

Water and carbon relations in the genus *Adesmia* (Papilionaceae) at different altitudes in the high north-central Chilean Andes

Relaciones hídricas y de carbono en el género *Adesmia* (Papilionaceae) a diferentes altitudes en los altos Andes del norte-centro de Chile

FERMIN RADA¹, FRANCISCO A. SQUEO², AURA AZOCAR¹
and HERNAN M. CABRERA³

¹ Centro de Investigaciones Ecológicas de los Andes Tropicales (CIELAT), Facultad de Ciencias, Universidad de los Andes, Mérida, Venezuela

² Departamento de Biología, Facultad de Ciencias, Universidad de La Serena, Casilla 599, La Serena, Chile

³ Instituto de Biología, Universidad Católica de Valparaíso, Casilla 4059, Valparaíso, Chile
E-mail: frada@ciens.ula.ve⁽¹⁾, fsqueo@elqui.cic.userena.cl⁽²⁾, hcabrera@ucv.cl⁽³⁾

ABSTRACT

The high north-central Chilean Andes present strong daily and seasonal temperature variations together with an extremely dry growing season, typical of mediterranean climates. *Adesmia* is highly diverse in terms of life-forms, and the most dominant plant genus in this region; therefore, it represents an opportunity to study plant responses to constraints imposed by water stress during the growing season. This paper characterizes variations in water relation parameters, which occur under low water availability conditions, and their effects on gas exchange characteristics in four *Adesmia* species with different life-forms and inhabiting different vegetation belts at different altitudes. Daily courses of gas exchange and water relations were performed on *A. hystrix* (3300 m), *A. aegiceras* (3300 and 3750 m), *A. echinus* (4200 m) and *A. subterranea* (3750 and 4200 m) in the growing season. Osmotic potential at full turgor and turgor loss and relative water content at turgor loss were also evaluated for each species. All *Adesmia* species show important stomatal control during most of the day as a response to low soil water availability. *A. aegiceras*, at both altitudes, exhibits maximum assimilation rates ($6-8 \mu\text{mol m}^{-2}\text{s}^{-1}$) compared to the other three species ($2-6 \mu\text{mol m}^{-2}\text{s}^{-1}$). Only *A. hystrix* at 3300 m and *A. aegiceras* at 3750 m lost turgor during the daily courses. Maximum CO_2 assimilation rates are low compared to other species from mid-latitude high mountains.

Key words: gas exchange, water stress, life-forms, desert mountains, *Adesmia*.

RESUMEN

Los altos Andes del Norte-Centro de Chile presentan fuertes variaciones diarias y estacionales de temperatura junto a una estación de crecimiento extremadamente seca, típica de climas mediterráneos. El género *Adesmia* es altamente diverso en términos de formas de vida y el más dominante entre las plantas de esta región, por lo tanto, representa una oportunidad para estudiar las respuestas de estas plantas a las restricciones ambientales impuestas por la baja disponibilidad de agua en el suelo. En este trabajo se caracterizan los cambios en los parámetros hídricos, que ocurren en condiciones de baja disponibilidad de agua, y su efecto sobre las características del intercambio de gases en cuatro especies de *Adesmia* con diferentes formas de vida y que habitan diferentes pisos de vegetación a diferentes altitudes. Se realizaron cursos diarios de intercambio de gases y relaciones hídricas en *A. hystrix* (3300 m), *A. aegiceras* (3300 y 3750 m), *A. echinus* (4200 m) y *A. subterranea* (3750 y 4200 m), durante el período de crecimiento. Además, en cada especie, se evaluaron el potencial osmótico a máximo turgor y en el punto de pérdida de turgor, así como el contenido relativo de agua en el punto de pérdida de turgor. Todas las especies de *Adesmia* mostraron un importante control estomático durante gran parte del día como respuesta a la baja disponibilidad de agua en el suelo. *A. aegiceras*, en ambas altitudes, exhibe las máximas tasas de asimilación de CO_2 ($6-8 \mu\text{mol m}^{-2}\text{s}^{-1}$) en comparación a las otras tres especies ($2-6 \mu\text{mol m}^{-2}\text{s}^{-1}$). Sólo *A. hystrix* a 3300 m y *A. aegiceras* a 3750 m perdieron turgor durante los cursos diarios. Las tasas máximas de asimilación son bajas si se comparan con otras especies de altas montañas de latitudes medias.

Palabras clave: intercambio de gases, estrés hídrico, formas de vida, montañas desérticas, *Adesmia*.

INTRODUCTION

Plants from high mountains are exposed to very unique environmental conditions, where water availability and low temperatures directly affect gas exchange characteristics, productivity, survival, and community structure (Schulze 1982, Schulze & Hall 1982, Kramer 1983, Sakai & Larcher 1987, Körner & Larcher 1988, Alberdi & Corcuera 1991, Jones 1986). Productivity of these ecosystems is probably limited more by water than any other environmental factor, while low temperature is most limiting to plant distribution (Parker 1963, Sarmiento 1986).

In contrast with high tropical mountains, where the temperature regime is characterized by large daily fluctuations without important seasonal variations (Azócar & Monasterio 1980), mid and high latitude mountains present strong daily and seasonal changes (Öquist & Martin 1986, Squeo et al. 1994). Besides these temporal extremes in temperature, plants in the north-central Chilean Andes with a mediterranean climate, are exposed to even harsher conditions due to an increasing water stress during the short growing season, while soil water stored during winter is being depleted.

In terms of general ecological characteristics, plant communities from high mountains have a particular physiognomy (Hedberg 1964, Coe 1967, Cuatrecasas 1968, Smith & Young 1987). With a few exceptions, high mountain vascular plants belong to four conspicuous growth forms which are used to define different vegetation belts: herbaceous, mostly perennial; cushions; subshrubs and shrubs (Villagrán et al. 1983, Monasterio 1986, Arroyo et al. 1988, Körner & Larcher 1988, Arroyo & Squeo 1990, Squeo et al. 1993). *Adesmia* (Papilionaceae) is the most dominant plant genus of the north-central Chilean Andes (Squeo et al. 1993, 1994). This genus represents an opportunity to study plant responses to environmental constraints since its species show all the life-forms described above and have a widespread distribution along the altitudinal gradient.

Studies on the ecophysiology of plants from high desert Chilean mountains are scarce. Squeo et al. (1996) describe cold resistance mechanisms in plants from this environment. This paper describes a first attempt to characterize carbon and water relations of four *Adesmia* species with different life-forms and inhabiting different vegetation belts at different altitudes.

MATERIALS AND METHODS

Study site and plant species

Four species of the genus *Adesmia* were chosen at Valle del Río Malo in the north-central Chilean Andes (Cordillera de Doña Ana, 29° 45'S, 69° 59'W) between 3300 and 4200 m. These high elevation mountains show an arid mediterranean climate with cold, wet winters and dry, warm summers. At 3750 m, the mean annual temperature is 4.3 °C. July is the coldest month (-1.8 °C), while January and February are the warmest months (9.9 °C) (Squeo et al. 1994). The annual precipitation of 242 mm falls mainly (97%) from May to October, mostly as snow.

There are three vegetation belts in the Cordillera Doña Ana (Squeo et al. 1993, 1994): subalpine (from 2700 to 3500 m) with shrubs between 0.5 to 1.5 m tall; low alpine (from 3500 to 4250 m) with subshrubs and cushion plants; and high alpine (from 4250 m to vegetation limit at 4450 m) with small rosettes. We selected three sites located in the subalpine belt (ca. 3300 m) and low alpine belt (ca. 3700 m and 4200 m). Vegetation cover at the subalpine belt was 40%, where shrubs (e.g., *Adesmia hystrix*, *Ephedra breana*), sub-shrubs (e.g. *Adesmia aegiceras*, *Viviania martifolia*), perennial herbs (e.g., *Astragalus cruckshanksii*, *Phacelia cumingii*) and annuals (e.g., *Viola chrysantha*) coexist. Vegetation cover at the low alpine belt were 27% (3750 m) and 12% (4200 m), with subshrubs (e.g., *Adesmia aegiceras*, *A. echinus*), cushion plants (e.g., *Calceolaria pinnifolia*, *Adesmia subterranea*) and perennial herbs (e.g., *Viola* spp., *Chaetanthera* spp.) present.

The studies were performed using adult individuals of *A. hystrix* Phil. (3300 m), *A. aegiceras* Phil. (3300 and 3750 m), *A. echinus* K.Presl. (4200 m) and *A. subterranea* Clos (3750 and 4200 m) during February of 1991, the middle of the growing season, which extends from the end of November to early April (Arroyo et al. 1981, Squeo et al. 1994, 1996).

Gas exchange and water relation measurements

Diurnal courses of gas exchange and leaf water potential were carried out in two independent days for each species at each elevation, during the first two weeks of February 1991. A fully portable system, consisting of a leaf chamber with humidity, temperature and quantum sensors, 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, ADC Ltd., United Kingdom). Gas exchange calculations were conducted according to von Caemmerer and Farquhar (1981). Fully expanded leaves ($n=9$ to 12) from three different individuals of the species studied were chosen for each measurement interval.

Diurnal courses of leaf water potential (Ψ_L) were carried out for each species and altitude at 2-hour intervals. Measurements were obtained from adult leaves ($n=4$) with a pressure chamber (PMS Instrument Co., Corvallis, Oregon, USA). Water volume-turgor relations, for three different plants of each species and altitude, were measured by the pressure-volume method as described by Tyree and Hammel (1972) and Koide et al. (1991).

RESULTS

For the genus *Adesmia*, water stress is a major factor affecting plant response in terms of stomatal control and its effects on CO_2 assimilation rates (A) for the different life-forms studied. A representative daily cycle with the different ecophysiological parameters measured for the shrub *A. hystrix* (3300 m) is shown in figure 1. As Ψ_L de-

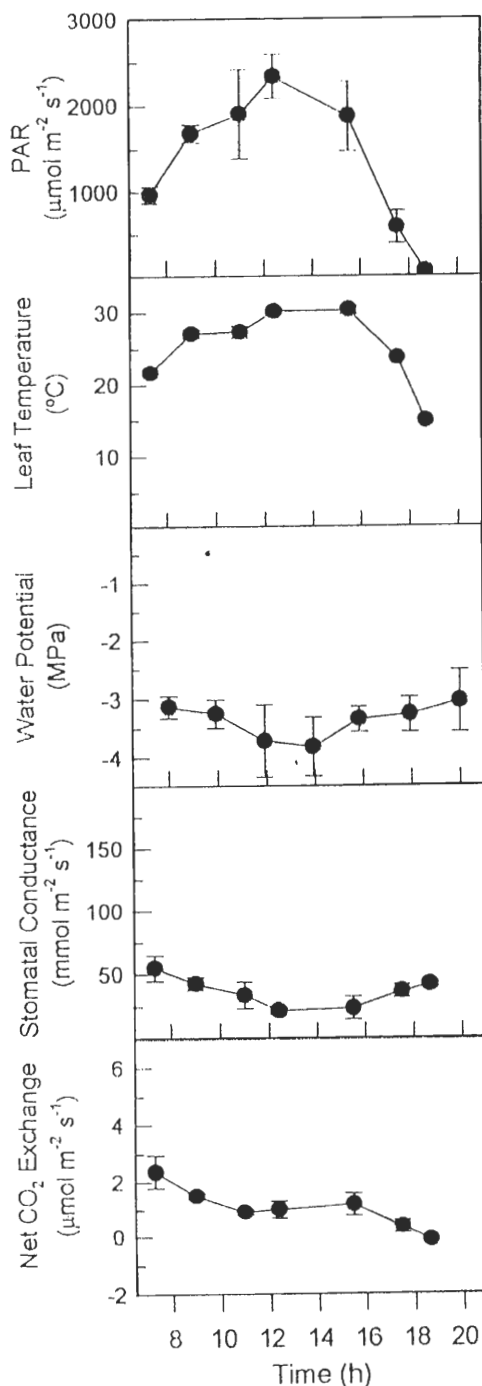


Fig. 1: Diurnal courses of photosynthetically active radiation (PAR), leaf temperature, leaf water potential, stomatal conductance and net CO_2 exchange for *A. hystrix* at 3300 m. Vertical bars represent standard error.

Cursos diarios de radiación fotosintéticamente activa (PAR), temperatura foliar, potencial hídrico foliar, conductancia estomática e intercambio neto de CO_2 para *A. hystrix* a 3300 m. Las barras verticales representan el error estándar.

creased due to a greater air evaporative demand, leaf conductance (g_s) also decreased. In general, maximum CO_2 assimilation rates ($A_{\text{max}} = 2.4 \mu\text{mol m}^{-2}\text{s}^{-1}$) were obtained in the early morning and decreased during the rest of the day.

Compared to *A. hystrix*, *A. aegiceras* showed a greater CO_2 assimilation rate for both altitudes, 3300 m and 3750 m, with A_{max} close to $6.5 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Fig. 2). *A. aegiceras* at 3300 showed a unimodal curve, while at 3750 m the curve had a midday depression and the A_{max} occurred at midafternoon. Leaf conductance for plants at the lower altitude showed a slight decrease after midmorning, which did not affect the assimilation rate. Leaf conductance for plants at the higher altitude decreased considerably due to minimum Ψ_L , which reached -4.07 MPa , below the turgor loss point, and which clearly affected CO_2

assimilation. Ψ_L in *A. aegiceras* at 3300 m decreased to a minimum of -2.8 MPa at midday. This species showed the highest assimilation rates of the four species studied.

Similar to *A. hystrix* and *A. aegiceras* at 3750 m, *A. subterranea* at 3750 m also presented stomatal closure (decrease in g_s) towards midday hours (Fig. 3a). This stomatal closure allowed leaf water potential to be relatively constant, even showing a slight increase during midday. In the case of this species, stomatal closure seemed to slightly affect CO_2 assimilation rate as it decreased throughout the day and it was only in the midafternoon that an increase in A was observed ($A_{\text{max}} = 2.3 \mu\text{mol m}^{-2}\text{s}^{-1}$), when stomatal conductance also increased (Fig. 3a). If we compare *A. subterranea* at this altitude with the same species at a higher altitude (4200 m, Fig. 3b), there

TABLE 1

Average values for the different parameters measured during the different daily cycles (two for each species at each altitude) along the altitudinal gradient. TL (leaf temperature, $^{\circ}\text{C}$), g_s (leaf conductance, $\text{mmol m}^{-2}\text{s}^{-1}$), E (transpiration rate, $\text{mmol m}^{-2}\text{s}^{-1}$), A (assimilation rate, $\mu\text{mol m}^{-2}\text{s}^{-1}$) and A/E (water use efficiency, μmol of CO_2/mmol of H_2O). Only values of photosynthetically active radiation (PAR) above $700 \mu\text{mol m}^{-2}\text{s}^{-1}$ were considered (Average PAR was between 1750 and 1990 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for all species and daily cycles studied). Values are means \pm standard error, numbers in parenthesis are maximum values measured

Valores promedio de los diferentes parámetros medidos durante los cursos diurnos (dos para cada especie y para cada altura) a lo largo del gradiente altitudinal. TL (temperatura foliar, $^{\circ}\text{C}$), g_s (conductancia foliar, $\text{mmol m}^{-2}\text{s}^{-1}$), E (tasa de transpiración, $\text{mmol m}^{-2}\text{s}^{-1}$), A (tasa de asimilación, $\mu\text{mol m}^{-2}\text{s}^{-1}$) y A/E (eficiencia en el uso del agua, μmol de CO_2/mmol de H_2O). Se consideraron sólo los datos obtenidos con valores de radiación fotosintéticamente activa (PAR) sobre $700 \mu\text{mol m}^{-2}\text{s}^{-1}$ (la PAR promedio estuvo entre 1750 y 1990 $\mu\text{mol m}^{-2}\text{s}^{-1}$ para todas las especies y cursos diarios estudiados).

Los valores son promedios \pm error estándar; el número entre paréntesis es el valor máximo

Species	Altitude (masl)	TL	g_s	E	A	A/E
<i>A. hystrix</i>	3300	26.5 \pm 1.0 (29.5)	37 \pm 12 (55)	1.29 \pm .23 (2.8)	1.89 \pm .50 (4.3)	0.91 \pm .48
<i>A. aegiceras</i>	3300	25.2 \pm 1.4 (28.3)	152 \pm 27 (180)	2.20 \pm .26 (4.9)	5.10 \pm 1.07 (6.8)	1.50 \pm .63
<i>A. aegiceras</i>	3750	23.3 \pm 1.4 (30.3)	67 \pm 50 (150)	1.37 \pm .25 (3.73)	3.70 \pm .53 (6.4)	1.34 \pm .52
<i>A. subterranea</i>	3750	25.9 \pm 1.1 (30.5)	43 \pm 9 (54)	1.69 \pm .16 (4.55)	1.55 \pm .35 (2.3)	0.42 \pm .26
<i>A. subterranea</i>	4200	19.6 \pm 0.7 (22.8)	77 \pm 21 (97)	2.02 \pm .36 (3.15)	1.35 \pm .28 (2.2)	0.62 \pm .33
<i>A. echinus</i>	4200	19.7 \pm 0.8 (23.2)	50 \pm 16 (76)	1.50 \pm .41 (3.45)	2.69 \pm .65 (5.5)	1.33 \pm .58

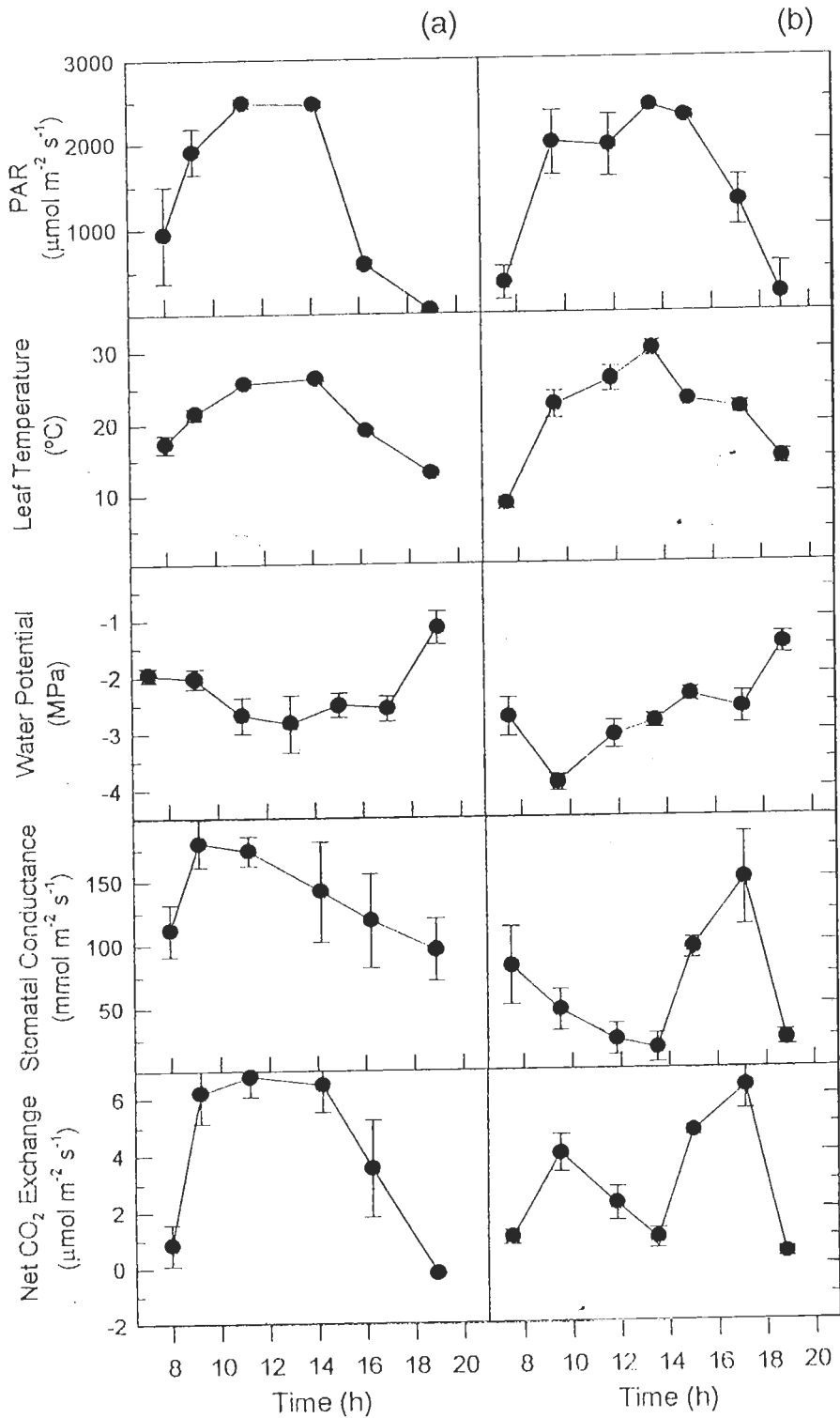


Fig. 2: Diurnal courses of photosynthetically active radiation (PAR), leaf temperature, leaf water potential, stomatal conductance and net CO₂ exchange for *A. aegiceras* at (a) 3300 m and (b) 3750 m. Vertical bars represent standard error.

Cursos diarios de radiación fotosintéticamente activa (PAR), temperatura foliar, potencial hídrico foliar, conductancia estomática e intercambio neto de CO₂ para *A. aegiceras* a (a) 3300 m y (b) 3750 m. Las barras verticales representan el error estándar.

were few differences in the parameters measured. Ψ_L remained slightly more positive at the higher altitude. This may be explained by severe stomatal closure throughout the cycle. At this altitude, the highest stomatal conductance measured occurred in the early morning hours and then decreased the rest of the day, even though average leaf conductance was higher at this altitude.

The representative daily course for *A. echinus*, at 4200 m (Fig. 4), showed a similar pattern compared to *A. subterranea* at the same altitude. Ψ_L were relatively high compared to *A. hystrix* and *A. aegiceras*, with a minimum of -2.6 MPa at midmorning and remaining more or less constant close to -2.0 MPa the rest of the day. Leaf conductance showed its maximum in the early morning ($76 \text{ mmol m}^{-2}\text{s}^{-1}$), decreased until the early afternoon and then remained relatively constant close to $50 \text{ mmol m}^{-2}\text{s}^{-1}$ the rest of the day (Fig. 4). This low stomatal conductance also resulted in lower CO_2 assimilation rates for this species ($A_{\text{max}} = 3.5 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$) compared with *A. aegiceras* (Fig. 2), species with a similar life-form.

Mean values for gas exchange parameters resulting from all the daily courses carried out for each species and altitude exhibited different response patterns (Table

1). In terms of stomatal conductance, *A. hystrix* and *A. aegiceras*, both species growing at 3300 m, showed the lowest and highest g_s values, respectively. As expected, transpiration followed g_s closely (Table 1). In average, the highest CO_2 assimilation rates were found in *A. aegiceras*, with rates of 5.1 and $3.7 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$ at 3300 and 3750 m, respectively. Due to this high A and low g_s which, in turn, decreased the transpiration rate, *A. aegiceras* at both altitudes showed the highest average water use efficiency. Lowest average water use efficiencies were found in *A. subterranea* at 3750 and 4200 m due to low CO_2 assimilation rates throughout the daily cycles.

Comparing minimum leaf water potential (Ψ_L^{min}) with osmotic potential at turgor loss ($\Psi\pi^0$), the shrub *A. hystrix* at 3300 m and *A. aegiceras* at 3750 m exhibited an important turgor loss during the daily courses (Table 2). *A. subterranea* at 3750 m also showed turgor loss during midmorning, but a fast reduction in stomatal conductance between midmorning and midday resulted in a recovery of leaf water potential (compare Table 2 with Fig. 3a). In contrast, Ψ_L^{min} of *A. subterranea* at 4200 m was 0.5 MPa above $\Psi\pi^0$, which indicates that at this altitude turgor was maintained throughout the day. *A. aegiceras* at the lower altitude

TABLE 2

Diurnal leaf water potential and pressure-volume curve parameters for four *Adesmia* species along the altitudinal gradient in north-central Chilean Andes. Ψ_L = Mean leaf water potential, Ψ_L^{min} = minimum leaf water potential, $\Psi\pi^{100}$ = osmotic potential at full turgor, $\Psi\pi^0$ = osmotic potential at turgor loss, RWC^0 = relative water content at turgor loss

Potencial hídrico foliar diurno y parámetros de las curvas presión-volumen para las cuatro especies de *Adesmia* a lo largo del gradiente altitudinal en los Andes de Chile norte-central. Ψ_L = potencial hídrico foliar promedio, Ψ_L^{min} = potencial hídrico foliar mínimo, $\Psi\pi^{100}$ = potencial osmótico a máximo turgor, $\Psi\pi^0$ = potencial osmótico en el punto de pérdida de turgor, RWC^0 = contenido relativo de agua en el punto de pérdida de turgor

Species	Altitude (m)	Ψ_L (MPa)	Ψ_L^{min} (MPa)	$\Psi\pi^{100}$ (MPa)	$\Psi\pi^0$ (MPa)	RWC^0 (%)
<i>A. hystrix</i>	3300	-3.46±1.3	-4.00	-1.89±0.19	-3.20±0.21	75±2
<i>A. aegiceras</i>	3300	-2.45±1.7	-3.20	-1.96±0.42	-3.26±0.34	69±3
<i>A. aegiceras</i>	3750	-2.72±1.7	-4.07	-2.25±0.17	-3.30±0.25	74±3
<i>A. subterranea</i>	3750	-2.35±1.4	-2.87	-1.87±0.11	-2.70±0.27	75±4
<i>A. subterranea</i>	4200	-2.08±1.1	-2.20	-1.92±0.23	-2.70±0.42	72±2
<i>A. echinus</i>	4200	-2.38±2.0	-2.63	-	-	-

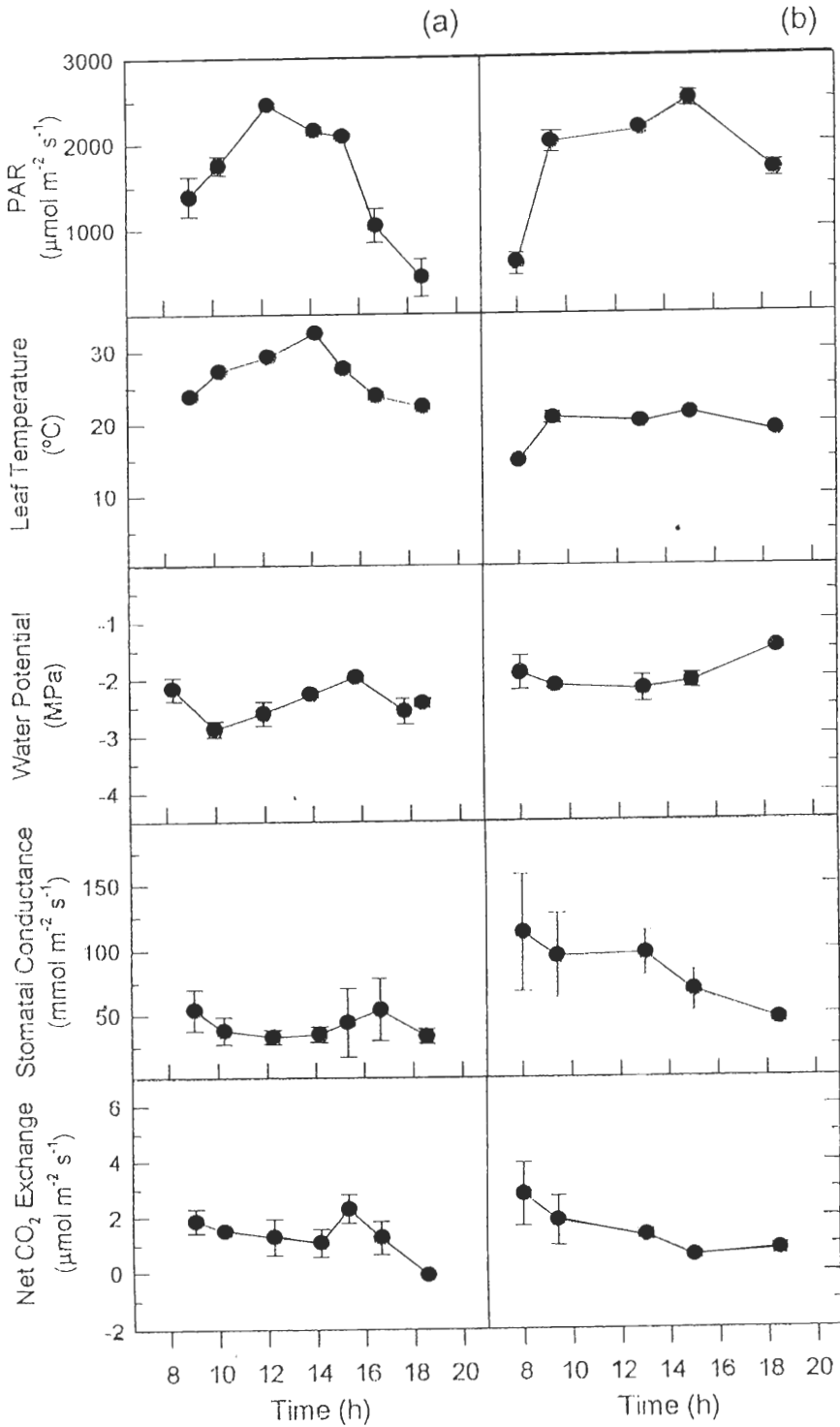


Fig. 3: Diurnal courses of photosynthetically active radiation (PAR), leaf temperature, leaf water potential, stomatal conductance and net CO₂ exchange for *A. subterranea* at (a) 3750 m and (b) 4200 m. Vertical bars represent standard error.

Cursos diarios de radiación fotosintéticamente activa (PAR), temperatura foliar, potencial hídrico foliar, conductancia estomática e intercambio neto de CO₂ para *A. subterranea* a (a) 3750 m y (b) 4200 m. Las barras verticales representan el error estándar.

and *A. subterranea* at 3750 m had Ψ_L^{\min} close to $\Psi\pi^0$. Relative water contents at turgor loss (RWC^0) were between 69% and 75% for all species.

DISCUSSION

This study has revealed a number of eco-physiological characteristics of the genus *Adesmia* growing at different altitudes. All *Adesmia* species respond to water stress conditions through stomatal closure or low stomatal conductances throughout the day to maintain turgor. However, in spite of relatively low leaf conductances, *A. hystrix* at 3300 m loses turgor during the day. This may be due to their presence in drier equatorial facing slopes, with a thin soil layer and abundant rocks which are associated to lower water availability and higher temperature (Rada et al. 1985a, Squeo et al. 1996). Turgor loss may be a mechanism which enables the plant to lower leaf water potentials creating a larger gradient between plant and soil and therefore permitting the plant to absorb soil water which otherwise would not be available (Meinzer et al. 1986, Rada et al. 1989). On the other hand, *A. aegiceras* at this same altitude, but on different slopes, presents a more favorable water status, which permits it to maintain a relatively high stomatal conductance, and therefore, higher assimilation rates. It is interesting to note that this same species at the higher altitude loses turgor, resulting in stomatal closure and a reduction in CO_2 assimilation, even though temperature and PAR conditions are favorable. These two species, *A. hystrix* and *A. aegiceras*, seem to be the most tolerant to these water stress conditions. *A. subterranea* and *A. echinus* maintained higher leaf water potentials and low stomatal conductances throughout the courses studied, an indication of avoidance as a mechanism to survive low water availability. These results support Squeo et al. (1994) who describe the sites where these last two species are found as areas with gentle slopes and more humid due to the accumulation of winter snow melt.

In terms of assimilation capacity, *Adesmia*'s different life-forms show low

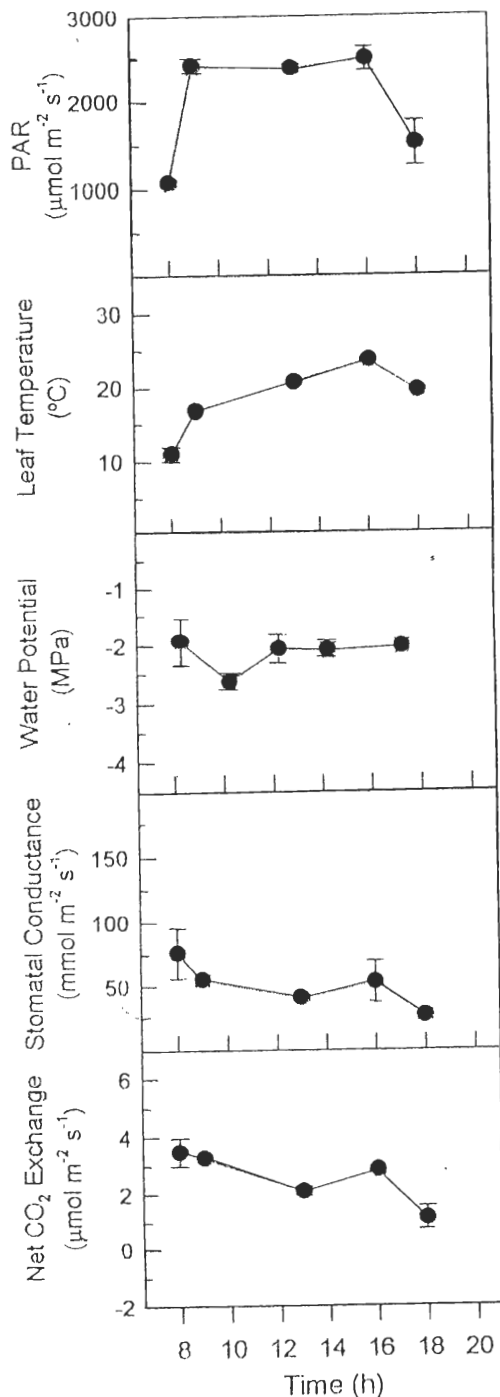


Fig. 4: Diurnal courses of photosynthetically active radiation (PAR), leaf temperature, leaf water potential, stomatal conductance and net CO_2 exchange for *A. echinus* at 4200 m. Vertical bars represent standard error.

Cursoros diarios de radiación fotosintéticamente activa (PAR), temperatura foliar, potencial hídrico foliar, conductancia estomática e intercambio neto de CO_2 para *A. echinus* a 4200 m. Las barras verticales representan el error estándar.

maximum assimilation rates ($2-7 \mu\text{mol m}^{-2}\text{s}^{-1}$) compared to other mid-latitude alpine environments, but are similar to those reported for the high tropical Andes. Subalpine perennial herbs and deciduous shrubs in the Rocky Mountains and in the Alps have maximum assimilation rates of $15-18 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Körner & Diemer 1987, Körner & Larcher 1988, Knapp & Smith 1987). All life forms studied (perennial herbs, acaulescent and giant caulescent rosettes, shrubs and trees) in the high tropical mountains have maximum assimilation rates between $4-11 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Schulze et al. 1985, Goldstein et al. 1989, 1994, Rada et al. 1992, 1996, 1998).

On an annual basis, productivity in alpine vegetation is quite low compared to the rest of the biosphere, only extreme deserts are lower, because these areas are only productive 10 to 25% of the year, under low temperatures and occasional drought stress (Billings 1979). Although assimilation rates are similar for the high tropical and north-central Chilean desert Andean plants, differences in productivity must exist. Even though there is a distinct dry season in the tropical high mountains, which may affect plant productivity for a short period, growth and development carries on all year-round (Estrada et al. 1991, Monasterio & Sarmiento 1991). In the case of the Chilean Andes, biomass production concentrates in a shorter, water stressed growing season (November to April) characteristic of desert ecosystems and which may affect mean annual productivity (Squeo et al. 1993). On an annual basis, considering that this maximum relative growth rate may occur for only a short period of time, total biomass production must be significantly reduced. In addition, because deciduousness is the most important low temperature resistance mechanism during winter, annual total biomass accumulation must be lower if compared to tropical mountain ecosystems, where evergreens are dominant.

Cold resistance mechanisms have been described for the tropical Andes (Rada et al. 1985a,b, 1987, Goldstein et al. 1985, Azócar et al. 1988, Squeo et al. 1991) and for the north-central desert Andes (Squeo et al. 1996). For both environments, a soil-

air temperature gradient is the main determinant of the mechanisms used by different plants to resist nighttime freezing temperatures (freezing tolerance for ground level plants and avoidance mechanisms for plants further away from the soil). For the high north-central Chilean Andes several questions remain open: What is the effect of this differentiation in terms of tolerance and avoidance on plant behavior during the early morning hours considering tolerant plants have to unfreeze before resuming diurnal physiological processes? Opposite to the soil-air temperature gradient produced at night (ground level temperatures lower than air temperatures), during the day temperatures at the soil surface are high compared to air temperatures. What is the effect of this diurnal temperature gradient on water and carbon balance parameters; i.e. optimum temperature for photosynthesis, CO_2 compensation points, maximum assimilation rates for the different life-forms? How do the species that have greater height behave in terms of water and carbon balance during their initial stages when growing close to the ground? Are there changes in the different parameters mentioned above as younger plants move away from the soil surface?

ACKNOWLEDGMENTS

This study was partially supported by Red Latinoamericana de Botánica (RLB), Universidad de La Serena and Compañía Minera El Indio grants.

LITERATURE CITED

- ALBERDI M & LJ CORCUERA (1991) Cold acclimation in plants. *Phytochemistry* 30: 3177-3184.
- ARROYO MTK & FA SQUEO (1990) Relationship between plant breeding systems and pollination. In: Kawano S (ed) *Biological approaches and evolutionary trends in plants*: 206-227. Academic Press, London.
- ARROYO MTK, JJ ARMESTO & C VILLAGRAN (1981) Plant phenological patterns in the high andean cordillera of central Chile. *Journal of Ecology* 69: 205-223.
- ARROYO MTK, FA SQUEO, JJ ARMESTO & C VILLAGRAN (1988) Effects of aridity on plant diversity in the Northern Chilean Andes: results of a natural experiment. *Annals of the Missouri Botanical Garden* 75: 55-78.

- AZOCAR A & M MONASTERIO (1980) Estudio de la variabilidad meso y microclimática en el Páramo de Mucubají. In: Monasterio M (ed) Estudios ecológicos en los páramos andinos: 255-262. Ediciones de la Universidad de los Andes. Mérida, Venezuela.
- AZOCAR A, F RADA & G GOLDSTEIN (1988) Freezing tolerance in *Draba chionophila*, a 'miniature' caulescent rosette species. *Oecologia* 75: 156-160.
- BILLINGS WD (1979) High mountain ecosystems: evolution, structure, operation and maintenance. In: Webber PJ (ed) High altitude geoecology: 97-125. Westview Press, Colorado.
- CAEMMERER S VON & GD FARQUHAR (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376-387.
- COE MJ (1967) The ecology of the alpine zone of Mt. Kenya. *Monographs in Biology*, 17. The Hague: W. Junk. 136 pp.
- CUATRECASAS (1968) Paramo vegetation and its life forms. In: Troll C (ed) Geo-ecology of the mountain regions of the tropical Americas: 163-186. Proceedings of the UNESCO, Mexico Symposium.
- ESTRADA C, G GOLDSTEIN & M MONASTERIO (1991) Leaf dynamics and water relations of *Espeletia spicata* and *E. timotensis*, two giant rosettes of the desert páramo in the tropical Andes. *Acta Oecologica* 12: 603-616.
- GOLDSTEIN G, F RADA & A AZOCAR (1985) Cold hardiness and supercooling along an altitudinal gradient in andean giant rosette species. *Oecologia* 68: 147-152.
- GOLDSTEIN G, F RADA, MO CANALES & O ZABALA (1989) Leaf gas exchange of two giant caulescent rosette species. *Oecologia Plantarum* 10: 359-370.
- GOLDSTEIN G, F MEINZER & F RADA (1994) Environmental Biology of a tropical treeline species, *Polylepis sericea*. In: Rundel PW, AP Smith & FC Meinzer (eds) Tropical alpine environments, plant form and function: 129-149. Cambridge University Press, Cambridge.
- HEDBERG O (1964) Features of Afroalpine plant ecology. *Acta Phytogeographica Suecica* 49: 1-44.
- JONES HG (1986) Plants and Microclimate. Cambridge University Press, New York. 321 pp.
- KNAPP AK & WK SMITH (1987) Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. *Oecologia* 74: 62-67.
- KOIDE RT, RH ROBICHAUX, SR MORSE & CM SMITH (1991) Plant water status, hydraulic resistance and capacitance. In: Pearcy RW, J Ehleringer, HA Mooney & PW Rundel (eds) *Plant Physiological Ecology*: 161-183. Chapman & Hall, London.
- KÖRNER CH & M DIEMER (1987) In situ photosynthetic responses to light temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology* 1: 179-194.
- KÖRNER CH & W LARCHER (1988) Plant life in cold climates. In: Long SP & FI Woodward (eds) *Plants and temperature*: 25-57. *Symp. Soc. Exp. Biol.*, 42. Cambridge.
- KRAMER PJ (1983) *Water Relations of Plants*. Academic Press, Orlando. 482 pp.
- MEINZER FC, PW RUNDEL, MR SHARIFI & E NIELSEN (1986) Turgor and osmotic relations of the desert shrub *Larrea tridentata*. *Plant, Cell & Environment* 9: 467-475.
- MONASTERIO M (1986) Recherches ecologiques sur les Espeletia du páramo désertique des hautes Andes tropicales du Venezuela. Doctor's Thesis. Université Perre et Marie Curie. Paris, France. 123 pp.
- MONASTERIO M & L SARMIENTO (1991) Adaptive radiation of *Espeletia* in the cold Andean tropics. *Trends in Ecology and Evolution* 6: 387-391.
- PARKER J (1963) Cold resistance in woody plants. *Botanical Review* 29: 123-201.
- ÖQUIT G & B MARTIN (1986) Cold climates. In: Baker NR & SP Long (eds) *Photosynthesis in contrasting environments*: 237-293. Amsterdam: Elsevier.
- RADA F, G GOLDSTEIN, A AZOCAR & F MEINZER (1985a) Daily and seasonal osmotic changes in a tropical treeline species. *Journal of Experimental Botany* 36: 987-1000.
- RADA F, G GOLDSTEIN, A AZOCAR & F MEINZER (1985b) Freezing avoidance in Andean giant rosette plants. *Plant, Cell & Environment* 8: 501-507.
- RADA F, G GOLDSTEIN, A AZOCAR & F TORRES (1987) Supercooling along an altitudinal gradient in *Espeletia schultzii*, a caulescent giant rosette species. *Journal of Experimental Botany* 38: 491-497.
- RADA F, G GOLDSTEIN, A OROZCO, M MONTILLA, O ZABALA & A AZOCAR (1989) Osmotic and turgor relations of three mangrove ecosystem species. *Australian Journal of Plant Physiology* 16: 477-486.
- RADA F, J GONZALEZ, A AZOCAR, B BRICEÑO & R JAIMEZ (1992) Net photosynthesis-leaf temperature relations in plant species with different height along an altitudinal gradient. *Acta Oecologica* 13: 535-542.
- RADA F, A AZOCAR, B BRICEÑO, J GONZALEZ & C GARCIA-NUÑEZ (1996) Carbon and water balance in *Polylepis sericea*, a tropical treeline species. *Trees* 10: 218-222.
- RADA F, A AZOCAR, J GONZALEZ & B BRICEÑO (1998) Leaf gas exchange in *Espeletia schultzii* Wedd, a giantcaulescent rosette species, along an altitudinal gradient in the Venezuelan Andes. *Acta Oecologica* 19: 73-79.
- SAKAI A & W LARCHER (1987) Frost survival of plants. In: Billings WD, F Golley, OL Lange, JS Olson & H Remmert (eds) *Ecological studies* 62. Berlin-Springer.
- SARMIENTO G (1986) Ecologically crucial features of climate in high tropical mountains. In: Vuilleumier F & M Monasterio (eds) *High altitude tropical biogeography*. Oxford University Press, Oxford.
- SCHULZE ED (1982) Plant life forms and their carbon, water and nutrient relations. In: Lange OL, PS Nobel, CB Osmond & H Ziegler (eds) *Encyclopedia of plant physiology, physiological plant ecology II*, Vol 12B: 616-676. Springer, Berlin.
- SCHULZE ED & AE HALL (1982) Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In: Lange OL, PS Nobel, CB Osmond & H Ziegler (eds) *Encyclopedia of plant physiology, physiological plant ecology II*, Vol 12B: 181-230. Springer, Berlin.
- SCHULZE ED, E BECK, R SCHEIBE & H ZIEGLER (1985) Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. *Oecologia* 65: 207-213.
- SMITH AP & TP YOUNG (1987) Tropical Alpine plant ecology. *Annual Review of Ecology and Systematics* 18: 137-158.

- SQUEO FA, F RADA, A AZOCAR & G GOLDSTEIN (1991) Freezing tolerance and avoidance in high tropical Andean plants: is it equally represented in species with different plant height? *Oecologia* 86: 378-382.
- SQUEO FA, H VEIT, G ARANCIO, JR GUTIERREZ, MTK ARROYO & N OLIVARES (1993) Spatial heterogeneity of high mountain vegetation in the andean desert zone of Chile. *Mountain Research and Development* 13: 1-10.
- SQUEO FA, R OSORIO & G ARANCIO (1994) Flora de Los Andes de Coquimbo: Cordillera de Doña Ana. Ediciones Universidad de La Serena, Chile. 168 pp.
- SQUEO FA, F RADA, CE GARCIA, ME PONCE, AL ROJAS & A AZOCAR (1996) Cold resistance mechanisms in high desert Andean plants. *Oecologia* 105: 552-555.
- TYREE MT & HT HAMMEL (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* 23: 267-282.
- VILLAGRAN C, MTK ARROYO & C MARTICORENA (1983) Efectos de la desertización en la distribución de la flora andina de Chile. *Revista Chilena de Historia Natural* 56: 137-157.