3± 4.6
Duration (da)	20.9± 2.9	19.3± 1.6	20.1± 2.4

*Significantly different at the P>0.05 level of probability.

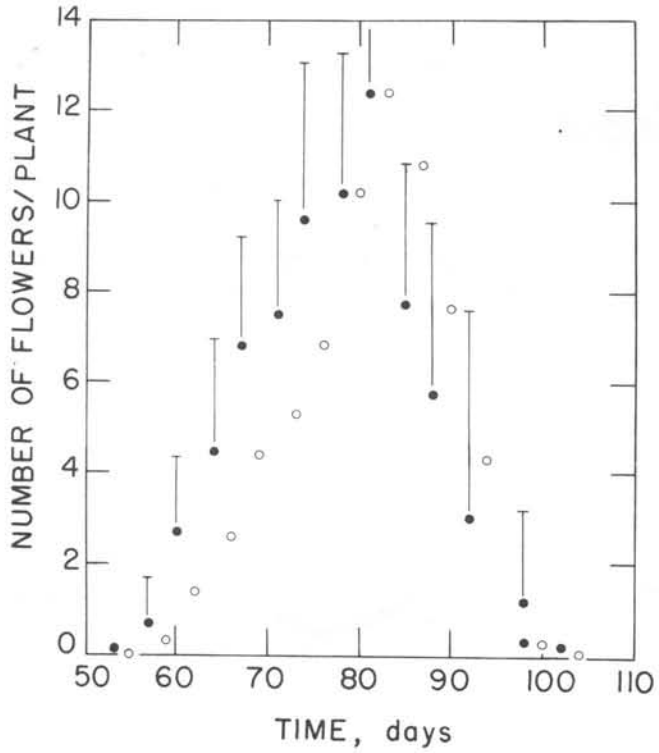

Fig. 4 The average number of open flowers of control (•) and split-night (o) tomato plants. The I bar indicates the standard deviation from the sample mean.

The average number of leaves per tomato plant did not differ between control and split-night populations, and increased linearly at one leaf every 5 days from day 1 to 70.

Figures 4 and 5 show that control and split-night plants flowered and set fruit at the same rate but the split-night plants lagged several days. This lag became smaller as plant development and fruit-set progressed.

The only statistically significant difference between the control and split-night populations during fruit growth was in the final yield of fruit. Control tomato fruit grew slightly faster and longer than the split-night fruit. These small differences led to a 13% decrease in yield (significant at the 5% probability level). The difference in yield for a large population of plants grown under the conditions of this experiment could vary from 5 to 22% within the standard error of the mean of the sample studied.

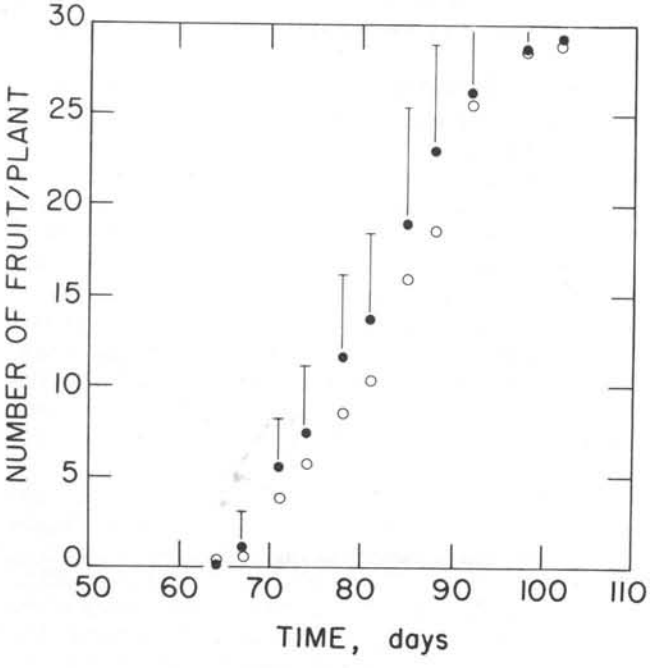

Fig. 5 The average number of fruit of control (•) and split-night (o) tomato plants and the standard deviation, I.

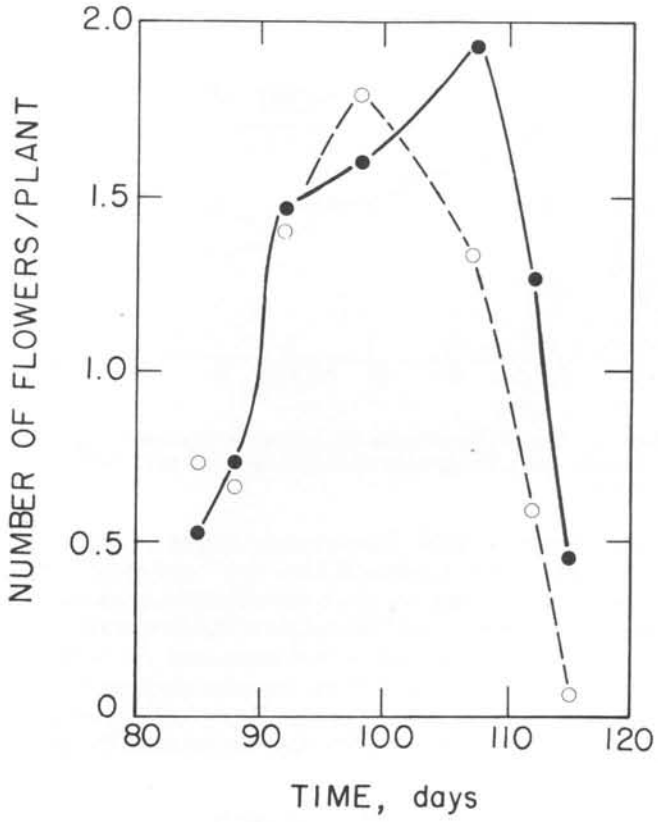

Fig. 6 The average number of open flowers of control (•) and split-night (o) Easter lilies.

The control tobacco plants grew considerably faster than the split-night plants. Although plant-to-plant variability obscured the difference in the elongation rate of individual leaves, visual observation of the size and number of leaves after a month of growth suggested that the controls grew about 50% faster than the split-night plants.

The growth and flowering of Easter lilies were affected little by the temperature at night. The cooling near the lilies however, was not as great as in other parts of the split-night greenhouse because they were closest to the

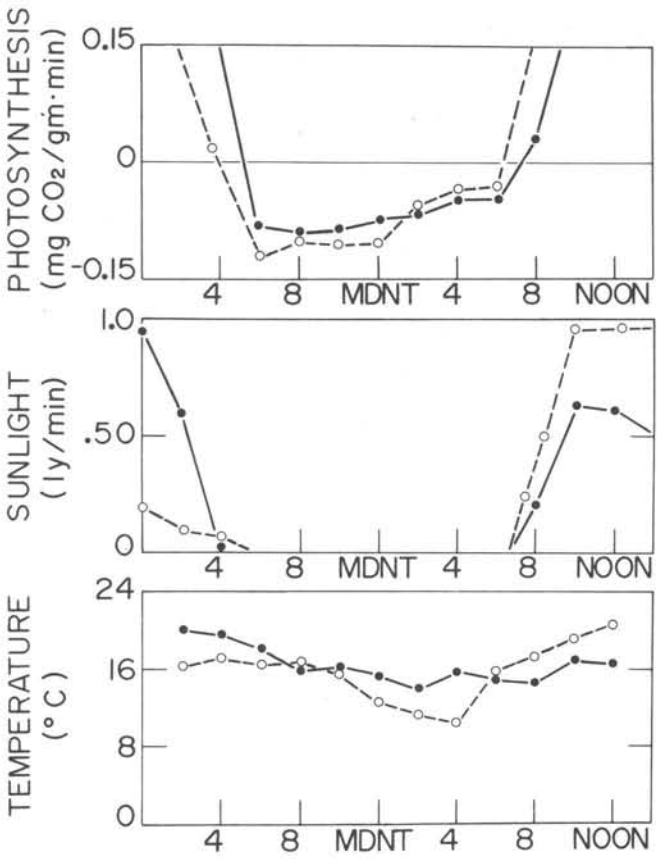

Fig. 7 Net photosynthesis of a control (●) and a split-night (o) tomato plant. The control and split-night data are for different days.

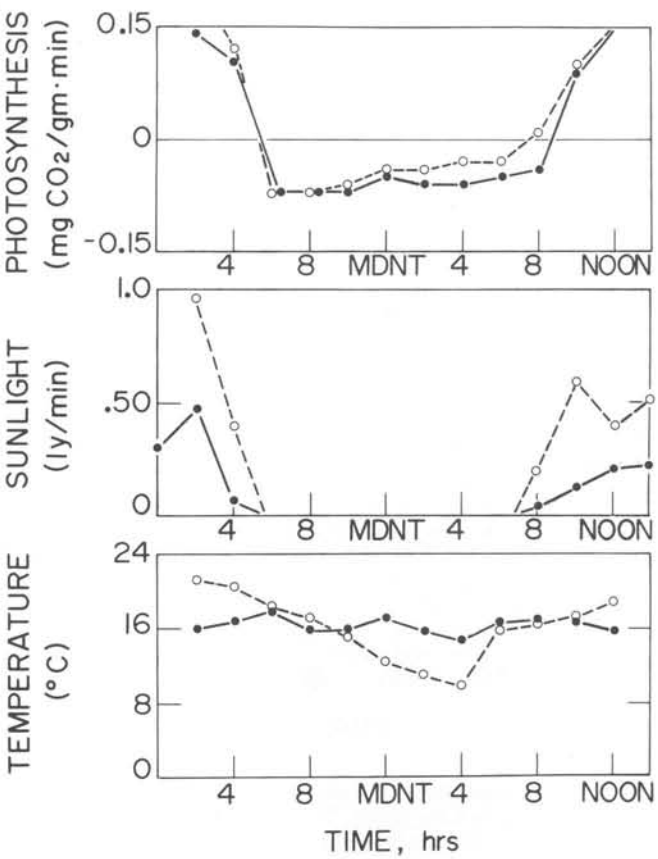

Fig. 8 Net photosynthesis of a control (●) and a split-night (o) tobacco plant. The control and split-night data are for different days.

steam heating pipes. The average height of the lilies increased linearly at about 0.5 cm · day^{-1} and at any time was about the same for both the control and the split-night plants. The mean final height of 42 cm was attained on day 80. The timing of flowering and the average number of flowers open per day was also the same for the two growth conditions (Fig. 6). However, the control plants seemed to flower a few days longer than the split-night plants.

Diurnal Course of Net Photosynthesis and Stomatal Opening

To learn if different levels of respiration and transpiration during the cool part of the night may persist to the following morning, we measured the net photosynthesis and transpiration of individual plants for a day. Figures 7 and 8 show net photosynthesis, normalized by the dry weight of the plant, for tomato and tobacco plants and show the sunlight and temperature. Since control and split-night plants were measured on different days, their photosynthesis cannot be directly compared. When the sun rose, however, photosynthesis in split-night plants rose as fast as in the control plants. Photosynthetic efficiency in the early morning is especially important in winter since days often become cloudy by mid-morning and remain cloudy for the rest of the day. Thus, a significant reduction of photosynthesis from 7 am to 10 am could include up to 30% of the total photosynthesis for the day.

Figures 7 and 8 show that photosynthesis depends on the sunlight. To compare the behavior of split-night and control tomato plants, the photosynthesis data from six experiments are plotted against sunlight intensity in Fig. 9. On the average, plants from both treatments respired at the rate of 0.06 mg CO_2 g^{-1} min^{-1} in the dark. The rate of photosynthesis rises linearly to 0.42 mg CO_2 g^{-1}min^{-1} at a sunlight intensity of 0.25 langley · min^{-1}. During cloudy winter weather, photosynthesis is saturated at only 25% of full sunlight. In the brightest sun, control plants fixed CO_2 at a slightly higher rate than the split-night plants. The data corresponding to light intensities of 0.0 to 0.20 langley · min^{-1}, which include the early morning hours, show that cool nights do not reduce photosynthesis during the early morning. In the dim sunlight during winter there is little difference in the photosynthesis of control and split-night plants.

Respiration during the night depends on temperature; thus, there was a noticeable decrease in respiration of the split-night plants during the cool part of the night. The split-night tobacco clearly showed this effect (Fig. 8). While not quite so obvious for tomato (Fig. 7), respiration decreased when the temperature of the split-night

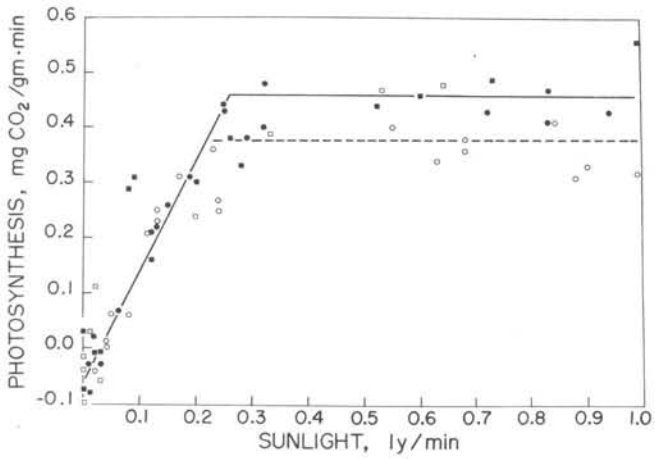

Fig. 9 Net photosynthesis of individual tomato plants from six separate experiments as a function of sunlight intensity. Filled symbols (●, ■) represent control and open symbols (o, □) represent split-night plants. The circles are for measurements in the morning and the squares are for the afternoon.

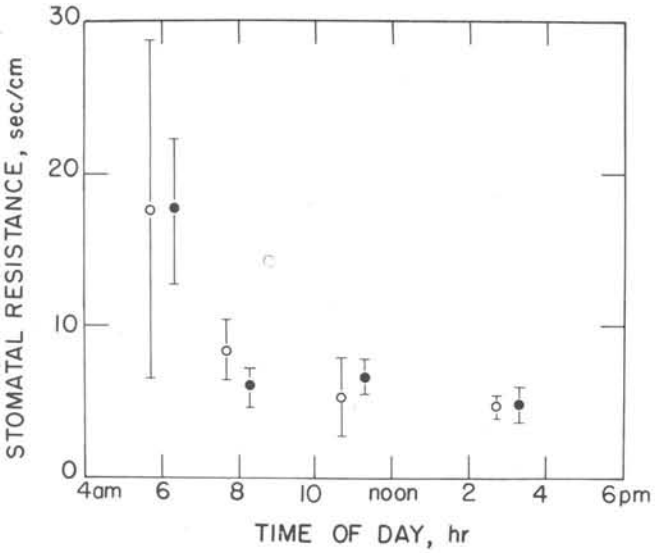

Fig. 10 The stomatal resistance to diffusion of water from the leaves of control (●) and split-night (o) tobacco plants. Filled symbols represent control and open symbols represent split-night. The I represents the standard deviation.

plant fell; there was no corresponding decrease in respiration of the control plant during the night. Although this behavior might seem beneficial for conserving assimilated CO_2, the growth analysis suggests that this decreased respiration was accompanied by decreased metabolism and development of the split-night plants.

Measurement of net photosynthesis under controlled laboratory conditions confirmed the independence of photosynthetic efficiency from previous night temperatures. Leaf discs of tobacco sampled at 9 am under control and split-night environments had the same photosynthetic rates. There was no significant difference between

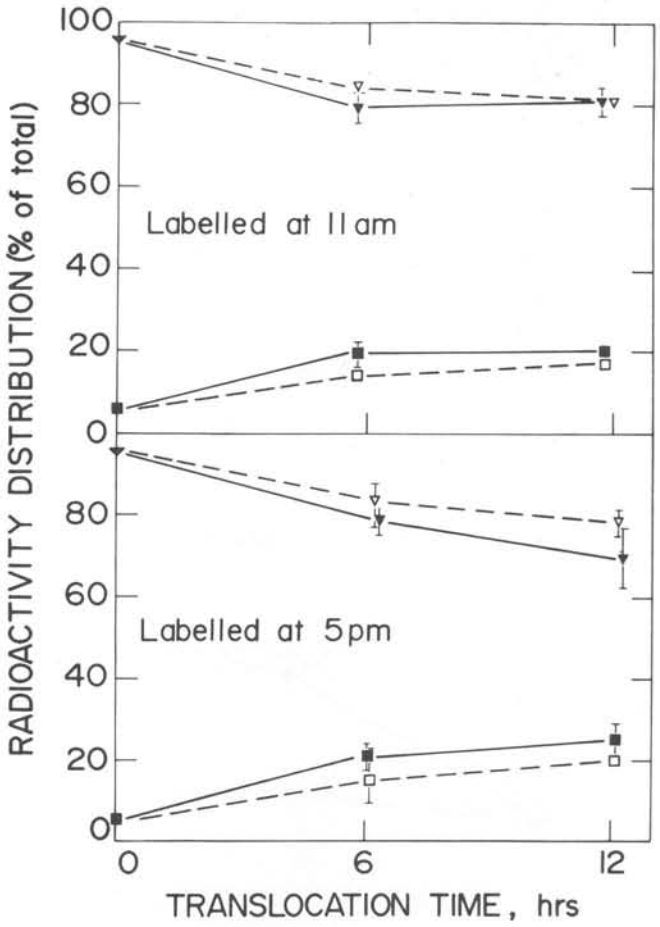

Fig. 11 The percentage of the total radioactivity found in the leaves (▼,▽) and stem (■, □) of tomato plants during vegetative growth. Filled symbols represent controls and open symbols represent split-night plants. The I represents the standard deviation.

the 0.73 ± 0.04 mg $CO_2 \cdot gm^{-1} \cdot min^{-1}$ of split-night plants and the 0.77 ± 0.07 mg $CO_2 \cdot gm^{-1} \cdot min^{-1}$ of the controls.

Stomatal opening can be inhibited or delayed by cold (Drake and Salisbury, 1972), and although greater stomatal resistance could reduce CO_2 assimilation in split-night plants, the diurnal records in Figs. 7 and 8 showed no reduced photosynthesis. Moreover, transpiration depended only on sunlight and concurrent temperature rather than on the previous temperature of the plant. Figure 10 shows leaf resistance measured at four times during a day. No significant differences in the average leaf resistance between control and split-night plants occurred at any time, even at 6:00-6:30 am, just after the greenhouse began heating. However, the variability of stomatal resistance among individual leaves did differ significantly. Thus, at 6 am the standard deviation for 15 measurements of split-night plants was ± 11 sec $\cdot$ cm^{-1} which is more than twice the standard deviation (± 4 cm $\cdot$ sec^{-1}) for the same number of measurements on control plants. This scatter gradually disappeared as the day progressed.

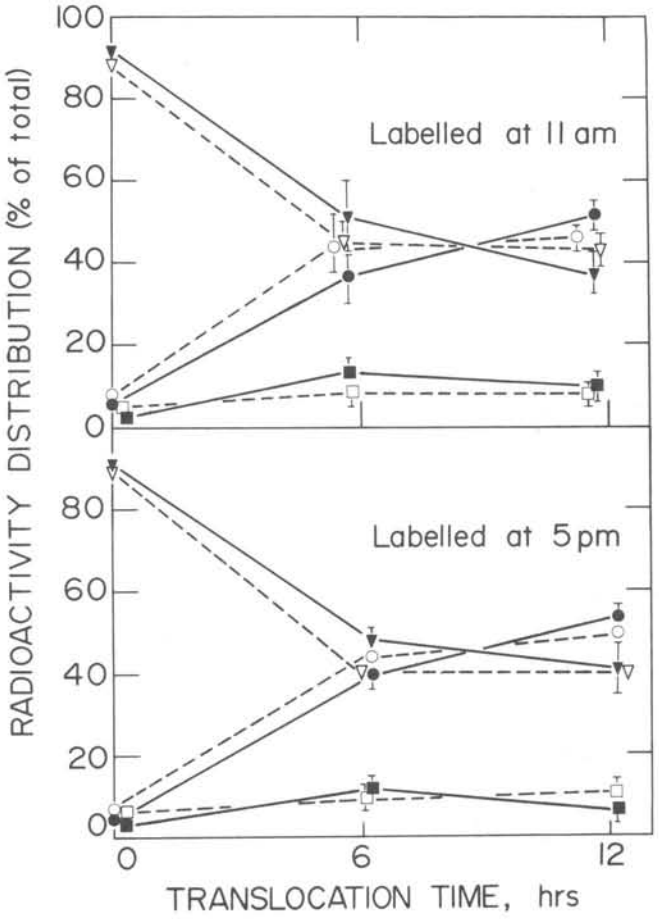

Fig. 12 The percentage of the total radioactivity found in the leaves (▼,▽), stem (■, □) and fruit (●, o) of tomato plants during reproductive growth. Filled symbols represent control and open symbols represent split-night plants. The I represents the standard deviation.

Diurnal Course of Translocation

The rate of movement and partitioning of recently assimilated photosynthate was determined both at flowering and early fruit filling stages. In Figs. 11 and 12 the radioactivity in the roots, stems, leaves and fruit of the plants 6 and 12 hours after $^{14}CO_2$ labelling is compared to the amount initially in the leaves. There were much greater differences between the plants at the two dates than between the control and split-night plants for a given time. During vegetative growth, little assimilated ^{14}C was exported from the leaf, and 70-80% of the radioactivity remained in the leaves, even after 12 hours (Fig. 11). During reproductive growth, however, ^{14}C-labelled sugars were swiftly transported, primarily to the fruit, and after 6 hours about 40% of the radioactivity was recovered from the fruit. This amount increased to more than 50% by 12 hours (Fig. 12). Thus, the movement of sugars out of the leaf is much greater during fruit filling than during vegetative growth.

In either developmental stage, both the control and split-night plants translocated a slightly higher percentage of radioactivity in the evening than during the day, as can be seen by comparing plants labelled at 5 pm to plants labelled at 11 am. The control plants continued to translocate ^{14}C-labelled sugars rapidly during the latter part of the constant temperature night (11 pm to 5 am). The reduction of translocation in split-night plants during the cool part of the night was the most obvious difference between the control and split-night plants in both translocation experiments.

During fruit filling more radioactivity was exported in 6 hours from the leaves of split-night plants than from controls. This occurred for both the 11 am and 5 pm labelling times. The rapid translocation between 5 and 11 pm by the split-night plants largely counteracted the slow translocation during the next 6-hour period so that after 12 hours there was little difference between the total amount of radioactivity translocated in the two treatments. The split-night plants had only 2-3% less ^{14}C in the fruit, even after 6 hours of cool night temperatures (see the 5 pm label in Fig. 12).

The radioactivity in the root tissues was only about 1% of the total radioactivity in split-night and control plants, except for the plants harvested at 5 am after 12 hours of translocation. At 5 am during vegetative growth, the roots of the control plants contained substantially more radioactivity than the roots of the split-night plants (4.8% vs. 2.9%). During reproductive growth, however, there was less radioactivity in the roots and no difference between split-night and control plants.

Diurnal Course of Carbohydrate

The first carbohydrate analyses were made when the plants were about 28 cm tall, had 12 leaves, and were beginning to flower. On February 28, 1979, following a sunny day, sugars had accumulated to similar levels in the leaves of control and split-night plants (see Fig. 13A,B). Starch was the major storage product, and had accumulated to approximately 12% of leaf dry weight by 5 pm. Starch levels were depleted in the leaves of control plants at a nearly linear rate to 4.9% at 5 am, after which no further metabolism was observed (Fig. 13A). Starch depletion in leaves of split-night plants was rapid only between 5 and 11 pm when the plants were at 60 F (15 C) or above, and more starch remained in these leaves than in the warmer control leaves. There were no significant differences in amount of sucrose, the major translocated sugar, between leaves of the two treatments.

Both sucrose and starch accumulated in tomato stems (Fig. 13). In stems of control plants, starch remained high until 11 pm but was lower by 5 am. In stems of split-night plants, on the other hand, starch was depleted during the early evening but during the cool part of the night, accumulated to the previous level (Fig. 13B) and then was depleted again after the greenhouse temperature rose. Initially, levels of sucrose in the stems were high for both treatment groups (about 5.5%). Sucrose levels in the controls then declined during the night to 2.8% (Fig. 13C) as observed in the leaf, but sucrose levels in stems of split-night plants remained between 4 and 5% throughout the day and night.

Direct effects of temperature on the carbohydrate

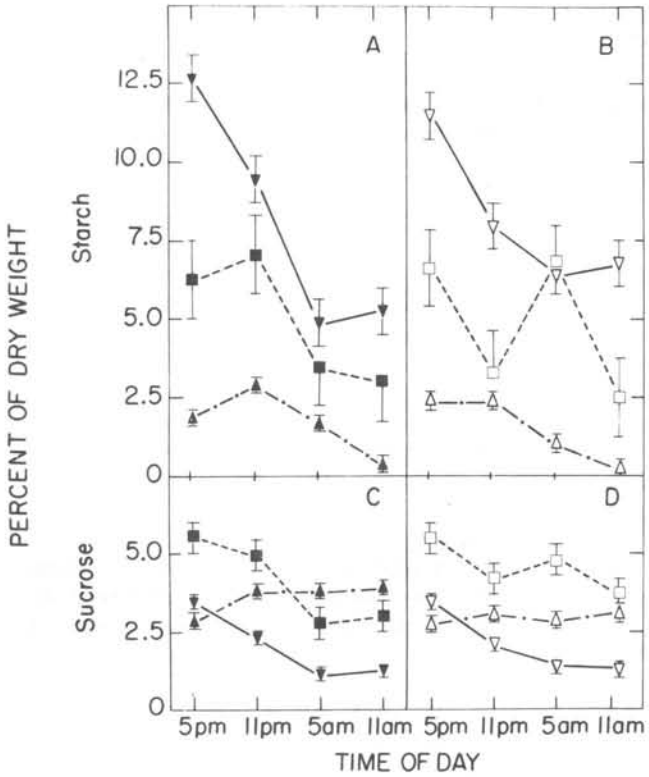

Fig. 13 Carbohydrate levels during the vegetative growth of tomato. Starch levels in percent of dry weight (panels A and B) and sucrose levels in percent of dry weight (panels C and D) are shown for the leaves (▼,▽), stems (■, □) and the roots (▲, △). Filled symbols represent control and open symbols represent split-night plants. The I represents the standard deviation.

metabolism of the roots were not readily apparent (Fig. 13). Roots of split-night plants, however, had lower carbohydrate levels at nearly all times, indicating a decreased availability of carbohydrate. In both treatments starch decreased sharply after 11 pm while sucrose remained constant, suggesting that starch, rather than imported sucrose, is the carbon for root respiration at night.

The second carbohydrate analyses were when the plants were about 60 cm tall, had 14 to 16 leaves, and seven immature fruit weighing 13 g. Harvests were again made on a clear, sunny day following two cloudy, overcast days. Accumulation and depletion of carbohydrates was more sensitive than translocation to the cool night.

Figures 14A and B illustrate the diurnal trends in starch in the leaf. Apparently because of the cool night, the normal periods of accumulation and depletion were offset in time. By 5 pm, leaves of both populations had accumulated substantial amounts of starch, 14.9% in control and 13.7% in split-night leaves. Degradation of starch in the leaves of control plants was rapid only after 11 pm. Leaves of split-night plants, however, had degraded their starch levels to 8.1% prior to the onset of the cool period at 11 pm. During the cooler part of the night, a slight but not significant accumulation was detected. At 5 am, leaves of split-night and control plants contained almost the same amounts of photosynthate. Sucrose levels remained constant at 1.5% during these large fluctuations in starch accumulation.

The differences between control and split-night plants in the time of accumulation and degradation of starch were especially apparent in the stem. Stems of control plants were only beginning to accumulate starch by 5 pm of a clear, sunny day, but starch continued to accumulate from 11% to a maximum of 19.9% by 11 pm. In stems of split-night plants, however, starch accumulation had apparently peaked several hours before 5 pm, and the level of starch continued to decline to a minimum of 11.2% at 11 pm. During the cool part of the night, starch rapidly accumulated in the stems of split-night plants (Fig. 14B). Sucrose dropped from 7.8% to 4.6% during this period of starch synthesis in the stem (Fig. 14D).

The decline in starch in stems of control plants between 5 am and 11 am came approximately 6 hours after the decline in leaf starch. By 11 am, leaves and stems of split-night plants had declined to approximately the same level of starch.

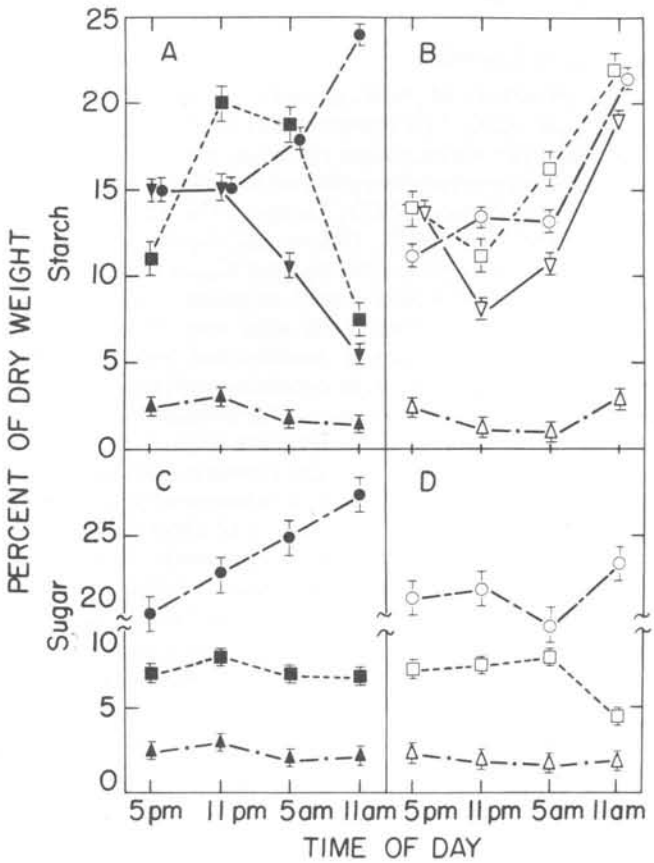

Fig. 14 Carbohydrate levels during the reproductive growth of tomato. Starch levels in percent of dry weight (panels A and B) and sucrose levels for the leaves and stems, and reducing sugar levels for the fruit, as percent of dry weight (panels C and D) are shown for the leaves (▼,▽), stems (■, □) and fruit (●, o). Filled symbols represent control and open symbols represent split-night plants. The I represents the standard deviation.

As expected, fruits were the major sink for photosynthate. Sucrose is the form in which carbon is translocated from the leaves, but no diurnal fluctuations in sucrose in the fruit were observed in plants of either treatment. Instead, soon after arrival in the fruit, sucrose was hydrolyzed to the reducing sugars fructose and glucose before starch synthesis. The control fruit accumulated sugars linearly throughout the night to 27.4%, while starch accumulated after a 6 hour lag to a nearly identical level (Figures 14A, C). In the fruit of split-night plants, no significant accumulation of reducing sugars or starch occurred during the night. After dawn, starch in the fruit rose from 13% to 21.4% by 11 am. Final starch and sugar at 11 am were generally, but not significantly, less in fruit of split-night plants.

Relatively low levels of carbohydrates were observed in roots of all plants. Roots of control plants contained 2.5% sucrose and starch, while roots of split-night plants contained about 2% sucrose and 1.5% starch. Variability in measurement rendered most comparisons nonsignificant.

DISCUSSION

Change in Growth

A comparison of plants grown in constant (15 C) and split-night (15 C/7 C) temperatures shows only a small retardation by the cool night on the growth, development, and yield. This generally agrees with the findings of others (Carow and Zimmer, 1977; Parups, 1978; Shanks, 1978; Shanks and Link, 1979; Thorne and Jaynes, 1977).

The inhibition of growth by cool nights may be small only because of the slow growth of plants in winter. Dim sunlight intensities and short days limit plant growth during winter. Permanent biochemical and structural adaptations to the dim light preclude rapid photosynthesis on the infrequent sunny days. For example, the tomato plants had maximum photosynthesis at only 25% of full sun (Fig. 9). Prolonged sunlight provides accumulations of starch that supply the plant on subsequent cloudy days. The relatively slow winter-time growth observed for both split-night and control plants is probably due to this fluctuating, and often limiting, supply of carbohydrate.

The effects of split-nights, half warm (15 C) and half cool (7 C), were much less than would be expected from the behavior of tomato plants grown at constant temperatures. At a constant 7 C, little weight accumulates and stems elongate little (Hussey, 1965; Went, 1944), while at a constant 15 C, the rate of growth would be fully half the maximum reached at 26 C. A naive calculation from the rates at 7 and 15 C would predict that 8 hours at 7 C should decrease the vegetative growth of split-night tomato plants by 33%. The difference in the rate of growth, however, was only 15%. Even this small difference was insignificant for development as plants in both treatments reached the same final size and produced the same numbers of flowers and fruit.

The split-night temperature of 7 C did not inhibit flowering of tomato nor promote fruit abortion, in contradiction to the widely held belief that temperatures below 10 C prevent fruit formation. The belief could have been initiated by Went (1944) or by the prevention of fruit formation by cool nights in the field. Our success may be due to the choice of short-season varieties, to the fertilization of flowers by vibration of the stem, or because the plants were repeatedly exposed to cold.

Although the growth rate of fruit was not significantly different between control and split-night plants, the final yield was decreased by 13% in the split-night plants due to slightly slower growth rate combined with a shorter development time. At constant temperature, the growth of tomato fruit at 7.5 C is one-third that at 15 C (Walker and Thornley, 1977). Thus, fruit growth rate should decrease by 25% for split-night plants if the timing of the cool period is unimportant. In fact, we found that the rate of fruit growth was only 5% less. Cool nights retard fruit growth much less than vegetative growth. This effect is also seen in sweet pepper (Rylski, 1973).

The lilies did not show any discernable effects of cool nights on growth or flowering. The development and flowering of several other plants have been shown to be insensitive to a split-night regime as long as the cool period is less than 12 hours (Carow and Zimmer 1977, Parups 1978, Shanks 1978, Shanks and Link, 1979). Of the species tested here, tobacco growth was reduced the most by cool nights.

Change in Physiology

Most processes were severely inhibited in the split-night tomato plants during the cool period. Therefore, their uninhibited growth requires two conditions: 1) Assimilation processes, such as photosynthesis and nutrient uptake, are not inhibited by previous cool temperatures; 2) Temperature-dependent growth processes are completed before the onset of the cool period. The second condition also implies that the metabolism of split-night plants may be especially active during the warm period.

We tested one aspect of the first condition: the rate of assimilation of CO_2 or net photosynthesis. No substantial inhibition due to split-night temperature was observed. In particular, early in the morning and soon after being warmed to 15 C, the photosynthesis of the leaves of split-night plants responded to light the same as controls. This response explains much of the success of the split-night scheme. Others found that plants subjected to regular cold nights showed the same photosynthesis as warm-night plants when tested under identical warm, controlled conditions (Hurd and Enoch, 1976; Kohl and Thigpen, 1979). However, plants grown at a steady warm temperature and then suddenly cooled to 5 or 10 C do not recover photosynthetic capacity when rewarmed (Taylor and Rowley, 1971; Crookston et al., 1974). This irreversible behavior is caused by loss of stomatal control and general tissue disruption (Drake and Salisbury, 1972; Breidenbach and Waring, 1977; Lyons, 1973; Chatterton et al., 1972; Ivory and Whiteman, 1978). Apparently, long adaptation to cool nights plays an important part in eliminating harmful effects on stomatal function and photosynthesis. The high photosynthetic capability soon

after a cool night satisfies the first requirement necessary for split-night plants to grow as fast as the controls.

During the entire winter, the growth of both split-night and control tomato plants was slow because carbohydrate was lacking. Following cloudy days and little photosynthesis, fewer hours of warm night temperatures should be needed for distribution and metabolism of the photosynthate than following sunny days. Thus, temperature-dependent growth processes might not be affected simply because they could be completed before the onset of the cool period, without any other adaptation or change in metabolism of the plants. This hypothesis was not directly tested here, since the diurnal harvests for the determination of translocation rates and carbohydrate levels were always made during and after sunny days. After growing for 52 and 86 days under split-night conditions, however, the plants continued in a long established diurnal rhythm of physiological processes.

Our experiments showed that the split-night regime distinctly accelerated the translocation and metabolism of carbohydrate relative to the controls before the cool part of the night. In this way the plants adapted to the split-night regime and completed temperature-dependent processes during the warm early evening.

Both translocation and metabolism of carbohydrate are necessary for growth. These two processes are not independent because starch reserves must be converted to sucrose to be translocated from the leaves. Likewise, the sucrose must be metabolized in the fruit and stems for continued influx of sucrose. Both translocation and metabolism were substantially inhibited during the cool portion of the split-night regime. Translocation from the leaves was inhibited by half or more (Figs. 11B, 12B) in agreement with results of translocation in tomato under constant temperature conditions (Walker and Ho, 1977). Carbohydrate metabolism as measured by CO_2 respiration, was also reduced about half when the temperature fell from 15 C to 7 C (Figs. 7 and 8). Specifically, the conversion of starch to sucrose was inhibited by the cool temperature. Starch levels in the split-night plants tended to rise from 11 pm to 5 am, even in the leaves, although the net carbohydrate reserves must be depleted during these hours of net respiration (Figs. 13B and 14B).

Split-night tomato plants did not adapt their metabolism to the cool temperatures *per se*. Instead, the translocation and metabolism of carbohydrate was faster during the afternoon and early evening in the split-night plants. This behavior was most pronounced during fruit filling, probably because the efficient translocation of carbohydrate is necessary for fast fruit growth. The amount of radioactive carbohydrate moved from the leaves to fruit was greater in split-night plants during the afternoon and evening (Fig. 12). Starch was degraded rapidly during the warm period from 5 pm to 11 pm in both the stems and leaves of split-night plants, causing levels below those found in the control plants 6 hours later (Fig. 14). In contrast, the starch levels in control plants did not peak until after 5 pm and starch degradation continued throughout the night. Thus, split-night tomato plants showed a definite, although indirect, adaptation to the repeated cool temperatures during reproductive growth that allowed a growth rate comparable to the controls.

The vegetative and reproductive stages of tomato growth must be considered separately in an analysis of the economic benefits of split-night greenhouse management. The split-night regime did not change the diurnal cycle of translocation and carbohydrate metabolism in vegetative plants and their rate of growth was reduced. However, the plants did reach the same final size and fruit bearing capacity by extending growth for several days. Thus, the split-night regime seems to be suitable for producing bedding plants. The economic benefit of split-night management can be found simply by subtracting the cost of extending the growing season by a few days from the savings due to the split-night temperature.

Reproductive plants acclimated to the split-night regime by speeding translocation and carbohydrate metabolism during the day, and the rate of growth of their fruit was not significantly reduced. However, fruit production in split-night plants declined faster than in the controls; the duration of fruit growth was shorter; and the final yield was significantly reduced. It may be possible to alleviate the faster decline in split-night plants by adjusting soil temperature, fertility or watering. Nevertheless, the time required to produce tomato fruit from seedlings under split-night temperatures was about the same as under constant temperature; thus, a significant amount of fuel was saved. To calculate the economic benefit, this savings must be compared to the reduction in economic yield of the fruit.

ACKNOWLEDGEMENTS

Mr. William Loefstedt introduced to us the idea of growing plants in split-night temperatures and has provided many stimulating discussions.

Mr. James Perito provided most of the assistance during the course of the experiment. He took care of the plants, measured their growth and development, and accomplished the initial data reduction. Dr. George R. Stephens provided valuable advice on the watering and fertilization of the plants and arranged for the supply of Easter lilies. Cindy Sudarsky did many of the carbohydrate analyses. Finally, Dr. David Oliver measured the tobacco photosynthesis under controlled conditions.

APPENDIX

Calculation of Heating Degree Days During Split-Night

Instead of measuring the fuel used in the greenhouse at different temperatures, we calculated the savings from reduced temperature by a modification of the familiar method of degree-days. First, we define a heating degree-day (HDD) that accounts for different inside temperatures at different times of the day, then we examine how the sun warms the greenhouse and affects HDD, and finally we calculate the energy needed to warm a cold greenhouse in the morning.

Heating degree-days are simply the differences between a desired minimum temperature inside a greenhouse and the daily mean temperature (TMN) outdoors, with negative values omitted. For a residence, we simply subtract TMN from 65 F (18.5 C) where TMN is the mean of the maximum and minimum outside temperatures, TMAX and TMIN. This simple method serves because the *same* inside temperature is assumed for all hours. To calculate degree-days for heating the inside to different temperatures at different hours, however, requires that we specify the outside temperature, hour-by-hour.

The daily course of temperature outside is generally a steady rise from TMIN at 6 am to TMAX at 2 pm and a fall to TMIN at 6 am that can be approximated by the two straight lines AB and BC shown in Fig. A1. Thus, the temperature T at time t hours after 6 am is approximately

$$T = \mathrm{TMIN} + t/8\,(\mathrm{TMAX} - \mathrm{TMIN}) \qquad \text{(A1)}$$

from 6 am to 2 pm, and

$$T = \mathrm{TMAX} - (t-8)/16\,(\mathrm{TMAX} - \mathrm{TMIN}) \qquad \text{(A2)}$$

from 2 pm to 6 am. In general, the minimum temperature differs from one day to the next and TMIN at point A is not equal to TMIN at point C in Fig. A1. It can be shown, however, that calculations using equations (A1) and (A2) give essentially the same results as do more complicated equations that account for this difference in TMIN. Therefore, we use the simpler equations (A1) and (A2).

From equations (A1) and (A2) for outside temperature at every hour we can calculate a mean outside temperature for three periods of steady inside temperature. One period is at night between 10 pm and 6 am when the greenhouse is allowed to cool. We call the mean temperature for this period $\overline{\mathrm{TN}}$ for "temperature-night." A second period is when the sun heats the inside. Generally this is between 9 am and 3 pm and we call the mean temperature for this period $\overline{\mathrm{TS}}$ for "temperature-sun." During the 10 remaining hours, 6 am to 9 am and 3 pm to 10 pm the greenhouse would generally be held at a warm temperature by burning fuel. The mean temperature for this 10-hour period is called $\overline{\mathrm{TD}}$ for "temperature-day." The mean temperatures $\overline{\mathrm{TN}}$, $\overline{\mathrm{TS}}$, and $\overline{\mathrm{TD}}$ are simply found by integrating the outside temperatures given by equations (A1) and (A2) between appropriate limits. The results of these integrations are:

for hours 10 pm to 6 am

$$\overline{\mathrm{TN}} = 0.25 \cdot \mathrm{TMAX} + 0.75 \cdot \mathrm{TMIN} \qquad \text{(A3)}$$

for hours 9 am to 3 pm

$$\overline{\mathrm{TS}} = 0.735 \cdot \mathrm{TMAX} + 0.265 \cdot \mathrm{TMIN} \qquad \text{(A4)}$$

for hours 6 am to 9 am, and 3 pm to 10 pm

$$\overline{\mathrm{TD}} = 0.56 \cdot \mathrm{TMAX} + 0.44 \cdot \mathrm{TMIN} \qquad \text{(A5)}$$

The HDD for a greenhouse maintained at temperature TB for 24 hours of a day is simply the sum of the three periods given by:

$$\mathrm{HDD}_{24} = 8/24\,(\mathrm{TB} - \overline{\mathrm{TN}}) + 6/24\,(\mathrm{TB} - \overline{\mathrm{TS}}) + 10/24\,(\mathrm{TB} - \overline{\mathrm{TD}}) \qquad \text{(A6)}$$

and is equivalent to the standard calculation of heating degree days for a residence at a steady temperature. To determine the relative fuel savings afforded by reducing

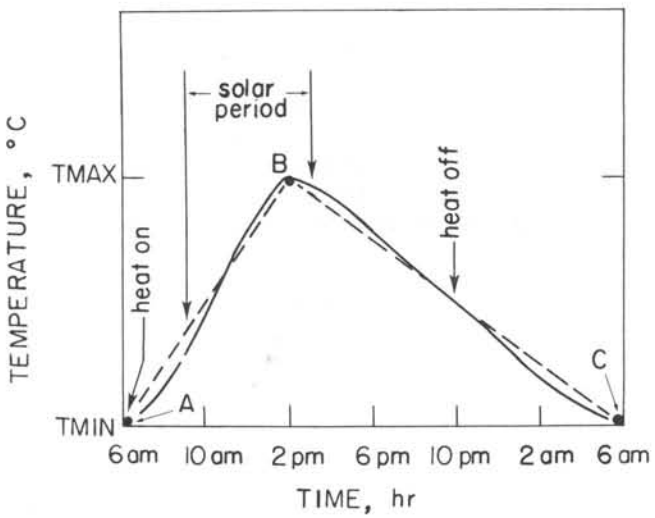

Fig. A1 The variation of outdoor temperature during a winter day is shown by the solid line. The dashed lines AB and BC approximate the actual temperature variation.

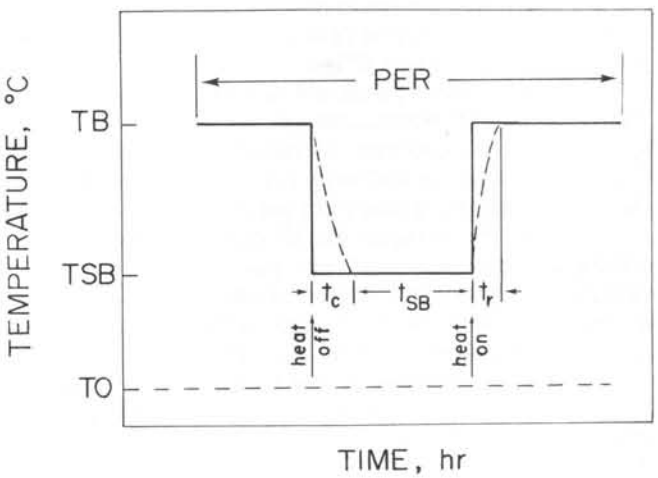

Fig. A2 The temperature response to a reduced thermostat setting for a greenhouse with time constant RC = 0 (solid line) and for one with RC greater than zero (dashed line).

the greenhouse temperature for 8 hours we must calculate how much fuel would normally be used without the reduction and how much would be used with the reduction and then compare the two numbers. To facilitate this comparison we calculate separately the amount of these HDD_{24} that is accumulated other than at night since this will be the same with or without temperature reduction:

$$HDD' = 6/24\,(TB - \overline{TS}) + 10/24\,(TB - \overline{TD}). \quad (A7)$$

To obtain an estimate of the fuel savings due to temperature reduction at night we calculate the HDD at night when the temperature is set back to TSB, add this result to HDD′ and subtract the sum from HDD_{24}. That is, the savings S are given by:

$$S \cong HDD_{24}\,(TB) - [HDD'(TB) + HDD_N\,(TSB)]. \quad (A8)$$

We now examine the effect of solar heating on our calculation. The bright sun sometimes heats the greenhouse above TB for a few hours so that no fuel is required during this time. From pyrheliometer recordings, we have derived a daily solar factor SR, which is either 1 or 0: SR is set equal to 1 if the day had full or nearly full sun, otherwise SR is set as 0. We obtained SR during the months of December, January, February, March and April for the last 5 years. Likewise, the HDD calculations described below use TMAX and TMIN data for these same periods.

To determine the influence of sun, we calculate a greenhouse heating degree-day $GHHDD_{24}$ defined by:

$$GHHDD_{24} = 8/24\,(TB - \overline{TN}) + 6/24\,(1 - SR) \cdot (TB - \overline{TS}) + 10/24\,(TB - \overline{TD}) \quad (A9)$$

Clearly, for days with little or no sun:

$$GHHDD_{24} = HDD_{24}$$

since SR = 0. For sunny days, no heating is required during the solar period. Thus, SR = 1 and $GHHDD_{24} < HDD_{24}$.

As above, we calculate a

$$GHHDD' = 6/24\,(1 - SR) \cdot (TB - \overline{TS}) + 10/24\,(TB - \overline{TD})$$

for the part of the day that does not include 10 pm to 6 am. Finally, since at night there is no sun and $GHHDD_N = HDD_N$, we obtain the savings:

$$S \cong GHHDD_{24}\,(TB) - [GHHDD'(TB) + HDD_N(TSB)] \quad (A10)$$

Energy Savings Due to Split-Night Regime

The absolute savings and the percent savings of HDD according to equation (A8), which ignores solar heating, are shown in Table A1 for December, January, February, March and April during the last 5 years. The average savings due to a reduction to 7.2 C compared with a 15.5 C setting is 19% during the entire winter. Finally, the calculated savings according to equation (A10), which includes the effects of solar heating, are shown in Table A2. The average savings for a 7.2 C reduction compared with the standard 15.5 C is 21.5%.

Heating Inefficiency Due to Changing the Temperature

In the above calculation of fuel savings we have assumed that the greenhouse temperature instantaneously becomes equal to the thermostat setting; that is, we have ignored the thermal inertia of the greenhouse. We examine the effects of finite cooling and reheating times for the simple case of a constant outside temperature and no heat supplied by the sun, i.e., an overcast day. The temperature history of the greenhouse in this case is shown in Fig. A2. The three temperatures TB, TSB and TO refer to the upper thermostat setting, the lower thermostat setting and the outside temperature, respectively. Four times must be considered: The time t_c is the time required for the greenhouse to cool from TB to TSB, t_r is the time to reheat from TSB to TB, t_{SB} is the time the greenhouse remains at TSB and PER is the entire heating period, in this case, 1 day.

For a hot-air heating system, no heat is required during cooling. The heat, QSB, required during 1 day using the reduced temperature regime is:

$$QSB = q_B \cdot t_B + q_{SB} \cdot t_{SB} + q_r \cdot t_r \quad (A11)$$

where q_B, q_{SB} and q_r are the rates of heat (cal/sec) supplied by the furnace during the steady upper temperature, during the steady lower temperature and during reheating, respectively. The percent savings due to temperature reduction is obtained by dividing equation (A11) by the heating required if the temperature is not reduced, i.e., $Q = q_B \cdot PER$. Denoting the fractional times by f, e.g.,

$t_{SB}/PER = f_{SB}$, the fractional savings S is $(Q - QSB)/Q$ or

$$S = [1 - f_B - (q_{SB}/q_B) f_{SB}) - (q_r/q_B) f_r] \quad (A12)$$

If the greenhouse has an overall heat capacity C (cal/°C) and an overall resistance to heat transfer R (sec °C/cal), cooling and reheating will be characterized by a time constant $R \cdot C$. During cooling to TSB the temperature obeys

$$TSB - TO = (TB - TO) \exp(-t_c/RC) \quad (A13)$$

while during reheating

$$TB - TO - q_r R = (TSB - TO - q_r R) \exp(-t_r/RC) \quad (A14)$$

In addition, during steady state at TB and at TSB we have

$$q_B = (1/R)\,(TB - TO) \quad (A15)$$

$$q_{SB} = (1/R)\,(TSB - TO) \quad (A16)$$

Solving equation (A14) for t_r and using this result together with equations (A15) and (A16) in equation (A12), we obtain

$$S = 1 - f_B - [(TSB - TO)/(TB - TO)] f_{SB} - (q_r/q_B) f_r \quad (A17)$$

where

$$f_r = (RC/PER) \ln[(1 - q_{SB}/q_r)/(1 - q_B/q_r)] \quad (A18)$$

If the greenhouse time constant is very small, and heating takes little time, the savings are approximately

$$S \cong 1 - f_B - [(TSB - TO)/(TB - TO)]f_{SB} \quad (A19)$$

Equation (A19) for the case of constant outside temperature is equivalent to our method of calculating the savings presented earlier in Tables A1 and A2.

To calculate the effect of reheating on the savings given by equation (A17), we must know the ratios of heating rates q_{SB}/q_r and q_B/q_r. As an example, we assume that $q_B/q_r = 0.35$. Then, if TB = 15.6°C, TSB = 7.2°C and TO = -1.1°C, we have $q_{SB}/q_B \cong 0.5$ and $q_{SB}/q_r = 0.175$. For our greenhouse, RC/PER = 0.25 so that $f_r \cong 0.06$. We must also have $f_B + f_c + f_{SB} + f_r = 1$. For an 8-hour temperature reduction, the savings calculated by equation (A17) are about 2.5% less than the savings calculated by equation (A19). Of course, if reheating is done inefficiently, the savings will be reduced somewhat more (Zabinsky and Parlange, 1977).

In our experiments, we added a certain amount of water at temperature TB to the plants in the experimental greenhouse each morning to speed the warming of the soil. However, if no heat is expended for warming the water during the cooling period, i.e., during time t_c, then this added heat is entirely accounted for by our calculations and will not affect the results.

In conclusion, an 8-hour temperature reduction during the winter months in Connecticut should afford a relative fuel savings of about 18%.

Table A1 Split-night fuel savings calculated from heating degree days assuming that greenhouse temperature is reduced from 15.5 to 7.2C from 10 pm to 6 am each day.

Month	HDD_{24} base 15.5°C	HDD' base 15.5°C	HDD_N base 7.2°C	HDD_{24} (set-back)	Savings	% Savings
December	870	536	179	715	155	17.8
January	1025	637	233	870	155	15.1
February	853	523	190	713	140	16.4
March	664	389	123	511	152	22.9
April	351	185	41	226	125	35.6
Total for Heating Season	3764	—	—	—	727	19.3%

Table A2 Split-night fuel savings calculated as in Table A1 except that an allowance for solar hearting is included.

Month	$GHHDD_{24}$ base 15.5C°	GHHDD' base 15.5°C	HDD_N base 7.2°C	$GHHDD_{24}$ (set-back)	Savings	% Savings
December	810	477	179	656	154	19.0
January	908	520	233	753	155	17.1
February	743	413	190	603	140	18.8
March	590	315	123	438	152	25.8
April	322	156	41	197	125	38.8
Total for Heating Season	3373	—	—	—	726	21.5%

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