Phyton (Horn, Austria)	**Vol. 42**	Fasc. 2	291–304	20. 12. 2002

Ecophysiological Studies on the Water Relations in a *Pinus canariensis* Stand, Tenerife, Canary Islands

By

G. Wieser*), J. Peters**), V. C. Luis**), D. Morales**)

and M. S. Jimenez**)

With 6 figures

Received April 22, 2002

Accepted May 8, 2002

Key words: Conductance, needle water relations, *Pinus canariensis*, sap flow, soil water relations, transpiration.

Summary

Wieser G., Peters J., Luis V. C., Morales D. & Jimenez M. S. 2002. Ecophysiological studies on the water relations in a *Pinus canariensis* stand, Tenerife, Canary Islands. – Phyton (Horn, Austria) 42 (2): 291–304, with 6 figures. – English with German summary.

Diurnal courses of sap flow density, changes in stem radius, needle level transpiration, and needle water potential were measured in 50-year old *Pinus canariensis* trees at a forest stand in 1650 m a.s.l. in Tenerife, Canary islands, Spain. A direct comparison of sap flow density estimated at the stem base and canopy transpiration measured at the needle level showed only small deviations in their diurnal courses. Needle water potential and stem radius decreased from the onset of canopy transpiration, reached minimum values at noon, when sapflow was highest, and then continuously increased. Within the canopy however, gas exchange was highly variable among differently orientated twigs. Depending on the inclination of the sun a steep microclimatic gradient across the canopy affected apparent transpiration, leaf conductance and needle water potential. However, there were no significant differ-

*) Wieser G., Austrian Federal Office and Research Centre for Forests, Div. Forest Tree Physiology, Rennweg 1, A-6020 Innsbruck, Austria. E-mail: Gerhard.Wieser@uibk.ac.at

**) Peters J., Luis V. C., Morales D. and Jimenez M. S., Departamento de Biologia Vegetal, Universidad de La Laguna, E-38207 La Laguna, Tenerife, Spain.

ences in the amount of water transpired during a day between differently orientated twigs. Thus, our results suggest that sap flow sensors are a suitable tool for estimating canopy transpiration of pine trees in an environment where the crowns are often enveloped by mist or fog, which is typically for pine forests at higher elevations in the western Canary islands.

Zusammenfassung

WIESER G., PETERS J., LUIS V. C., MORALES D. & JIMENEZ M. S. 2002. Ökophysiologische Untersuchungen zum Wasserhaushalt in einem *Pinus canariensis* Bestand auf Teneriffa, Kanarische Inseln. – Phyton (Horn, Österreich) 42 (2): 291–304, 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In einem auf 1650 m Seehöhe gelegenen 50-Jahr alten *Pinus canariensis* Bestand in Teneriffa, Kanarische Inseln, Spanien wurden die tageszeitlichen Verläufe des Stammdurchflusses, der Änderung im Stammradius, der Transpiration und des Nadelwasserpotentials vergleichend gemessen. Dabei ergaben sich keine gravierenden Unterschiede im tageszeitlichen Verlauf des Stammdurchflusses, und der Transpiration im Kronenbereich. Nadelwasserpotential und der Stammradius nahmen mit dem Einsetzten der Transpiration kontinuierlich ab, erreichten zu Mittag minimale Werte und stiegen dann wieder kontinuierlich an. Innerhalb der Baumkrone entwickelte sich in Abhängigkeit vom Sonnenstand ein steiler mikroklimatischer Gradient, der sich auf den tageszeitlichen Verlauf des Nadelwasserhaushaltes auswirkte, nicht jedoch auf die Tagessumme der Transpiration. Unsere Ergebnisse zeigen, dass in Gebieten, wo Baumkronen des öfteren in Nebel gehüllt sind, Stammdurchflussmeßsysteme gut zur Abschätzung der Kronentranspiration geeignet sind.

Introduction

Pinus canariensis Chr. Sm. ex DC in Buch, is an endemic conifer of the Canary Islands a region of volcanic origin. Natural pine forests are usually located in the western Canary Islands where it grows spontaneously from near see level up to about 2200 m in a Mediterranean climate (BRAMWELL & BRAMWELL 1990, DEL ARCO & al. 1992). As a result of high solar irradiance, air, and soil drought pine forests in the Canary islands experience a high evaporative demand. Dryness however, is often mitigated due to the influence of the trade winds coming from North East. These winds bring moisture from the sea and cause a high relative humidity of the air and a certain amount of throughfall due to the interception of small mist droplets (KÄMMER 1974, ABOAL & al. 2000).

Survival during dry periods usually implies that the stomata maximise carbon gain while minimising water loss as shown for evergreen woody Mediterranean species by ABRIL & HANANO 1998. Changes in stomatal aperture occurs as an integrated effect of changes in environmental factors above-ground as well as in soil water availability (KÖRNER 1994, MONTEITH 1995, NONAMI & al. 1990, SCHULZE 1986, TENHUNEN & al. 1994). Although water loss by the plants is regulated by the stomata and driven by the atmospheric demand; transpiration can not exceed the supply rate through the woody tissue (JACKSON & al. 2000).

Beside the water taken up by the roots, water stored within the woody tissue may contribute substantially to transpiration (LASSIOE 1973, WARING & al. 1979), and this may make stems fluctuate in size (KOZLOWSKY & al. 1991, HERZOG & al. 1995). Generally, such observations have been thought to reflect differences in the water status of the stem during the course of the day (HINCKLEY & BRUCKERHOFF 1975, OFFENTHALER & al. 2001). Furthermore, it was shown that diurnal changes in stem diameter were closely related to the kinetics of sap flow (HERZOG & al. 1995, UEDA & SHIBATA 2001).

Therefore, in this study we present (1) the relationship between soil water content and soil matric potential and (2) short-term observations on water transport in the stem and canopy transpiration of *Pinus canariensis* trees in order to explore the potential of sap flow sensors and dendrometers for a long-term monitoring of the water status of *Pinus canariensis* trees.

Material and Methods

Site description: The experiments were part of a year round investigation on the gas exchange of a 50-year old *Pinus canariensis* stand, growing on a north-north-east slope at 1650 m a.s.l. in the Mountains of La Victoria approximately 20 km SW of La Laguna (28°35′N, 27°60′W), Tenerife, Canary Islands (PETERS 2001). The field site is characterised by a Mediterranean climate with an average annual air temperature of 12.6 °C, an average relative humidity of 52% (data source: El Gaitero weather station period 1986–94), and the annual sum of precipitation is 1000 mm (PETERS 2001). During the summer months drought is often mitigated by a high relative humidity of the air and a high frequency of clouds due to the north east trade winds. The measurements were carried out during a warm period in July 2000 (Table 1).

Table 1.
Weather conditions at the experimental site from 7 to 14 July 2000. Measurements were made just 2 m above the canopy.

	Mean	Maximum	Minimum
Irradiance [W m^{-2}]	362	1110	0
Air temperature [°C]	19.9	28.6	8.2
Water vapour pressure deficit [hPa]	18.8	35.7	0
Wind velocity [m s^{-1}]	1.3	6.9	0
Precipitation [mm d^{-1}]*	0.3	1.0	0

* throughfall resulting from fog interception during 00:00 and 04:30.

Estimation of soil properties

For the determination of soil-water relationships core samples were collected in 5–10, 10–15 cm, and 40–45 cm soil depth using beveled edge cylinders of 5.6 cm diameter and 4 cm depth for minimising internal disturbance of the sample cores. In the laboratory the soil cores were slowly saturated for 48 h. Soil matric potential (Ψ_{soil}) was then estimated from volumetric water content (θ_v) using tension tables and a pressure membrane apparatus (SCHLICHTING & al. 1995). Additionally, representative bulk soil samples were taken from each soil depth, air dried, ground to pass a 2-mm sieve, and used for the analysis of physical properties. Particle-size analysis was performed by means of sieves (2000 to 40 µm) and a Particle Size analyser (<40 µm; Shimadzu SA-CP2/10). Organic matter was analysed in a muffle-furnace (SCHLICHTING & al. 1995).

Measurements of sap flow and thickness change in the trunk: Xylem sap flow density (F) was monitored with 2-cm long continuously heated sap flowmeters (UP Umweltanalytische Produkte GmbH. Munich, Germany) according to the method described previously by GRANIER (1985, 1987). The sensors were inserted into the xylem (North-West aspect) of 2 trees at breast height. Protection from high solar irradiation was ensured by isolating shields placed over the sensors. Data were recorded with a Campbell CR10 data logger (Campbell Scientific Ltd. Shepshed, U.K.) programmed to record 15- minute means of measurements taken every minute. F was then calculated according to the equation:

$$F = 0.0714 * (\Delta T_{max}/(\Delta T_{act})-1)^{1.231}$$

where ΔT_{max} is the maximum temperature difference recorded at night when transpiration is close to zero and ΔT_{act} is the momentary temperature difference.

At the same trees we also installed point dendrometers at breast height (LORIS 1981) for monitoring changes in stem radius (Δr). They consisted of a precision linear displacement transducer (MM10, Megatron, Putzbrunn, Munich, Germany) mounted on an aluminium frame which was anchored from both sides into the hydroinactive xylem. Thus, the stem remained intact where it was contacted by the sensor. At the contact point of the sensor the bark was removed so that only changes in phloem and xylem diameter were recorded. Each dendrometer was individually calibrated and a 2 µm change in radius corresponded to approximately 1 mV. Radius changes on the north-facing side of the trees were monitored in 15 minutes intervals with a Campbell CR10 data logger.

Diurnal courses of needle water relations: Scaffolding provided access to branches to the upper sun crown at 17 m tree height. Stomatal conductance to water vapour (G_{wv}), transpiration (Tr), needle water potential (Ψ_{needle}), and relative water content (RWC) of 1-year old needles (9 branches, 3 per tree) were measured from sunrise to sunset in one- to two hour intervals.

Gas exchange measurements were made in situ with a portable gas exchange system (LCA4, ADC, Hoddesdon, UK) equipped with a 6.25 cm^2 PLC(B) leaf chamber (ADC, UK). For these measurements fascicles (ten needles per twig) were marked at the base to ensure that the same needles were measured throughout a daily course. Gas exchange parameters were calculated according to VON CAEMMERER & FARQUHAR 1981 and related to projected needle surface area. Projected needle surface area was estimated by measuring the length and the diameter of the needle portion contained in the gas exchange cuvette. Measurements indicated that the needle diameter approximated at an average of 1.2 mm, as also observed by BLANCO & al. 1989. The length of the gas exchange cuvette was 25 mm, thus the projected surface area of the fascicle was assumed to be 300 mm^2. The specific leaf area was 38.73 ± 3.67 cm^2 of projected surface area per g needle dry weight.

Needles attached to the same twig as those used for gas exchange measurements were used for estimating Ψ_{needle} and RWC. Ψ_{needle} was measured with a Scholander pressure chamber (PMS, Instruments, Corvallis, OR, USA) on two single needles per tree. If values differed by more than 0.1 MPa during the dawn and more than 0.2 MPa during the day a third measurement was made. The mean of these values was taken as the Ψ_{needle} of the tree.

For the estimation of RWC 10 to 15 needle bundles were cut from the branches, immediately placed in plastic bags, sealed, and stored under dark at 5 °C or below in a cooling box and transported to the laboratory. In the laboratory the fresh (FW), turgid (TW) and dry (DW) weights of the needles were determined with an analytical balance (Mettler, Greifensee, Switzerland). For the estimation of the turgid weight the needles were rehydrated overnight in a saturated atmosphere. Dry weight was obtained after drying at 80 °C for 48 h. Needle RWC was calculated as:

$$RWC = (FW-DW)/(TW-DW)*100.$$

Environmental measurements: Climatic conditions were recorded by a meteorological station installed at the top of the scaffolding tower. It consisted of a DL2 data logger with temperature and humidity sensors (Delta-T, Cambridge, U.K.); a silicon cell pyranometer, an anemometer, and a rain gauge (Skye Ins. Landrindod, UK). In addition the volumetric water content of the soil was obtained in 45 cm soil depth with a ThetaProbe (Delta-T, Cambridge, U.K).

Results

According to the USDA taxonomic classification the soil is classified as an andosol. There was a shallow layer of 3 to 5 cm needle litter and the top 50 cm mineral soil horizon was enriched with 10% of organic matter. Physical analysis indicated that the soil is dominated by the sand fraction which was at an average higher than 65%. Clay was much less than slit, varying from 2 to 3%. The relationship between Ψ_{soil} and θ_v indicated no significant differences in water retention of the soil depths investigated (Fig. 1).

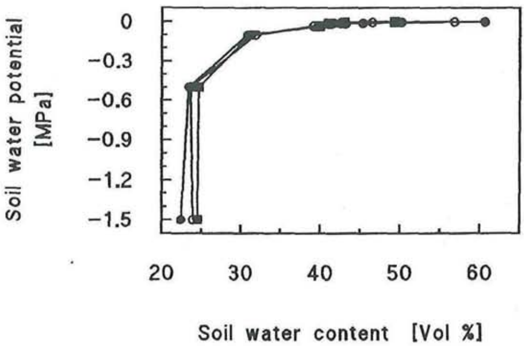

Fig. 1. The relationship between volumetric soil water content and soil water potential in 5–10 (●), 10–15 (○) and 40–45 cm (■) soil depth.

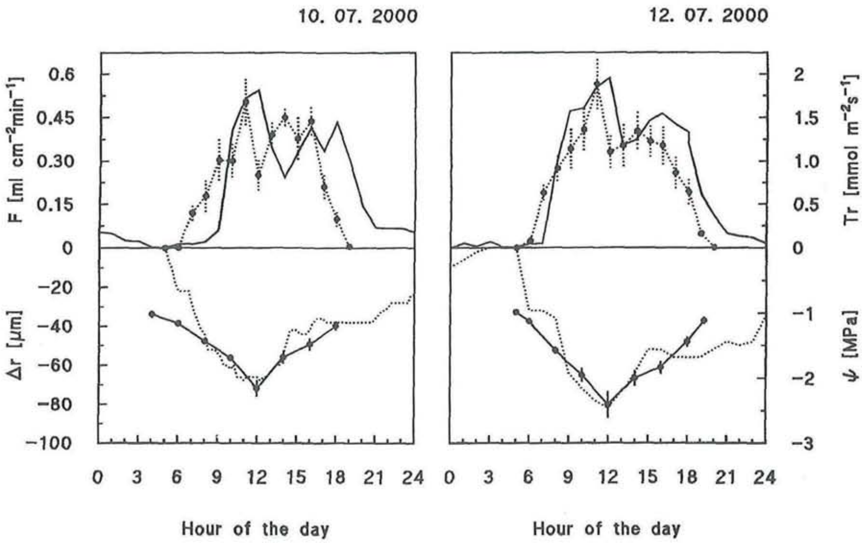

Fig. 2. Diurnal changes in sap flow density (F, solid line) and change in stem radius (Δr, dotted line) in 1.5 m height, as well as transpiration (Tr, dotted line and ●), and needle water potential (Ψ_{needle}; solid line and ●) in the upper canopy of *Pinus canariensis* on 10 (left) and 12 July 2000 (right). n = 9 needle fascicles ± SD.

Changes in Tr, F, Δr, and Ψ_{needle} showed marked diurnal patterns (Fig. 2). On both days investigated, F lagged significantly behind Tr. In the morning, F started later, increased more abruptly, and reached the maximum later than Tr. In the afternoon and the evening by contrast, F decreased more slowly than Tr.

Δr and Ψ_{needle} varied in parallel over the day. Both parameters continuously decreased from the onset of Tr and reached minimum values at 12:00, when F was highest (Fig. 2). Sunsequently, the Δr, and Ψ_{needle} increased.

Within the canopy however, there were marked differences in the diurnal patterns of incident photosynthetic photon flux density (PPFD) and leaf to air vapour pressure difference (Δw) (Fig. 3). Needles of east-facing twigs experienced higher PPFD and Δw values during the morning hours, whereas needles on west-facing twigs were exposed to higher PPFD and higher Δw in the afternoon. As a result Tr and G_{wv} of east-facing and west-facing twigs was high during the morning and during the afternoon, respectively. A trend which was much more pronounced on the dry July 12 than on July 10. However, there were no differences in the amount of water transpired during the day between east- and west-facing twigs neither on July 10 nor on July 12 (Fig. 3). Corresponding values of cumulative daily Tr were 126 and 142 mol H_2O per m^{-2}, respectively.

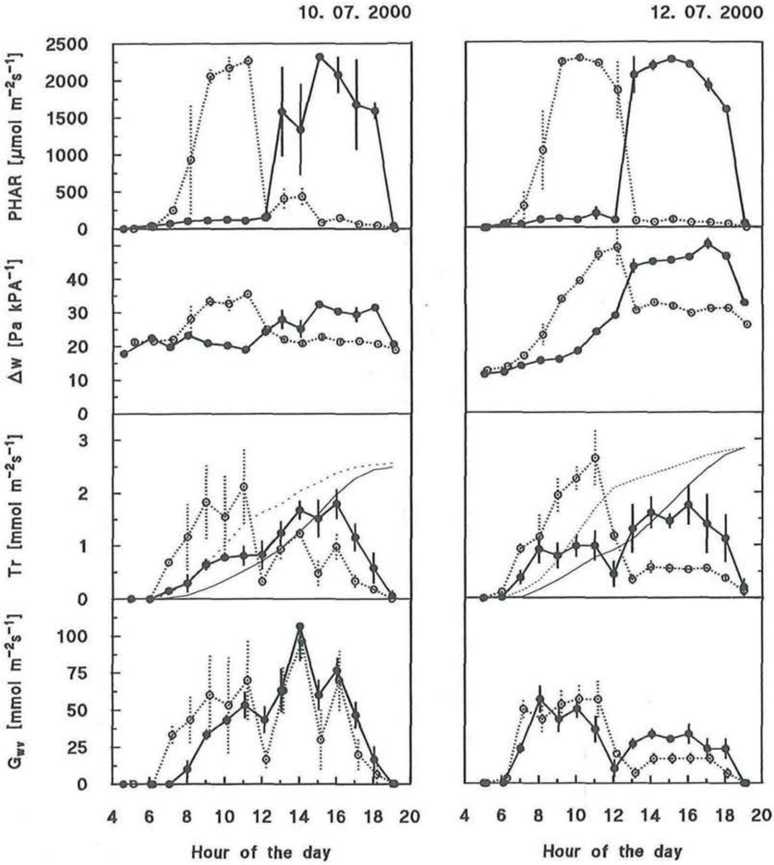

Fig. 3. Diurnal courses of photosynthetic photon flux density (PPFD) and leaf to air vapour pressure difference (Δw) at the needle level, actual transpiration rate (Tr), and cumulative transpiration (Tr_{cum}; fine lines) and stomatal conductance for water vapour of *Pinus canariensis* needles (G_{wv}) on east- (dotted line and ○) and west-facing twigs (solid line and ●). n = 3 needle fascicles per tree ± SD.

On both days investigated, Ψ_{needle} was significantly lower in west- than in east-facing twigs, especially during midday and in the afternoon (Fig. 4). The RWC of the needles by contrast, remained more or less constant throughout the day and was at an average 87.7±3.5% in both west- and east-facing twigs (Fig. 4).

When Tr and G_{WV} were plotted against PPFD, both parameters were light saturated at a PPFD of 250 µmol m^{-2} s^{-1} (Fig. 5).

Under conditions of light saturation G_{WV} decreased with increasing Δw, while Tr tended to increase with increasing Δw (Fig. 6). At Δw values higher than 30 Pa kPa^{-1}, however Tr decreased as a result of stomatal closure.

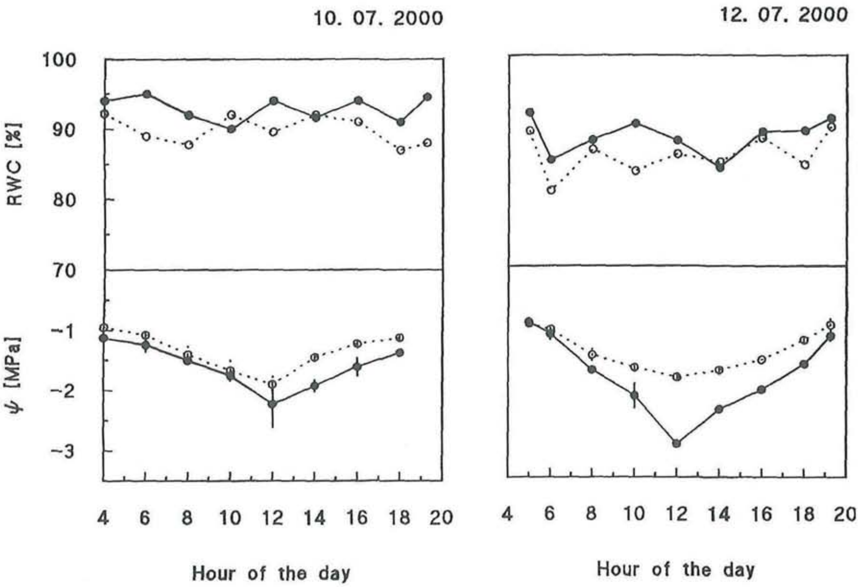

Fig. 4. Diurnal courses of the relative water content (RWC) and the needle water potential (Ψ_{needle}) of *Pinus canariensis* needles on east- (dotted line and ○) and west-facing twigs (solid line and ●). n = 3 needle fascicles per tree ± SD.

Discussion

In this study we focused on the water relations of a *Pinus canariensis* stand in Tenerife, Canary Islands. Water loss of the foliage is regulated by external and internal factors (JONES 1992, KÖRNER 1994, LEE & BOWLING 1995, TESKEY & al. 1995). The diurnal trends in average canopy transpiration are similar to those reported for other evergreen woody Mediterranean species (ABRIL & HANANO, 1998; MANES & al. 1997). However, within the uppermost canopy gas exchange was highly variable among differently orientated twigs. There was a steep photosynthetic photon flux density gradient across the canopy depending on the inclination of the sun, which affected the interaction between the canopy and the environment of east- and west-facing twigs. Diurnal patterns of transpiration of needles on east- and west-facing twigs paralleled changes in incident photosynthetic photon flux density (Fig. 3). Thus, both sets of needles achieved similar maximum transpiration rates at different times of the day. Similar diurnal differences in microclimate at the leaf level and in gas exchange patterns were also reported for differently orientated leaves within in the canopy of *Macaranga conifera* (ISHIDA & al. 1999) and *Clusia hilariana* (FRANCO & al. 1999) trees.

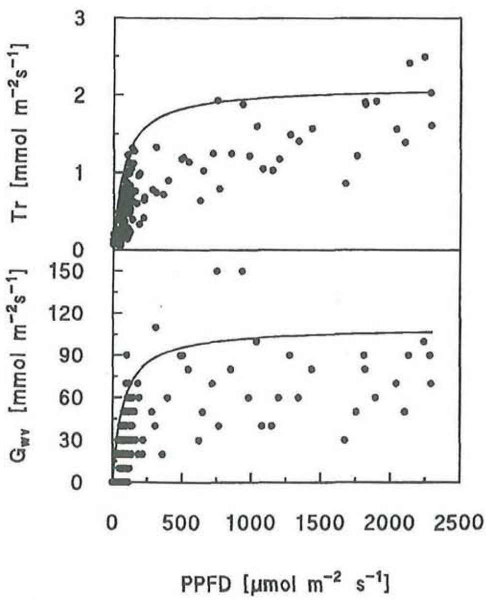

Fig. 5. Boundary line analysis representing the relationship between transpiration (Tr) and stomatal conductance for water vapour (G_{wv}) of *Pinus canariensis* needles and photosynthetic photon flux density (PPFD) at a leaf to air vapour pressure difference values <30Pa kPa^{-1}.

During the afternoon however, increasing leaf to air vapour pressure difference prevented stomatal opening in needles of west-facing twigs when compared to morning values in east-facing twigs (day 12. 07. 2002; Fig. 3). Thus, the same climatic conditions caused a higher stomatal conductance for water vapour during the morning than in the afternoon (HAVRANEK & WIESER 1993, JARVIS 1976, KÖRNER & COCHRANE 1985, KÜPPERS & al. 1986, PEREIA & al. 1987, VYGODSKAYA & al. 1997). The afternoon reduction of stomatal conductance compared to morning values under equal climatic conditions was in the order of up to 20%. Although no ABA measurements have been undertaken such time-dependent reductions in stomatal conductance relative to morning values might be associated with water stress as suggested by SCHULZE 1994. This idea is further corroborated by the observation that during the afternoon needle water potential was lower in west- than in east-facing twigs (Fig. 4). The lower needle water potential in west-facing twigs might result from an imbalance between needle transpiration and sap flow at the stem base (Fig. 2) and thus resulting in diurnal changes in water storage within the tree above the point of sap flow measurement (HOGG & HURDLEY 1997, PALLARDY & al. 1995). Transpiration started before sap flow in the morning when water in the trunk was easily available, and also finished before in the afternoon

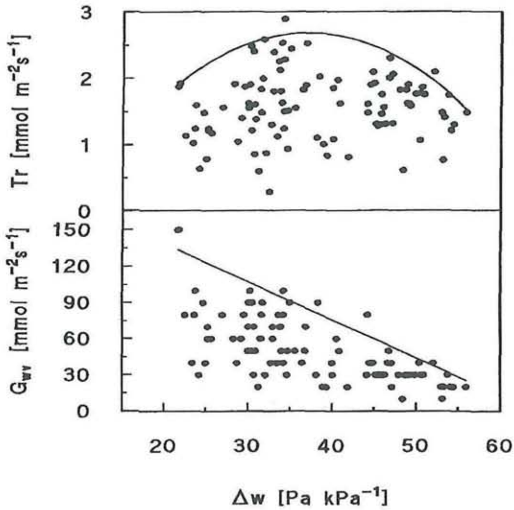

Fig. 6. Boundary line analysis representing the relationship between transpiration (Tr) and stomatal conductance for water vapour (G_{wv}) of *Pinus canariensis* needles and leaf to air vapour pressure difference (Δw) at PPFD values (600 µmol m^{-2} s^{-1}.

when empty reservoirs will be refilled (CERMAK al. 1982, 1984, SCHULZE & al. 1985).

The simultaneous recording of sap flow and changes in stem radius at the stem base revealed a close relationship between both factors, as also observed in Norway spruce (HERZOG & al. 1995, OFFENTHALER & al. 2001). Both factors responded rapidly to changes in climatic conditions of the free atmosphere above the canopy (data not shown). Thus changes in stem radius might have been driven by changes in needle water potential resulting from transpiration (OFFENTHALER & al. 2001).

The response of transpiration and stomatal conductance in the uppermost canopy to environmental conditions however, was similar to that found in other conifer species (cf. KÖRNER 1994, TESKEY & al. 1995). Stomatal response to photosynthetic photon flux density showed the usual hyperbolic trend with complete stomatal opening at photosynthetic photon flux density values around 250 µmol m^{-2} s^{-1} (Fig. 5). Under conditions of light saturation stomatal conductance decreased with increasing leaf to air vapour pressure difference (Fig. 6). Thus, the observed decrease in transpiration at a leaf to air vapour pressure difference >30 Pa kPa^{-1} resulted from stomatal closure (Fig. 6). Stomatal sensitivity to increasing leaf to air vapour pressure difference is an obvious advantage to minimise water loss under conditions of high evaporative demand as well as in droughty areas and has been documented in various pine species (SANDFORD & JARVIS 1986). Furthermore, is necessary to maximise carbon gain relative to the transpirational water loss as proposed in the optimisation theory by COWAN & FARQUHAR 1977. On a relative scale however, in *Pinus canariensis* stomatal conductance decreased at about 30% per 10 Pa kPa^{-1} increase in leaf to air vapour pressure difference as also observed in conifers of the temperate (WIESER 1999) and boreal zone (DANG & al. 1997, VYGODSKAYA & al. 1997).

Conclusions

Gas exchange measurements at the leaf level in the upper crown give detailed information how Tr is influenced by environmental variables. However, on the long term under the climatic conditions in the Canary islands this assessment of transpiration is a difficult task (GONZÁLEZ-RODRÍGUEZ & al. 2001, PETERS 2001) because crowns are periodically wet due to the influence of the trade winds bring moisture from the sea. Sap flow sensors by contrast, give long term records and enable the automatic recording of whole canopy transpiration on the tree level. Additional measurements of Δr will reflect diurnal patterns of Tr. In combination with the knowledge on soil water relationships such measurements are an important contribution to the water balance of *Pinus canariensis* forests.

References

ABOAL J. R., JIMÉNEZ M. S., MORALES D. & GIL P. 2000. Effects of thinning on throughfall in Canary Islands pine forest – The role of fog. – Journal of Hydrology 238: 218–230.

ABRIL M. & HANANO R. 1998. Ecophysiological responses of three evergreen woody Mediterranean species to water stress. – Acta Oecologia 19: 377–387.

BLANCO A., CASTROVIEJO M., FRAILE J. L., GANDULLO J. M., MUNOZ L. A. & SÁNCHEZ-PALMERA O. 1989. Estudio ecológico del pino canario. – Ministerio de Agricultura, Pesca y Alimentación, ICONA, Serie técnica Nr. 6, Madrid, 199 p.

BRAMWELL D. & BRAMWELL Z. I. 1990. Flores silvestres de las Islas Canarias. – Rueda, Madrid, 284p.

CERMAK J., ULEHLA J., KUCERA J. & PENKA M. 1982. Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimension. – Biol. Plant. 24: 34-41.

— , JELINK J., KUCERA J. & ZIDEK V. 1984. Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes in environment. – Oecologia 64: 145–151.

COWAN I. R. & FARQUHAR G. D. 1977. Stomatal function in relation to leaf metabolism and environment. – Symp. Soc. Exp. Biol. 31: 471–505.

DANG Q. L, MARGOLIS H. A., COYEA M. R., SY M. & COLLATZ G. J. 1997. Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. – Tree Physiol. 17: 521–535.

DEL ARCO AGUILAR M. J., PÉREZ DE PAZ P. L., RODRÍGUEZ O., SALAS M. & WILDPRET W. 1992. Atlas cartográfico de los pinares de Canarias II. Tenerife. Dirección general de Medio Ambiente y Conservación de la Naturalez. – Gobierno de Canarias. Santa Cruz de Tenerife. 228 p.

FRANCO A. C., HERZOG B., HÜBNER C., DE MATTOS E. A., SCARANO F. R., BALL E. & LÜTTGE U. 1999. Diurnal changes in chlorophyll a fluorescence, CO_2-exchange and organic acid decarboxylation in the tropical CAM tree *Clusis hilatiana*. – Tree Physiol. 19: 635–644.

GONZALEZ-RODRIGUEZ A., MORALES D. & JIMENEZ M. 2001. Gas exchange characteristics of a Canarian laurel forest tree species (*Laurus azorica*) in relation to environmental conditions and leaf canopy position. – Tree Physiol. 21: 1039–1045.

GRANIER A. 1985. Une nouvelle methode pour la mesure du flux de seve brute le tronc des arbes. – Ann. Sci. For. 42: 193–200.

— 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow meters. – Tree Physiol. 3: 309–320.

HAVRANEK W. M & WIESER G. 1993. Zur Ozontoleranz der europäischen Lärche (*Larix decidua* Mill.). – Forstw. Cbl. 112: 56–64.

HERZOG K. M., HÄSLER R. & THUM R. 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. – Trees 10: 94–101.

HINCKLEY T. M. & BRUCKERHOFF D. N. 1975. The effect of drought on water relations and stem shrinkage of *Quercus alba*. – Can. J. Bot. 53: 62–72.

HOGG E. H. & HURDLEY P. A. 1997. Sap flow in trembling aspen: implications for stomatal response to vapour pressure deficit. – Tree Physiol. 17: 501–509.

ISHIDA A., TOMA T. & MARJENAH 1999. Leaf gas exchange and chlorophyll fluorescence in relation to leaf angle, azimuth, and canopy position in the tropical tree, *Macaranga conifera*. – Tree Physiol. 19: 117–124.

JACKSON R. B., SPERRY J. S. & DAWSON T. E. 2000 Root water uptake and transport: using physiological processes in global predictions. – Trends in Plant Science 5: 482–488.

JARVIS P. G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. – Philos. Trans. R. Soc. London B. 273: 593–610.

JONES H. G. 1992. Plants and microclimate. A quantitative approach to environmental plant physiology. – Cambridge, University Press, 428p.

KÄMMER CH. 1974. Klima und Vegetation auf Teneriffa besonders im Hinblick auf Nebelniederschlag. – Scripta Geobotanica Vol. 7. Edit. Erich Goltze K.G. Göttingen.

KÖRNER CH. 1994. Leaf diffusive conductances in the major vegetation types of the globe. – In: SCHULZE E. D. & CALDWELL M. M. (Eds.), Ecophysiology of photosynthesis, pp 463–490. – Ecological Studies Vol. 100, Springer Verlag, Berlin.

— & COCHRANE P. M. 1985. Stomatal response and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. – Oecologia 66: 443–455.

KOZLOWSKY T. T. KRAMER P. J. & PALLARDY S. G. 1991. The physiological ecology of woody plants. – Academic Press, San Diego.

KÜPPERS M., MATYSSEK R. & SCHULZE E. D. 1986. Diurnal variations of light-saturated CO_2 assimilation and intercellular carbon dioxide concentration are not related to leaf water potential. – Oecologia 69: 477–480.

LASSIOE J. P. 1973. Diurnal dimensional fluctuations in a Douglas fir stem in response to tree water status. – For. Sci. 19: 251–255.

LEE J. S. & BOWLING D. F. J. 1995. Viewpoint: influence of the mesophyll on stomatal opening. – Aust. J. Plant. Physiol. 22: 357–363.

LORIS K. 1981. Dickenwachstum von Zirbe, Fichte und Lärche an der alpinen Waldgrenze/Patscherkofel. Ergebnisse der Dendrometermessungen 1976/79. – Mitt. Forstl. Bundesversuchsanstalt Wien 142/II: 417–441.

MANES F., SEUFERT G. & VITALE M. 1997. Ecophysiological studies of Mediterranean plant species at the Castelporziano Estate. – Atmosp. Environ. 31: 51–60.

MONTEITH J. L. 1995. A reinterpretation of stomatal responses to humidity. – Plant, Cell Environm. 18: 357–364.

NONAMI H., SCHULZE E. D. & ZIEGLER H. 1990. Mechanisms of stomatal movement in response to air humidity, irradiance and xylem water potential. – Oecologia 183: 57–64.

OFFENTHALER I., HIETZ P. & RICHTER H. 2001. Wood diameter indicates diurnal and long-term patterns of xylem water potential in Norway spruce. – Trees 15: 215–221

PALLARDY S. G., CERMAK J., EWERS F. W., KAUFMANN M. R., PARKER W. C. & SPERRY J. S. 1995. Water transport dynamics in trees and stands. – In: SMITH W. K. & HINCKLEY T. M. (Eds.), Resource physiology of conifers acquisition, allocation and utilization, pp 301–389. – Academic Press, San Diego, Ca.

PEREIA J. S., TENHUNEN J. D. & LANGE O. L. 1987. Stomatal control of photosynthesis of *Eucalyptus globulus* Labill. trees under field conditions in Portugal. – J. Exp. Bot. 38: 1678–1688.

PETERS J. 2001. Ecofisiologia del Pino canario. – PhD La Laguna University (Tenerife, Spain). 257 p.

SANDFORD A. P. & JARVIS P. G. 1986. Stomatal response to humidity in selected conifers. – Tree Physiol. 2: 89–104.

SCHLICHTING E., BLUME H. P. & STAHR K. 1995. Bodenkundliches Praktikum. – Blackwell Wissenschafts-Verlag, Berlin, Wien, 295 p.

SCHULZE E. D. 1986. Carbon dioxide and water vapout exchange in response to drought in the atmosphere and the soil. – Ann. Rev. Plant Physiol. 37: 247–274.

— 1994. The regulation of plant transpiration: interactions of feedforward, feedback, and futile cycles.- In: SCHULZE E. D. (Ed.), Flux control in biological systems. From enzymes to populations and ecosystems, pp. 203–236. – Academic press San Diego Ca..

— , CERMAK J., MATYSSEK R., PENKA M., ZIMMERMANN R., VASICEK F., GRIES W. & KUCERA J. 1985. Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees – a comparison of xylem flow, porometer and cuvette measurements. – Oecologia 66: 475–483.

TENHUNEN J. D., HANANO R., ABRIL M., WEILER E. W. & HARTUNG W. 1994. Above- and below-ground environmental influences on leaf conductance of *Ceanothus thyrsifolius* growing in a chapparal environment: drought response and the role of abscisic acid. – Oecologia 99: 306–314.

TESKEY R. O., SHERIFF D. W., HOLLINGER D. Y. & THOMAS R. B. 1995. External and internal factors regulating photosynthesis. – In: SMITH W. K. & HINCKLEY T. M. (Eds.), Resource physiology of conifers acquisition, allocation and utilization, pp. 105–140. – Academic Press, San Diego, Ca.

UEDA M. & SHIBATA E. 2001. Diurnal changes in branch diameter as indicator of water status of Hinoki cypress *Chamaecyparis obtusa*. – Trees 15: 315–318.

VON CAEMMERER S. & FARQUHAR G. D. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta 153: 376–387.

VYGODSKAYA N. N., MILYUKOVA I., VARLAGIN A., TATARINOV F., SOGACHEV A., KOBAK K. I., DESYATKIN R., BAUER G., HOLLINGER D. Y., KELLIHER F. M. & SCHULZE E. D. 1997. Leaf conductance and CO_2 assimilation of *Larix gmelinii* growing in an eastern Siberian boreal forest. – Tree Physiol. 17: 607–615.

WARING R. H., WHITEHEAD D. & JARVIS P. G. 1979. The contribution of stored water to transpiration in Scots pine. – Plant Cell Environm. 2: 309–317.

WIESER G. 1999. Evaluation of the impact of ozone on conifers in the Alps: a case study on spruce, pine and larch in the Austrian Alps. – Phyton 39: 241–252.