

SHORT COMMUNICATION

Crassulacean acid metabolism (CAM) in high elevation tropical cactus

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Abstract. Several taxa of cacti are distributed in high elevation tropical alpine habitats between 4000–4700 m in central Peru. This region has a marked dry season with soil water potentials as low as -25 MPa. The barrel type cactus *Oroya peruviana* and the low caespitose *Tephrocactus floccosus* (both the typical hairy form and a hairless form) all exhibited diurnal fluctuations of malic acid (10 – 100 $\mu\text{mol/g}$ FW), indicative of CAM photosynthesis. $\delta^{13}\text{C}$ carbon isotope ratios were -13 to -14 suggesting that for these CAM plants the bulk of the net carbon gain is through night-time carbon uptake. This occurs in spite of overnight temperatures below 0°C . CAM activity was observed on nights when air temperature dropped to -8°C and subepidermal temperatures reached as low as -3°C . In central Peru, the typical form of *T. floccosus* has a dense covering of long silvery white hairs. Comparisons with an adjacent 'hairless' form showed that the hairy morph maintained a subepidermal temperature several degrees higher during the night. At a site where the 'hairless' morph was rare, the hairy *T. floccosus* had substantially higher overnight acid accumulation. At another site where the 'hairless' morph was abundant, the hairy *T. floccosus* had substantially lower acid accumulation relative to the 'hairless' form.

Key-words: CAM; photosynthesis; cactus; tropics; alpine.

Crassulacean Acid Metabolism, involving night-time fixation of CO_2 , is a photosynthetic pathway found in many succulent plants, particularly species in the families Crassulaceae and Cactaceae. Due to daytime stomatal closure, these plants exhibit high water use efficiency and these species are often distributed in hot xeric desert environments (Kluge & Ting, 1978). It is not surprising then, that these families are less common at high latitudes and high elevations (Teeri, Stowe & Murawski, 1978). Thus, the occurrence of cacti in the alpine puna vegetation of central Peru is of some interest.

Tephrocactus floccosus is a low-growing (< 25 cm) caespitose cactus readily distinguishable by the dense

coat of long white hairs; see for example, Fig. 5.25 in Gibson & Nobel (1986). In some populations, similar 'hairless' morphs occur in association with typical *T. floccosus*. *Tephrocactus floccosus* is frequent on equator-facing slopes above 4000 m in central Peru and personal observations reveal that it extends to above 4700 m; for example, circa Laguna Caprichosa, south of La Oroya, Peru. Also associated with these caespitose cacti is a barrel-type cactus *Oroya peruviana*. The purpose of this communication is to report on observation of microclimate patterns and capacity for Crassulacean Acid Metabolism (CAM) in these taxa.

Two populations were studied. Both were located north of La Oroya (Departemento Junin) in central Peru. One site (referred to as the Tarma Site) was south of the road to Tarma, 4.7 km east of the intersection with La Oroya-Junin Route 33 (elevation 4270 m, $11^\circ 25'\text{S}$, $75^\circ 48'\text{W}$). The puna vegetation typical of this area consists of low bunch grasses with cacti restricted to north-facing slopes usually on thin soils on slightly elevated ridges between drainages. Three taxa were studied at this site *Oroya peruviana* (K. Schum.) Britt. & Rose, the typically hairy *Tephrocactus floccosus* (Salm-Dyck) Backeb., and an unnamed 'hairless' taxon doubtfully distinct from *T. floccosus*. The second site (the Junin Site) was situated on a rocky north-facing slope on the northwest side of Lago Junin, 16.2 km southwest of shelby (elevation 4190 m, $10^\circ 55'\text{S}$, $76^\circ 16'\text{W}$). At this site, only the two *Tephrocactus* taxa were present.

Tissue acidity was measured by grinding samples in deionized water and titrating to pH 7.0 with 0.01 kmol m^{-3} NaOH. Malic acid concentrations were determined on a subsample of tissue extract which was returned to the lab and assayed as described in (Gutman & Wahlefeld, 1974). $\delta^{13}\text{C}$ isotope ratios were determined on tissue samples as described in Sternberg, DeNiro & Keeley (1984).

Tissue and soil water potential were determined using a Decagon SC-10 Thermocouple Psychrometer Sample Changer read with a NT-3 Nanovoltmeter Thermometer. The sample changer was insulated with a styrofoam jacket and samples were allowed 4–8 h equilibrium time prior to measurement.

Table 1. Climatic data for nearest station*

	Mean maximum temperature (°C)	Mean minimum temperature (°C)	Precipitation (mm)
January	16.5	2.9	60.7
February	16.0	3.9	70.6
March	18.2	3.4	74.9
April	17.5	3.1	31.0
May	18.0	0.1	3.5
June	17.0	-0.7	0.9
July	15.8	0.9	22.1
August	16.8	0.9	8.5
September	16.0	3.3	61.2
October	19.1	3.7	35.7
November	19.0	3.7	43.6
December	17.7	2.2	43.2

*Data for La Oroya, Departamento Junin, Peru, 11°31'S, 75°56'W, 3712 m, from unpublished data (5-year period) supplied by Dr Carlos Lopez Ocaña, Centro de Investigacion de Zonas Aridas, Universidad Nacional Agraria, Lima, Peru.

Micrometeorology data was collected from sensors calibrated and read by a 21X Micrologger (Campbell Instruments). Temperatures were made with copper-constantan thermocouples, relative humidity with CSI Model 207 RH probe, wind speed with an anemometer type CSI 014A wind speed sensor and irradiance with a LI-190SB quantum sensor.

Table 1 illustrates climatic data for the part of central Peru in which this study was conducted. The nearest station, La Oroya, is 500 m lower than the study sites and, thus, the mean temperatures at the authors' sites are surely lower than those shown for La Oroya. This region has a distinct wet and dry season. Being in the southern hemisphere, higher temperatures would be expected during the wet season months of November to March than during the dry season months of May to August. This is the case for overnight minimum temperatures but, due to the high incidence of cloud cover during the wet season, the

Table 2. Water potential estimates for soil and plant tissue

Site	Date	Water potential (MPa)
Tarma, 11 November 1985		
Soil at 5 cm		-0.12, -0.21
<i>Oroya peruviana</i>		-0.78, -0.85
<i>Tephrocactus floccosus</i> :		
hairy morph		-0.74, -0.80
hairless morph		-0.70, -0.84
Tarma, 29 and 31 July 1986		
Soil at 5 cm		-1.59, -1.85, -1.93, -3.50
<i>Oroya peruviana</i>		-0.67, -0.89
<i>Tephrocactus floccosus</i> :		
hairy morph		-0.80, -1.01
hairless morph		-0.89, -0.91
Junin, 1 August 1986		
Soil at 5 cm		-8.58, -11.11, -28.37, -29.57
<i>Tephrocactus floccosus</i> :		
hairy morph		-0.39, -0.57
hairless morph		-0.24, -0.61

daytime maximum temperatures are not higher than for the dry season months of May to August.

These areas were visited during both the beginning of the wet season in 1985 and the middle of the dry season in 1986. During the first visit three cacti taxa were studied at the Tarma Site. At this site there was a small population (approximately 50) of the barrel-type cactus *Oroya peruviana* scattered over several hectares, interspersed amongst > 1000 clones of the typical hairy form of *Tephrocactus floccosus*. At this site there were only two individuals of the 'hairless' morph. During the second trip in the dry season, the Junin Site was included because of the very high frequency of the 'hairless' morph (> 60% of the *Tephrocactus floccosus* at this site were the 'hairless' form).

Not surprisingly, at the Tarma Site, soil water potentials were an order of magnitude lower during the dry season than during the wet season (Table 2).

Table 3. Malic acid concentrations in Andean cacti

Site	Date	Malic Acid ($\mu\text{mol g}^{-1}$ fresh weight)			
		1800 h $\bar{X} \pm \text{SD}^a$	2400 h $\bar{X} \pm \text{SD}$	0600 h $\bar{X} \pm \text{SD}$	1200 h $\bar{X} \pm \text{SD}$
<i>Oroya peruviana</i>					
Tarma, 11 November 1985		26 \pm 4	—	137 \pm 73	—
Tarma, 29 July 1985		24 \pm 9	—	68 \pm 11	—
<i>Tephrocactus floccosus</i> (typical hairy morph)					
Tarma, 11 November 1985		48 \pm 14	—	66 \pm 9	—
Tarma, 29 July 1986		67 \pm 8	89 \pm 13	101 \pm 11	95 \pm 10
Junin, 30 July 1986		84 \pm 14	—	99 \pm 27	—
<i>Tephrocactus floccosus</i> (hairless morph)					
Tarma, 11 November 1985		17 \pm 8	—	69 \pm 22	—
Tarma, 29 July 1986		24 \pm 2	—	35 \pm 5	—
Junin, 30 July 1986		50 \pm 10	—	98 \pm 5	—

^aMean \pm standard deviation, $n = 3$.

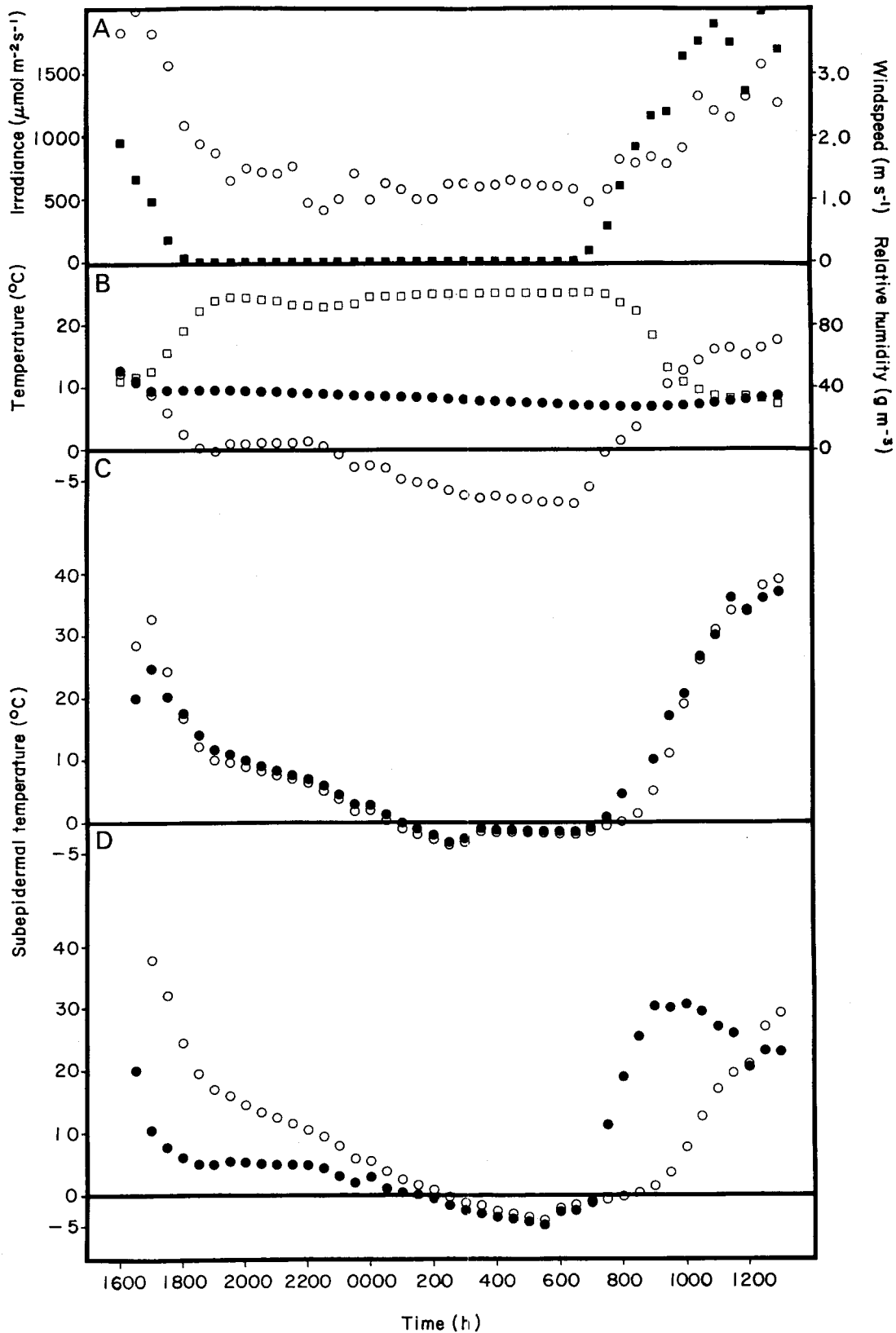


Figure 1. Microclimate data for 29 July 1986 at the Tarma Site. (A) Irradiance (closed squares), windspeed (open circles); (B) relative humidity (open squares), air temperature (open circles), soil temperature (closed circles); (C) subepidermal temperatures on the west-facing side (open circles) and east-facing side (closed circles) of typical hairy *Tephrocactus floccosus*; (D) subepidermal temperatures on the west-facing side (open circles) and east-facing side (closed circles) of *Oroya peruviana*.

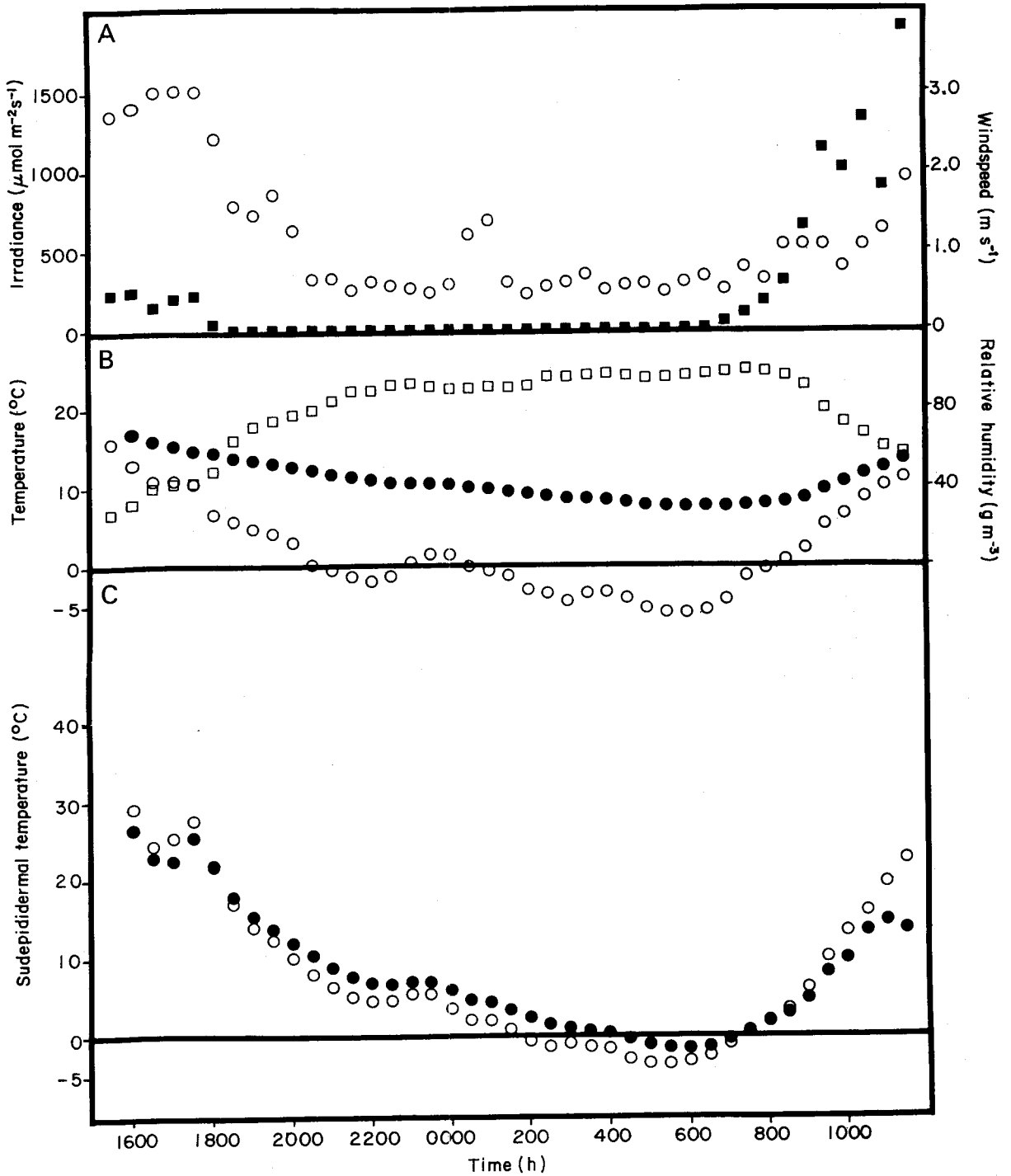


Figure 2. Microclimate data for 30 July 1986 at the Junin Site. (A) Irradiance (closed squares), windspeed (open circles); (B) relative humidity (open squares), air temperature (open circles), soil temperature (closed circles); (C) subepidermal temperatures on the west-facing side of the 'hairless' taxon (open circles) and hairy taxon (closed circles) of *Tephrocactus floccosus*.

In light of the similar elevation and proximity of the two sites, it was of some surprise that the soil water potentials during the dry season were nearly an order of magnitude more negative at the Junin Site than at the Tarma Site. Despite the spatial and temporal differences in soil water potential, relatively little

difference in tissue water potential was observed.

Stable carbon isotope ratios for the three taxa were -13.9 , -14.0 , and -14.6% for *O. peruviana*, *T. floccosus* (hairy form) and the 'hairless' form, respectively, for new growth collected in November from the Tarma Site.

In both the wet and dry season, all three taxa had higher malic acid concentrations in the morning than in the evening (Table 3). Due to logistical problems with the deionized water, titrations were not done in November. However, titrations on the July samples verified that the diurnal fluctuations in malate/malic acid were due to the acid form. This acid fluctuation was restricted to the subepidermal photosynthetic tissue; deeper layers of cactus tissue showed no diurnal fluctuation in acidity or malic acid. At the Tarma Site, both the 'hairless' *Tephrocactus floccosus* and the (hairless) *Oroya peruviana* exhibited higher diurnal acid fluxes in November than in July. Of interest is the observation that the hairy *Tephrocactus floccosus* had a higher acid accumulation at the Tarma Site where it greatly outnumbered the 'hairless' form. At the Junin Site the 'hairless' form was most abundant and showed the highest acid fluctuation.

The microclimate during the two nights for which acidity samples were taken (in the dry season) is shown in Figs 1 and 2. Both sites were similar in that overnight, windspeed dropped, relative humidity remained above 80 g m^{-3} , and air temperature dropped below zero. The sites differed in the early morning irradiance levels. Due to morning fog associated with Lago Junin, the Junin Site had relatively low irradiance levels early in the morning.

Subepidermal temperatures on the cacti approached 40°C at mid-day and dropped to close to -5°C at night. Due to self shading by the large barrel-like growth form of *Oroya peruviana*, afternoon temperatures on the west-facing side were more than 10°C higher than on the east-facing side and the temperature on this side of the plant remained higher throughout the night. Of course, the east-facing side showed the same pattern in the morning. Possibly due to the lower growth form and dense cover of white hairs this temperature differential was much less pronounced in *Tephrocactus floccosus*.

A comparison of subepidermal temperature on adjacent hairy and 'hairless' forms of *Tephrocactus floccosus* at the Junin Site are shown in Fig. 2. In general, temperatures on the 'hairless' form were several degrees higher during the day but several degrees lower at night.

The three tropical alpine cacti studied here appear to be Crassulacean Acid Metabolism (CAM) plants. In addition to possessing overnight acid accumulation, the $\delta^{13}\text{C}$ ratios are in the range of those for CAM plants that obtain the bulk of their carbon from dark CO_2 uptake (Edwards & Walker, 1983). Although the demonstration of CAM in succulents from cold environments is not new (Medina & Delgado, 1976; Nobel, 1981), the activity of this pathway on nights when air temperatures drop below 0°C is of some interest. Medina & Delgado (1976) found that for the tropical alpine CAM plant *Echeveria columbiana*, nocturnal acid accumulation was two-thirds lower when the plants were maintained overnight at 0°C than when maintained at 10°C .

Thus, it is not surprising that for *Tephrocactus floccosus*, two-thirds of the overnight acid accumulation occurred by midnight (Table 1). However, it is noteworthy that a substantial fraction of acid accumulation occurred after midnight when subepidermal temperatures were below 0°C .

The scope of this study was too limited to thoroughly evaluate the factors involved in the role of hairs in the two *Tephrocactus* taxa; however, a few observations are worth noting. For the one night of study at each site, the level of acid accumulation was greatest in the form (hairy or 'hairless') which was most abundant at that site. It is unknown to what degree hairs affect acid accumulation; however, it is clear that hairs play a role in insulating the stem tissues; for example, subepidermal temperature in the hairy form remained above 0°C for nearly 3 h longer than in the 'hairless' form (Fig. 2). Hairs, however, would have a marked effect on reducing day time absorption of photosynthetically active radiation (PAR) which could affect total carbon gain (Ehleringer, Bjorkman & Mooney, 1976) and, thus, carbohydrate substrates for CAM. Nobel (1983) has shown such an effect due to spines. In cacti, spines substantially reduce PAR interception and this reduces nocturnal acid accumulation. A dense coat of hairs may have a similar effect in reducing overnight acid accumulation. Such an effect would be exacerbated at the Junin Site where morning fog reduces total daytime irradiance, and this may account for the greater frequency of hairless morphs at this site and the greater nocturnal acid accumulation by that form over the hairy morph.

In conclusion, this communication extends the upper elevational limit of CAM species to 4700 m and illustrates that malic acid accumulation occurs at subepidermal temperatures below 0°C .

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