

EFFECT OF NIGHT TEMPERATURE ON THE ASSIMILATION OF CARBON DIOXIDE BY MATURE PINEAPPLE PLANTS, *ANANAS COMOSUS* (L.) MERR.

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[Manuscript received 27 November 1972]

Abstract

The influence of a range of ambient night temperatures (15–35°C) on the CO₂-exchange patterns of mature pineapple plants is described. As night temperatures are increased (with day temperatures held constant at 27.5°C) the net assimilation of CO₂ at night decreased, while that by day increased. An 8-hr night at 35°C induced a net night-time efflux of CO₂ and a continuous uptake of CO₂ throughout the 16-hr day. The proportion of the total net assimilation of CO₂ over a complete 24-hr cycle that was assimilated at night ranged from 100 to 0%, depending upon night temperature and photoperiod.

I. INTRODUCTION

Two of the essential characteristics that distinguish crassulacean acid metabolism (CAM) (Bennet-Clark 1933) plants are the ability to accumulate titratable acidity at night and the concomitant "dark" assimilation of atmospheric CO₂ (Thomas 1949). These characteristics, coupled with an "inverted" stomatal rhythm, confer a diurnal gas-exchange pattern quite different from the "square wave" rhythm of CO₂ exchange of "normal" plants of the C₃ or C₄ photosynthetic mode (Neales *et al.* 1968). The many descriptions of this pattern of CO₂ assimilation by CAM plants, from at least five families, have recently lead to the view that CAM metabolism represents a third, alternative, mechanism of carbon acquisition by plants (Laetsch 1971), rather than an oddity of carbon metabolism possessed by some succulent plants.

The intensity with which CAM metabolism is carried on by a plant species has long been known to be influenced by environmental factors: notably by the night temperature (Bennet-Clark 1933). Recently also, Winter and von Willett (1972) have shown that a CAM-type CO₂ assimilation pattern in *Mesembryanthemum crystallinum* can be evoked by the addition of 500 mM NaCl to the rooting medium in which the plants were grown.

The problems which arise therefore are (1) the extent to which, in any one species, the mode of CO₂ assimilation can be changed from the CAM to the non-CAM form; and (2) the nature of factors (environmental or genetic) that induce this change. These queries lead to considerations, not investigated here, of the mechanisms of CO₂ assimilation in the light and dark parts of the diurnal cycle of CAM plants.

This paper describes the effect of variation in night temperature on the diurnal patterns of CO₂ assimilation in mature pineapple plants—a species that has long been

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known to possess CAM characteristics (Sideris *et al.* 1948), although this is not mentioned in a text on the pineapple (Collins 1960).

II. METHODS

Eight vegetative pineapple plants that had been grown for 12 months in soil in a glasshouse in pots of 21-cm diameter were used. The plants were watered every 2 days. They were placed in a growth cabinet of volume 4.28 m^3 and floor area of 1.68 m^2 . Illuminance at the top of the plants, which had *c.* 30 leaves and were *c.* 50 cm high, was *c.* 2500 f.c. The light source was 30 120-W Sylvania "cool white" tubes plus 22 40-W Mazda incandescent globes.

The cabinet was constructed so that it could be made gas-tight, when it constituted a closed system in which the CO_2 content of the internally circulating air was continuously measured by infra-red gas analysis. From the rate of change of the CO_2 concentration of the air inside the cabinet the influx or efflux of CO_2 attributable to the plants (tops plus roots plus soil), was derived. The cabinet was opened daily to equilibrate the CO_2 content of the internal and external atmosphere. During the 25 days of the experiment the mean CO_2 concentration at "lights off" (beginning of dark period) was 355 p.p.m. and at "lights on" (beginning of light period) was 327 p.p.m. The largest depletion recorded during the night was -170 p.p.m. (425 to 255) and the largest increase in CO_2 content (35°C night temperature) was $+153$ p.p.m. (250 to 443). During the day the largest depletion of CO_2 in the cabinet was -225 p.p.m. (605 to 380) and the largest addition was $+163$ p.p.m. (205 to 368).

Estimates of the respiratory efflux of CO_2 from the soil and plant roots were obtained by decapitating the plants at the end of the series of experiments, sealing the cut stem with wax, and measuring the CO_2 efflux rates of pots plus soil over the range of temperatures used. Assimilation rates are presented as the net CO_2 exchange of the tops of eight plants (mg CO_2 /hr, or mg CO_2 per light or dark period). The experimental design was such that the day temperature was kept constant (27.5°C) and the night temperature was varied in steps between 15 and 35°C . The experiments were conducted sequentially over 25 days. Two photoperiod regimes were used: 16 hr light/8 hr dark and 10 hr light/14 hr dark. In the light, leaf temperatures (ambient air temperature 27.5°C) ranged from 27.9 to 29.2°C . In what follows, the light part of the cycle is referred to as "day" and the dark part as "night".

TABLE 1
EFFECT OF TWO NIGHT TEMPERATURES ON THE MEAN NET CO_2 FLUXES OF THE TOPS
OF EIGHT PINEAPPLE PLANTS
— = net CO_2 uptake; + = CO_2 output

Night		Day		Plant CO_2 exchange (mg CO_2 per period)	
Temp. ($^\circ\text{C}$)	Duration (hr)	Temp. ($^\circ\text{C}$)	Duration (hr)	By night	By day
15	8	27.5	16	-1327	-805
35	8	27.5	16	+112	-2692
15	14	27.5	10	-1848	+284
35	14	27.5	10	-617	-2357

III. RESULTS

(a) Effects of Night Temperature on the Total Net CO_2 Exchange by Night and Day

The data in Table 1 illustrate quantitatively the extent to which the net CO_2 exchange of pineapple plants (tops only) is affected by variation in night temperature. The day temperature of the subsequent day was kept constant at 27.5°C . At both the photoperiod regimes used (8 hr and 14 hr night), high night temperatures greatly

reduced the night uptake of CO_2 compared to that of nights of 15°C . A night temperature of 35°C induced a small net efflux of CO_2 over an 8-hr night (Table 1). Also, the CO_2 exchange during the subsequent day was greatly influenced by the temperature of the previous night (Table 1). Under conditions inducing low night CO_2 influx (high night temperatures) there were large net influxes of CO_2 by day and, conversely, when a large night CO_2 influx was induced by low night temperatures, the net daytime CO_2 influx was decreased. A net daytime efflux of CO_2 resulted after a 14-hr night at 15°C .

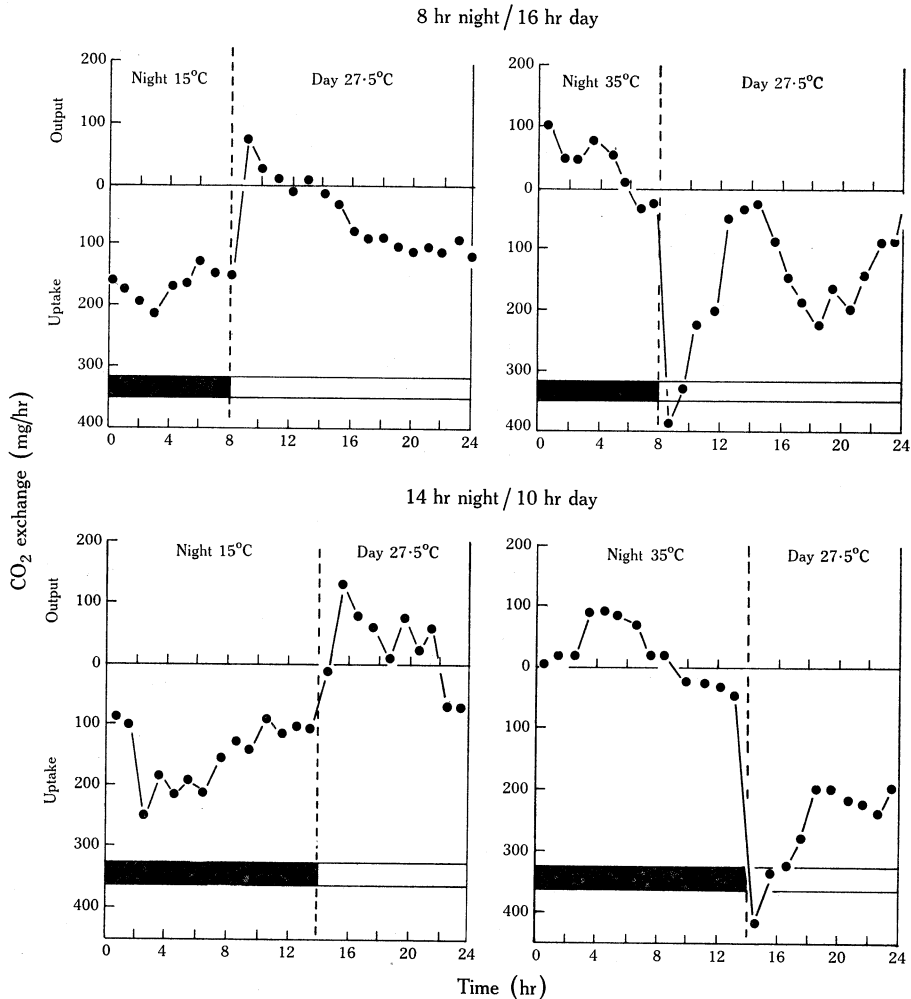


Fig. 1.—Effect of night temperature and duration on the pattern of CO_2 assimilation of the tops of pineapple plants.

(b) Effect of Night Temperature on the Patterns of Net CO_2 Exchange

Figure 1 is a plot of the hourly values of net CO_2 exchange for the two night temperatures (15°C and 35°C) and two night lengths (8 hr and 14 hr). The pattern

of the night CO_2 exchange at 15°C is similar for night periods of 8 hr and 14 hr—considerable CO_2 uptake takes place throughout the night. At night temperatures of 35°C there is initially an efflux of CO_2 followed, towards the end of the night, by a CO_2 influx.

The pattern of day CO_2 exchange is greatly affected by that of the previous night. Night temperatures of 15°C induce initial daytime effluxes of CO_2 followed by a period of CO_2 influx (Fig. 1). However, night temperatures of 35°C evoke a CO_2 influx as soon as the lights come on which is sustained throughout the day. It is apparent that a large night CO_2 influx induces a low (or negative) daytime CO_2 influx and *vice versa*.

(c) *Effect of Night Temperature on the Total Net Night CO_2 Exchange*

Figure 2 shows the relationship between night temperature and the observed total net CO_2 fluxes. Four curves have been drawn. Curves A and B are for the observed CO_2 fluxes of the whole plants, including root and soil respiration, for 8-hr (A) and 14-hr (B) nights. Curves C and D are plots of the estimated CO_2 exchange of the plant tops alone for 8-hr (C) and 14-hr (D) nights.

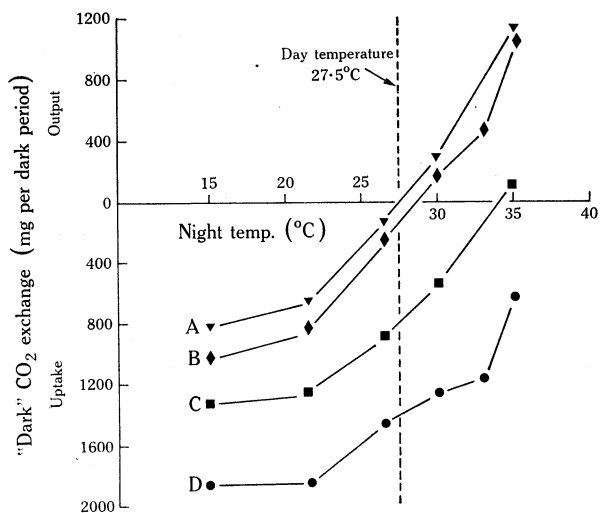


Fig. 2.—Effect of night temperature on the total net night-time CO_2 exchange.

- A, 8-hr night:
plant tops+roots+soil
- B, 14-hr night:
plant tops+roots+soil.
- C, 8-hr night:
plant tops only.
- D, 14-hr night:
plant tops only.

These data indicate that night-time CO_2 influx progressively decreases with increase in night temperature (T_N). At high night temperatures ($T_N = 35.0^\circ\text{C}$) and short night periods, a net CO_2 efflux in the dark was observed. For night lengths of 14 hr, however, the high night temperature of 35.0°C continued to support a net CO_2 influx. Thus at $T_N = 35^\circ\text{C}$, when the night was warmer than the day by 7.5°C , little net total CO_2 efflux at night was observed. Hence it may be concluded that the "dark" carboxylations in the leaves of pineapple are not completely inhibited by night temperatures that exceed day temperatures. However, if soil and root respiration are included (curves A and B, Fig. 2), then night temperatures in excess of day temperature induce a state of net carbon loss at night (Fig. 2).

(d) Relationship between Total Net Daytime CO₂ Exchange and that of the Previous Night

It is clear (Table 1; Fig. 1) that the CO₂-exchange pattern of pineapple plants at night influences the CO₂ exchange of the following day, although day temperatures were held constant at 27·5°C. The dependence of day net CO₂ exchange on that of the previous night is illustrated in Figure 3. Curve B is for the plant tops alone and curve A is for whole plants and soil. It is evident that a negative correlation exists between night and day CO₂ exchange: conditions that favour night CO₂ uptake are associated with low (or negative) daytime CO₂ influx, and *vice versa*.

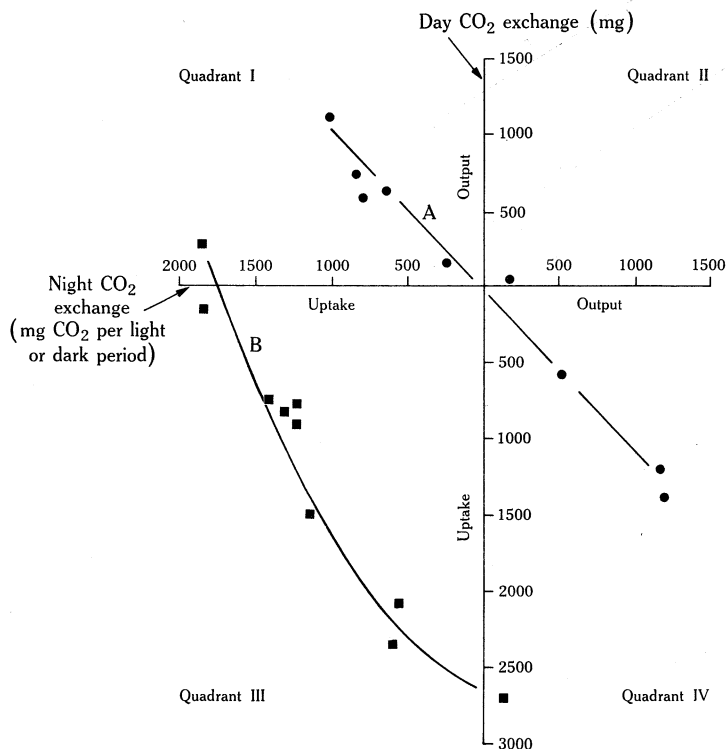


Fig. 3.—Relationship between the day and night total net CO₂ fluxes of pineapple plants.

A, plants + roots + soil.

B, plant tops only.

Curve B (CO₂ exchange of plant tops alone) lies predominantly in quadrant III of Figure 3 which denotes night *and* day CO₂ uptake, whilst curve A (CO₂ exchange of plant tops plus roots plus soil) lies equally (Fig. 3) in quadrant I (night uptake/day output of CO₂) and in quadrant IV (night output/day uptake). This indicates that, for whole pineapple plants, the two modes of CO₂ acquisition (night uptake/day output or day uptake/night output) may be regarded as alternatives controlled by the night temperature.

IV. DISCUSSION

(a) CO₂ Assimilation in the Pineapple

The results described above substantiate previous reports that CO₂ assimilation in the pineapple is of the CAM type (Joshi *et al.* 1955; Neales *et al.* 1968; Aubert

1971; Bartholomew and Conelly 1971). The data also agree with (and amplify) the brief report in abstract of Bartholomew and Conelly (1971), that the CO_2 -exchange pattern of single pineapple leaves by day and night were greatly affected by night temperature.

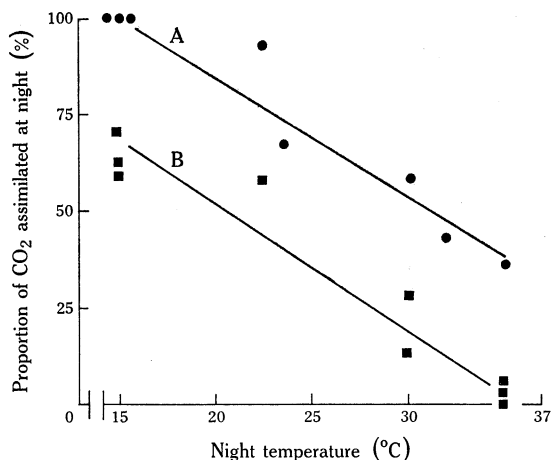


Fig. 4.—Effect of night temperature on the proportion of the CO_2 assimilated at night to that assimilated over 24 hr.
A, 14-hr dark period.
B, 8-hr dark period.

Figure 4 demonstrates that the proportion of the total net CO_2 influx over 24 hr that is assimilated at night decreases as the night temperature increases. As might be expected, this proportion is greater for 14-hr nights (curve A, Fig. 4). Collins (1960, p. 133) gives the average minimum temperatures for pineapple-growing areas as follows: Hawaii 10°C , Malaya 26°C , Australia 12°C , S. Africa 5°C . Thus it would appear likely (Fig. 4) that a high proportion of carbon assimilation in pineapple crops is due initially to “dark” carboxylations. Ekern’s (1965) data for the daily trends of evapotranspiration rate of this crop in Hawaii point to the same conclusion. A direct test of this suggestion could be made by the field measurement of CO_2 fluxes into a pineapple crop using established (Lemon *et al.* 1971) micrometeorological methods.

(b) Control of the Diurnal Pattern of CO_2 Assimilation in the Pineapple

Thomas and Ransome (1960) discussed the “varying CAM power in a single plant” (p. 87), and mentioned plant age, season, photoperiod, and night temperature as relevant factors. The large influence of night temperature on patterns of CO_2 assimilation in the pineapple reported above (Table 1; Fig. 1) appear to agree with the observations and suggestions of Kluge (1971) and Avadhani *et al.* (1971). They suggested that the pattern of daytime CO_2 assimilation in *Bryophyllum tubiflorum* was controlled by the malic acid status of the phyllodes at the end of the dark period. In “high malate” phyllodes, CO_2 assimilation via phosphopyruvate carboxylase (PPC) was inhibited and sugars were a more predominant product of CO_2 assimilation than was malate. In the experiments reported above using pineapple plants, night temperatures of 35°C greatly reduced dark CO_2 assimilation (Fig. 2) and hence these plants entered the light phase as “low malate” plants, in which considerable net CO_2

assimilation was induced as soon as the plants were illuminated (Fig. 1). On the other hand, it may be inferred that cool night temperatures (15°C) produced high malate plants in which light induced a CO₂ efflux at the beginning of the light period (Fig. 1). This has been called the "light deacidification" phase of the CAM cycle (Thomas and Ransome 1960) and perhaps corresponds to the internal release of CO₂ which is not reassimilated because of the inhibition of PPC (Kluge 1971) and the lower affinity for CO₂ of the alternative, ribulosediphosphate carboxylase, carboxylating system. In this sense, night temperature may be one of the factors that controls the pattern and mechanism of CO₂ assimilation in CAM plants. There is also evidence from another source that CAM plants assimilate CO₂ by either the C₃ or the C₄ system. Lerman (1972) has recorded that the discrimination against ¹³C (as δ¹³C‰ values) of succulent plants (cactus, *Agave*, pineapple, *Tillandsia*, etc.) was $-17 \pm 8\%$ which is a value intermediate between that of C₃ (δ¹³C = $-27 \pm 4\%$) and C₄ plants ($-10 \pm 3\%$). Also, Bender (1971) gives δ¹³C‰ values for seven crassulacean plants that range from -27.6% (*Sedum spurium* Bieb.) to -13.8% for *S. rubrotinatum* Clausen.

V. ACKNOWLEDGMENTS

I am grateful for financial support from the Australian Research Grants Committee and the Water Research Foundation of Australia. Miss Robin Duke provided competent technical assistance and I benefited from useful discussions with Dr. C. B. Osmond.

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