

Fluctuations in Leaf Carbon Assimilation as Affected by Root-zone Temperature and Growth Environment

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Abstract. Short-term effects of root-zone temperatures (RZT) of 28, 33, 38, and 43C for 6 hours daily on container-grown *Musa* spp. (AAA) 'Grande Naine' and *Ixora chinensis* L. 'Maui' were determined under greenhouse and growth room conditions. Diurnal fluctuation of leaf carbon assimilation (LCA) was altered by treatments. In the growth room at 43C, the maximum LCA occurred about midday for banana, but not until afternoon in ixora. LCA was highest (0.53 mg CO₂/m² per sec) in banana with a 33C RZT under greenhouse conditions, while it was equally high (0.74 mg CO₂/m² per sec) at 33 and 38C in a growth room. In ixora, 33C induced the highest LCA (0.40 mg CO₂/m² per sec) in the greenhouse at 1200 HR, but there were no apparent differences in midday LCA between plants with RZT of 28, 33, and 38C in the growth room. Effects of RZT and environment on the daily fluctuations of gaseous exchange processes raise questions about using measurements at only one time during the day to separate treatment effects.

High root-zone temperatures (RZT) reduce plant growth (Ingram, 1981; Ingram et al., 1986; Ketallepper, 1960) and affect many physiological processes (Gosselin and Trudel, 1984, 1986; Guinn and Hunter, 1968; Itai et al., 1973). Soil temperatures as high as 52C have been recorded in the tropics (Franco, 1958), and temperatures in this range are lethal for some tropical (Franco, 1958; Itai et al., 1973) and subtropical crops (Ingram and Buchanan, 1984). Container media approach 50C daily, with temperatures above 40C maintained for 5 to 6 h daily in the Virgin Islands (Ingram and Ramcharan, unpublished). The number of ornamental plants, such as *Ixora chinensis*, being produced in containers in the tropics has increased in recent years, and the production cycle of banana often includes a containerization phase to prepare

micropropagules for field transplanting.

Growth and dry-weight partitioning in banana (*Musa* spp. AAA) were influenced by air temperature (Turner and Lahav, 1963), and mineral composition was highly influenced by air temperatures from 18 to 33C (Turner and Lahav, 1965). An RZT of 33C was found to be optimum for growth and transpiration in coffee (Franco, 1958), a member of the same subfamily of Rubiaceae to which ixora belongs (Bailey and Bailey, 1976).

Our study investigated the short-term effects of RZT on daily fluctuations of LCA in container-grown 'Grande Naine' banana and 'Maui' ixora in a greenhouse and a growth room. Such knowledge would help determine the optimum time of day to measure gaseous exchange processes as a function of root-zone temperatures in the two environments.

Ten- to 12-cm-tall, tissue-cultured 'Grande Naine' banana plants and similar-sized, uniform 'Maui' ixora rooted cuttings were obtained from commercial nurseries. Plants were hardened in intermittent mist (6 sec-min⁻¹) for 1 week under 80% light exclusion and then moved to 40% light exclusion for 1 week. Plants were transplanted to 4-cm-diameter × 21-cm-high conical containers (150 cm³) using Metro-Mix 300 growth medium (Grace-Sierra, Cambridge, Mass.). Plants were fertilized weekly with a soluble 20N-8.8P-16.6K fertilizer (Peters 20-20-20, Grace-Sierra) at 150 mg N/liter.

Following preliminary experimentation, an experiment was initiated in Aug. 1985 in an air-conditioned glasshouse with a mean maximum daily photosynthetic photon flux (PPF) of 600 to 700 μmol·m⁻²·s⁻¹ and 25 to 30C/day and 18 to 21C/night air. Relative humidity was not controlled and varied generally between 40% at midday to 80% at midnight. Continuous air movement within the plant canopy was provided by overhead fans. Recently transplanted banana and ixora plants were watered thoroughly each day and allowed to acclimate for 1 week before treatment initiation.

Plants were held in Styrofoam-lined wooden air-bath boxes (1 × 1 × 0.20 m) described by Ingram et al. (1986). The temperature in each box was verified daily with a thermocouple thermometer. An automatic drip irrigation system provided 120 ± 5 ml of water to each plant daily at 2200 HR.

Growth medium temperatures approaching those causing direct injury to roots occur for ≈ 6 h daily in nursery containers exposed to full sun (Ingram, 1981). Therefore, boxes were heated daily from 1000 to 1600 HR to maintain the root zones at 28, 33, 38, or 43 ± 1C. Temperature in the boxes equilibrated to ambient between heating periods. Each box contained six ixora and six banana plants, and there were three replicate boxes for each treatment temperature arranged in a randomized complete-block design. An analysis of variance was performed to determine RZT treatment effects on each genus. Treatment means and standard errors were calculated for the three replications and two plants per experimental unit at each sampling time.

After 14 days, diurnal measurements of

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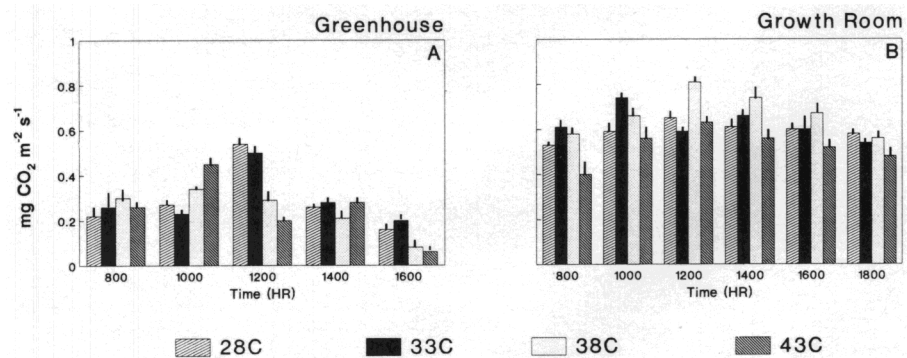


Fig. 1. Daily fluctuations of 'Grande Naine' banana leaf carbon assimilation in response to root-zone temperature under greenhouse (A) and growth room (B) conditions. Standard errors are indicated by vertical bars.

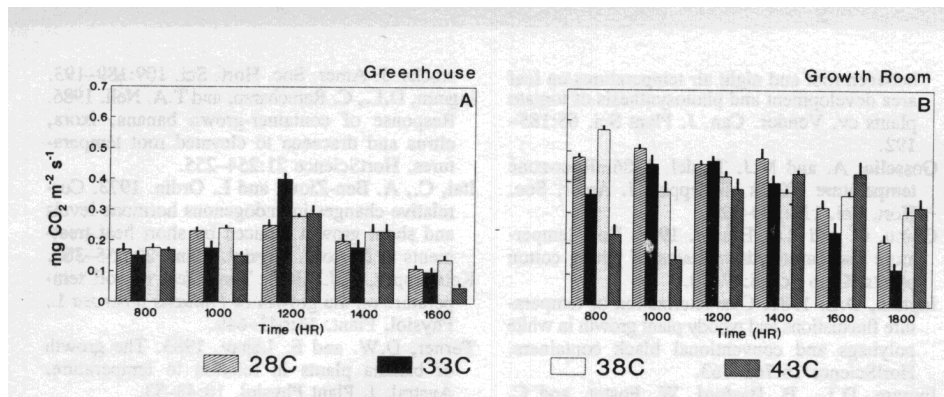


Fig. 2. Daily fluctuations of 'Maui' ixora leaf carbon assimilation in response to root-zone temperature under greenhouse (A) and growth room (B) conditions. Standard errors are indicated by vertical bars.

LCA and conductance were made using a portable photosynthesis system (LI-6000 model, LI-COR, Lincoln, Neb.). Measurements were initiated at 0800 HR Eastern Daylight Time on a clear day and taken every 2 h on all plants through 1600 HR. PPF at canopy height was ≈ 175 , 800, and 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 0800, 1200, and 1600 HR, respectively. A 1-liter cuvette was used and the mean of eight consecutive 30-sec observations constituted a measurement. Mean cuvette conditions were: $\text{CO}_2 = 330 \mu\text{g}\cdot\text{liter}^{-1}$, leaf temperature = 29C, and relative humidity = 60%. The third most recently expanded leaf in banana was used for gaseous exchange measurements. This leaf has been shown to be the most responsive and the youngest with fully developed stomata (Turner and Lahav, 1983). For ixora, the most recently matured leaf was used for LCA and conductance measurements.

To further monitor the physiological responses of 'Grande Naine' banana and 'Maui' ixora to RZT under more precisely controlled environmental conditions, an experiment was conducted in a $3.0 \times 7.6\text{-m}$ walk-in growth room. A PPF of $1100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was supplied at canopy height from 0600 to 1830 HR by 1000-W phosphor-coated metal-arc HID lamps (GTE Sylvania Corp., Manchester, N.H.). Air was maintained at $28 \pm 2\text{C}/\text{day}$ and $21 \pm 2\text{C}/\text{night}$ with relative humidity near 40%/day and 80%/night. Each conical container with a transplant was suspended through a tightly fitting Styrofoam ring within a specially constructed root heating tube with solid-state, electronic controllers described by Ingram et al. (1990). RZTs of 28, 33, 38, and $43 \pm 0.8\text{C}$ were maintained from 1000 to 1600 HR daily. Sampling techniques and physiological measurements were performed after 14 days, as in the greenhouse experiment.

The design in the growth room experiment was a randomized complete block with 36 plants of each species per RZT arranged in six blocks. An analysis of variance was performed to determine RZT treatment effects on each genus. Means and standard errors were calculated for each sampling time.

The highest LCA fluxes in banana (0.53 and 0.50 $\text{mg CO}_2/\text{m}^2$ per sec) in the greenhouse were at midday for the 33 and 28C RZT treatments (Fig. 1A). Maximum LCA in plants at 43C (0.43 $\text{mg CO}_2/\text{m}^2$ per sec)

was recorded at 1000 HR, while LCA for plants at 38C was highest at 1000 and 1200 HR. Leaf conductance fluctuations were similar to the patterns for LCA (data not shown). No symptoms of water stress were visible.

The highest LCA for banana plants with a RZT of 38C in the growth room, recorded at 1200 HR, was 0.81 $\text{mg CO}_2/\text{m}^2$ per sec (Fig. 1B), which was a 54% increase over the highest recorded value in the greenhouse (Fig. 1A). The highest values for plants at 33C (0.74 $\text{mg CO}_2/\text{m}^2$ per sec) occurred at 1000 HR and for plants at 43C (0.65 $\text{mg CO}_2/\text{m}^2$ per sec) it was midday. Plants with RZT of 43C exhibited lower LCA through the afternoon hours than those at 33 and 38C (Fig. 1B). Daily leaf conductance fluctuations were similar to those for LCA (data not shown). Under sunlit growth room conditions, a 33C day/26C night cycle for air was reported as being optimum for growth and partitioning in Cavendish banana; 37C caused leaf injury (Turner and Lahav, 1983, 1985).

Ixora LCA increased from 0800 HR to midday for all treatments and midday LCA was highest in plants exposed to an RZT of 33C in the greenhouse (Fig. 2A). Midday LCA was reduced by 39%, 32%, and 30% by the 28, 38, and 43C RZT, respectively, when compared to the 33C RZT (0.41 $\text{mg CO}_2/\text{m}^2$ per sec). At 1400 HR, however, LCA fluxes were similar for all RZT, with LCA for 33C being slightly lower than the others. At 1600 HR, LCA for the 28, 33, and 38C-treated plants were similar and the LCA for 43C was lowest. Leaf conductance (data not shown) generally paralleled LCA, with the maximum midday value occurring in plants at 33C. Visible symptoms of water stress were never apparent in these plants. Although LCA was not measured, Franco (1958) reported that a 33C RZT was optimum for coffee in terms of transpiration and root and shoot dry weights. Transpiration and plant dry weights were reduced with increasing RZT above 33C and plants died at 48C.

Daily LCA and conductance fluctuations for ixora in the growth room were dissimilar to those in the greenhouse, which were characterized by midday maxima followed by distinct declines (Fig. 2A). The air temperature and relative humidity of the greenhouse and growth room environments were similar at midday. The primary differences in these environments were the consistent, higher light

intensity in the growth room and the fact that air temperature, light intensity, and relative humidity changed gradually in the greenhouse during the early morning and late afternoon hours. LCA at 1000 HR was $\approx 0.5 \text{ mg CO}_2/\text{m}^2$ per sec in plants subjected to 28 and 33C RZTs in the growth room. LCA for these treatments gradually declined throughout the day to 0.21 and 0.12 $\text{mg CO}_2/\text{m}^2$ per sec, respectively, at 1800 HR (Fig. 2B). LCA was 0.57 $\text{mg CO}_2/\text{m}^2$ per sec at 0800 HR for 38C RZT and had declined significantly by 1000 HR, with no further decreases for the rest of the day. LCA was lower during the morning hours in plants with roots at 43C relative to the other treatments but was similar to that of other treatments from 1400 through 1800 HR, except for those at 33C at 1800 HR.

RZT influenced the time of day at which the highest LCA was recorded for banana in both the greenhouse and growth room. Midday LCA in banana plants was highest in plants at the 28 and 33C RZT in the greenhouse and at the 38C RZT in the growth room. The higher light intensity in the growth room compared to the greenhouse appeared to compensate for the higher RZT up to 38C. However, when measured at 1000 HR, the 43C RZT resulted in the highest LCA in the greenhouse and the 33C RZT resulted in the highest values in the growth room. This difference indicates that measurement of gaseous exchange processes at one time during the lighted period may not provide an adequate characterization of stress by supraoptimal RZT.

The highest LCA values in ixora were recorded at 1200 HR for all RZT treatments in the greenhouse. Ixora with roots at 38C had the highest LCA at 0800 HR in the growth room, but decreased significantly in response to the initiation of RZT treatments at 1000 HR. The relatively low LCA and conductance early in the day, with subsequent increases at later hours, in plants at 43C suggests modification of stomatal responsiveness at this temperature. There may have been an effect of the high and constant light intensity, relative humidity, and/or air temperature during the illumination period in the growth room, which maintained the higher midday LCA to later hours than in the greenhouse. However, the decline in gas exchange processes in ixora by 1800 HR in the growth room suggests that stomata may not have completely lost the diurnal pattern evident under greenhouse conditions.

Results of these experiments indicate that banana, although a herbaceous mesophyte, could tolerate daily root-zone temperatures up to 38C for 14 days, while this temperature appeared supraoptimal for ixora, a woody flowering shrub. Gas exchange was generally higher in both plants in the growth room than in the lower and gradually fluctuating light conditions of the greenhouse. It appears that RZT and environment may have interactively affected LCA; however, these experiments were not designed to measure such an interaction. RZT and growth environment affected the daily fluctuation in both species,

and measuring gas exchange processes only one time during the day would have provided misleading data in some cases. If one-time-of-day measurements are to be used to separate plant response to environmental treatments, the lack of treatment effect on daily fluctuations in these processes must be documented.

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