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Gas Exchange Characteristics of *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (Tagasaste) Measured in Spring-Summer under Field Conditions

By

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With 5 figures

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Summary

González-Rodríguez A. M., Martín-Olivera A., Morales D. & Jiménez M. S. 2002. Gas exchange characteristics of *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (tagasaste) measured in spring-summer under field conditions. – Phyton (Horn, Austria) 42 (2): 225–236, with 5 figures. – English with German summary.

Carbon assimilation rate (A), stomatal behaviour and transpiration (E) of *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (tagasaste) were studied in spring-summer in natural conditions in the North-West slope of Tenerife. Daily courses of this species did not show midday depression of A. A_{max} measured in tagasaste (10 µmol m^{-2} s^{-1}) is in the limits given to tropical rain forest trees and trees of broadleaved evergreens of the subtropics and warm-temperate regions. Stomatal closure was shown under conditions of high air vapour pressure deficit (VPD) and leaf temperature, showing a relatively good stomatal control, better than other tree species of the Canarian laurel forest. Instantaneous water use efficiency decreased with higher evaporative demand, in contrast to intrinsic water use efficiency (A/g_s) that did not change significantly under different environmental conditions. In both

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cases these parameters were higher than those found in trees of the Canarian laurel forest, an ecosystem with similar distribution area to that of tagasaste. These characteristics together with a better stomatal control could make this species able to live outside of its natural distribution area and enable its use for revegetation in semiarid zones.

Zusammenfassung

González-Rodríguez A. M., Martín-Olivera A., Morales D. & Jiménez M. S. 2002. Die Gaswechseleigenschaften von *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (Tagasaste) im Frühling und im Sommer unter Freilandbedingungen. – Phyton (Horn, Austria) 42 (2): 225–236, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Kohlenstoffassimilationsrate (A), das Spaltöffnungsverhalten und die Transpiration (E) von *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (Tagasaste) wurde im Frühling und Sommer unter Freilandbedingungen am Nortwestabfall von Teneriffa untersucht. Der Tagesgang wies keine mittägliche Depression von *A* auf. Die bei Tagasaste gemessene A_{max} (10 μmol m^{-2} s^{-1}) liegt im Bereich der Bäume tropischer Regenwälder und immergrüner Laubbäume der Subtropen sowie warm temperierter Gebiete. Spaltöffnungsschluss konnte unter Bedingungen hoher Dampfdruckdefizite (VPD) und Blatttemperaturen festgestellt werden, was auf eine relativ gute stomatäre Kontrolle weist, welche viel besser ist als bei anderen Arten des kanarischen Lorbeerwaldes. Die momentane „water use efficiency" sank mit größer werdender Beanspruchung der Wasserabgabe, was im Gegensatz zur wirklichen „water use efficiency" (A/g_s) steht, welche sich nicht signifikant unter den verschiedenen Umweltbedingungen verändert. In beiden Fällen waren diese Parameter größer als bei den anderen Bäumen des kanarischen Lorbeerwaldes, einem Ökosystem mit ähnlicher Verbreitung wie von Tagasaste. Diese Eigenschaften, gemeinsam mit einer besseren Spaltöffnungskontrolle, könnten diese Art befähigen, auch außerhalb ihres natürlichen Verbreitungsgebiets vorzukommen und würde sie zur Wiederbepflanzung semiarider Zonen eignen.

Introduction

Tagasaste (*Chamaecytisus proliferus* (L. fil.) Link ssp. *proliferus* var. *palmensis* (Christ)) is a perennial leguminous shrub endemic of the Canary Islands (Acebes Ginovés & al. 1991, Francisco-Ortega & al. 1993) where it has been traditionally used as fodder for local herds. It was introduced in Australia and New Zealand in the XIX century (Francisco-Ortega & al. 1991), and its cultivation has been greatly extended to feed livestock not only in these countries where it has gained economic importance, but also in others, such as Chile and Ethiopia (Kaitho & al. 1997, Arredondo & al. 1998, Assefa 1998). Most studies have been conducted about its biomass yield and quality (Arredondo & al. 1998, Assefa 1998), nutritive value and palatability (Borens & Poppi 1990, Méndez 1993, Tolera & al. 1997), however little is known about its physiological response under environmental conditions. Recent studies have been carried out on water use efficiency and water balance of tagasaste in south-western Australia (LEFROY & al. 2001a, b) although nothing is known about its gas exchange characteristics under native field conditions.

In the Canary Islands, tagasaste is mainly present from 300/400 to 1300/1400 m of altitude in gaps and boundary zones of forests in N and NE slopes of the islands (PÉREZ DE PAZ & al. 1986) in a humid Mediterranean climate. Since many legume shrubs, because their ability for fixing nitrogen, are able to grow in low quality soils (VAN ANDEL & al. 1993) and have been used for revegetation of abandoned, altered or drought fields, tagasaste could be used for this purpose. This work is a preliminary study to know the behaviour of tagasaste in its native environment by evaluating photosynthetic and transpiration rates, and stomatal conductance. This will give insight to the general knowledge of the behaviour of this species in its native environment and also will constitute the basis for a possible use of this forage plant outside of its natural distribution area, not only in the Canary Island but also in other Mediterranean countries where more arid conditions occur.

Material and Methods

The study was conducted in adult plants of *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* (tagasaste) from March to August of 2000 in Tenerife, Canary Islands. The experimental site is situated at an altitude of 950 m, facing NO and has a humid Mediterranean climate with a mean annual temperature between 10–13 °C.

Carbon assimilation rate, measured as CO_2 uptake (A), stomatal conductance (g_s) and transpiration rate, measured as water vapour efflux (E) were determined on attached apical non-woody shoots with a portable Infrared Gas Analyser (LCA2, Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.) every hour from the early morning to the evening.

Gas exchange rates were calculated using equations developed by VON CAEMMERER & FARQUHAR 1981. Leaf temperature (T_{leaf}) was determined from air temperature and calculated energy fluxes (PARKINSON 1985).

Approximately 10 diurnal courses were measured from March to August 2000 on six attached apical non-woody shoots in different plants.

In the global analysis we included all data obtained during all measured days. Applying boundary lines to the resulting data clouds we obtained approximations of optimal ranges of gas exchange variation with environmental and physiological factors. This kind of results are very common in field measurements and has been evaluated in the same way by other authors (MASAROVICOVA & ELIAS 1986, CHEESEMAN & al. 1991, LARCHER 1995, CHEESEMAN & LEXA 1996).

Results

Figure 1 shows the diurnal courses of gas exchange during two sunny days with contrasting environmental conditions. On 25 April, a cloudless day, with a vapour pressure deficit (VPD) low (<0.58 kPa) and T_{leaf} below

26 °C, A_{max} reached 8.4 μmol m^{-2} s^{-1} and high values of g_s were recorded (150 mmol m^{-2} s^{-1}). No values of g_s below 130 mmol m^{-2} s^{-1} were recorded. In contrast, during the weather conditions of 31 July, when VPD was high (mean value >2kPa) reaching maximum values of 5 kPa and T_{leaf} reached 39 °C, A_{max} was only 5 μmol m^{-2} s^{-1}, because it was limited by low g_s (80 mmol m^{-2} s^{-1}). On both days, *A* paralleled diurnal pattern of PPFD.

On the day with low VPD and T_{leaf} (25 April), *E* reached maximum mean values below 3 mmol $m^{-2}s^{-1}$. This value increased to 4 mmol $m^{-2}s^{-1}$ under high VPD and T_{leaf} conditions on 31 July.

As a result of the increase of VPD, a decrease in instantaneous water use efficiency (WUE) was shown, varying from 3.2 μmol $mmol^{-1}$ on 25 April to 1.3 μmol $mmol^{-1}$ on 31 July. Intrinsic water use efficiency (A/g_s) did not change significantly, remaining around 60 μmol $mmol^{-1}$ (Fig. 1).

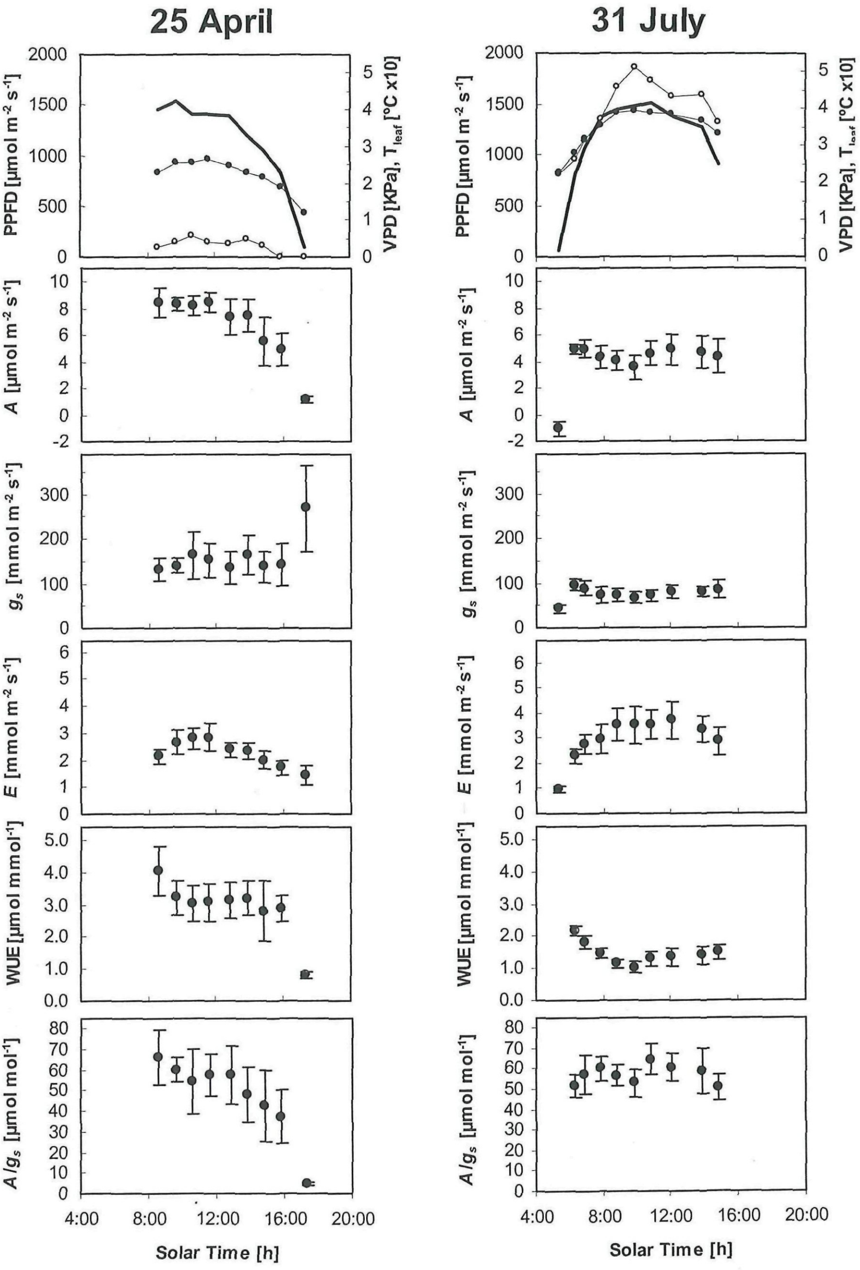
In order to analyse the total data we used boundary-line analysis using all data of each parameter plotted against every variable, to estimate the maximal parameter values when other variables were not limiting. The relationship between *A* and T_{leaf} indicated that the optimum temperature was 22 °C. On the basis of measurements of CO_2 gas exchange, a 90% of the photosynthetic rate at optimum temperature were obtained between 17.5 and 28 °C and a reduction of 50% of *A* was reached at temperature below 12 °C and above 40 °C (Fig. 2).

Response of *A* to PPFD yielded an A_{max} of 10 μmol m^{-2} s^{-1} and indicated that *A* reached light saturation above 700 μmol m^{-2} s^{-1}. The plot of *A* versus g_s did not pass through the origin because the stomata were partly open when *A* was zero. Values of g_s above 150 mmol m^{-2} s^{-1} were considered to be non-limiting (Fig. 3).

Response of *A* to VPD followed a characteristic tendency in which higher VPD values led to lower *A* values. The curve showed optimal photosynthetic values until VPD values of 0.6 kPa and a progressive decrease of *A* at higher VPD values. This species maintained 50% of its A_{max} until 5 kPa of VPD (Fig. 3).

Relationships between g_s and PPFD and VPD are shown in figure 4. Values of g_s above 200 mmol m^{-2} s^{-1} were exhibited at low PPFD (34 μmol m^{-2} s^{-1}) and g_s began to decrease at 0.5 kPa and was less than 50% of maximum above 1.5 kPa.

Fig. 1. Diurnal courses of photosynthetic photon flux density (PPFD) at leaf surface, leaf temperature (T_{leaf}), air vapour pressure deficit (VPD), carbon assimilation rate (*A*), transpiration (*E*), stomatal conductance (g_s), instantaneous water use efficiency (WUE= A/E) and intrinsic water use efficiency (A/g_s) of *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis* measured on 25 April (a day with low VPD) and on 31 July (a day with high VPD). Each point represents the mean of six measurements with their standard deviations. Upper graphics show PPFD (solid line), VPD (○) and T_{leaf} (●).


25 April
31 July
PPFD [µmol m-2 s-1]
VPD [KPa], Tleaf [°C x10]
A [µmol m-2 s-1]
gs [mmol m-2 s-1]
E [mmol m-2 s-1]
WUE [µmol mmol-1]
A/gs [µmol mol-1]
4:00
8:00
12:00
16:00
20:00
Solar Time [h]

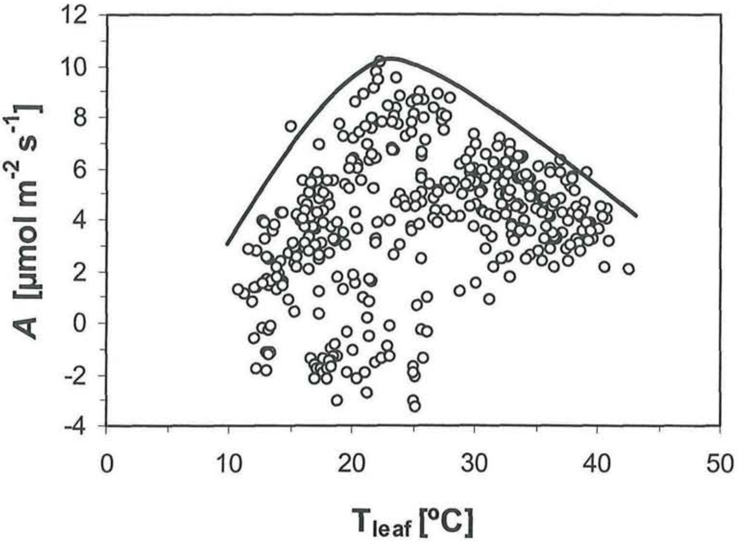


Fig. 2. Relationships between carbon assimilation rate (A) and leaf temperature (T_{leaf}), in *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis*. Each point is an individual measurement.

Maximum values of E (5 mmol m^{-2} s^{-1}) were reached at 3 kPa of VPD and A_{max} (optimum T_{leaf} 22 °C) was reached at values of E close to 3.5 mmol m^{-2} s^{-1} (Fig. 5).

Discussion

Daily courses of gas exchange were different depending on environmental conditions. On days with low VPD, A, E and g_s were mainly controlled by PPFD; however, on days in which the VPD was high, A was lower because g_s was also lower throughout the whole day. Midday depression of A has been reported for temperate-zone plants (HODGES 1967, DOUGHERTY & HINCKLEY 1981), Mediterranean climate plants (TENHUNEN & al. 1981, PEREIRA & al. 1986) and tropical trees (MEDINA & al. 1978, ZOTZ & al. 1995, PATHRE & al. 1998, ISHIDA & al. 1999), however, we did not find midday depression of A in all studied days.

The increase of VPD to 5 kPa produced a reduction in A about 50%, mainly due to low g_s. Despite stomatal closure, E increased, producing a

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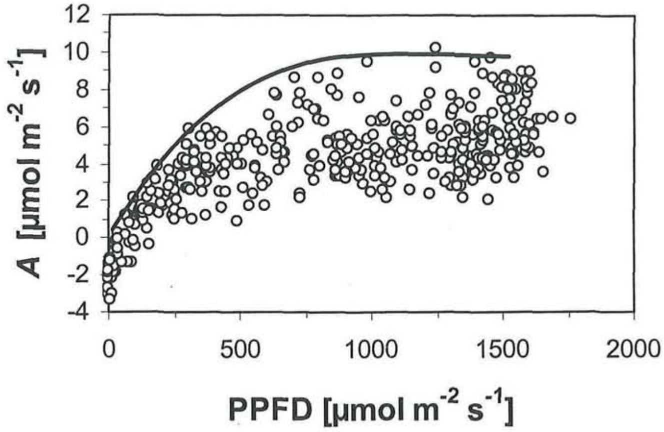
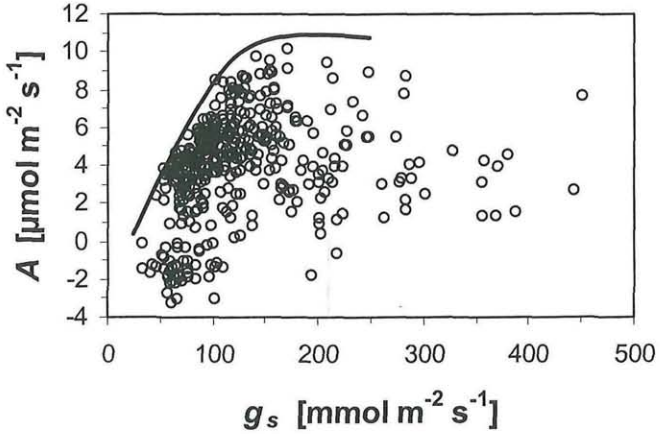
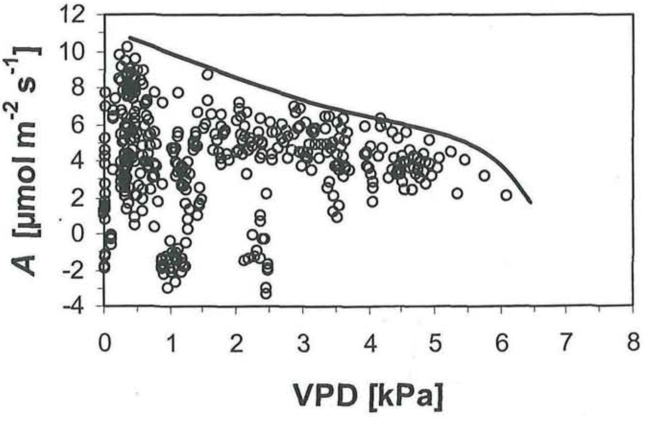
Fig. 3. Relationships between carbon assimilation rate (A) and photosynthetic photon flux density (PPFD) at the leaf surface, water vapour stomatal conductance (g_s) and air vapour pressure deficit (VPD) in *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis*. Each point is an individual measurement.


12
10
8
6
4
2
0
-2
-4
A [µmol m-2 s-1]
0
500
1000
1500
2000
PPFD [µmol m-2 s-1]


12
10
8
6
4
2
0
-2
-4
A [µmol m-2 s-1]
0
100
200
300
400
500
gs [mmol m-2 s-1]


12
10
8
6
4
2
0
-2
-4
A [µmol m-2 s-1]
0
1
2
3
4
5
6
7
8
VPD [kPa]

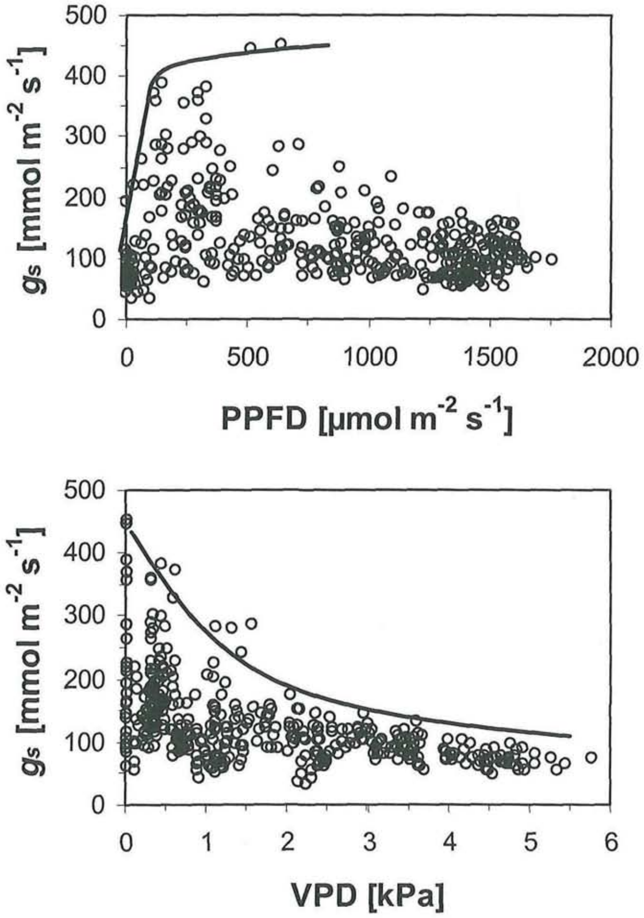


Fig. 4. Relationships between water vapour stomatal conductance (g_s) and photosynthetic photon flux density (PPFD) at the leaf surface, and air vapour pressure deficit (VPD) in *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis*. Each point is an individual measurement.

decrease in WUE. However, the values of WUE obtained were higher than those found in the Canarian laurel forest trees (GONZÁLEZ-RODRÍGUEZ & al. 2001, 2002). In the same way, values of A/g_s were also higher than in Canarian laurel forest trees (GONZÁLEZ-RODRÍGUEZ & al. 2001, 2002). A significant increase of this ratio during the summer has been shown in some Mediterranean shrubs and trees (PEÑUELAS & al. 1998, FLEXAS & al. 2001), optimising their photosynthetic rate under drought conditions, nevertheless this parameter did not change significantly under different environmental conditions in tagasaste.

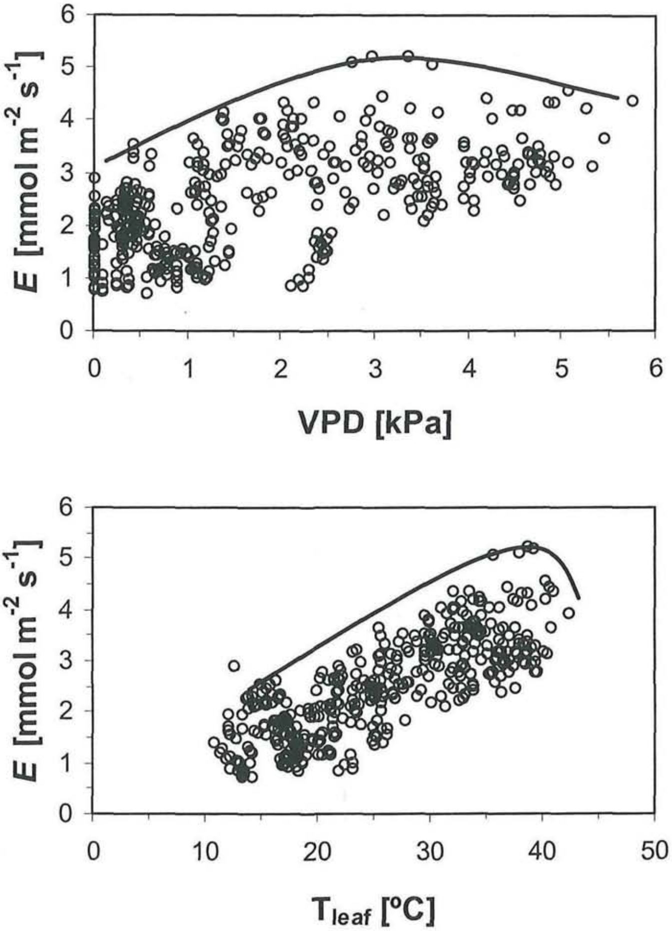


Fig. 5. Relationships between transpiration rate (E) and leaf temperature (T_{leaf}), and air vapour pressure deficit (VPD) in *Chamaecytisus proliferus* subsp. *proliferus* var. *palmensis*. Each point is an individual measurement.

Leaf photosynthesis in trees is variable since its maximum value under natural conditions ranges from roughly 3 to 30 μmol m^{-2} s^{-1} (CEULEMANS & SAUGIER 1991). Generally, photosynthetic rates of tropical rain forest trees are relatively higher (between 10-16 μmol m^{-2} s^{-1}) than trees of broadleaved evergreens of the subtropics and warm-temperate regions (between 6-12 μmol m^{-2} s^{-1}) (LARCHER 1995). The maximum value of A measured in tagasaste (10 μmol m^{-2} s^{-1}) is in the limits of both ranges.

A_{max} is reached with values of PPFD above 700 μmol m^{-2} s^{-1}, this value is in the range given by sun leaves of tropical forest trees and non-tropical evergreen broadleaved trees (LARCHER 1995). Temperature optimum of A (22 °C) is similar to those found to evergreen broadleaved trees of the tropics and subtropics.

Stomatal conductance was sensitive to increasing VPD over the range 0 to 5 kPa, decreasing exponentially to values below 100 mmol m^{-2} s^{-1}. Maximum values of g_s in tagasaste were relatively high compared with Mediterranean evergreen shrubs (KÖRNER 1995) and lower than in Canarian laurel forest trees (GONZÁLEZ-RODRÍGUEZ & al. 2001, 2002).

All these characteristics fit well with the environment where this shrub lives: in a subtropical region but with humid Mediterranean climate in the limits of the laurel forest distribution area. The WUE and A/g_s values higher than Canarian laurel forest trees and the better stomatal control as a response to the increase of VPD could make this species able to live outside of its natural distribution area, although more studies focused on drought responses of this shrub are needed before its use in semiarid zones for revegetation.

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