

## Water relations of European silver fir (*Abies alba* Mill) in 2 natural stands in the French Alps subject to contrasting climatic conditions

P Guicherd

Université Joseph-Fourier, Centre de Biologie Alpine, BP 53, 38041 Grenoble cedex 9, France

(Received 30 November 1992; accepted 26 January 1994)

**Summary** — This paper reports on the diurnal and seasonal variations in water potential, stomatal conductance, and transpiration of twigs from silver fir in a mesohydrophilic stand of the external French Alps, and in a mesoxerophilic stand in the inner French Alps where this fir grows near its ecological limits. In both stands, predawn needle water potential was always 0.2–0.4 MPa below the potential of the driest soil layer. In the first one, it was maintained at about –0.4 MPa. Maximum stomatal conductance and maximum transpiration, which could reach 200 mmol/m<sup>2</sup>/s and 1 mmol/m<sup>2</sup>/s, respectively, occurred at the same time which corresponded to minimum leaf water potential. In the dry stand, predawn needle water potential never dropped below –1.14 MPa, yet a general browning of older needles was already observed. The decrease of predawn needle water potential was accompanied by the decrease of maximum stomatal conductance and transpiration to 15% of their highest value, which reached 150 mmol/m<sup>2</sup>/s and 1 mmol/m<sup>2</sup>/s, respectively, at this stand. Maximum stomatal conductance occurred in general before UT 07.00, and maximum transpiration 5–6 h later, irrespective of predawn needle water potential. Furthermore, in both stands, stomata closed at vapor pressure deficit value as low as 0.3 kPa. This extremely early reaction to water stress exhibited by European silver fir is consistent with its well-known sensitivity to atmospheric humidity and soil water availability. It indicates a strong avoidance strategy, which we have hitherto attributed only to species better adapted to drought.

***Abies alba* Mill = European silver fir / Alps / stomata / water potential / water deficit**

**Abbreviations and units:** E = transpiration (mmol (H<sub>2</sub>O)/m<sup>2</sup>/s); E<sub>max</sub> = maximal transpiration (mmol (H<sub>2</sub>O)/m<sup>2</sup>/s); G<sub>s</sub> = stomatal conductance (mmol(H<sub>2</sub>O)/m<sup>2</sup>/s); G<sub>smax</sub> = maximal stomatal conductance (mmol(H<sub>2</sub>O)/m<sup>2</sup>/s); L<sub>p</sub> = soil-to-leaf hydraulic conductance (mmol/m<sup>2</sup>/s/–MPa); PFD = photon flux density (μE/m<sup>2</sup>/s); VPD = vapor pressure deficit (kPa); ψ<sub>l</sub> = leaf water potential (MPa); ψ<sub>lmin</sub> = minimum leaf water potential (MPa); ψ<sub>p</sub> = predawn needle water potential (MPa); ψ<sub>s</sub> = soil water potential (MPa); Δψ = ψ<sub>lmin</sub> – ψ<sub>p</sub> (MPa).

**Résumé — Comportement hydrique du sapin pectiné (*Abies alba* Mill) dans 2 stations des Alpes françaises climatiquement contrastées.** L'article décrit les variations diurnes et saisonnières du potentiel hydrique foliaire, de la conductance stomatique et de la transpiration de rameaux de sapin dans une station mésohygrophile des Alpes externes, et dans une station mésoxérophile des Alpes internes en limite écologique de l'essence. Dans les 2 stations, le potentiel hydrique de base est toujours inférieur de 0,2 à 0,4 MPa au potentiel hydrique des couches de sol les plus sèches. Dans la première, il s'est maintenu aux environs de -0,4 MPa. La conductance stomatique et la transpiration maximales, pouvant atteindre respectivement 200 mmol/m<sup>2</sup>/s et 1 mmol/m<sup>2</sup>/s, ont toujours eu lieu au même moment, qui correspondait au potentiel hydrique foliaire minimum. Dans la station sèche, le potentiel hydrique de base n'est jamais descendu en dessous de -1,14 MPa, mais on pouvait déjà observer un brunissement généralisé des plus vieilles aiguilles. Cette diminution du potentiel de base s'est accompagnée d'une diminution de la conductance et de la transpiration maximales pour atteindre 15% de leur plus forte valeur, qui pour cette station sont respectivement de 150 mmol/m<sup>2</sup>/s et 1 mmol/m<sup>2</sup>/s. La conductance stomatique maximale a le plus souvent eu lieu avant 7 h TU, et la transpiration maximale 5 ou 6 h après, indépendamment du potentiel de base. De plus, dans les 2 stations, les stomates se ferment quand le déficit de pression de vapeur atteint seulement 0,3 kPa. Cette réaction extrêmement précoce au stress hydrique est cohérente avec la légendaire sensibilité du sapin à l'humidité atmosphérique ainsi qu'à l'eau dans le sol. Elle dénote chez cette essence une nette stratégie d'évitement que l'on croyait jusqu'alors être l'apanage d'espèces mieux adaptées à la sécheresse.

***Abies alba* Mill = sapin pectiné / Alpes / stomates / potentiel hydrique / déficit hydrique**

## INTRODUCTION

European silver fir is one of the most important forest-trees in France, covering one-million hectares (Jacamon, 1987). Our understanding of its ecological amplitude is essentially based on the study of its natural range; this conifer cannot tolerate late frosts and dry summers and is the major component of mountain forests (900 to 1 500 m of elevation) where atmospheric humidity is high. Dendrochronological and dendro-ecological studies emphasize the high sensitivity of silver fir to water stress (Bîndiu, 1971; Serre-Bachet, 1986; Lévy and Becker, 1987; Becker, 1989) while experiments on young potted trees show that it conserves water quite well (Becker, 1970, 1977) and in particular better than Norway spruce (*Picea excelsa* Link) with which it is frequently mixed in mountain stands. However, silver fir appears to delay the regulation of its water-vapor exchanges, which classifies it among species that are poorly adapted to drought (Aussenac, 1980).

In the French Alps, fir forests grow from the very humid external belt to the most xeric areas of the internal one. All along this transect of increasing continentality, changes in climatic conditions modify floristic composition and decrease productivity (Oberlinkels *et al*, 1990). How does this species, which is believed to display a low plasticity in its response to environmental conditions, survive and grow at the limits of its natural range, especially when it is found in the vicinity of other drought-resistant species such as pines? As little is known about the physiological ecology of this fir, we attempted to understand the water relations of this species in the field. The aim of this work was:

- to collect information about diurnal and seasonal variations in water potential, stomatal conductance and transpiration of fir twigs in 2 contrasting habitats;
- to understand interrelations between these variables and their interactions with microclimatic and edaphic factors; and
- to search for a possible strategy adopted by silver fir in dry stands.

## MATERIALS AND METHODS

### Study sites

Two north-facing fir forests each typical of a particular bioclimatic zone and a productivity level were chosen on calcareous bedrocks in the Dauphiné Alps (near Grenoble). One is located in the external Alps, as defined by Ozenda (1985) by a Gams angle  $< 40^\circ$ , at a place named Valombré in the commune of Saint-Pierre-de-Chartreuse (abbreviated SPC). It is located in the National Forest of Grande-Chartreuse, at an elevation of 1 000 m ( $45^\circ 20' 25''$  N;  $5^\circ 46' 5''$  E). This mesohygrophilic stand was called 'fir forest with tall herbaceous layer' by Richard and Pautou (1982). The rainfall here exceeds 2 000 mm per year and dominant trees in the forest reach heights of 45 m. The second site is located in the French internal Alps, characterised by a Gams angle  $> 50^\circ$ , in a centre of xericity called Briançonnais (near Briançon). It is located in the Council Forest of Montgenèvre (abbreviated MTG) at a place named Bois des Bans at a mean elevation of 1 700 m ( $44^\circ 55' 10''$  N;  $6^\circ 41' 13''$  E). This mesoxerophylic site was described by Oberlinkels *et al* (1990) as a fir forest with *Melampyrum sylvaticum* and *Carex australpina*. The rainfall here is about 700 mm per year with a marked summer drought. The height of dominant trees does not exceed 25 m. Adult trees were chosen at each site with respect to the exposure of the crown and accessibility of twigs at a height of about 5 m. The main characteristics of studied trees are presented in table I.

### Soil water potential

At SPC, the soil water potential was measured at depths of 20, 40, 60, 80 and 105 cm with a

Nardeux DTE 1000 tensiometry system. At MTG, thermocouple dewpoint hygrometers Wescor PCT-55 connected to a Wescor HR-33 T microvoltmeter buried in the soil at depths of 10, 35 and 80 cm were also used (Pallardy *et al*, 1991). Measurements were made early in the morning.

### Microclimatic factors

A meteorological station was set up in the open forest at MTG, and in a clearing at SPC. Temperature, relative humidity, solar radiation, wind speed and rainfall data were stored in a Campbell 21 X micrologger every 10 min, throughout the 1990 and 1991 growing seasons from June to October. The photon flux density values used (PPFD,  $\mu\text{E}/\text{m}^2/\text{s}$ ) were recorded with a LI-COR 190 SB sensor integral with the porometer, just before the transpiration was measured. The vapor pressure deficit (VPD, kPa) was calculated with interpolated values of relative humidity and temperature stored by the station.

### Transpiration, stomatal conductance and leaf water potential

The stomatal conductance of twigs was measured with a LI-COR 1600 porometer. The resistance ( $\text{s}/\text{cm}$ ) was converted into conductance ( $G_s$ ,  $\text{mmol}/\text{m}^2/\text{s}$ ) according to Körner and Cochrane (1985). Transpiration ( $E$ ,  $\text{mmol}/\text{m}^2/\text{s}$ ) was computed from the resistance measured by porometer, relative humidity and temperature, which were stored by the meteorological station. Leaf temperature was considered to be equal to air temperature. Resistance of the boundary layer is taken as 0.2  $\text{s}/\text{cm}$ , a value which is set in the porometer. Measurements made when the relative

**Table I.** Main characteristics of studied trees in both stands.

	SPC		MTG			
	A	D	E	G	H	I
Height (m)	17.5	8	10.5	17.8	12	10
Diameter at 1.30 m (cm)	24.2	11.2	19.6	37.6	20.4	19
Age at 1.30 m (years)	29	38	50	88	180	66
Position of studied twigs within the crown	Lower	Middle	Middle	Lower	Lower	Middle

humidity was above 90% have been eliminated. Leaf area was determined by weighing a paper copy of enlarged views of needles obtained with an overhead projector, considering that fir needles are nearly plane; abaxial and adaxial sides were taken into account. The transpiration and stomatal conductance values presented in diurnal and seasonal time-courses are averages of 5 measurements per tree achieved on south-facing twigs at a height of 4 to 5 m, except for 3 trees where only 3 twigs were studied; the same twigs were used throughout the growing season. Simultaneously, leaf water potential of previous year needles from adjacent twigs were measured with a pressure chamber (Scholander *et al.*, 1965); 5 to 7 measures were made, each taking less than 2 min. All these measurements were repeated 10–13 times a day; hours are UT hours.

When sufficient ( $E$ ,  $\psi_l$ ) paired data were available, soil-to-leaf hydraulic conductance ( $L_p$ ,  $\text{mmol/m}^2/\text{s}/\text{MPa}$ ) was indirectly calculated as the absolute value of the slope of the linear regression between transpiration and leaf water potential (Reich and Hinckley, 1989). All correlations were significant at  $p < 0.05$ .

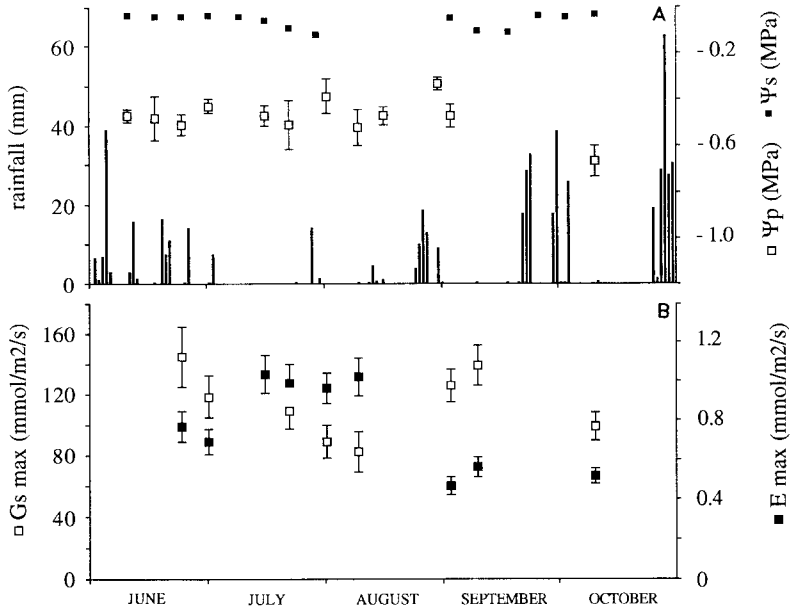
### Statistical tests

Correlations have been tested with Pearson  $r$  ( $r^2$ ), or with Spearman  $r$  ( $r_s$ ) when the former was not appropriate (Sokal and Rohlf, 1981). In the following \* means  $p < 0.05$ ; \*\* means  $p < 0.01$ ; NS means that correlation was not significant.

## RESULTS

### Rainfall and seasonal trend of $\psi_p$ (predawn needle water potential) during 1990

At SPC considerable rainfall (300 mm from June to September) and good soil water retention maintained the soil water potential ( $\psi_s$ ) at a high level (fig 1A). The tensiometry system failed for 3 weeks at 20 cm depth and never below 40 cm. Conse-



**Fig 1.** Seasonal trend of (A) predawn needle water potential, soil water potential at 20 cm depth ( $\psi_s$ ) and rainfall; and (B) maximal daily stomatal conductance ( $G_{smax}$ ) and maximal daily transpiration ( $E_{max}$ ) of fir in the humid stand during 1990. Vertical bars represent  $\pm$  SE.

quently,  $\psi_p$  remained about  $-0.4$  MPa throughout the growing period.

At MTG, low rainfall (162 mm from June to September) resulted in a gradual decrease of  $\psi_p$  which reached  $-1$  MPa (fig 2A). Data collected during 1991 show that  $\psi_p$  was  $0.2$ – $0.4$  MPa below the potential of the driest soil layer, though this, as at the other site, depended on the trees.  $\psi_p$  fell to  $-1.14$  MPa in 1991 and the oldest needles of all trees already exhibited browning.

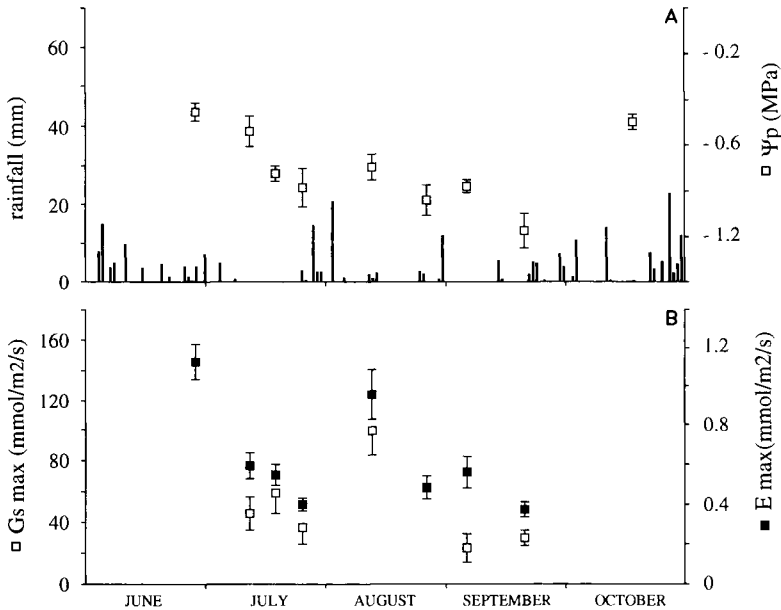
### Typical and noteworthy diurnal time-courses in each stand

Over 40 diurnal time-courses have been obtained from the 2 stands. Each exhibits one typical pattern, with some noteworthy variations at MTG.

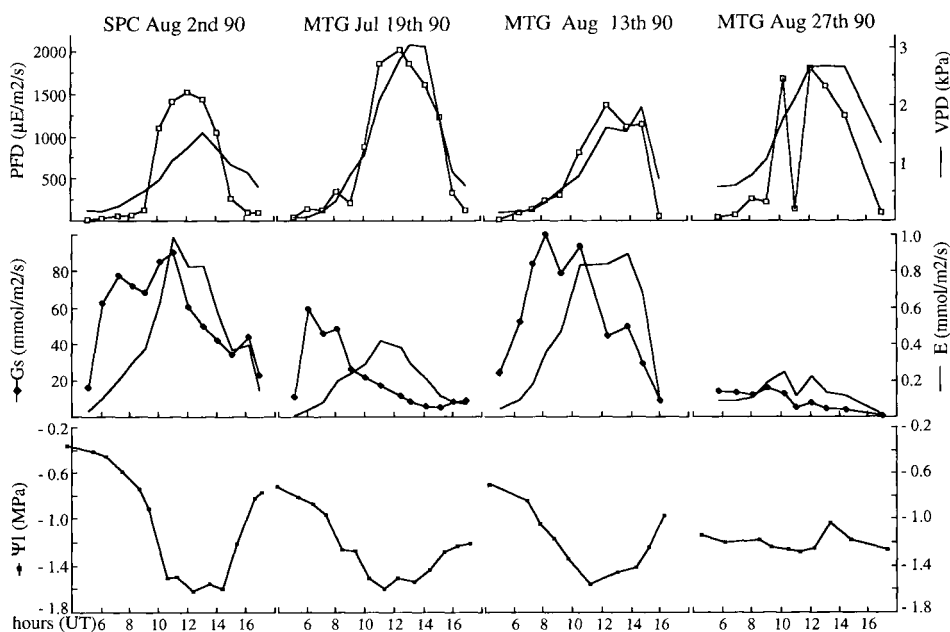
At SPC, due to high relative humidity, daily VPD never exceeded  $1.6$  kPa, and PFD

$1800 \mu\text{E}/\text{m}^2/\text{s}$ . A typical pattern is illustrated on August 2 1990 (fig 3). Stomata opened widely from the early morning and reached the maximum aperture at about 10.00–11.00 h, and then closed as quickly as they opened. At 18.00 h, they were nearly entirely closed (the slight decrease of  $G_s$  which occurs frequently at about 07.00 h was probably due to irradiance which becomes important only from 10.00 h owing to tree position in the clearing).  $G_{s\text{max}}$ ,  $E_{\text{max}}$  and  $\psi_{\text{Imin}}$  occurred at the same time. Stomatal closure immediately induced a decrease of water flow through the leaf and stabilized  $\psi_1$ , which then enabled its quick recovery. Depending on climatic conditions, the maximum values reached by each variable can of course change. A cloudy spell may also induce a shift in the model, but the general shape of the curves and especially coincidence of the peaks is always the rule.

At MTG, microclimatic conditions are very different. PFD may reach  $2\ 200 \mu\text{E}/\text{m}^2/\text{s}$



**Fig 2.** Seasonal trend of (A) predawn needle water potential ( $\psi_p$ ) and rainfall; and (B) maximal daily stomatal conductance ( $G_{s\text{max}}$ ) and maximal daily transpiration ( $E_{\text{max}}$ ) of fir in the dry stand during 1990. Vertical bars represents  $\pm$  SE.



**Fig 3.** Four diurnal time-courses of microclimate conditions (photon flux density, PFD and vapor pressure deficit, VPD), stomatal conductance ( $G_s$ ) transpiration ( $E$ ) and leaf water potential ( $\psi_l$ ) of the previous year's needles. Each point is an average of 5 measurements obtained from tree A and SPC and tree E at MTG except on August 27 1990 (tree D).

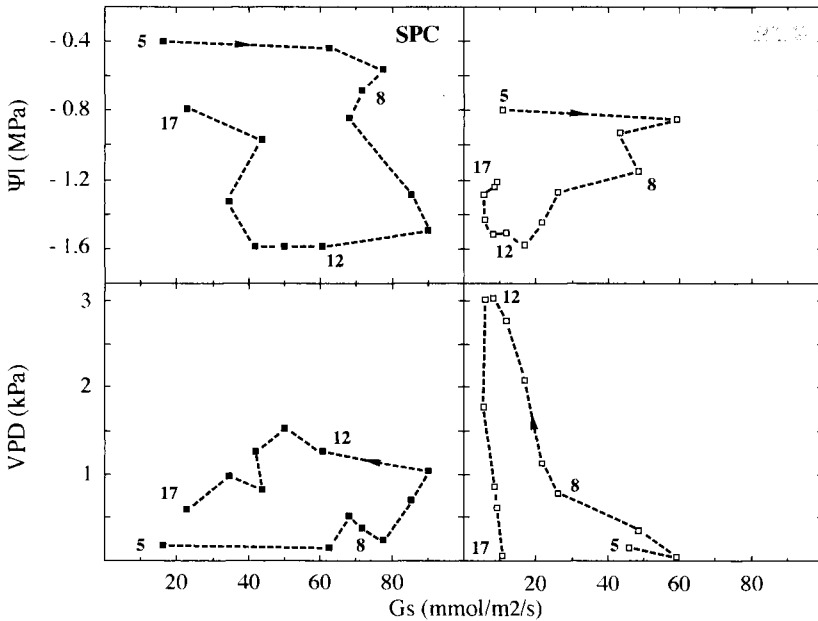
and VPD 4 kPa during sunny summer days. The typical pattern is illustrated for July 19 1990 (fig 3). It is characteristic in showing the movement of maximum stomatal conductance towards the early hours of the morning, irrespective of  $\psi_p$ . Furthermore,  $E_{\max}$  occurs 5–6 h after  $G_{s\max}$  due to high values of VPD in the late afternoon.

Nevertheless, this general pattern may be disrupted if a rainy spell has occurred recently (August 13 1990). The few millimeters that fell on August 12 1990 after 8 dry days enhanced stomatal aperture, causing the daily transpiration of the tree to increase significantly, although  $\psi_p$  was still equal to  $-0.7$  MPa.

The third diurnal time-course (August 27 1991) was obtained after a 2 month rain-

less period, when  $\psi_p$  was equal to  $-1.14$  MPa, and  $\psi_s$  to  $-0.8$  MPa for the driest soil layer. Transpiration was still significant, but stomata opened to no more than 15% of their maximum aperture. Because of a very low transpiration,  $\Delta\psi$  reached only  $-0.14$  MPa on this day. Graphs showing the strong reduction in water flow can be seen in figure 3.

The graphs in figure 4 allow us to grasp better the typical diurnal course of  $G_s$  in relation to  $\psi_l$  and VPD in both stands. The curves obtained from the dry site (MTG) are very remarkable insofar as stomatal closure occurs before VPD reaches significant values but does not stop the decrease of water potential, due to increasing  $E$ . On the contrary, stomatal closure immediately stabi-



**Fig 4.** Typical relationships of stomatal conductance with leaf water potential and vapor pressure deficit in both stands; measurements on August 2 at SPC (■) and July 19 at MTG (□); the same values as presented in figure 3. Chronological order is indicated by the arrows and UT hours near the points.

lizes  $\psi_l$  in the humid stand (SPC) which then recovers a high level by the end of the afternoon because of good water availability.

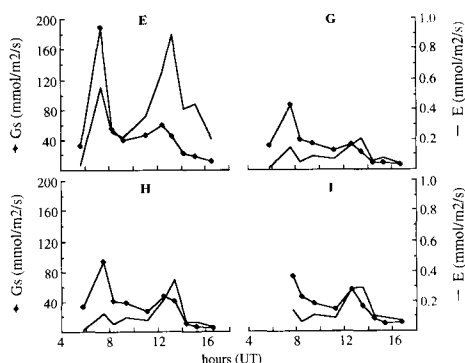
#### **Variability between trees and needle years**

Is the particular diurnal course of stomata at MTG representative of forest water relations or just characteristic of the few trees we studied? On August 27 1990 transpiration and stomatal conductance were followed in 4 trees (fig 5). Obviously, this pattern is typical of this stand. The maximum values differ from tree to tree for several reasons (age, water status and competition with other trees), but all of them exhibit an early stomatal closure.

Concerning variability between current-year needles and one-year needles, transpiration and stomatal conductance have been simultaneously measured 5 times at SPC and 4 times at MTG. When there were differences (3 times at SPC and twice at MTG), they were in the same direction, that is, a markedly later opening of current-year needles' stomata, and a slightly earlier closing (fig 6). We note this whilst recognizing that there could be such differences between immature and mature needles.

#### **Correlations with microclimatic factors and seasonal trend of $G_{smax}$ and $E_{max}$**

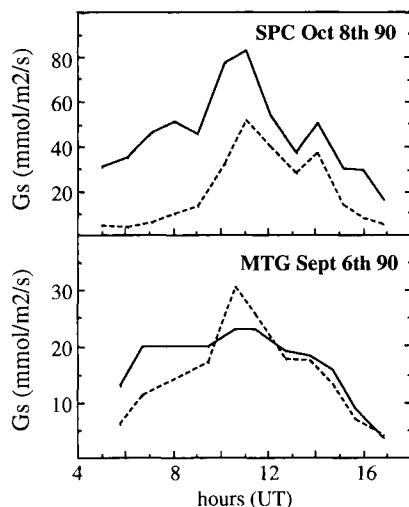
At SPC, the only significant correlation was observed between  $E_{max}$  and  $VPD_{max}$  ( $r_s =$



**Fig 5.** Comparison of the diurnal course of stomatal conductance and transpiration of previous year needles in 4 trees of the dry stand (MTG) on August 27 1990. Microclimatic conditions are similar for both trees.

0.82\*\*,  $n = 11$ , tree A). In fact, when  $\psi_s$  is high,  $\psi_p$  and  $G_{smax}$  are fairly constant (fig 1B) and VPD seemed to determine the intensity of transpiration and partly  $\Delta\psi$  ( $r_s = 0.49^{NS}$ ,  $n = 10$ , tree A) of which mean value was  $-1\text{MPa}$ . In both stands,  $\psi_{imin}$  never dropped below  $-1.8\text{MPa}$  and  $E_{max}$  reached  $1\text{mmol/m}^2/\text{s}$ .

At MTG,  $G_{smax}$  decreases when  $\psi_p$  decreases ( $r_s = 0.745^{**}$ ,  $n = 11$ , trees E + D) and so does  $E_{max}$  ( $r_s = 0.783^{**}$ ,  $n = 13$ , trees E + D).  $L_p$  is reduced from 80% when  $\psi_p$  decreases from  $-0.46$  to  $-0.78\text{MPa}$ . Moreover,  $E_{max}$  and  $G_{smax}$  are correlated ( $r_s = 0.711^*$ ,  $n = 11$ , trees E + D). VPD is no longer correlated with  $E_{max}$ , but linked to  $\Delta\psi$  ( $r_s = -0.75^*$ ,  $n = 9$ , trees E + D), which only reached  $-0.8\text{MPa}$  on average due to lower  $\psi_p$ , except on August 27 1991. Possible causalities revealed by these correlations show that a decreasing predawn needle water potential may reduce maximum stomatal conductance and consequently transpiration. This is in evidence in figure 2B. The intensity of transpiration determines the diurnal decrease of leaf water potential.



**Fig 6.** Two examples of the diurnal course of stomatal conductance differing between previous year needles (—) and current year needles (-----) obtained from tree A (SPC) and tree E (MTG).

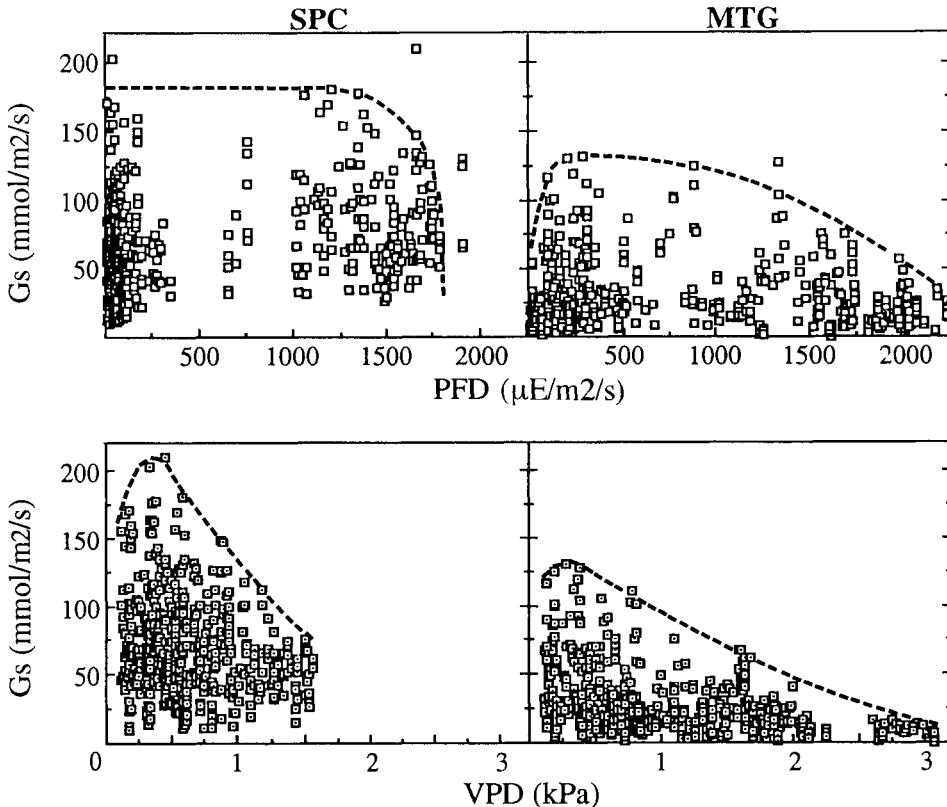
#### **Relationship of stomatal conductance to irradiance, vapor pressure deficit and tree water status**

Stomatal aperture is not associated with any constant PFD, VPD, or  $\psi_l$  value, which is common in such studies. Nevertheless, the large amount of data allows us to indirectly determine stomatal sensitivity to these factors. In fact, according to Jarvis (1976), provided that enough measurements have been made to cover the variable space, the upper limit of a scatter diagram would delineate the response of  $G_s$  to a particular independent variable when the others are not limiting. This latter condition is not always fulfilled, but boundary line analyses are reliable in such field studies (Hinckley *et al*, 1980). At SPC, maximum stomatal conductance is reached at very low irradiance, as is frequently the

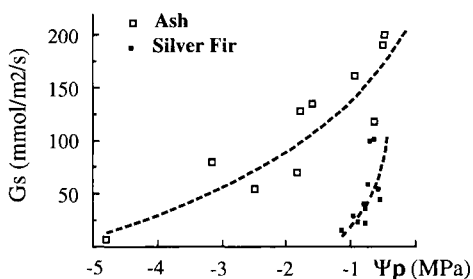


case in the field, and  $G_s$  stays at this level up to high PFD values (fig 7). At MTG, another factor interferes with PFD, probably VPD insofar as the scatter diagrams are similar. The response to VPD is particularly surprising, because it is the same at the 2 stands, and stomatal closure occurs for very low VPD values, about 0.3 kPa. Is the decrease of  $G_s$  with increasing VPD also due to the decrease of  $\psi_1$ ? As expected, these 2 parameters are correlated at both stands ( $r^2 = 0.634^{**}$ ,  $n = 90$  at SPC;  $r^2 = 0.291^{**}$ ,  $n = 80$  at MTG). So we can suppose that diagrams of  $G_s$ /VPD inte-

grate the influence of  $\psi_1$ . Nevertheless,  $\psi_1$  values corresponding to a 0.3 kPa VPD are  $-0.75$  MPa for SPC and  $-1$  MPa for MTG (refer to regression equations). These values are much higher than those which are known to occur at stomatal closure in conifers and are reported in the literature (Kaufmann, 1976; Running, 1976; Lopushinsky, 1969 in Kramer and Kozlowski, 1979). This does not prove that VPD may influence stomatal conductance in the field before bulk leaf water potential but it is suggestive. Of course, they can act simultaneously and in synergy later.



**Fig 7.** Scatter diagram of stomatal conductance plotted against irradiance (upper) and pressure vapor deficit (lower) for previous year needles. All measurements are taken into account. SPC (tree A):  $n = 497$ ; MTG (trees E + D):  $n = 627$ .



**Fig 8.** Comparison of decreasing of maximal stomatal conductance with decreasing predawn needle water potential between silver fir (trees E + D) and ash tree (*Fraxinus excelsior* L); from Carlier *et al* (1992) for data concerning ash, with the permission of the journal.

## DISCUSSION

The aim of this work was first to collect quantitative data concerning water relations of silver fir in a natural environment. Even at one dry stand where fir was growing near its ecological limits, the predawn needle water potential never fell below  $-1.14$  MPa, which generally represents a moderate water stress. Nevertheless, firs still suffered considerably, since all trees without exception and even mountain pines (*Pinus uncinata* Mill) showed a browning of their older needles, due to the strong reduction of water flow through the leaf for several days. Moreover,  $\Delta\psi$  was equal to  $-0.14$  MPa on this day. If a critical predawn needle water potential as defined by Aussenac and Granier (1978) exists, it is about  $-1$  MPa, a value higher than that observed in other pine species (Aussenac and Valette, 1982). Moreover,  $-1.8$  MPa seems to be the lower limit of leaf water potential reached by silver fir in the field, at least for previous-year needles of the middle crown. This value is close to that measured in *P. pinaster* (Loustau *et al*, 1990), and is much higher than that of *Cedrus atlantica* at Mont-Ventoux (Aussenac and Valette, 1982). Comparison of the main physiological parameters shows

similar observations in firs at the 2 stands. Maximal stomatal conductance is higher at SPC than at MTG. This is probably due to the lack of measurements at high soil water potential at this latter stand. The maximal value ( $150$ – $200$  mmol/m<sup>2</sup>/s, *ie* approximately  $0.4$ – $0.5$  cm/s) is high compared with other conifers (Hinckley *et al*, 1978).

A decrease of maximal stomatal conductance with decreasing predawn needle water potential has been known for years in the field (Running, 1976; Reich and Hinckley, 1989) as well as in controlled environments (Acherar *et al*, 1991). However, this decrease is dramatic in silver fir (fig 8). Like fir, the ash tree appreciates good water availability but frequently tolerates meso-xerophil conditions. Because of stomatal adjustment (Carlier *et al*, 1992), this species can maintain transpiration until a  $-5$  MPa predawn leaf water potential, whereas fir reaches the same level of transpiration when  $\psi_p$  is about  $-1$  MPa. In the same way,  $L_p$  is strongly reduced when a slight decrease of  $\psi_p$  occurs but recovers a high level just after a rainy spell irrespective of  $\psi_p$ , like stomatal conductance. Numerous hypotheses have been made concerning the increase of  $L_p$  during a period of drought (cavitation, death of fine roots, increasing of soil resistance, or alterations in root function) and any discussion would be useless. We will merely note the potential rapidity of the decrease. So, according to the variables we studied, fir exhibits a marked 'avoidance' strategy as defined by Ludlow (1989). This early response to drought of silver fir is somewhat stronger than that of other fir species which are known for their better adaptation to drought, such as *Abies bornmulleriana* originating in northern Turkey (Granier and Colin, 1990; Guehl *et al*, 1991).

What about stomatal sensitivity to VPD or leaf water potential? The fact that these 2 factors act in a concerted and similar manner makes the discrimination of their relative influences very difficult. It now seems clear

that humidity is not sensed by plants by a specific sensor but through the evaporation rate (Grantz, 1990), although detailed mechanisms remain unknown. Depending on the effects on decreasing  $G_s$  and  $E$  of leaf water potential when VPD increases, 2 types of response are exhibited by plants: a feedback response (probably the more common response); and a feedforward response as defined by Farquhar (1978), observed in some conifers (Jarvis, 1980; Meinzer, 1982). On a daily basis, the precocity of silver fir's stomatal closure before any sufficient transpiration leading to a significant decrease of leaf water potential, plus stomatal sensitivity to VPD as shown in figure 7, may be consistent with a feedforward response or at least indicates that the feedback response is not the only mechanism involved in stomatal closure. Furthermore, the feedforward response on cut twigs of *A. alba* has been observed by Guehl and Aussenac (1987) under controlled conditions, based on the only valid criterion, *ie*  $\Delta E/\Delta VPD < 0$  when VPD increases (Schulze, 1986).

Soil water conditions in the vicinity of roots can also directly influence stomatal movements. Bates and Hail (1981) have demonstrated that stomatal closure is not necessarily associated with changes in bulk leaf water potential but might be mediated by information coming from roots. Since then, evidence has been found that ABA or other phytohormones produced in the roots can influence stomatal conductance during water stress, even if only a part of the root is affected (Zhang *et al*, 1987; Davies *et al*, 1990). Changes in concentration of ABA in xylem sap cannot induce daily stomatal closure, but are related to the range of maximum stomatal conductance during the course of a drying cycle (Wartinger *et al*, 1990). These processes occur also in the field (Tardieu *et al*, 1992a,b). We have seen that during a dry period of several days silver fir trees integrate stress conditions, in particular by an early stomatal closure, but

that few millimetres of rainfall can selectively cause a large stomatal conductance, irrespective of predawn needle water potential. Actually, it is very difficult in such field studies to say whether this water modifies root–shoot communication, is rapidly conveyed at the vicinity of the surface roots and absorbed, or whether it modifies some cells water status in the leaf and increases stomatal aperture. Several mechanisms are surely implied. Whatever the case, this opportunistic behaviour allows silver fir to take advantage of the few summer rain spells in the dry stand.

Do firs native of the southern Alps represent an ecotype as proposed by some phytogeographers (Ozenda, 1964; Barbéro and Quèzel, 1975)? None of our results agrees with this assumption, except the lower decrease of stomatal conductance after the VPD threshold observed in MTG (fig 7). However, the considerable importance of natural regeneration in this area where seedlings are always exposed to full sunlight indicates that fir exhibits particular adaptation abilities. Larsen and Mekic (1991) have shown that origins of *A. alba* native of southern Italy are distinguishable from provenances of central Europe by a notably higher water-use efficiency of older needles. This may be the case for fir native of Briançonnais, as Guehl and Aussenac (1987) have also found differences between 2 provenances of *A. alba* concerning this physiological characteristic, with a better preservation of water-use efficiency during a period of drought for firs originating from dry areas.

What is the contribution of these results to the understanding of the ecology of silver fir? Water relations of fir are very close to that of pines despite marked differences in resistance to drought and geographical distribution. Actually, the ecological requirements of species can certainly not be understood by taking into account only one aspect of mature trees' physiology. The survival strategy of one species in a particular habi-

tat is also related to other characteristics like phenology or capacity of seed germination, and to other limiting factors like temperature. The 'avoidance' strategy is favourable for pines because it is linked to an optimal behaviour throughout the season, whereas fir does probably not optimize its water relations as soon as water fails. Monitoring photosynthesis and transpiration throughout the growing season now appears essential to prove this hypothesis and confirm the low water-use efficiency of twigs during water stress and observed under controlled environment.

Nevertheless, it now seems well established that fir's well-known sensitivity to atmospheric and edaphic drought is based more on the precociousness of its physiological reaction than the late reducing of its water vapor exchanges. However, differences on this point between provenances are not ruled out.

## CONCLUSION

Maximal stomatal conductance, maximal transpiration and soil-to-leaf hydraulic conductance of European silver fir decrease by 80% when predawn needle water potential reaches  $-1.1$  MPa. Furthermore, stomatal conductance decreases as soon as a  $0.3$  kPa VPD is reached, and minimum leaf water potential never dropped below  $-1.8$  MPa. Silver fir can exhibit similar water relation characteristics to pines and drought-resistant *Abies* species. Obviously, a strong avoidance strategy does not necessarily reveal a gain in resistance to drought, particularly for silver fir which likes habitats with good soil water retention and high rainfalls.

## ACKNOWLEDGMENTS

The author thanks JP Peltier for helpful suggestions during preparation of the manuscript, and

is also very grateful to the personnel of ONF (Office National des Forêts) and particularly to JM Brezard at Grenoble and P Clauss, JM Puthod and A Imbert at Briançon.

## REFERENCES

- Acherar M, Rambal S, Lepart J (1991) Evolution du potentiel hydrique foliaire et de la conductance stomatique de quatre chênes méditerranéens lors d'une période de dessèchement. *Ann Sci For* 48, 561-573
- Aussenac G (1980) Comportement hydrique de rameaux excisés de quelques espèces de Sapins et de Pin noir en phase de dessiccation. *Ann Sci For* 37, 201-215
- Aussenac G, Granier A (1978) Quelques résultats de cinétique journalière du potentiel de sève chez les arbres forestiers. *Ann Sci For* 35, 19-32
- Aussenac G, Valette JC (1982) Comportement hydrique estival de *Cedrus atlantica* Manetti, *Quercus ilex* L et *Quercus pubescens* Willd et de divers pins dans le Mont Ventoux. *Ann Sci For* 39, 41-62
- Barbéro M, Quèzel P (1975) Les forêts de Sapin sur le pourtour méditerranéen. *Ann Inst Bot Cavanilles* 32, 1245-1289
- Bates LM, Hall AE (1981) Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. *Öcologia (Berl)* 50, 62-65
- Becker M (1970) Transpiration et comportement vis-à-vis de la sécheresse de jeunes plants forestiers (*Abies alba* Mill *Picea abies* (L) Karsten *Pinus nigra* ARN ssp *laricio* Poir, *Pinus strobus* L). *Ann Sci For* 27, 401-420
- Becker M (1977) Contribution à l'étude de la transpiration et de l'adaptation à la sécheresse de jeunes plants résineux – Exemple de 3 sapins du pourtour méditerranéen (*Abies alba*, *A Nordmanniana*, *A numidica*). *Ann Sci For* 137-158
- Becker M (1989) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Can J For Res* 19, 1110-1117
- Bîndiu C (1971) Le régime hydrique, facteur limitatif pour l'accroissement radial du sapin. *Rev Roum Biol Botanique* 16, 405-412
- Carlier G, Peltier JP, Gielly L (1992) Comportement hydrique du frêne (*Fraxinus excelsior* L) dans une formation montagnarde mésoxérophile. *Ann Sci For* 49, 207-223
- Davies WJ, Mansfield TA, Hetherington AM (1990) Sensing of soil water status and the regulation of plant growth and development. *Plant Cell Environ* 13, 709-719
- Farquhar GD (1978) Feedforward responses to humidity. *Aust J Plant Physiol* 5, 787-800
- Granier A, Colin F (1990) Effets d'une sécheresse édaphique sur le fonctionnement hydrique d'*Abies*

- bornmulleriana* en condition naturelles. *Ann Sci For* 47, 189-200
- Grantz DA (1990) Plant response to atmospheric humidity. *Plant Cell Environ* 13, 667-679
- Guehl JM, Aussenac G (1987) Photosynthesis decrease and stomatal control of gas exchange in *Abies alba* Mill in response to vapor pressure difference. *Plant Physiol* 83, 316-322
- Guehl JM, Aussenac G, Bouachrine J *et al* (1991) Sensitivity of leaf gas exchange to atmospheric drought, soil drought, and water-use-efficiency in some Mediterranean *Abies* species. *Can J For Res* 21, 1507-1515
- Hinckley TM, Lassoie JP, Running SW (1978) Temporal and spatial variations in the water status of forest trees. *For Sci* 24, Monograph 20, 79 p
- Hinckley TM, Duhme F, Hinckley AR, Richter H (1980) Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. *Plant Cell Environ* 3, 131-140
- Jacamon M (1987) Guide de dendrologie – Tome I : conifères. ENGREF, Nancy, France, 88 p
- Jarvis PG (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies and in the field. *Phil Trans R Soc Lond* 273, 593-610
- Jarvis PG (1980) Stomatal response to water stress in conifers. In: *Adaptations of Plants to Water and High Temperature Stress* (NC Turner, PJ Kramer, eds), J Wiley and Sons, Interscience Publication, New York, USA, 105-122
- Kaufmann MR (1976) Stomatal response of Engelmann Spruce to humidity, light and water stress. *Plant Physiol* 57, 898-901
- Körner C, Cochrane PM (1985) Stomatal responses and water relations of *Eucalyptus pauciflora* along an elevational gradient. *Æcologia* 6, 443-455
- Kramer PJ, Kozlowski TT (1979) *Physiology of Woody Plants*. Academic Press, New York, USA, 811 p
- Larsen JB, Mekic F (1991) The geographic variation in European silver fir (*Abies alba* Mill). Gas exchange and needle cast in relation to needle age, growth rate dry matter partitioning and wood density by 15 different provenances at age 6. *Silvae genetica* 40, 188-198
- Levy G, Becker M (1987) Le dépérissement du sapin dans les Vosges : rôle primordial de déficits d'alimentation en eau. *Ann Sci For* 44, 379-402
- Loustau D, Granier A, El Hadj Moussa F (1990) Evolution saisonnière du flux de sève dans un peuplement de pins maritimes. *Ann Sci For* 21, 599-618
- Ludlow M (1989) Strategies of response to water stress. In: *Structural and Functional Responses to Environmental Stresses* (KH Kreeb, H Richter and TM Hinckley, eds) SPB Acad Publ bv, The Hague, The Netherlands, 269-281
- Meinzer FC (1982) The effect of vapor pressure on stomatal control of gas exchange in douglas fir (*Pseudotsuga menziesii*) saplings. *Æcologia (Berl)* 54, 236-242
- Oberlinkels M, Cadel G, Pautou G, Lachet B (1990) Zonation biogéographique des Alpes dauphinoises à partir de l'étude comparative des sapinières à *Abies alba* et des pessières à *Picea abies*. *Ann Sci For* 47, 461-481
- Ozenda P (1964) *Biogéographie Végétale*. Doin, Paris, France, 374 p
- Ozenda P (1985) La Végétation de la Chaîne Alpine dans l'Espace Montagnard Européen. Masson, Paris, France, 330 p
- Pallardy SG, Pereira JS, Parker WC (1991) Measuring the state of water in tree systems. In: *Techniques and Approaches in Forest Tree Ecophysiology* (JP Lassoie and TM Hinckley, eds) CRC press, Boca Raton, 27-76
- Reich PB, Hinckley TM (1989) Influence of predawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance of two oak species. *Funct Ecol* 3, 719-726
- Richard L, Pautou G (1982) Alpes du nord et Jura méridional. Notice détaillée de la carte de la végétation de la France au 1/200 000, feuilles d'Annecy et de Grenoble. CNRS, 316 p
- Running SW (1976) Environmental control of leaf water conductance in conifers. *Can J For Res* 6, 104-112
- Scholander PM, Hammel HT, Brastreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. *Science* 148, 339-346
- Schulze ED (1986) Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Ann Rev Plant Physiol* 37, 247-274
- Serre-Bachet F (1986) Une chronologie maîtresse du Sapin (*Abies alba* Mill) du Mont Ventoux (France). *Dendrochronologia* 4, 87-96
- Sokal RR, Rohlf FJ (1981) *Biometry. The Principles and Practice of Statistics in Biological Research*. Freeman and Co, 859 p
- Tardieu F, Zhang J, Davies WJ (1992a) What information is conveyed by an ABA signal from maize roots in drying field soil? *Plant Cell Environ* 15, 185-191
- Tardieu F, Zhang J, Katerji N, Bethenod O, Palmer S, Davies WJ (1992b) Xylem ABA controls the stomatal conductance of field-grown maize subjected to soil compaction or soil drying. *Plant Cell Environ* 15, 193-197
- Wartinger A, Heilmeier H, Hartung W, Schulze ED (1990) Daily and seasonal course of leaf conductance and abscisic acid in the xylem sap of almond trees (*Prunus dulcis* (Miller) DA WEBB under desert conditions. *New Phytol* 116, 581-587
- Zhang J, Schurr U, Davies WJ (1987) Control of stomatal behaviour by abscisic acid which apparently originates in the roots. *J Exp Bot* 38, 1174-1181