

## Leaf gas exchange of two giant caulescent rosette species

G. Goldstein (\*), F. Rada, M. O. Canales and O. Zabala

Departamento de Biología,  
Facultad de Ciencias,  
Universidad de Los Andes, Merida, Venezuela.

(\* Present address:

Laboratory of Biomedical and Environmental Sciences,  
University of California,  
900 Veteran Ave., Los Angeles,  
California 90024, U.S.A.

### ABSTRACT

Gas exchange characteristics were studied under field conditions in two giant caulescent rosette species, *Espeletia timotensis* and *Espeletia spicata*, which grow at elevations up to 4,600 m in the high tropical Andes.

Gas exchange measurements were obtained at the end of the wet season and during the dry season in a tropical alpine environment at 4,200 m elevation. Spectral properties as well as nitrogen content were measured in leaves of different developmental stages. Maximum light levels were never measured at midday due to the vertical orientation of the rosette leaves. Reduced net assimilation rates during the day were associated with reduced irradiance due to the erect position of the leaves and with low stomatal conductances.

Conductance was maximal at midmorning and late in the afternoon, while exhibiting a midday decline. Low nocturnal temperatures affected the gas exchange behaviour of both species only temporarily, as full photosynthetic capacity was regained within one hour following a night with subzero temperatures. Net CO<sub>2</sub> assimilation was strongly influenced by leaf orientation in *E. spicata*. *E. timotensis* exhibited lower photosynthetic rates than *E. spicata*, which can partly be explained by relatively low leaf nitrogen content and by the presence of a thicker pubescent layer. The physiological costs and benefits of leaf pubescence for giant caulescent rosette plants is discussed.

KEY WORDS: tropical alpine environment, *Espeletia timotensis*, *Espeletia spicata*, photosynthesis, gas exchange, low temperature effects, leaf pubescence.

### RÉSUMÉ

Les caractéristiques des échanges gazeux ont été établies en condition naturelle pour deux espèces « géantes » à rosettes caulescentes *Espeletia timotensis* et *Espeletia spicata* qui poussent jusqu'à 4 600 m d'altitude dans les Andes tropicales.

Les échanges gazeux ont été mesurés à la fin de la saison humide et durant la saison sèche, dans un milieu tropical de haute montagne (4 200 m). Les propriétés spectrales, tout comme la teneur en azote des feuilles à différents stades de développement ont été déterminées. Les maximums d'éclairement ne se situent pas à midi par suite de la disposition verticale des feuilles en rosette. La diminution du taux d'assimilations au milieu de la journée est associée à la réduction de la lumière par suite de la position érigée des feuilles et de leur faible conductance stomatique. La conductance était au maximum au milieu de la matinée et tard dans l'après midi, avec une dépression aux alentours de midi. Les basses

températures nocturnes n'affectent que temporairement les échanges gazeux des deux espèces. Une heure, après une nuit durant laquelle la température était négative, la capacité photosynthétique était entièrement récupérée.

L'assimilation nette de CO<sub>2</sub> était fortement dépendante de l'orientation des feuilles d'*E. spicata*. *E. timotensis* indiquant des taux photosynthétiques plus faibles que *E. spicata*, expliqués partiellement par une teneur relativement faible en azote des feuilles et par la présence d'une pilosité plus dense.

Les coûts et les avantages des feuilles couvertes de poils pour les plantes à rosettes caulescentes géantes font l'objet d'une discussion.

MOTS CLÉS : milieux tropicaux de haute montagne, *Espeletia timotensis*, *Espeletia spicata*, photosynthèse, échanges gazeux, effet des basses températures, pilosité des feuilles.

## INTRODUCTION

Giant rosette species belonging to the genus *Espeletia* occur at elevations up to 4,600 m in the tropical Andes. The high tropical environments where these caulescent rosettes grow are characterized by daily rather than seasonal temperature fluctuations and by frequent nocturnal freezing temperatures. Rainfall, however, is distinctly seasonal, and in some Venezuelan paramos (tropical alpine) the dry season may be severe enough to significantly reduce the rate of leaf expansion in *Espeletia* species (SMITH, 1981).

High elevation *Espeletia* species have one terminal rosette of spirally arranged leaves separated by very compressed internodes, a thick pubescent layer which covers both upper and lower leaf surfaces, a stem protected from nocturnal freezing temperatures by a layer of marcescent leaves, and a voluminous central water storage made up of parenchymatous stem tissue (GOLDSTEIN & MEINZER, 1983; GOLDSTEIN *et al.*, 1984; MEINZER & GOLDSTEIN, 1986).

Plants growing in cold tropical environments lacking temperature seasonality are not subjected to the same constraints as those growing in cold temperate climates. For example, giant rosette plants would be expected to exhibit a more or less constant level of physiological activity throughout the year rather than relying on dormancy as a mechanism for withstanding short periods of nocturnal freezing temperatures. Actual freezing of the leaf tissue does not occur in species of the genus *Espeletia* because they endure the nocturnal frost period in an unfrozen, supercooled state (RADA *et al.*, 1985; GOLDSTEIN *et al.*, 1985*b*; RADA *et al.*, 1987). The minimum night-time temperatures are, however, low enough to produce metabolic disturbances in plants not adapted to such conditions.

This study documents carbon assimilation rates and gas exchange parameters of two giant rosette species using infrared gas analysis in the field. A major focus of this work was to investigate environmental and morphological constraints imposed on carbon assimilation by cold tropical habitats. For example, thick pubescence on *Espeletia* leaves permits a certain degree of thermoregulation by uncoupling leaf temperature from air temperature variations (MEINZER & GOLDSTEIN, 1985), but may also shade the leaf and affect CO<sub>2</sub> uptake through increasing boundary layer resistance. We consider here leaf age, orientation, nitrogen content, pubescent thickness, and spectral properties, as well as environmental variables such as vapor pressure deficits and quantum flux density, in relation to gas exchange characteristics.

## MATERIALS AND METHODS

### SITE CHARACTERISTICS AND PLANT MATERIAL

Gas exchange was measured in leaves of *E. timotensis* Cuatrecasas and *E. spicata* Sch. Bip. found in the Paramo de Piedras Blancas (08°52'N, 70°48'S) at 4,200 m elevation. The mean annual temperature is 2.8°C, night-time temperatures frequently drop to -3°C, and the difference in mean monthly temperature between the coldest and warmest months does not exceed 3.0°C. The annual precipitation of 800 mm falls primarily between April and December, with the intensity of the dry season varying greatly from year to year. Fog and mist commonly occur after midday in the rainy season, being less frequently during the dry season.

*E. timotensis* grows on stony and sandy slopes where soils are poor in nutrients and very well drained. *E. spicata*, on the other hand, tends to grow in open depressions where soils are relatively rich in organic matter. Both species have a single stem surrounded by a thick layer (20-30 cm) of dead leaves and a conspicuous central pith. Expanded leaves of *E. timotensis* are 4 to 5 cm wide, while those of *E. spicata* are only 2 to 3 cm in width. This study was carried out with individuals approximately 1 to 1.5 m tall with a terminal rosette of more than 60 expanded leaves. Comparative measurements were made on fully developed leaves of different orientations. Daily cycles of gas exchange and microclimatic variables (quantum flux density, relative humidity, leaf and air temperature) were measured at the end of the wet season and throughout the dry season, between December 2, 1986 and March 10, 1987.

### GAS EXCHANGE MEASUREMENTS

A fully portable system, consisting of a leaf chamber, an air supply unit, and an infrared gas analyser unit, operating in the open mode was used to measure gas exchange in the field (LCA-2 System, The Analytical Development Co. Ltd., Hoddesdon, Herts, England). The leaf chamber, within which a portion of the leaf is sealed during measurements for less than 30 s, contained a solid state humidity sensor, a thermistor for air temperature measurements, and a quantum sensor for photosynthetic active radiation measurements.

The infrared gas analyser was calibrated *in situ* with a gas mixture containing 326 ppm of CO<sub>2</sub>. The air supply unit was fitted with a variable area flow meter that was also calibrated *in situ* with a soap-bubble flow meter. A variable drier by-pass was used to allow a certain degree of humidity control inside the leaf chamber.

Gas exchange rates were determined from flow rates, projected leaf surface area sealed within the chamber, and CO<sub>2</sub> and water vapor concentration differences between reference and analysis air. Gas exchange calculations were conducted according to VON CAEMMERER and FARQUHAR (1981). A correction factor provided by the manufacturer, that takes into account the diluting effect of transpirational water vapor in the leaf chamber, was introduced into the final gas exchange calculations.

Leaf temperatures were measured with fine-wire copper-constantan thermocouples attached to the lower leaf surface. Air humidity was measured with ventilated wet and dry bulb psychrometers installed at 1.0 m above ground. The humidity values were corrected to take into account the relatively low barometric pressure at the study site.

### LEAF SPECTRAL PROPERTIES AND NITROGEN CONTENT

Spectral properties of leaves in relation to solar radiation in the 400-700 nm wavelength range were estimated in the laboratory with a LI-COR LI-1800 Integrating sphere (LI-COR, Inc., Lincoln, Nebraska) fitted with a LI-COR LI-190SB quantum sensor. Mature plants were transported to the laboratory and absorptance, reflectance, and transmittance measurements were taken within a few minutes following leaf excision. Twelve leaves from five different developmental stages were used for each species. The hairs were then plucked from the same series of leaves and placed on transparent tape in an attempt to maintain the structure of the pubescent layer. Spectral properties of the pubescent layer were immediately estimated with the integrating sphere. The spectral properties of the transparent

tape alone were determined and subtracted from the previous reading. The thickness of the pubescent layer was measured under a microscope ( $M \times 40$ ) using ten leaves of each of the five leaf age classes. Nitrogen content of leaves was determined in six leaf samples from two different individuals of each species, by a Kjeldahl procedure which includes an acid digestion, followed by a distillation process, and titration with HCl 0.01 N (BREMNER, 1965).

## RESULTS

### LEAF PUBESCENCE, NITROGEN CONTENT, AND ORIENTATION IN RELATION TO PHOTOSYNTHETIC CAPACITY

Total leaf absorbance increased with age, from approximately 40% absorbance in very young leaves to 70% in old leaves (table I). In contrast to this pattern,

TABLE I. — Summary of physical and spectral characteristics of five different leaf age classes for *E. spicata* and *E. timotensis*. Age 1 corresponds to small expanding leaves and age 5 to senescent leaves. Average absorbances and reflectances of leaves and pubescent layer were estimated for the 400-700 nm wavelength range. Values are means  $\pm$  standard error ( $n=10$ ). Spectra properties and thickness of the pubescent layer for the first two age classes of *E. spicata* leaves were difficult to determine.

Age Class	Leaf absorbance (%)	Leaf transmittance (%)	Pubescence absorbance (%)	Pubescence transmittance (%)	Pubescence thickness (mm)
<i>E. spicata</i>					
1	40.7 $\pm$ 1.9	2.8	—	—	—
2	52.2 $\pm$ 0.8	2.0	—	—	0.66 $\pm$ .04
3	54.7 $\pm$ 0.7	2.2	6.5 $\pm$ 2.6	74.5	0.63 $\pm$ .02
4	61.3 $\pm$ 2.9	2.3	5.5 $\pm$ 2.3	76.8	0.60 $\pm$ .02
5	69.0 $\pm$ 0.9	2.0	8.6 $\pm$ 3.2	77.9	0.62 $\pm$ .02
<i>E. timotensis</i>					
1	43.7 $\pm$ 0.9	0.8	4.4 $\pm$ 1.8	51.0	1.45 $\pm$ .06
2	51.3 $\pm$ 1.4	1.1	13.2 $\pm$ 6.4	52.4	1.36 $\pm$ .05
3	53.2 $\pm$ 0.8	1.3	13.1 $\pm$ 3.9	54.7	1.30 $\pm$ .08
4	57.5 $\pm$ 1.5	1.2	15.3 $\pm$ 1.7	55.5	1.34 $\pm$ .05
5	68.2 $\pm$ 1.3	0.7	17.0 $\pm$ 3.6	60.6	0.69 $\pm$ .02

leaf reflectance decreased with increasing leaf age (data not shown), resulting in transmitted light through leaf relatively independent of age class. Similarly for the pubescence layer, the absorbance increased with leaf age and the percent of light transmitted through the pubescence (i. e. % reaching the lamina) was also relatively independent of age class. The pubescence layer of *E. timotensis* was about two times thicker and intercepted about 10% more photosynthetically active radiation than the pubescence of *E. spicata*. The lamina of *E. timotensis* leaves, therefore, receive relatively low levels of irradiance.

Leaf nitrogen content was higher in *E. spicata* than in *E. timotensis* for all five leaf age classes (table II). In both species, leaf nitrogen content declined in the two older age classes.

Diurnal variations of incident solar radiation in partially erect leaves of intermediate age were influenced by leaf orientation (azimuth) in *E. spicata* (fig. 1).

TABLE 2. — Nitrogen content (mg N/g leaf dry weight) for five different leaf age classes in *E. timotensis* and *E. spicata*. Age 1 corresponds to small expanding leaves and age 5 to senescent leaves. The other leaf age classes are intermediate stages of development between classes 1 and 5. Values are means  $\pm$  standard error ( $n=4$ ).

Age class	1	2	3	4	5
<i>E. timotensis</i>	6.48 $\pm$ 0.87	6.83 $\pm$ 0.57	6.83 $\pm$ 0.64	5.69 $\pm$ 0.31	4.69 $\pm$ 0.21
<i>E. spicata</i>	10.33 $\pm$ 0.93	10.55 $\pm$ 1.14	10.54 $\pm$ 0.46	7.97 $\pm$ 0.65	5.99 $\pm$ 0.45

The upper leaf surface on the east-facing side of the rosette received more irradiance during the morning hours, whereas the upper surface of leaves on the west side received more irradiance during the afternoon hours. Net assimilation of leaves with different orientations followed the pattern of irradiance closely. However, leaf

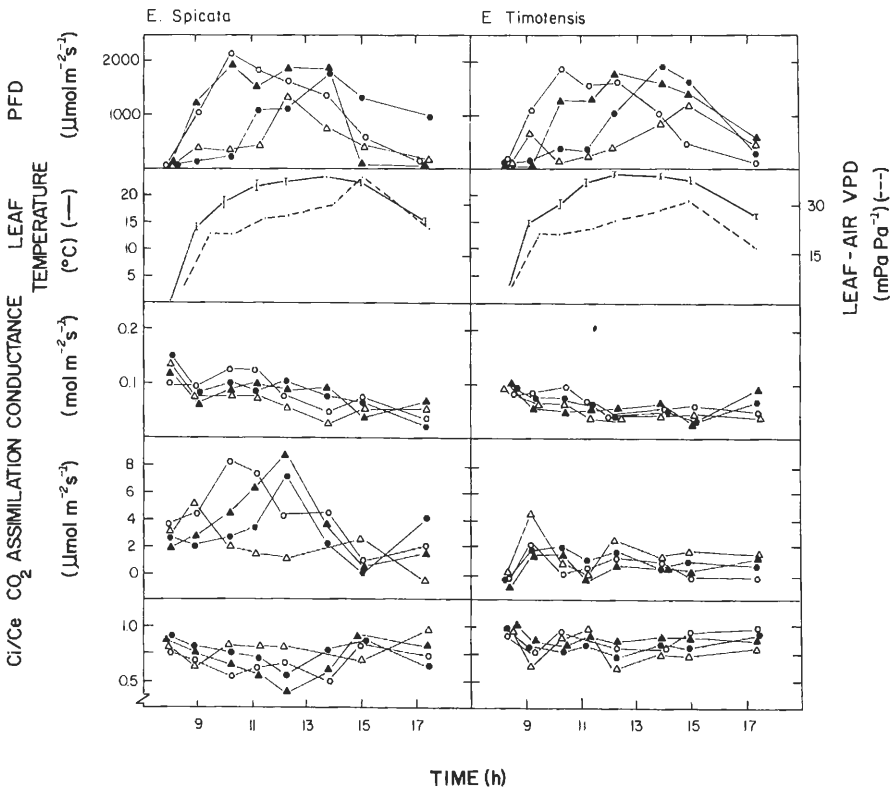


FIG. 1. — Daily courses of photon flux density (PFD), average leaf temperature, vapor pressure deficit (Leaf-Air VPD), CO<sub>2</sub> assimilation, and the ratio of internal to external CO<sub>2</sub> concentration (Ci/Ce) in leaves with four different orientations: East (○), South (▲), North (△), and West (●), on a clear day (27 February 1987). The quantum sensor was held perpendicular to the leaf lamina.

orientation did not significantly influence net assimilation of individual leaves of *E. timotensis*; CO<sub>2</sub> uptake during the day was very similar for all leaves measured.

#### DIURNAL COURSES OF GAS EXCHANGE

Diurnal variations in average photon flux density (PFD), leaf temperature, leaf-air vapour pressure deficit (VPD), leaf conductance, transpiration, net assimilation and the ratios between internal and external CO<sub>2</sub> concentration are shown in

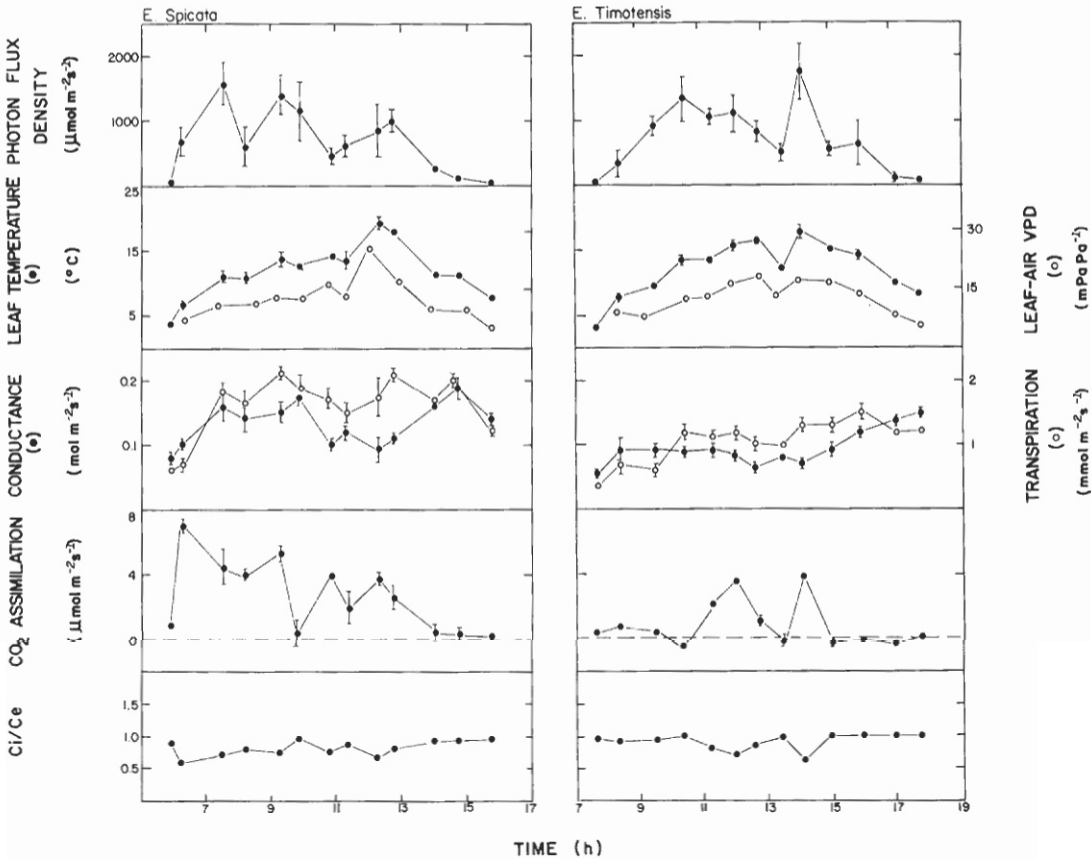


FIG. 2. — Daily courses of photon flux density (quantum sensor held perpendicular to the leaf lamina), leaf temperature, leaf-air vapor pressure deficit (Leaf-Air VPD), transpiration rate, leaf conductance, CO<sub>2</sub> assimilation and the ratio of internal to external CO<sub>2</sub> concentration (Ci/Ce) during the middle of the dry season (21 January 1987) for *E. spicata* and *E. timotensis*. Bars are  $\pm 1$  SE of the mean ( $n=4$ ).

figures 2 and 3 for leaves of *E. spicata* and *E. timotensis*. Figure 2 shows data collected during the peak of the 1987 dry season, while figure 3 shows data collected

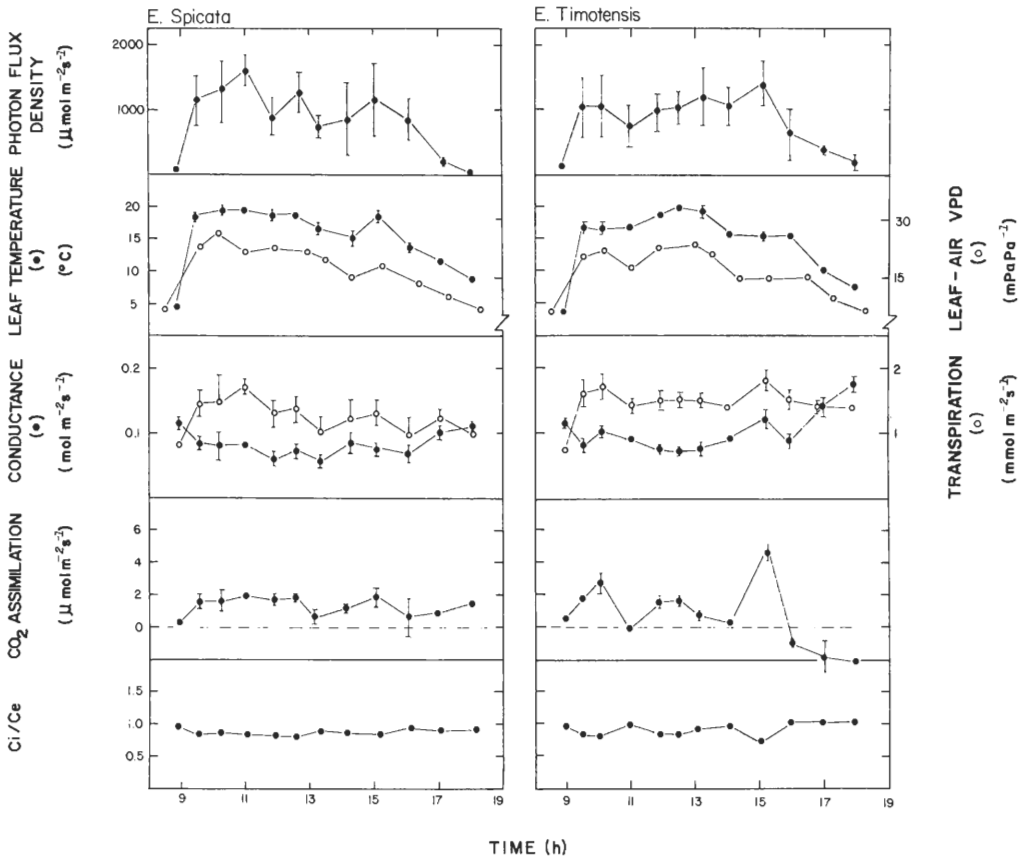


FIG. 3. — Daily courses of photon flux density (quantum sensor held perpendicular to the leaf lamina), leaf temperature, leaf-air vapor pressure deficit (leaf-air VPD), transpiration rate, leaf conductance,  $\text{CO}_2$  assimilation, and the ratio of internal to external  $\text{CO}_2$  concentration ( $C_i/C_e$ ), during the second half of the dry season (10 February 1987) for *E. spicata* and *E. timotensis*. Bars are  $\pm 1$  SE of the mean ( $n=4$ ).

during a period of sporadic rains which occur prior to the onset of the rainy season. Maximum light levels were never measured at midday due to the vertical orientation of the fully expanded leaves of intermediate age, used in this part of the study, which reduce light interception when the sun is at the zenith. Maximum leaf temperatures and VPDs were generally measured either before or after midday. The lowest conductance values were obtained at high VPD's and high leaf temperatures. The opposite pattern of variation between VPD and conductance was clearly evident on February 10 (fig. 3) during which maximum values of stomatal conductance were observed in the early morning and late afternoon hours, the periods of lowest VPD's. During midday it is not possible to distinguish between light and

VPD effects on stomatal conductance since VPD changes in parallel to light, due to the erect leaf position.

Very low values of  $\text{CO}_2$  uptake were observed in both species. In fact in one of the species, *E. timotensis*, even negative net assimilation rates were frequently measured during the daytime. The strong decline in carbon uptake in leaves of both species appears to be associated with relatively low PFD and low stomatal conductances (figs. 2 and 3). Mean internal  $\text{CO}_2$  concentrations in *E. spicata* and in *E. timotensis* were about 273 and 295 ppm, respectively. These internal  $\text{CO}_2$  concentrations appear to be relatively high compared to recently published results of high altitude species from temperate regions (KÖRNER & DIEMER, 1987). Nevertheless, the values were consistent with both the low carbon assimilation and the relatively high conductances exhibited by both species. External  $\text{CO}_2$  concentrations, during the field measurements, varied approximately from 320 to 345 ppm.

Similar diurnal variations in the ratio of internal to external  $\text{CO}_2$  were observed in both species despite the fact that *E. spicata* exhibited larger variations in carbon uptake. This indicates that this species can maintain a higher constancy in internal

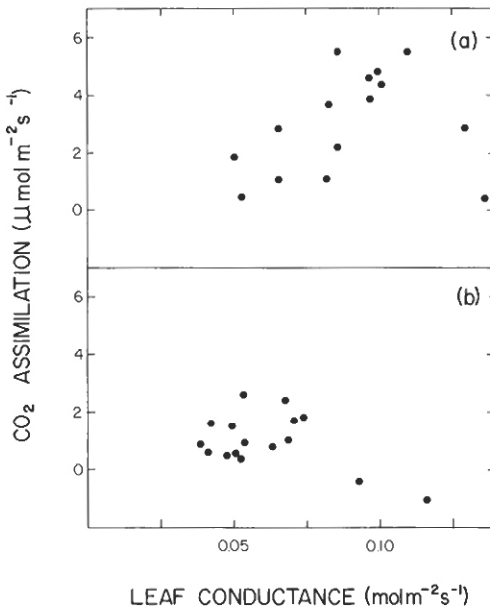


FIG. 4. — Relationship between  $\text{CO}_2$  assimilation and leaf conductance for (a) *E. spicata* and (b) *E. timotensis* leaves of age class 3 during a clear day (27 February 1987).

$\text{CO}_2$  concentrations. The cause of this different behaviour is revealed in figure 4 where carbon uptake measurements obtained on an unusually clear day were plotted as a function of stomatal opening. The two data points on the lower right hand side of each panel represent the first measurements taken in the early morning. If one temporarily omits these data points from the analysis of the relationship depicted in figure 4 (see below), it is clear that photosynthesis tends to increase in a more or less linear fashion with increasing leaf conductance in *E. spicata* while no correlation between assimilation and conductance can be observed in



*E. timotensis*. A high degree of coupling between assimilation and conductance will result in relatively constant internal  $\text{CO}_2$  concentrations throughout the day.

Low values of photosynthesis associated with relatively high values of stomatal conductances measured in the early morning indicate that the photosynthetic apparatus was more affected by the low temperatures that prevail at night than were the mechanisms responsible for the opening and closure of stomates. Leaves, however, appear to recover full photosynthetic capacity less than one hour after sunrise. The pubescent layer was thoroughly inspected and measurements were only taken if dew formation was absent. We believe that the high conductances values observed in the early morning were not an artifact of humidity trapped in the pubescent layer.

The stomates of both species appear to be responsive to changes in VPD. Pooled data from different daily courses showed that conductances tend to decline

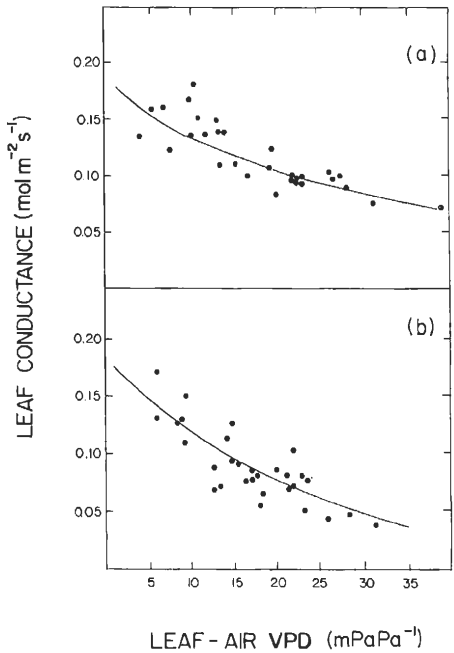


FIG. 5. — Relationship between stomatal conductance ( $g_s$ ) and leaf-air vapor pressure deficit (VPD) for (a) *E. spicata*,  $g_s = 0.175 e^{-0.423 \text{ VPD}}$ ,  $R = 0.87$ ,  $SE = 0.12$  and (b) *E. timotensis*,  $g_s = 0.185 e^{-0.764 \text{ VPD}}$ ,  $R = 0.83$ ,  $SE = 0.20$ . Leaves of age class 3 were used. All data for 4 days of field observations were included in the figure.

with increasing VPD (fig. 5). The negative exponential correlation observed between these two variables was very high given that measurements were not obtained under controlled conditions, and that light levels were highly variable during the course of the day. Stomatal conductance of *E. timotensis* declined more sharply as compared to *E. spicata* with increasing VPD. The net effect was that at low ambient humidities, stomatal conductances in *E. timotensis* were relatively low. This increase in the sensitivity of conductance to VPD was surprising in light of the morphological characteristics of *E. timotensis* leaves.

## DISCUSSION

## THE EFFECT OF PUBESCENCE ON CARBON UPTAKE

Pubescence may have a significant influence on leaf temperature as well as on carbon gain. MEINZER and GOLDSTEIN (1985) discussed the effects of pubescence on leaf energy balance. Leaf pubescence up to 3 mm thick in *E. timotensis*, increases both reflectance and resistance to heat transfer, resulting in leaf temperatures up to 7 or 8°C above ambient temperature. This is advantageous for plant growth under the low temperature conditions characteristic of the Paramo environment; however, the pubescent layer may reduce carbon gain *via* its effects on incident irradiance levels and the diffusive pathway.

Our results indicate that the pubescent layer of *E. timotensis* leaves reduces incoming solar radiation by as much as 13%. This reduction in incoming solar radiation due to the pubescence layer becomes important when PFD in the field is below the light saturation levels for photosynthesis. Under these conditions, carbon gain and light interception are reduced by approximately the same amount.

Leaf pubescence also likely decreased the rate of carbon dioxide diffusion into the leaf. Evaluating the effect of pubescence on CO<sub>2</sub> diffusion in *Espeletia* leaves is difficult by means of laboratory or field manipulative experiments because removal of the trichomes causes immediate damage to the stomatal apparatus. The effect of pubescence on the net assimilation rates was determined by a theoretical approach (NOBEL, 1983) and was found to decrease CO<sub>2</sub> uptake by 15% in *E. timotensis* and by 8% in *E. spicata*. Consequently, leaves of *E. timotensis* that have a relatively thick pubescent layer appear to have lower rates of net assimilation by virtue of the combined effects of reduced light levels and a higher boundary layer resistance to the diffusion of CO<sub>2</sub>. The higher photosynthetic capacity observed in *E. spicata* leaves may be the partial consequence of thinner pubescent layers. SCHULZE *et al.* (1985) measured higher rates of carbon uptake in glabrous Afroalpine giant caulescent rosette plants, similar in general morphology to the Andean rosette plants. If the detrimental effect of the leaf trichomes on carbon gain is eliminated, the photosynthetic levels of the two *Espeletia* species would be comparable to those measured by SCHULZE and coworkers in Afroalpine rosette plants.

## THE INFLUENCE OF AIR TEMPERATURE AND HUMIDITY ON GAS EXCHANGE

Light and VPD are dominant input signals modulating stomatal conductance in several species (e. g. THORPE *et al.*, 1980; KAUFMAN, 1982; GRANTZ *et al.*, 1987). Because of the influence of radiation on leaf temperature which is a major determinant of VPD, diurnal courses of both environmental factors are roughly parallel (e. g. fig. 3), and it is difficult to isolate the effects of light and VPD on stomatal behaviour from field observations. High irradiance causes stomatal opening, and increasing VPD causes stomatal closure. There are, however, strong indications that increasing VPD may be one of the main factors responsible for the decrease in conductance observed in this study (fig. 5). Additional laboratory experiments under controlled conditions are required to establish a more definite relationship.

Below-freezing leaf temperatures at night-time are frequently observed in the study site. Actual freezing of the leaf tissue, however, does not occur because the leaves of *Espeletia* species have the ability to supercool several degrees centigrade

below minimum nocturnal temperatures (RADA *et al.*, 1985; GOLDSTEIN *et al.*, 1985 *b*). Low nocturnal temperatures affect gas exchange activities of *E. timotensis* and *E. spicata* only temporarily (fig. 4), as both species appear to regain their full photosynthetic capacity in less than one hour following a night with subzero temperatures. Afroalpine rosette plants that tolerate ice formation in the intercellular spaces, however, do not exhibit after-effects in photosynthetic capacity following night frost (SCHULZE *et al.*, 1985). Despite differences in the freezing resistance mechanisms, both South American and African giant caulescent rosette plants are able to withstand freezing temperatures and large diurnal temperature fluctuations without significant reductions in carbon assimilation.

Similar to the afroalpine giant rosette plants (SCHULZE *et al.*, 1985) a very pronounced characteristic of both *Espeletia* species was the low photosynthetic rate that occasionally fell close to the CO<sub>2</sub> compensation point (zero net CO<sub>2</sub> gain) for short periods during midday. This considerable decline in CO<sub>2</sub> uptake is associated with low stomatal conductances and the vertical orientation of the rosette leaves. One might suspect that plants exhibiting this photosynthetic behaviour are subject to strong water deficits or other environmental stress. This was not the case, however, with the rosette plants used in the present study, because similar photosynthetic patterns were observed not only during the end of the dry season, but also during the transition period between wet and dry seasons. Although leaf water potential was not measured on a regular basis, occasional potential measurements suggested that the plants were not under severe water stress. The pith water storage not only delays the leaf water potential decrease at midday by supplying water to the transpiring rosette, but also fulfills a role in the water relations of giant rosette plants on a seasonal basis (GOLDSTEIN *et al.*, 1985 *a*).

Several morphological and physiological features of giant caulescent rosette plants in tropical South America have a clear adaptive value. For example, leaf pubescence increases the boundary layer resistance to convective and latent heat transfer resulting in relatively high leaf temperatures. This feature is advantageous in the environment where *E. timotensis* and *E. spicata* grow because diurnal temperatures during the rainy season are low. The results of this work, nevertheless, suggest that the cost of the pubescence for *E. timotensis* leaves is relatively high in terms of CO<sub>2</sub> acquisition. Pubescence may decrease net assimilation rates by 20-30%, particularly during periods of low irradiance, and may also increase the time required for the plant to respond to rapid fluctuations in environmental factors, such as solar radiation.

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