Shifts in the optimal temperature for nocturnal CO_2 uptake caused by changes in growth temperature for cacti and agaves

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When the day/night air temperatures were raised from 10°C/10°C to 30°C/30°C, the optimal tempearture for nocturnal CO_2 uptake by six species of cacti and three species of agave shifted from an average of 12°C to an average of 20°C. The maximum rate of CO_2 uptake was higher for *Agave americana* at the higher ambient temperature, lower for *A. deserti,* and much lower for *A. utahensis,* consistent with the relative mean temperatures of their native habitats. For the cactus *Coryphantha vivipara,* which had the greatest temperature shift observed (13°C), the halftime was 8 days for the upward shift and 4 days for the downward shift. The halftimes for the comparable shifts averaged 1.6 days for three other species of cacti and less than 1 day for two agave species. The shifts in the optimal temperature for nocturnal CO_2 uptake were in response to changes in nighttime temperature, at least for *C. vivipara,* and reflected temperature responses of both the stomates and the chlorenchyma.

Additional key-words: CAM, Crassulacean acid metabolism, photosynthesis.

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Introduction

The optimal temperature for photosynthesis can shift to match the ambient temperature of a plant's environment, a characteristic which has been known for many years (Semikhatova 1960, Mooney and West 1964, Strain and Chase 1966). Such shifts are generally considered adaptive acclimations having a biochemical basis. They can occur in periods as short as 24 h (Mooney and Shropshire 1967, Chabot 1979) as well as in response to seasonal changes in temperature. The highest photosynthetic rates in laboratory studies usually occur at temperatures similar to those of the natural habitat of the species in question, which also has obvious ecological implications (Chabot 1979, Berry and Björkman 1980, Osmond *et al.* 1980). These studies have dealt with plants having the C_3 or C_4 pathway for photosynthesis, while comparable attention has not been focused on plants having Crassulacean acid metabolism (CAM). Such plants open their stomates at night when tissue

temperatures are considerably less, and hence the water vapor concentration drop from the tissue to the air is much lower than during the daytime. This causes the transpirational water loss per unit time to be much lower. Such a strategy generally leads to a high water-use efficiency (mass CO_2 fixed/mass H_2O transpired), as shown by desert succulents such as cacti and agaves (Nobel 1976, 1977). These succulents usually have a fairly low optimal temperature for nocturnal CO_2 uptake, often in the range of 10°C to 15°C (Dinger and Patten 1972, Nobel 1977, Hanscom and Ting 1978, Nobel and Hartsock 1978).

There is some evidence that cacti can shift their optimal temperature for nocturnal CO_2 uptake. For example, the optimal temperature for nocturnal CO_2 uptake by *Coryphantha vivipara* shifted from 10°C to 6°C when the ambient temperature was lowered from 10°C to −10°C for one night (Nobel 1981). The upper temperature compensation point for nocturnal CO_2 uptake varies seasonally for *Opuntia phaeacantha* var.

discata from about 13°C in March to 24°C at the end of August (Nisbet and Patten 1974), which allows a positive carbon balance for a much larger fraction of the year. The optimal temperature for nocturnal CO_2 uptake by seedlings of *Ferocactus acanthodes* shifted from 24°C to 12°C when the day/night air temperature was lowered from 35°C/27°C to 15°C/10°C (Jordan and Nobel 1981). The present study examines the flexibility of the optimal temperature for nocturnal CO_2 uptake by a series of CAM plants maintained at low *versus* high growth temperatures. The plants chosen were native to the Sonoran desert, except for *Agave americana*, which presumably comes from eastern Mexico (Gentry 1972). *Coryphantha vivipara* is especially widespread, occurring from 30°N in northern Mexico to 50°N in southern Canada (Nobel 1981). The rates of change in optimal temperature for nocturnal CO_2 uptake in response to changes in the ambient temperature were also determined.

Materials and methods

Carnegiea gigantea (Engelm.) Britton & Rose (Cactaceae) was obtained at 33°46′N, 112°41′W, 500 m elevation; *Coryphantha vivipara* (Nutt.) Britton & Rose var. *deserti* (Engelm.) W. T. Marshall (Cactaceae) at 36°40′N, 116°1′W, 1100 m; *Ferocactus acanthodes* var. *lecontei* (Engelm.) Lindsay (Cactaceae) at 33°38′ N, 116°24′W, 840 m; *Opuntia bigelovii* Engelm. (Cactaceae) at 33°38′N, 116°24′W, 840 m; *Agave americana* L. (Agavaceae) from a commercial source; *A. deserti* Engelm. (Agavaceae) at 33°38′N, 116°24′W, 840 m; and *A. utahensis* Engelm. (Agavaceae) at 37°24′N, (Agavaceae) from a commercial source; *A. deserti* Engelm. (Agavaceae) at 33°38′N, 116°24′W, 840 m; and *A. utahensis* Engelm. (Agavaceae) at 37°24′N, 115°23′W, 1680 m. Nomenclature is according to Shreve and Wiggins (1964), Benson (1969), Munz (1974), or Beatley (1976).

Mature plants (at least 10 years old) were transplanted in desert soil and then maintained in environmental chambers with a 12-h daytime at 350 ± 30 μmol m^{-2} s^{-1} photosynthetically active radiation from 400 to 700 nm (determined with a Lambda Instruments LI-190S quantum sensor). Day/night air temperatures were either 10°C/10°C (in which case maximum day/minimum night tissue surface temperatures were 18.4 ± 1.7°C/9.3 ± 0.3°C) or 30°C/30°C (maximum day/minimum night tissue surface temperatures of 37.2 ± 1.8°C/29.4 ± 0.3°C). Plants were watered weekly with 1/10 Hoagland's solution No. 1 (Hoagland and Arnon 1950) so that the soil water potential near the roots (determined with Wescor PT 51–05 soil thermocouple psychrometers) was -0.2 ± 0.1 MPa (1 MPa $= 10^6$ N m^{-2} $= 10$ bars). Air temperature and tissue surface temperatures (0.5 mm below the surface at midheight on cactus stems or midlength on agave

leaves) were measured with 36-gauge (0.13 mm diameter) copper-constantan thermocouples.

Nocturnal gas exchange on at least two plants of each species (agreement in optimal temperature within $\pm$ 1°C) was determined as described in Nobel and Hartsock (1978) using an assimilation chamber containing 340 ± 4 μl l^{-1} CO_2 in air of $60 \pm 5\%$ relative humidity. Measurements were made 3 to 6 h after the beginning of the dark period, times when stomatal opening and net CO_2 uptake were maximal. The water vapor conductance equalled the transpiration rate per unit leaf or stem surface area divided by the water vapor concentration drop from the tissue to the air (circumscribing area was used for the irregular surfaces of cacti). The CO_2 residual conductance of the chlorenchyma equalled the net rate of CO_2 exchange per unit leaf or stem surface area divided by the CO_2 concentration in the intercellular air spaces just interior to the stomates (Nobel and Hartsock 1979).

Results

When the air temperature was increased from 10°C to 30°C, the optimal temperature for nocturnal CO_2 uptake by *Carnegiea gigantea* increased from about 14°C to 21°C (Fig. 1). At the higher ambient temperature, both the water vapor conductance and the CO_2 residual conductance were considerably lower, resulting in a 3-fold lower maximum rate of CO_2 uptake. When the plant was returned to an air temperature of 10°C, the
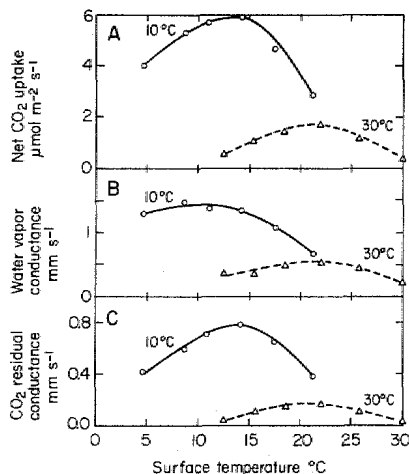

Fig. 1. Temperature response of nocturnal gas exchange by *Carnegiea gigantea*. A plant was maintained for 4 weeks with day/night air temperatures of 10°C/10°C, gas exchange was determined, and then the plant was switched to 30°C/30°C and gas exchange was determined again after 4 weeks. A) Net CO_2 uptake, B) stem water conductance, and C) CO_2 residual conductance.
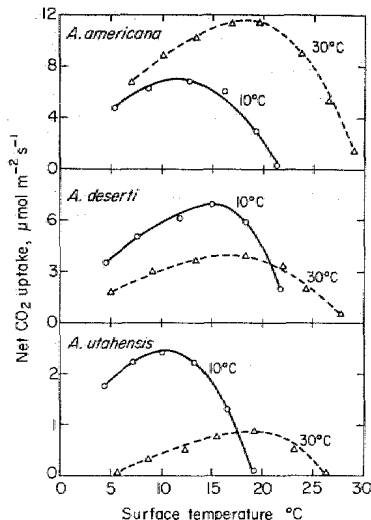
Fig. 2. Nocturnal CO_2 uptake for three species of *Agave* maintained for 4 weeks at day/night air temperatures of 10°C/10°C and then 4 weeks at 30°C/30°C.
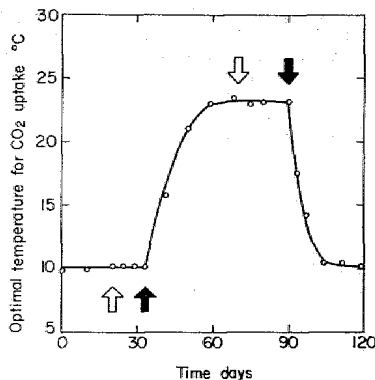

Fig. 3. Influence of day *versus* night temperature on the optimal temperature for nocturnal CO_2 uptake by *Coryphantha vivipara*. Daytime air temperature was increased from 10°C to 30°C on day 20 (upward open arrow; maximum stem surface temperature increased from 21°C to 40°C) and then reduced back to 10°C on day 70 (downward open arrow). Nighttime air temperature was increased from 10°C to 30°C on day 33 (upward closed arrow; nighttime stem surface temperatures were within 0.5°C of air temperature for the last 8 h of the night) and reduced back to 10°C on day 90 (downward closed arrow).

temperature dependencies and magnitudes of the conductances and net CO_2 uptake returned to their original values.

The optimal temperature for net CO_2 uptake was also influenced by the growth temperature for all three species of *Agave* considered. For *A. americana*, the net

Tab. 1. Summary of optimal temperatures for nocturnal CO_2 uptake for six species of cacti and three species of agave maintained at low or high ambient temperatures. Plants were kept for 4 weeks at day/night air temperatures of 10°C/10°C and gas exchange measured, and then they were shifted to day/night air temperatures of 30°C/30°C for 4 weeks and gas exchange measured again. In a second set of measurements, the plants were maintained at 30°C/30°C for 4 weeks, the temperature dependence of gas exchange determined, and then determined again after 4 weeks at 10°C/10°C. The optimal temperatures for nocturnal CO_2 uptake (determined graphically) were averaged for the two measurements under a particular condition, agreement generally being within ± 0.6°C.

Species	Optimal temperature for net CO_2 uptake (°C)	
	10°C/10°C	30°C/30°C
Carnegiea gigantea	14.2	21.2
Coryphantha vivipara	10.2	23.2
Ferocactus acanthodes	12.0	21.8
F. viridescens	13.0	19.2
Mammillaria dioica	12.6	16.0
Opuntia bigelovii	11.4	22.0
Agave americana	11.6	18.6
A. deserti	15.2	17.8
A. utahensis	10.4	19.8

CO_2 uptake was 66% higher for day/night air temperatures of 30°C/30°C than for 10°C/10°C, but it was 43% lower for *A. deserti* at the higher temperature and 65% lower for *A. utahensis* (Fig. 2). The shift in optimal temperature was about 3°C for *A. deserti*, 7°C for *A. americana*, and 9°C for *A. utahensis*.

The optimal temperatures for the three species of *Agave* and six species of cacti are summarized in Table 1. In all cases, the optimal temperature for net CO_2 uptake was higher for plants maintained at day/night air temperatures of 30°C/30°C than at 10°C/10°C. The largest shifts occurred for *Coryphantha vivipara* (13°C) and *Opuntia bigelovii* (11°C), and the smallest for *A. deserti* and *Mammillaria dioica* (3°C).

Since *Coryphantha vivipara* had the largest shift in the optimal temperature for nocturnal CO_2 uptake, both the time course of the shift as well as the effect of day *versus* night air temperature were checked for this species. Figure 3 shows that the daytime temperature did not influence the location of the optimum for nocturnal CO_2 uptake, while the nighttime temperature did. The halftime for the increase in the optimal temperature upon raising the air temperature was nearly 8 days, while the halftime for the decrease upon lowering the air temperature was just under 4 days (Fig. 3).

Table 2 summarizes the halftimes for the shifts in optimal temperatures for *Coryphantha vivipara* and the five other species of cacti and agaves tested. These other species all had shorter halftimes than did *C. vivipara*. In fact, for *Agave americana*, over half of the upward and downwards shifts in optimal temperatures occurred in less than 1 day (Tab. 2).

Tab. 2. Halftimes for the shift in optimal temperature for plants at low versus high ambient temperatures. Nocturnal gas exchange was measured at various times after shifting from day/night air temperatures of 10°C/10°C to 30°C/30°C or vice versa and the halftime for the shift in optimal temperature determined graphically (cf. Fig. 3).

Species	Halftime (days)	
	10°C-to-30°C shift	30°C-to-10°C shift
Carnegiea gigantea	1.8	1.6
Coryphantha vivipara	7.7	3.8
Ferocactus acanthodes	1.6	1.7
Opuntia bigelovii	1.8	1.3
Agave americana	0.6	≤0.5
A. utahensis	0.8	1.5

Discussion

The optimal temperature for nocturnal CO_2 uptake by six species of cacti and three species of agave depended on the growth temperature, increasing 3°C to 13°C as the day/night air temperature was raised from 10°C/10°C to 30°C/30°C (Tab. 1). For most non-CAM plants, the change in location of the optimal temperature for CO_2 uptake per degree change in growth temperature is 0.3 to 0.4 (Billings et al. 1971, Slatyer 1977, Mooney et al. 1977, Pearcy 1977, Berry and Björkman 1980), although some plants such as Heliotropium curassavicum can be over 0.6 (Mooney 1980). Thus, a shift of 6°C to 8°C in the optimal temperature might be expected for the conditions employed here, consistent with the observed mean shift of 8°C. Species exhibiting greater temperature plasticity might be expected to be more widely distributed or found in regions with greater seasonal temperature fluctuations, which is observed in comparing the widespread Coryphantha vivipara to the other cacti, in comparing Ferocactus acanthodes (widely distributed in Arizona and California) to F. viridescens (restricted to coastal southern California and northern Baja California), but not in comparing Agave deserti to the more restricted A. utahensis.

The temperature shift for the CAM plants depended on changes in the sensitivity of both the stomates and the chlorenchyma to temperature (shown in Fig. 1 for Carnegia gigantea and also observed for the other species). Similarly, the temperature shift for the C_3 plant Encelia californica represented changes in the temperature response of both stomatal conductance and mesophyll CO_2 conductance (Mooney and Harrison 1970). The stomatal response seems to be the more temperature-sensitive factor for Eucalyptus pauciflora (Slatyer 1977), but not for most plants (e.g. Mooney et al. 1977, Pearcy 1977, Berry and Björkman 1980, Osmond et al. 1980). The shift in optimal temperature for nocturnal CO_2 uptake was in response to changes in nighttime temperature, at least for Coryphantha vivi-

para (Fig. 3). Although this would be expected for a process occurring at night, it apparently has not been previously demonstrated.

Growth temperatures where the three species of Agave had their highest rates of nocturnal CO_2 uptake reflected the ambient temperatures in their typical habitats. Agave americana is subtropical and probably originated in eastern Mexico, perhaps in Tamaulipas (Gentry 1972), where mean annual air temperatures might be about 25°C. Agave deserti is common in the northern and western Sonoran desert, where mean annual temperatures are about 21°C (Shreve and Wiggins 1964), while A. utahensis occurs in southern Nevada in the Mojave desert, where the mean annual temperature is about 15°C (Beatley 1976). The latter species had much lower nocturnal CO_2 uptake rates at day/night air temperatures of 30°C/30°C than 10°C/10°C, while A. americana did much better at the higher temperatures and A. deserti had an intermediate pattern (Fig. 2).

The halftimes for the shifts between the optimal CO_2 uptake temperatures varied considerably for the various species. Agave americana completed over half of its upward or downward shift in less than 1 day, while Coryphantha vivipara required nearly 8 days for the upward shift and 4 days for the downward shift (Tab. 2). Shifting Opuntia basilaris from day/night temperatures of 20°C/10°C to 40°C/30°C caused essentially no CO_2 exchange for 1 day, but acclimation began by the next day (Gulmon and Bloom 1979). Earlier studies on Opuntia phaeacantha indicated that the shifts in the upper temperature compensation point for nocturnal CO_2 fixation lagged about 1 month behind changes in ambient temperature (Nisbet and Patten 1974), which is considerably slower than observed here, although the two sets of observations are not fully comparable. Studies on the C_3 plants Encelia californica and Polygonum bistortoides suggested that most of the shift in the optimal temperature for CO_2 uptake occurred in 24 h (Mooney and Shropshire 1967). For the moss Dicranum fuscescens, most of the shift occurred in 2 days for transitions between day/night air temperatures of 8°C/1°C and 18°C/7°C (Hicklenton and Oechel 1976). Temperature responses that occur in a few days would allow acclimation to individual weather fronts, thus maximizing the CO_2 uptake capacity.

References

Beatley, J. C. 1976. Vascular Plants of the Nevada Test Site and Central-Southern Nevada: Ecologic and Geographic Distribution. – Energy Research and Development Administration, Washington, D. C. ISBN 0-87079-033-1.

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Benson, L. 1969. The Native Cacti of California. – Stanford University Press, Stanford. ISBN 0-8047-0696-4.

Berry, J. & Björkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. – Annu. Rev. Plant Physiol. 31: 491–543.

Billings, W. D., Godfrey, P. J., Chabot, B. F. & Bourque, D. P. 1971. Metabolic acclimation to temperature in arctic and alpine ecotypes of Oxyria digyna. – Arctic Alpine Res. 3: 277–289.

Chabot, B. F. 1979. Metabolic and enzymatic adaptations to low temperature. – In Comparative Mechanisms of Cold Adaptation (L. S. Underwood, L. L. Tieszen, A. B. Callahan, and G. E. Folk, eds.), pp. 283–301. Academic Press, New York. ISBN 0-12-708750-8.

Dinger, B. E. & Patten, D. T. 1972. Carbon dioxide exchange in selected species of Echinocereus (Cactaceae). – Photosynthetica 6: 345–353.

Gentry, H. S. 1972. The Agave Family in Sonora. – Agricultural Research Service, U.S.D.A., Washington, D. C. Stock No. 0100-1237.

Gulmon, S. L. & Bloom, A. J. 1979. C_3 photosynthesis and high temperature acclimation of CAM in Opuntia basilaris Engelm. and Bigel. – Oecologia 38: 217–222.

Hanscom, Z. III & Ting, I. P. 1978. Irrigation magnifies CAM-photosynthesis in Opuntia basilaris (Cactaceae). – Ibid. 33: 1–15.

Hicklenton, P. R. & Oechel, W. C. 1976. Physiological aspects of the ecology of Dicranum fuscescens in the subarctic. I. Acclimation and acclimation potential of CO_2 exchange in relation to habitat, light, and temperature. – Can. J. Bot. 54: 1104–1119.

Hoagland, D. R. & Arnon, D. I. 1950. The water-culture method for growing plants without soil. – Calif. Agric. Exp. Stn. Circ. 347: 1–32.

Jordan, P. W. & Nobel, P. S. 1981. Seedling establishment of Ferocactus acanthodes in relation to drought. – Ecology 62: 901–906.

Mooney, H. A. 1980. Photosynthetic plasticity of populations of Heliotropium curassavicum L. originating from differing thermal regimes. – Oecologia 45: 372–376.

– & Harrison, A. T. 1970. The influence of conditioning temperature on subsequent temperature-related photosynthetic capacity in higher plants. – In Prediction and Measurement of Photosynthetic Productivity, pp. 411–417. Pudoc, Wageningen. ISBN 90-220-0323-X.

– & Shropshire, F. 1967. Population variability in temperature related photosynthetic acclimation. – Oecol. Plant. 2: 1–13.

– & West, M. 1964. Photosynthetic acclimation of plants of diverse origin. – Am. J. Bot. 51: 825–827.

– Björkman, O. & Collatz, G. J. 1977. Photosynthetic acclimation to temperature in the desert shrub, Larrea divaricata. I. Carbon dioxide exchange characteristics of intact leaves. – Plant Physiol. 61: 406–410.

Munz, P. A. 1974. A Flora of Southern California. – University of California Press, Los Angeles. ISBN 0-520-02146-0.

Nisbet, R. A. & Patten, D. T. 1974. Seasonal temperature acclimation of a prickly-pear cactus in southwestern Arizona. – Oecologia 15: 345–352.

Nobel, P. S. 1976. Water relations and photosynthesis of a desert CAM plant, Agave deserti. – Plant Physiol. 58: 576–582.

– 1977. Water relations and photosynthesis of a barrel cactus, Ferocactus acanthodes, in the Colorado desert. – Oecologia 27: 117–133.

– 1981. Influence of freezing temperatures on a cactus, Coryphantha vivipara. – Ibid. 48: 194–198.

– & Hartsock, T. L. 1978. Resistance analysis of nocturnal carbon dioxide uptake by a Crassulacean acid metabolism succulent, Agave deserti. – Plant Physiol. 61: 510–514.

– – 1979. Environmental influences on open stomates of a Crassulacean acid metabolism plant, Agave deserti. – Ibid. 63: 63–66.

Osmond, C. B., Björkman, O. & Anderson, D. J. 1980. Physiological Processes in Plant Ecology. – Springer-Verlag, Berlin. ISBN 3-540-10060-1.

Pearcy, R. W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in Atriplex lentiformis (Torr.) Wats. – Ibid. 59: 795–799.

Semikhatova, O. A. 1960. The after-effect of temperature on photosynthesis. – Bot. Zh. (Leningr.) 45: 1488–1501.

Shreve, F. & Wiggins, I. L. 1964. Vegetation and Flora of the Sonoran Deserts. – Vols. I and II. Stanford University Press, Stanford. Library of Congress No. 64-13366.

Slatyer, R. O. 1977. Altitudinal variation in the photosynthetic characteristics of snow gum, Eucalyptus pauciflora Sieb. ex Spreng. III. Temperature response of material grown in contrasting thermal environments. – Aust. J. Plant Physiol. 4: 301–312.

Strain, B. R. & Chase, V. C. 1966. Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. – Ecology 47: 1043–1045.

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