Leaf and canopy boundary layer conductances of two semiarid species (*Retama sphaerocarpa* L. Boiss, and *Stipa tenacissima* L.)

F. Domingo[1](*), M.J. Moro[2], G. Sanchez[1], A.J. Brenner[3] and P.R. van Gardingen[4]

SUMMARY

Canopy boundary layer conductance was calculated in the field by measuring the evaporation from artificially wet canopies of two main semi-arid species found in the Rambla Honda (Almería, South East of Spain), *Retama sphaerocarpa* (L.) Boiss, and *Stipa tenacissima* L. *R. sphaerocarpa* is a leafless perennial shrub having cylindrical cladodes arranged on randomly orientated stems constituting an open canopy. In contrast S. *tenacissima* is a perennial tussock grass having a dense canopy and leaves that can roll during periods of water stress. Values of leaf boundary layer conductance, taken from a previous study on the same species, obtained by the construction of cylindrical leaf replicas were extrapolated to the canopy.

The results from the current study emphasise the importance of shelter effects influencing wind speed and then boundary layer conductance. The comparison between the two species reflects the interaction between leaves in *Stipa*, sheltering each other, producing a lower boundary layer than for *R. sphaerocarpa*. Our results showed that the extrapolation from a leaf to the whole of the canopy is not simply the addition of leaf boundary layer conductances in dense canopies as *S. tenacissima*. However for *R. sphaerocarpa* the interaction between leaves is not significant and the extrapolation from a leaf to the whole canopy is possible.

RESUMEN

La conductancia aerodinámica a escala de copa en dos especies dominantes del área de Rambla Honda (Almería), *Retama sphaerocarpa* L. Boiss y *Stipa tenacissima* L., ha sido calculada en condiciones naturales a partir de la medida de la evaporación directa de copas saturadas de agua. *R. sphaerocarpa* es un arbusto perenne de copa abierta, con cladodios cilíndricos localizados en tallos que se distribuyen de forma aleatoria. *S. tenacissima* es una gramínea perenne de densa copa, con hojas que se enrollan sobre sí mismas en los periodos de estrés hídrico. La conductancia aerodinámica a escala foliar fue calculada a partir de réplicas foliares artificiales y extrapolada posteriormente al conjunto de la copa.

Los resultados de este estudio permiten incidir en la relevancia del efecto barrera entre las hojas de la copa, el cual ejerce una influencia significativa sobre la velocidad del viento y, en consecuencia sobre la conductancia aerodinámica. La comparación de los dos especies refleja una mayor interferencia entre las hojas de *Stipa*, produciendo una menor conductancia aerodinámica que en *Retama*. La comparación de los dos métodos de estima de conductancia aerodinámica a nivel de copa muestran que ésta no es simplemente la suma de las conductancias aerodinámicas foliares individuales en *Stipa*. Sin embargo en *Retama*, la interacción entre cladodios no es significativa y por tanto, esta extrapolación puede considerarse una aproximación válida.

Key words. Artificial replicas, boundary layer conductance, *Retama sphaerocarpa*, scaling- up, semi-arid Spain, *Stipa tenacissima*.

Palabras clave. Réplicas artificiales, conductancia aerodinámica, *Retama sphaerocarpa*, escalado, semiárido español, *Stipa tenacissima*.

INTRODUCTION

Estimations of boundary layer conductance at the scale of the individual leaf, using measurements of heat or water flux from leaves or replica leaves, have been made by many workers (Landsberg and Ludlow, 1970; Grace, Fasehun and Dixon, 1980; Leuning and Foster, 1990; Brenner and Jarvis, 1995, Domingo *et al.*, 1996). However the complexity of scaling this information to a canopy level depends upon the interactions between leaves in the canopy, and canopies in a stand and will depend on the extent to which plant elements interact with themselves and the atmosphere (Jarvis and McNaughton, 1986; McNaughton and Jarvis, 1991).

Heterogeneity of boundary layer conductance within the canopy has been investigated using heated leaf replicas to measure leaf conductance in various locations inside and outside the canopy (Grace, Fasehun and Dixon 1980). A steady state method for calculation of boundary layer conductance from heated leaf replicas was developed for continuous use by Leuning and Foster (1990) and Brenner and Jarvis (1995).

The main objective of the current study was to experimentally determine rules for scaling-up measure-

[1] Estación Experimental de Zonas Aridas (C.S.I.C.), Almería 04001, Spain.
[2] Departamento de Ecología, Universidad de Alicante, Alicante, Spain
[3] Department of Pure and Applied Biology, University of Leeds, Leeds LS2 9JT, UK.
Current address:
School of Natural Resources and Environment, The University of Michigan
Ann Abor, MI 48109-115, USA
[4] Institute of Ecology and Resource Management,
University of Edinburgh, Edinburgh EH9 3JG, UK
(*) Corresponding author.

ments of leaf boundary layer conductance to the level of a canopy for plants of contrasting growth forms. The study was focused on *Retama sphaerocarpa,* a woody perennial with an open canopy, and *Stipa tenacisssima*, a perennial tussock grass with a dense canopy. These species were chosen for their contrasting canopy characteristics and constitute two of the three main perennial species found in the Rambla Honda, Almería Province, south-east Spain (Fig. 1). A previous work on the same species (Domingo *et al.*, 1996) presented data collected in the field describing the transfer of heat and mass from *S. tenacissima* tussocks and *R. sphaerocapra* bushes using leaf replicas. The study found very different relationships between leaf boundary layer conductance and wind speed for the two species studied. These differences were related to differences in leaf shape and canopy structure. The present study tried to investigate how information gained at the leaf level can be combined to give realistic estimates of canopy level conductances. Therefore, the results presented in Domingo *et al.* (1996), at the level of leaf, are here compared with estimates of whole canopy boundary layer conductance by measuring the evaporation of water from wet canopies (Teklehaimanot and Jarvis, 1991).

MATERIALS AND METHODS

Measurements of leaf boundary layer conductance by energy balance of heated leaf replicas

Cylindrical leaf replicas were constructed and placed within the canopies of *R. sphaerocarpa*, and *S. tenacissima* (Domingo *et al.*, 1996), semi-arid species found in the Rambla Honda (Almería, south-eastern Spain, 37° 8'N, 2° 22'W, 630 m altitude) (Fig. 1). *R. sphaerocarpa* is a leafless leguminous shrub, up to 4 m tall, with cylindrical evergreen stems (cladodes). It has a deep root system which can penetrate to depths of > 25 m (Haase *et al.* 1995), giving access to deep, moist soil layers. *Stipa tenacissima* is a tall tussock grass, up to 1.5 m tall, with long narrow cylindrical evergreen leaves. The basic units of the tussock structure are the stems which are formed by a succession of rigid internodes and more plastic nodes. Each node supports one leaf. Sanchez and Puigdefábregas (1994) have observed that leaves are produced from autumn until late spring and that in general do not survive the next summer. After drying the leaves bend down to the soil and may persist for years tied together forming a rigid mat.

The boundary layer conductance of the leaf can be calculated based on a simple energy balance approach (Leuning and Foster, 1990; Monteith and Unsworth, 1990; van Gardingen and Grace, 1991; Brenner and Jarvis, 1995, Domingo *et al.*, 1996). Transfer characteristics of individual leaf replicas were measured and evaluated in controlled conditions for a range of wind speeds in a wind tunnel at The University of Edinburgh (Domingo *et al.*, 1996).

Pairs of replicas were attached to a square metal frame (400 mm x 400 mm) with nylon fishing line (diameter = 0.3 mm). A reference set of replicas was always mounted outside the canopies at the same height than the

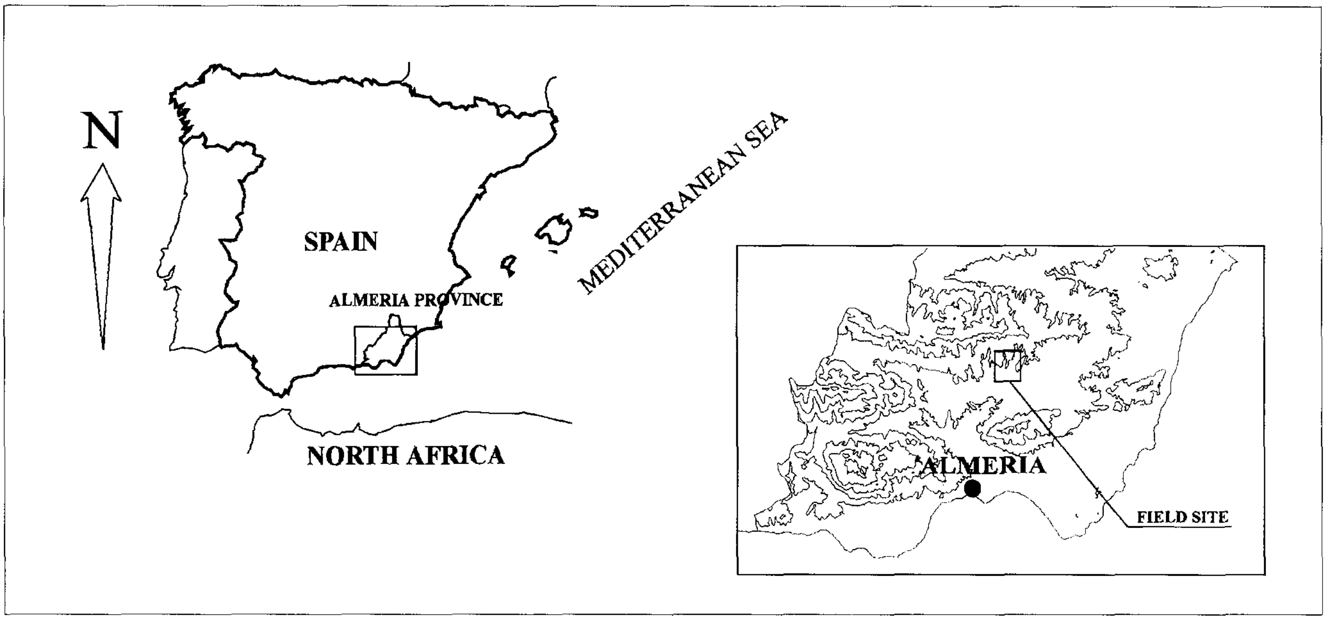

Figure 1.Location of the study area.

others at least 1 m away from the edge of the canopy. For the *R. sphaerocarpa* bushes pairs of replicas were positioned on vertical and horizontal transects through the canopy. For the *S. tenacissima* canopies, replicas were placed at three different heights, and positioned in the canopy at green or live part (two heights) and in standing dead/litterfall part. For a detailed description of the construction and operation of the leaf replicas see Domingo *et al.* (1996).

Cup anemometers (A100G, Vector Instrument, Rhyl, UK; starting speed 0.2 m s^{-1}) recorded horizontal wind speed *(u)* close to the replicas, at the height of the middle of the canopy, 1.25 m for *R. sphaerocarpa* and 0.6 m for *S. tenacissima.* Horizontal turbulence intensity was measured inside and outside canopies with four heated bead anemometers (AVM501, Prosser Scientific Instruments Ltd, Ipswich, UK) that had previously been calibrated against a pitot tube anemometer in a wind tunnel. The positions of the heated beads corresponded to those of the pairs of replicas. Turbulence intensity was calculated as $\frac{\sigma_u}{u}$ Measurements were recorded by a CR10 datalogger.

Measurements of canopy boundary layer conductance by evaporation from wet canopy

Whole canopy boundary layer conductance was calculated by measuring the drying rate of wetted canopies suspended from a load cell (Teklehaimanot and Jarvis, 1991). Tussocks of *S. tenacissima* and bushes of *R. sphaerocarpa* were cut at ground level, suspended from a load cell (25 kg, RS components Ltd., U.K.) connected to a data-logger (CR10). Mass of the plant was measured at a frecuency of 0.125 seconds and the average calculated every 10 seconds. Plants were wetted using a hand-held sprayer, until the increase in mass of the plant stopped and remained constant for several seconds. The change of mass of the plant was recorded as the plant dried out. Times when wetting of plant started and stopped, and when the rate of dripping became negligible and stopped were noted.

Simultaneous measurements of air temperature, vapour pressure (ventilated psychrometer, Allen *et al.*, 1994) windspeed (A100G), and surface temperature of canopy (0.3 mm copper-constantan thermocouples, type T, Omega Engineering, Leicestershire, UK) (4 on the inner leaves and 4 on the outer leaves).

The canopy boundary layer conductance was calculated from:

$$g_c = PE / [M\rho_a(e_l^* - e_a)] \qquad (7)$$

where g_c is canopy boundary layer conductance, P is atmospheric pressure, M is the ratio of molecular weights of water and air (=0.622), E is the rate of evaporation from the wet crown, r_a is density of air, e^*_l is the saturated vapour pressure at the temperature of the surface of the canopy and ea is vapour pressure of the air.

RESULTS

The relationship $g_a = au^b$ was fitted to field data using non-linear regression analysis from the package Sigmaplot for Windows (Kuo and Fox, 1993). Measured values for leaf boundary layer conductance obtained in canopies of *R. sphaerocarpa* and *S. tenacissima* are presented in Table 1 (extracted from Domingo *et al.* (1996). Replicas placed in the canopy of *R. sphaerocarpa* suggest that there was no significant effect of horizontal position within canopy on the boundary layer conductance of an individual leaf replica. Data for the vertical transect appear to show leaf boundary layer conductance increasing with height for a given wind speed. These results seem inconsistent with those obtained with the horizontal transect, but they reflect the expected pattern of increasing wind speed with height (Grace, 1983). The apparent differences in conductance between replica positions would be expected to be smaller if data had been available for wind speed for the vertical transect at the heights of the replicas.

	a	b	R^2
Open field	0.89±0.001*	0.49±0.017	0.55
***R. sphaerocarpa* canopy**	**a**	**b**	**R^2**
Top	0.103±0.001*	0.51±0.02	0.56
Centre	0.095±0.001*	0.52±0.02	0.54
Edge	0.093±0.002*	0.54±0.04	0.58
Bottom	0.076±0.001*	0.52±0.02*	0.66
***S. tenacissima* canopy**	**a**	**b**	**R^2**
Green foliage	0.061±0.008	0.45±0.02	0.75
Between bushes	0.069±0.001	0.32±0.03*	0.51
Dead foliage	0.052±0.001*	0.32±0.03*	0.46

Table 1. Values of the parameters *a* and *b* for the relationship $g_a=au^b$ obtained in different locations in the canopies of *R. Sphaerocarpa* and *S. tenacissima* and in open field (table extracted from Domingo *et al.*, 1996). Curves were fitted to field data using non linear regression. Figures of *a* and *b* marked (*) are significantly different ($p < 0.05$) from the coefficients of engineering equation ($a = 0.068$, $b = 0.47$). The reported values for the parameters are those obtained from the regression ± standard error.

The results obtained for the *S. tenacissima* contrast with those obtained for *R. sphaerocarpa* in that a significant effect is observed of canopy position on leaf boundary layer conductance (Table 1). The measured leaf boundary layer conductance was lower for all positions in the canopy when compared to values obtained in the open field. For any wind speed the highest boundary layer conductance was observed in the open field and lowest in dead foliage and litter (Domingo *et al.*, 1996).

The canopy of *R. sphaerocarpa* did not significantly influence the velocity or turbulence of the air flow impinging on individual cladodes within the canopy. In contrast the canopy of *S. tenacissima* seemed to reduce the mean velocity. Wind speeds measured outside and inside the *R. sphaerocarpa* and *S. tenacissima* canopies by heated bead anemometers (Fig.2) indicate that wind speed is much lower inside the *S. tenacissima* canopy than in open field and than in the *R. sphaerocarpa* canopy, for a given wind speed. Results also showed that the turbulence intensity measured inside the *S. tenacissima* (Fig. 3 and 4) is similar to that measured in open field. Therefore, measurements from the heated bead anemometer confirmed that the dense canopy of *S. tenacissima* was creating shelter and reduced mean wind speed at the location of the leaf replicas (Fig. 2). The importance of shelter in modifying the observed relationship leaf between boundary layer conductance and wind speed was previously suggested by Dixon and Grace (1984) based on results from a wind tun-

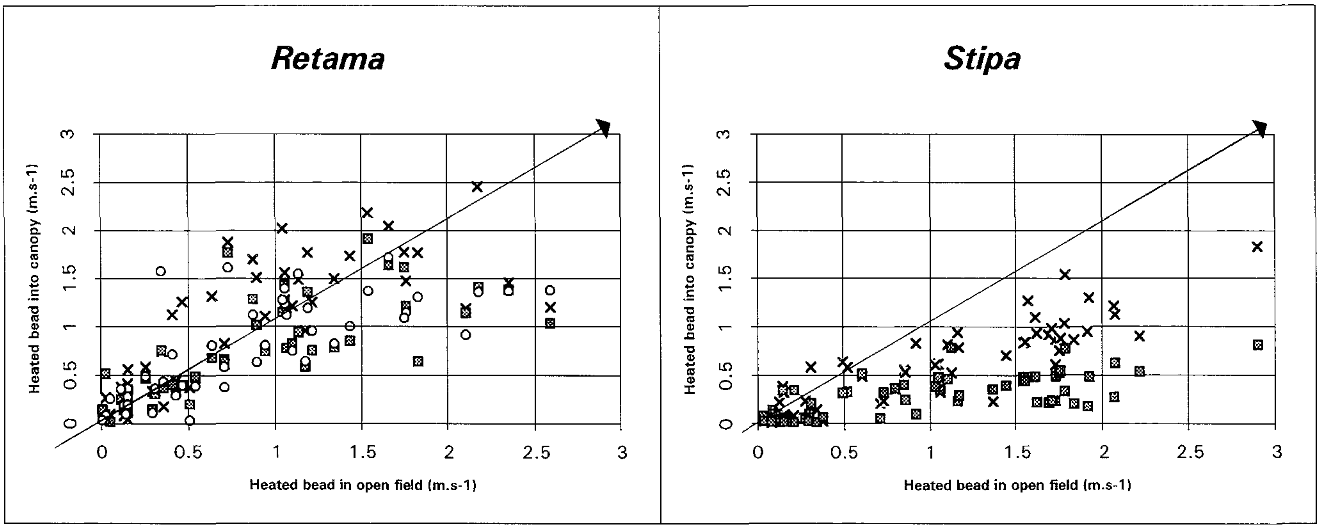

Figure 2. Figures comparing wind speeds measured outside and inside the canopies measured by heated bead anemometers for the two species. In the figure for *R. sphaercarpa*, the symbol X is for the heated bead positioned at the 'edge' of the canopy,□ at the 'middle' and ◎ at the other 'edge' of the canopy in the horizontal transect. In the figure for *S. tenacissima*, the symbol X is for the heated bead positioned at the 'live ' part and at the 'dead' (densest) part.

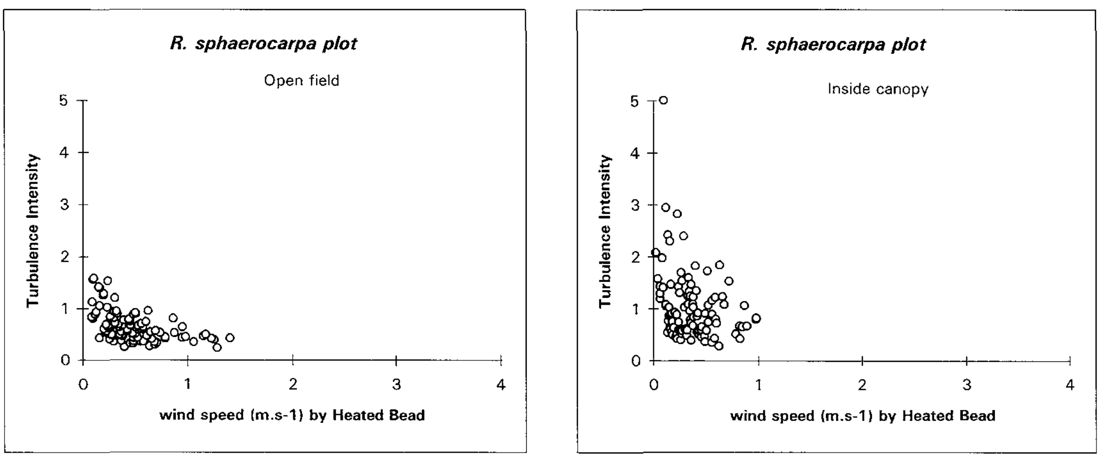

Figure 3 Figures showing turbulence intensity in open field and inside the canopies vs wind speed measured inside the canopies by the heated bead anemometers for *R. sphaerocarpa*.

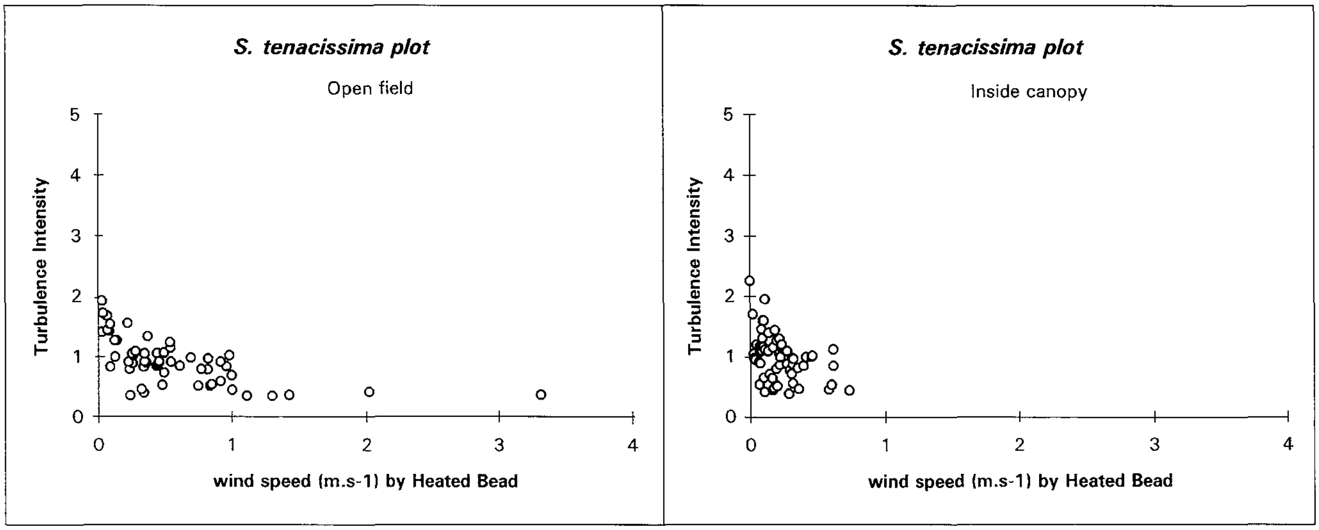

Figure 4 Figures showing turbulence intensity in open field and inside the canopies vs wind speed measured inside the canopies by the heated bead anemometers for *S. tenacissima*.

nel study. The current field based observations serve to reiterate their point.

Assuming conductances in parallel, the boundary layer conductance for the whole canopy (g_c) will be the addition from the individual leaf boundary layer conductances (g_a) measured by leaf replicas. Therefore

$$g_c = \Sigma 3.1416 L g_a$$

where L is the leaf area index, and g_a is obtained averaging the parameters a and b of the relationship between leaf boundary layer conductance and wind speed from all the positions and configurations of the replicas into the canopy and individual plants studied by Domingo *et al.* (1996) (see Table 1). In the case of *R. sphaerocarpa* the parameters were a= 0.094 and b= 0.53 (considering just the horizontal transect) and for *S. tenacissima* a= 0.060 and b= 0.363. For L, planar leaf area index, were used the values of 0.7 and 4 for *R. sphaerocarpa* and *S. tenacissima* respectively. The values of L corresponded to the average leaf area index of plants used for applying the Teklehimanot and Jarvis (1991) method of measuring canopy boundary layer conductance. Values of L were multiplied by 3.1416 to transform projected leaf area to total leaf surface area index, assuming that the cladodes were cylindrical.

This way of adding leaf boundary layer conductances is probably not correct since the real g_a is more like the sum of the g_a of different layers, i.e.

$$g_c = \Sigma 3.1416 L_i g_{ai}$$

i = 1 to i = n, where n is the number of layers, L_i and g_{ai} are the leaf area index and boundary layer respectively of the layer i. Because of the lack of information on verticalstructure of these studied species, it was assumed that every layer was uniform.

Figure 5 presents relationships between boundary layer per plant and wind speed obtained by the two methods, i.e. adding leaf conductances measured by leaf replicas and evaporation from wet canopy (Teklehimanot and Jarvis, 1991). For instance for a wind speed of 2 $m.s^{-1}$, the second method gives a canopy bondary layer of 0.17 $m.s^{-1}$ for *R. sphaerocarpa* and 0.08 $m.s^{-1}$ for *S. tenacissima*. Calculating g_a for the same wind speed from the relationships between g_a and wind speed obtained with the leaf replicas, the average figures are 0.20 $m.s^{-1}$ and 0.83 $m.s^{-1}$ for *R. sphaerocarpa* and *S. tenacissima* respectively. Therefore the values of g_a from the method of Teklehaimanot and Jarvis (1991) are more similar to those calculated from the leaf replicas in the case of *R. sphaerocarpa*, but quite differents for the case of *S. tenacissima* (about 950% lower).

DISCUSSION AND CONCLUSIONS

The observed results for field measurement of boundary layer conductance can be explained in terms of the structure of canopies of *R.. sphaerocarpa* and *S. tenacissima*. Plants of *R. sphaerocarpa* have an open canopy allowing a better penetration of the wind and creating less shelter for leaves. The canopy of *R. sphaerocarpa* does not significantly influence the velocity or turbulence of the air flow impinging on individual cladodes within the canopy (Fig. 3 and 4). In contrast the canopy of *S. tenacissima* reduces the mean velocity (Fig. 3 and 4). There is indirect

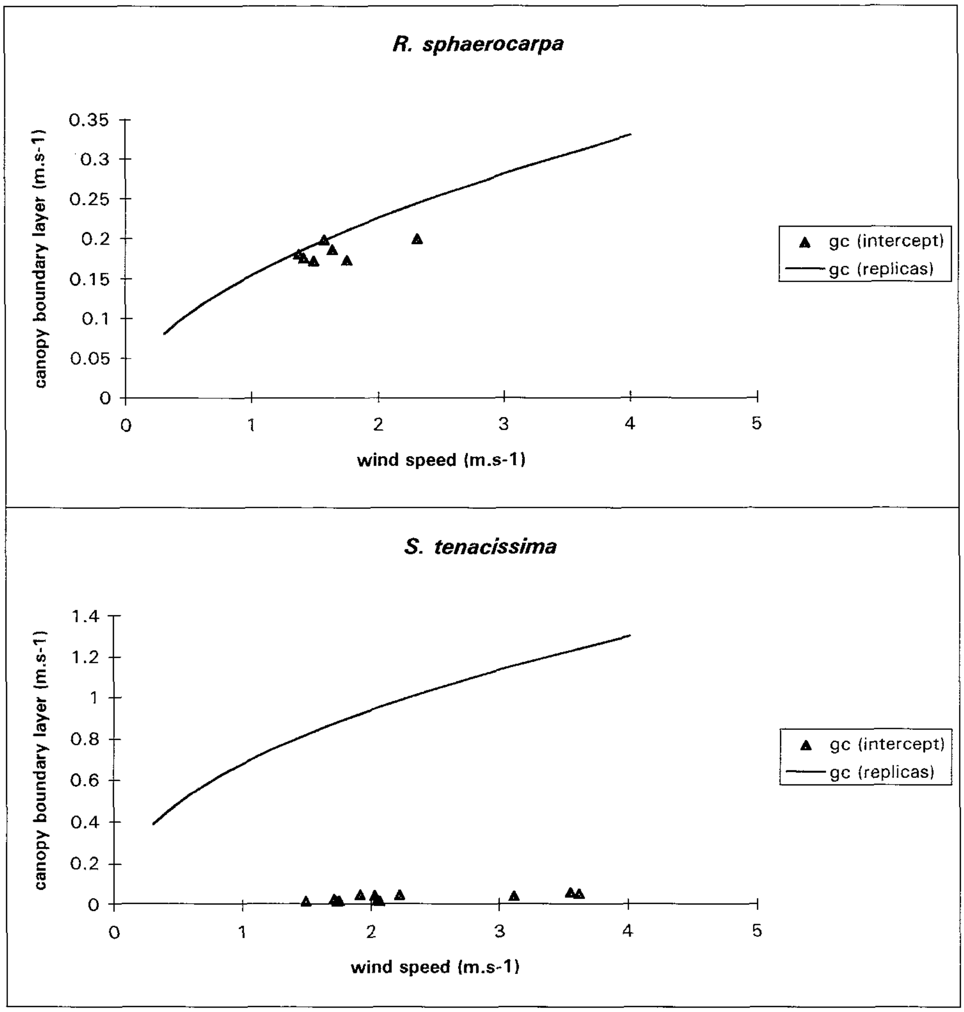

Figure 5. Relationship between canopy boundary layer conductance and wind speed for the two methods used for scaling up from leaf to whole canopy: energy balance of heated leaf replicas (g_c.replicas), and evaporation of water from wet canopy (Teklehimanot and Jarvis, 1991) (g_c.intercept).

evidence that turbulence intensity within canopies of *S. tenacissima* is not affected, since the values of the parameter *b* decrease (Domingo *et al.*, 1996). These would be expected to increase with increased turbulence.

Differences found between these species can be explained by their structural differences. *S. tenacissima* has a relatively dense canopy near the ground with a large accumulation of litter. The total biomass area index of *S. tenacissima* is higher compared with *R. sphaerocarpa.* The dense accumulation of dead foliage or litter under canopies of *S. tenacissima* may further increase the effective leaf area index for shelter and be up to six times higher (Puigdefábregas *et al.,* 1995) than the green area index. The velocity of the incident air flow is then reduced more effectively inside canopies of *S. tenacissima* than in canopies of *R. sphaerocarpa.*

The results from the current study emphasise the importance of shelter effects influencing wind speed and then boundary layer conductance. The comparison of the two methods of estimating canopy boundary layer conductance reflects the interaction between leaves in *Stipa,* sheltering each other, producing a lower boundary layer than for *R. sphaerocarpa*. The extrapolation from a leaf to the whole of the canopy is not simply the addition of leaf boundary layer conductances in dense canopies as *S. tenacissima.* However for *R. sphaerocarpa* the interaction between leaves is not significant and the extrapolation from a leaf to the whole canopy is possible.

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