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Environmental and endogenous controls on leaf- and stand-level water conductance in a Scots pine plantation

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Abstract – Measurements of leaf level gas exchange and conductance, tree transpiration via sapflow monitoring, soil moisture and water extraction, predawn water potential, and xylem abscisic acid (ABA) concentration were carried out over the course of the 1993 and 1994 summer seasons at the Hartheim *Pinus sylvestris* plantation on the Upper Rhein Plain, Germany. Periodic leaf level conductance determinations with porometry established a maximum value of ca 280 mmol m^{-2} s^{-1} (13.6 mm s^{-1}). Half maximal conductance was attained at 40 µmol m^{-2} s^{-1} and 90 % of light saturation occurred at ca 500 µmol m^{-2} s^{-1} PPFD. Conductance decreased strongly with increases in vapor pressure deficit above 10 hPa, while the temperature optimum was 22 °C at light saturation. Strong restrictions on maximum conductance at both leaf and stand levels were apparent below a soil moisture content of 16 volume percent. Although less strongly, conductance also decreased with initial drying of the upper soil layers and decreases in predawn water potential from –0.4 to –0.6 MPa. In this range of water potential change, xylem ABA increased to between 200 and 500 nmol L^{-1}. Thus, an immediate leaf-level reaction to the onset of summer weather conditions is observed, i.e. leaf conductance and water use decrease. We hypothesize that ABA functions as a key control on water balance, transmitting information about soil water status and endogenously modifying canopy response in order to budget water and avoid extensive cavitation damage in most years. Transpiration potential of the stand was reduced by thinning during autumn 1993 in approximate proportion to changes in leaf area index and sapwood area. Simultaneous observations of sapflow and conductance have allowed us to view the effects of leaf conductance on whole plant water use, while thinning revealed the effects of stand level phenomena on conductance regulation. (© Inra/Elsevier, Paris.)

conductance / transpiration / abscisic acid / drought / *Pinus sylvestris*

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Résumé – Contrôle environnemental et endogène de la conductance stomatique et du couvert dans une plantation de pins sylvestres. Des mesures de l'échange du gaz et de la conductance stomatique de l'eau, de la transpiration par deux méthodes de mesure du flux de sève, de l'humidité du sol et de l'extraction de l'eau du sol, du potentiel hydrique foliaire de base et de la concentration en acide absissique (ABA) dans l'aubier ont été réalisées au cours des étés 1993 et 1994 dans une plantation de pins sylvestres dans la plaine rhénane au sud-ouest de l'Allemagne, près du village de Hartheim. Les mesures périodiques de la conductance stomatique ont montré une valeur maximale de 280 mmol m^{-2} s^{-1} (13,6 mm s^{-1}). Le demi-maximum de la conductance stomatique était atteint pour un rayonnement de 40 μmol m^{-2} s^{-1} et la conductance était établie à 90 % du maximum lors d'une exposition à 500 μmol m^{-2} s^{-1}. La conductance était diminuée rapidement dès que le déficit de saturation de l'air dépassait 10 hPa. L'optimum de la conductance était atteint pour une température de 22 °C, en condition de lumière saturante. Au-dessous d'une humidité volumique du sol de 16 %, la conductance foliaire ainsi que la conductance du couvert étaient fortement limitées. La conductance diminuait aussi, mais moins fort, pour un dessèchement initial des couches supérieures du sol, correspondant à une diminution de –0,4 à –0,6 MPa du potentiel hydrique foliaire de base. Dans les limites de cette variation du potentiel hydrique, la concentration de l'ABA dans l'aubier est passée de 200 à 500 nmol l^{-1}. Ainsi, une réaction immédiate a pu être observée au niveau des feuilles au moment de l'installation des conditions estivales, c'est-à-dire une diminution de la conductance stomatique et de consommation en eau. Nous supposons que l'ABA occupe une position clé dans le bilan hydrique en transmettant des informations sur les conditions hydriques dans le sol et en modifiant la réponse du peuplement à ces conditions pour maintenir le budget d'eau, et pour protéger les arbres contre des dommages durables causés par cavitation. La transpiration potentielle du couvert a été diminuée par une éclaircie en automne 1993, approximativement proportionnellement aux modifications de la surface du bois d'aubier et de l'indice foliaire (LAI). Les mesures simultanées de flux de sève et de conductance nous ont permis d'examiner les effets de la conductance stomatique sur l'utilisation de l'eau à l'échelle de l'arbre, tandis que l'éclaircie révélait les effets des phénomènes à l'échelle du peuplement sur la régulation de la conductance stomatique. (© Inra/Elsevier, Paris.)

conductance stomatique / transpiration / acide abscissique / sécheresse / pin sylvestre

1. INTRODUCTION

The conductance for water vapor transfer from the vegetation to the atmosphere is a key parameter for describing ecosystem function and the environmental relations of plants. Due to tight atmospheric coupling in forest stands, this conductance is dominated by time-dependent physiological processes governing the opening and closing of the stomata, which determine patterns in water use, in energy balance, and in nutrient relations as well as the fixation of CO_2 and uptake of pollutants such as SO_2 and O_3 [25]. The relationship or response of conductance at both leaf and stand level to environmental variables is similar and reasonably well described [24, 26, 32, 51]; conductance increasing with increase in radiation, but decreasing with increase in leaf to air vapor pressure deficit and with decrease in soil water availability.

The strong correlation between leaf CO_2- and water vapor-exchange has been exploited to develop phenomenological stomatal models [4–6, 31] which offer promise in attempts to predict atmospheric coupling, forest stand growth and catchment water balances under conditions of elevated atmospheric CO_2, i.e. where carbon allocation considerations have suggested the manner in which CO_2-uptake potentials may change. Tenhunen et al. [45] demonstrated that the complex net photosynthesis response surface with respect to radiation, temperature and vapor pressure deficit along with an endogenous 'soil coupling' influence could be effectively related to daily, seasonal and annual changes in conductance of a Mediterranean oak species subjected to a large range in radiation, temperature and soil water availability.

Despite having gained knowledge during recent decades of the primary factors influencing stomatal conductance in natural habitats, surveys demonstrate that large unexplained regional and continental scale heterogeneity in response is found for well-studied species (e.g. Ogink-Hendrik [39], Peck and Mayer [41] and Alsheimer et al. [1] with respect to Norway spruce) which may be due to acclimation to natural gradients or to varying degrees of anthropogenic ecosystem impacts and manipulations [26, 42]. In addition, species-specific sensitivity with respect to stress factors is poorly described, e.g. a literature search provided little information on the shape of the response function for *Pinus sylvestris* with respect to soil water availability.

The purpose of the present study with *P. sylvestris* was to define the response sensitivities of conductance at both leaf and stand levels to radiation, vapor pressure deficit and soil water availability. We chose to study a long-term site which is regularly subjected to summer drought, but of varying degree. The comparison of leaf- and stand-level response provides important baseline data for the development of up-scaling gas exchange model hierarchies [13, 14]. The models can in turn be used to compare stands and to help identify differences in Scots pine forest controls on gas exchange along environmental gradients. Additionally, we examined the relationship between conductance and xylem sap abscisic acid (ABA) concentration which may act as an integrative root to shoot signal, conveying information on root system status [21, 46].

2. MATERIALS AND METHODS

Measurements were conducted in a 35-year-old *P. sylvestris* L. (Scots pine) plantation in southwest Germany. The site is situated on the alluvial floodplain of the Rhine River 20 km west of Freiburg im Breisgau and close to the village of Hartheim. As a consequence of water management measures in this region during the past 150 years, the bed of the Rhine River deepened by erosion and was subsequently sealed, such that vegetation on the alluvial terraces no longer has access to groundwater. Precipitation in the Upper Rhine Valley is strongly influenced by the north to south extension of the Vosges Mountains, which creates an obstacle to humid air masses from the main westerly wind direction [40]. The shallow nature of the top soil layer and the high portion of coarse textured soil increase the probability of extreme and extended drought exposure of the forest [20]. Further information about the Hartheim plantation is given by Jaeger and Kessler [23]. Stand characteristics before and after thinning in autumn 1993 are described in *table I*.

During the summers of 1993 and 1994, microclimate profiles were observed within the Hartheim forest stand. Meteorological data above the canopy, such as air temperature, air humidity and global radiation, were provided by the Meteorological Institute, University of Freiburg. A diffusion porometer (WALZ CQP130i, Effeltrich, Germany) with a H_2O/CO_2 differential BINOS infrared gas analyser (Leybold Heraeus, Hanau, Germany) was used on 38 d in 1994 to monitor transpiration, assimilation and conductance of terminal shoots. Observations were carried out in different crown levels of two Scots pine trees that were accessible from a tower. During each experiment, gas exchange was observed continuously on the same sample branch over the course of the day. Mean values of gas exchange were logged at 2-min intervals and these were then used to obtain 10-min mean values. Additionally, a LI-COR H_2O porometer (Li-1600, Lincoln, USA) was used in four crowns to measure daily courses of shoot transpiration and water vapor conductance. The time increment between measurements was 2 h for each branch sampled.

Xylem water potential was measured at predawn with a P70 pressure chamber (PMS, Corvallis, Oregon) with a sampling frequency of 1 week in 1993 and 2–3 d in 1994. Each

Table I. Characteristics of the Hartheim Scots pine stand before and after thinning.

General characteristics		
Location	southern Upper Rhine Valley, Germany:	
Geographical coordinates	47°56' N, 7°36' E	
Elevation	202 m a.s.l.	
Forest stand extension	ca 5 000*1 200 m; station in the center	
Tree species	*Pinus sylvestris*	
Major understory species; see Wedler et al. [47, 48]	*Brachypodium pinnatum, Carex flacca, Carex alba*	
Depth to groundwater	ca 7 m	
Age	36 years	
Soil		
Texture	sandy to silty on fluvial gravel and coarse sand	
Depth of the upper soil layer	15–75 cm; mean value 40 cm	
Field capacity (vol.%)	31.4	
Wilting point (vol.%)	11.7	
Tree stand	1992	1994
Projected LAI (m^2 m^{-2})	3	1.9
Density (trees ha^{-1})	3 753	1 754
Mean height (m)	11.5	12.3
Mean breast height diameter (cm)	10.8	12.9
Basal area (cm^2 m^{-2})	36.7	24.1
Sapwood area (cm^2 m^{-2})	33.4	22.1

observation time is recorded as the arithmetic mean value of 3–5 Scots pine shoots taken from the upper crown level. Xylem sap for determination of ABA was obtained from the same branch samples as for water potential determinations by increasing the pressure 0.2–0.3 MPa above the balancing pressure and collecting the exuded sap into a glass capillary. Samples were taken from approximately half of the branches used for predawn potential observations. Sample volume was between 10 and 50 μL. The samples were immediately frozen in liquid nitrogen and freeze dried prior to determination of xylem sap ABA concentration with the highly specific and sensitive ELISA immunoassay test as described by Mertens et al. [35].

Two methods for measuring xylem sapflow were employed to measure tree transpiration: thermal flowmeters constructed according to Granier [16, 17] and the steady-state, null-balance method of Cermák and co-workers [10, 28, 30]. With the Granier method, cylindrical heating and sensing elements were inserted into the trunks at breast height, one above the other ca 15 cm apart, and the upper element was heated with constant power. The temperature difference sensed between the two elements was influenced by the sap flux density in the vicinity of the heated element. Sap flux density was estimated via calibration factors established by Granier [16]. With the steady-state, null-balance method, a constant temperature difference of 3 K was maintained between a sapwood reference point and a heated stem segment. The mass flow of water through the xylem of the heated area is proportional to the energy required in heating. During 1993, 15 null-balance sensors were used to measure sapflow, while during the summer of 1994, five null-balance systems and ten installations of the Granier-type were employed. Data were logged every 10 s and averaged over 10-min intervals. To standardize the further processing of the data, the output values for both systems were converted to sapflux density (sapflow in kg cm^{-2} h^{-1}). As described in Köstner et al. [28, 29] no difference was observed between the range of flux densities and time-lag of the sapflow systems. The arithmetic mean sapflux density for all trees was multiplied by the stand sapwood area at the height of the sensor to obtain estimates of stand transpiration.

Six time domain reflectometry (TDR) sensors (Trime P3EZ, IMKO, Germany) were used to determine short-term fluctuations in soil moisture (5-min sampling intervals) in the upper soil layer and along one soil profile. In addition, ten soil cores were taken weekly to gravimetrically determine the spatial distribution of soil moisture content (integrating the water content from 0–40 cm) within the forest stand.

Canopy conductance was estimated as total water conductance assuming a tight atmospheric coupling and exclusive control by the stomata [27, 33]. The time-lag between transpiration and sapflow was variable (0–1 h) and not considered for the calculation of conductance:

$$g_{tw} = \frac{E}{D_a} \cdot \rho_a \cdot G_v \cdot T_a \qquad (1)$$

where g_{tw} is total water conductance at the canopy level (mm s^{-1}), E is transpiration per time increment (mm s^{-1}), D_a is air saturation deficit (kPa), ρ_a = density of air (kg m^{-3}), G_v is gas constant of water vapor (0.462 m^3 kPa kg^{-1} K^{-1}), and T_a is air temperature (K).

Water vapor conductance at the leaf level was calculated according to Field et al. [15], assuming a negligible boundary layer in the ventilated cuvette:

$$g_s = \frac{E\left(1 - \left(\frac{w_i + w_0}{2}\right)\right)}{w_i - w_0} \qquad (2)$$

where g_s is stomatal conductance for water vapor, E is measured transpiration in (mmol m^{-2} s^{-1}), w_i is water content of the air inside the leaf (mol mol^{-1}), and w_0 is water content of the air outside the leaf in the chamber (mol mol^{-1}).

All calculations of conductance at the leaf and at the stand scale are related to projected leaf area which is total leaf area divided by a factor of 2.57.

3. RESULTS

Plotting of observed conductances from daily courses as a function of a single environmental variable is extremely useful, despite the difficulties imposed by actual response to simultaneous change in several factors. While a highly scattered collection of points is obtained *(figure 1)*, these plots reveal:

a) the dependency of stomatal conductance in response to the variable in question under conditions optimal for other variables influencing response. This is seen as the upper limit or borderline of the plotted observations;

b) the influence of a secondary filtered variable on conductance, i.e. by limiting the range of observations selected for plotting with respect to a secondary variable, a series of borderlines may be defined which describe the interacting effects of the two variables;

c) information about the response to environmental factors that are difficult or impossible to investigate under laboratory conditions, such as the influence of soil moisture on the leaf conductance of large trees.

Nevertheless, many observations are required and sampling should be carried out over long periods [39]. *Figure 1* shows the distribution of observed shoot water vapor conductance values for *P. sylvestris* as related to temperature *(figure 1a)*, air saturation deficit *(figure 1b)*, and photosynthetically active photon flux density (PPFD; *figure 1c, d*). The plot of stomatal conductance against air temperature was more triangular than bell-shaped. Maximum conductance occurred at 22 °C which corresponds to the mean daily maximum temperature at the site from the beginning of May until October. The temperature response curve at otherwise optimum conditions may be approximated with two linear segments below and above 22 °C. With decreasing PPFD, maximum

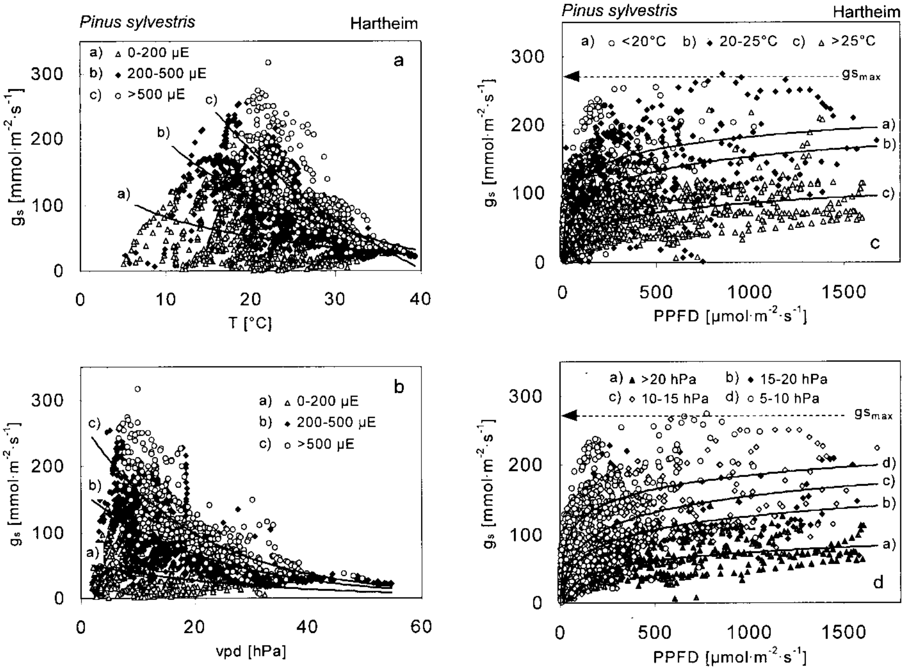

Figure 1. Conductance of branch ends determined by porometry during summer 1994 plotted versus: (a) ambient air temperature where logarithmic regressions are fit to the observations in different classes of irradiance as shown; (b) vapor pressure deficit where logarithmic regressions are fit to the observations in different classes of irradiance as shown; (c) irradiance where saturation curves are fit to the observations in different classes of temperature as shown and described in text; and (d) irradiance where saturation curves are fit to the observations in different classes of vapor pressure deficit as shown.

conductance occurs at lower temperatures as suggested by the logarithmic regressions applied to data in different PPFD ranges in the figure (best estimates for the optimum with PPFD of 500 µmol m^{-2} s^{-1} at approximately 19 °C; at 200 µmol m^{-2} s^{-1} approximately 17 °C).

Ignoring the question of whether a direct effect is observed or whether response is mediated via leaf water content [2, 3, 36, 37], air vapor pressure deficit strongly influences conductance of *P. sylvestris*. Stomatal conductance as related to water saturation deficit is left-skewed with a maximum at 10 hPa. Above this vpd value, the conductance decreases approximately logarithmically toward zero. During clear nights and in early morning hours, condensation was occasionally observed in the porometer cuvette and tubing. For this reason, values observed below 3 hPa have been excluded from the analysis. A shift in the maximum conductance or shape of the relationship between saturation deficit and conductance with differing irradiance was not apparent. However, the maximum conductance decreased from 280 mmol m^{-2} s^{-1} at PPFD observations > 500 µmol m^{-2} s^{-1} to 250 mmol m^{-2} s^{-1} with PPFD from

200–500 µmol m^{-2} s^{-1} and to 190 mmol m^{-2} s^{-1} with PPFD below 200 µmol m^{-2} s^{-1} (as judged from the upper limit of the scattergram).

The scatter obtained between stomatal conductance and irradiance *(figure 1c, d)* was examined with respect to a saturation response curve [i.e. $g_s = g_{smax}/(1 + K_s/\mathrm{PPFD})$]. The value of $g_{smax}/2$ (140 mmol m^{-2} s^{-1}) is reached at K_s = 40 µmol m^{-2} s^{-1}; 90 % of light saturation occurs at ca 500 µmol m^{-2} s^{-1}. Partitioning the data set into temperature or saturation deficit classes reveals the expected decrease of conductance at high temperatures and high values of vpd. There was no apparent change in the light saturation level of 500 µmol m^{-2} s^{-1} among temperature and vpd classes.

Based on the 2-min mean values of gas exchange, hysteresis was observed in the response of stomatal conductance to changing light conditions *(figure 2)* as found by others for *P. sylvestris* [38, 50]. In the example shown for 13 August 1994, air temperature and vpd remained relatively constant and in a range where maximum conductance could be attained. As seen in *figure 2,* the temporal maxima are not in phase with radiation changes but are delayed by 8–15 min. Thus, with frequent change in PPFD in the early afternoon, there is almost no stomatal response. While conductance changed slowly, the effects of fluctuating light on net photosynthesis were rapid, indicating that the cuvette system itself did not substantially contribute to the time lags seen. Greater conductance is observed during the morning hours than in the afternoon which cannot be explained as a response to above-ground microclimate conditions. This general time-dependent effect seems related to changes in internal water stores.

The relationship of maximum stomatal conductance on individual days to observed soil moisture is shown in *figure 3a.* The data suggest that maximum leaf level conductance without water stress was the same during both years. Due to the thinning of the Hartheim stand in autumn 1993 and due to higher precipita-

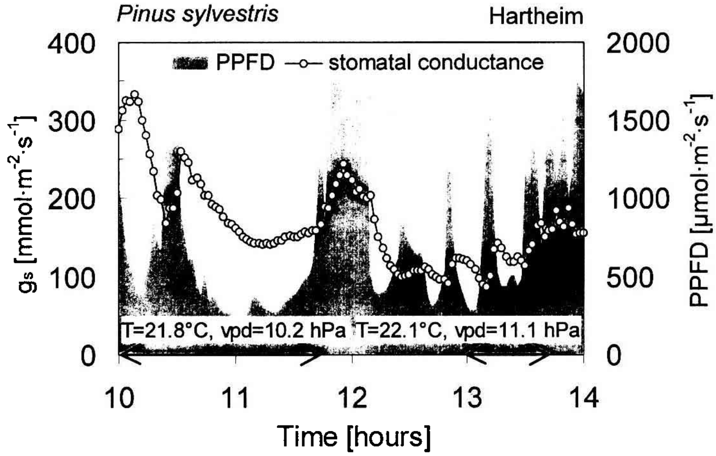

Figure 2. Time course of leaf level conductance in response to natural changes in PPFD on 13 August 1994 in the upper crown level. Arrows indicate periods with an almost constant temperature and vpd as indicated.

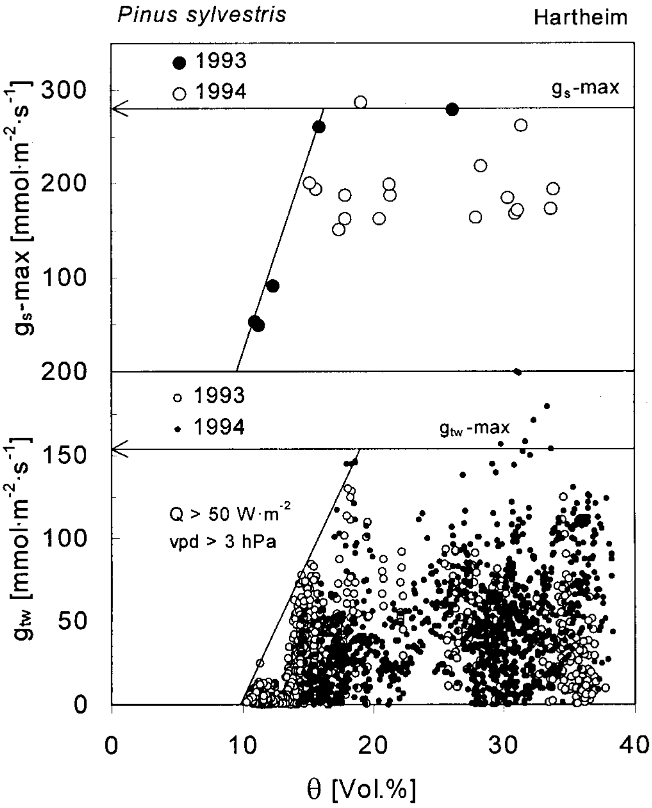

Figure 3. Water vapor conductances plotted versus soil water availability: (a) pooled maximum values at leaf level observed with porometry during diurnal courses in 1993 and 1994; (b) canopy conductance values scaled-up from sapflow measurements during 1993 and 1994.

tion input, the soil moisture in 1994 decreased only to ca 16 volume percent and had a limited effect on conductance. Pooled data from 1993 and 1994 reveal a strong limitation on maximum daily stomatal conductance as soon as soil water decreases below 16 volume percent. The maximum stomatal conductance of ca 280 mmol m^{-2} s^{-1} obtained with the LI-COR null-balance porometer agreed well with data from the WALZ measurement system. A more complete picture of response to water stress is obtained from the continuous tree transpiration measurements. At the limit of the scatter plot, maximum stand water conductance decreased linearly with reduced soil water content *(figure 3b)* below a soil moisture of ca 16 volume percent. Conductances at stand level are significantly lower than at the leaf level since they reflect the response of the average leaf under conditions of reduced light intensity. The absolute values of maximum stand conductance in 1993 (100 mmol m^{-2} s^{-1}) were in general much lower than in 1994 (200 mmol m^{-2} s^{-1}) despite greater LAI due to the effects of strong drought (discussed further below).

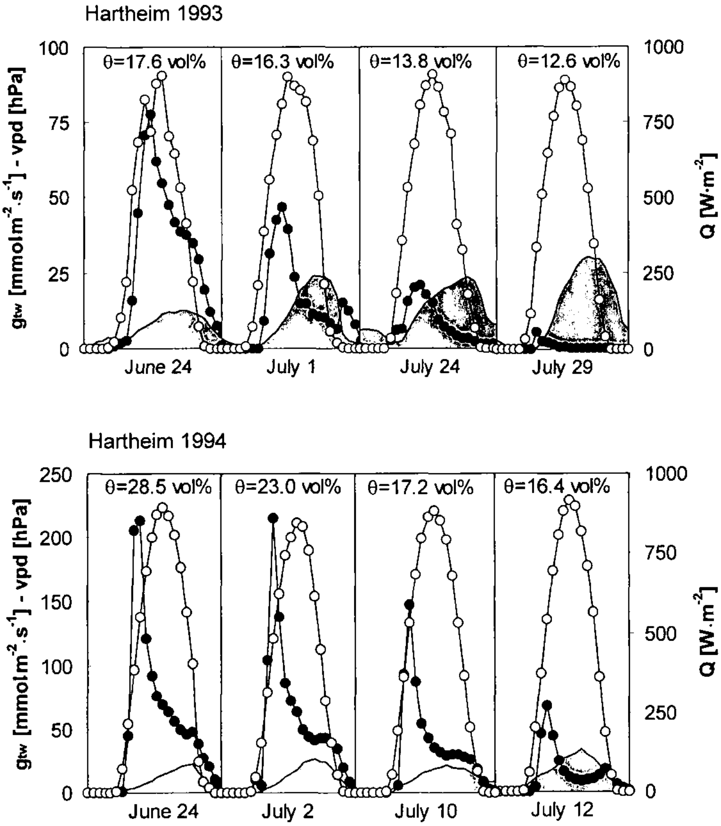

Figure 4. Daily patterns in canopy conductance (closed circles), global radiation (open circles), and vapor pressure deficit (shaded) on clear days and at different stages of soil drying during 1993 (a) and 1994 (b).

The effects of successive reductions in soil water availability on daily courses of stand conductance are illustrated for the summer periods of 1993 and 1994 in *figure 4.* Four clear days with comparable meteorological conditions have been chosen. Maximum conductance is reached in the morning hours and decreases as vpd increases and as water is removed from plant internal storage over the course of the day. Maximum conductance decreases continously with decreasing water availability as illustrated in *figure 3.* The daily pattern of water use remains much the same. In the driest situation observed on 29 July 1993, stand conductance was essentially zero throughout the day.

Seasonal changes in tree physiological parameters during 1993 and 1994 are shown in *figures 5* and *6*. A long period of restricted water availability occurred during July 1993 which was terminated with thunderstorms at the beginning of August. Predawn water potential of the pines decreased during drought to −1.5 MPa (*figure 5* upper panel), increased with the precipitation in August to –0.6 MPa, and recovered with additional precipitation to

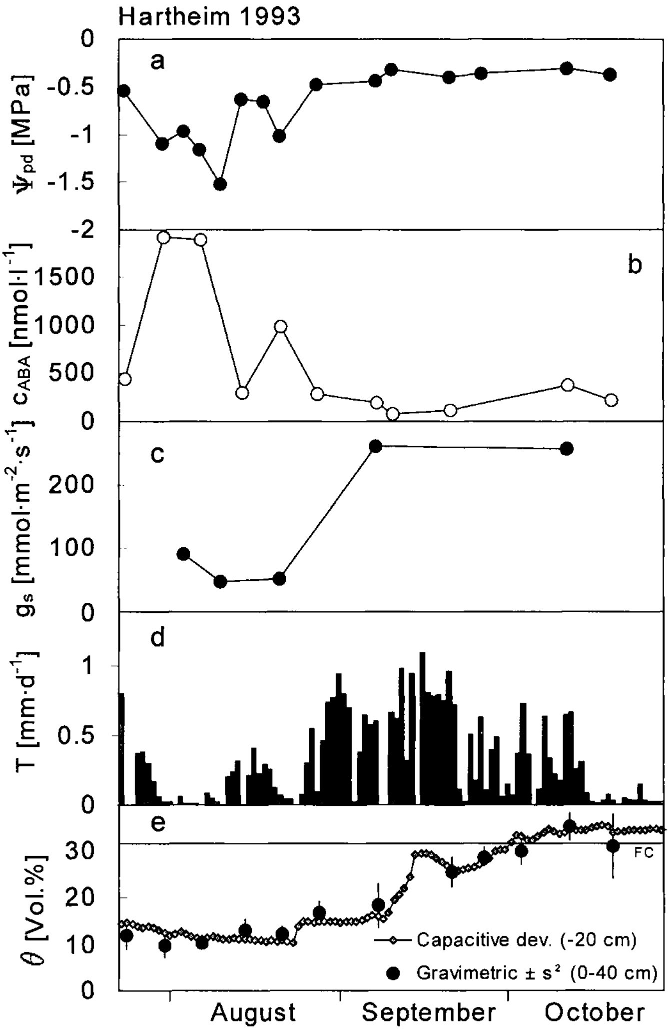

Figure 5. Observed seasonal courses during summer 1993 for (a) predawn water potential; (b) xylem sap abscisic acid concentration; (c) shoot maximum daily conductance; (d) daily sums of stand transpiration; and (e) soil moisture. FC = field capacity.

the winter level of –0.4 MPa. While a general correlation is seen with soil moisture measured at 20 cm and the store integrated from 0–40 cm, it is obvious that the trees are reacting strongly to precipitation input to the upper soil layer. Water potential recovery is much more rapid than are increases in these soil moisture measures. Xylem ABA concentration is strongly correlated with predawn water potential (*figure 5*). Maximum values of about 2000 nmol L^{-1} were recorded at the beginning of August during severe drought. After recovery from drought in the fall,

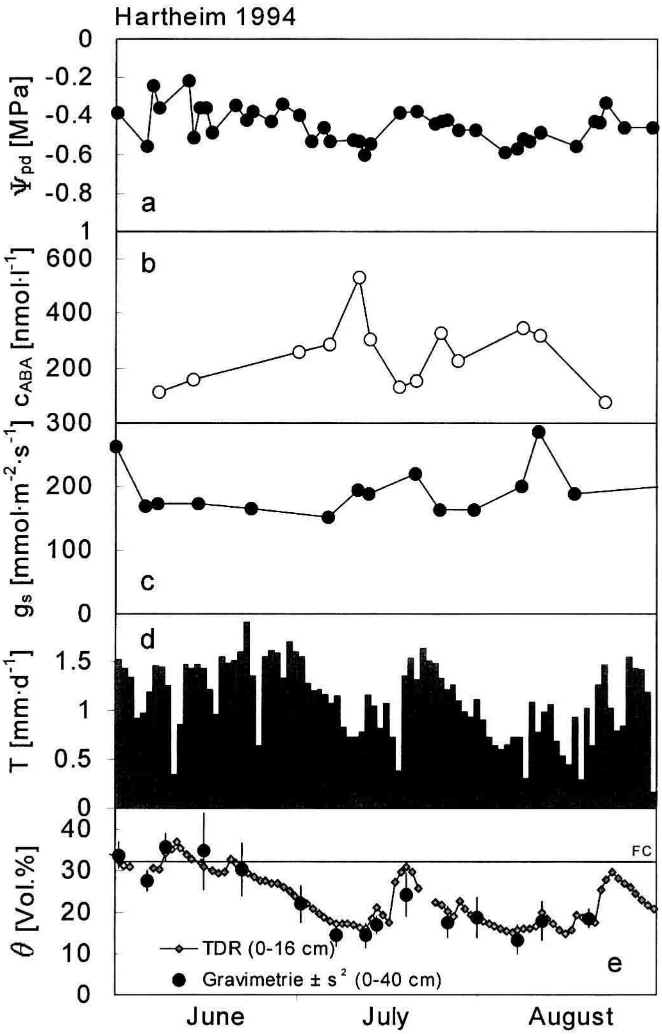

Figure 6. Observed seasonal courses during summer 1994 for (a) predawn water potential; (b) xylem sap abscisic acid concentration; (c) shoot maximum daily conductance; (d) daily sums of stand transpiration; and (e) soil moisture. FC = field capacity.

ABA concentration remains between 100 and 200 nmol L^{-1}. The observed maximum conductances at leaf level decreased to < 50 mmol m^{-2} s^{-1} during stress *(figure 3)* and recovered to 250 mmol m^{-2} s^{-1} in the fall. While nighttime water storage permitted conductance values of 50 during the morning hours in summer, daily transpiration was severely restricted due to subsequent strong reductions in conductance *(figure 4)*. Stand transpiration was strongly correlated with predawn water potential and xylem ABA concentration. A sensitive reaction to ABA appeared to occur between 0 and 1 000 nmol L^{-1}. Refilling of the soil water store in September 1993 increased daily transpiration to about 1 mm d^{-1}. This relatively low value is due to low available energy during this period.

Due to frequent rains, soil moisture was more variable during summer 1994 *(figure 6)*. The soil water store was rapidly emptied by transpiration but replenished by rainfall events. Due to rainfall and thinning of the stand during the previous winter, trees were not subjected to strong reductions in water availability. Predawn water potential remained between –0.4 and –0.6 MPa throughout the summer. Nevertheless, soil moisture reductions in mid-July and beginning to mid-August are sensed by *P. sylvestris* as seen in the time course for xylem ABA. Effects of the small reductions in predawn water potential are seen on stomatal conductance as previously reported for Mediterranean shrubs [46]. The response to reductions in available water may be amplified via the ABA control mechanism. Maximum conductance at the leaf level decreased to 150 mmol m^{-2} s^{-1} with moderate water shortage. Despite reduction in LAI from 3 to 2, water use (1.5 mm d^{-1}) remained above the levels measured during summer 1993 due to greater leaf conductances and large atmospheric demand. The importance of integrating soil moisture effects on conductance over daily courses is evident; coincidence between changes in the soil moisture store and the seasonal course of daily transpiration is high.

The most important correlations resulting from the seasonal observations are summarized in *figure 7a–f. Figure 7a, b* illustrates the overall relationship between maximum water conductance, shoot predawn water potential and soil moisture content. Based on the curvi-linear fits shown, a predawn potential value of approximately –0.6 MPa can be viewed as separating two phases of stomatal response to drought (cf. [44]). Initial

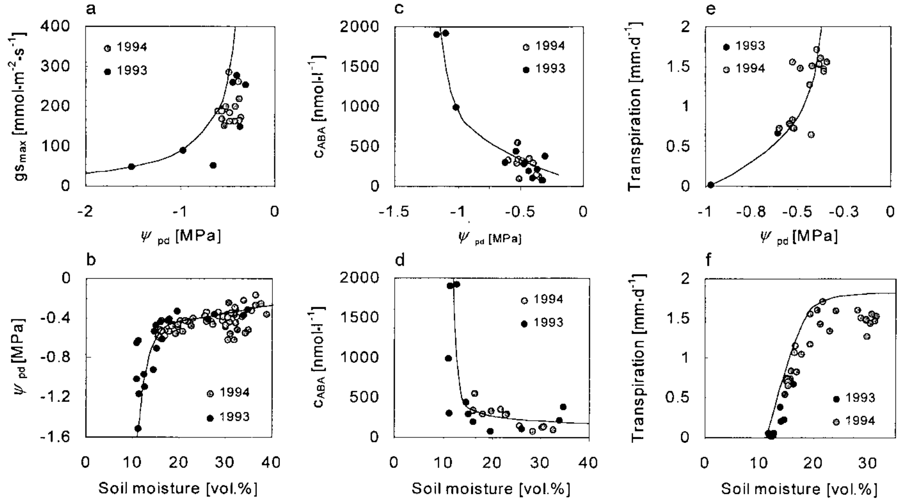

Figure 7. Relationships observed between predawn water potential or soil moisture and shoot conductance, xylem sap ABA concentration, and daily sums of stand transpiration. For both (e) and (f) only data from clear days are plotted.

decreases in water potential (–0.4 to –0.6 MPa with no obvious threshold) associated with drying of the upper soil layers lead to strong stomatal closure and savings of water. The largest changes in conductance occur during this phase. During the second phase as water potential decreases below –0.6 MPa and even lower soil levels dry, 'very conservative behavior' is exhibited by the plants with stomata opening for only very brief periods during the morning to replenish carbon pools. At this point, physiological mechanisms are no longer able to stabilize predawn water potential and water relations. Changes in xylem ABA concentration at predawn similarly suggest two phases in response to drought. Increased ABA concentrations in the range 0 to 500 nmol L^{-1} occur as water balance is maintained within a restricted range via reduced stomatal conductance. As soil drying results in the inability to maintain predawn water potential above –0.6 MPa *(figure 7c)*, very strong increases in ABA are associated with conservative controls on water use mentioned above (cf. [21, 46]). Assuming that plant available water is stored in the upper 40 cm of the soil, the wilting point is at 11.7 volume percent and that field capacity is 31.4 volume percent (see *table I*), maximum extractable water is ca 79 mm. The transition or change in plant behavior discussed above occurs at a soil water storage of ca 17 mm.

In terms of changes in stand transpiration, transitions in response are not observed at the same soil moisture levels as for conductance and ABA. Instead a gradual change in daily water use occurs. It must be remembered that over the course of these measurements both vpd and temperature are changing which results in a longer period of maximal transpiration despite initial restriction of water use via stomatal closure. Despite thinning which decreased stand density by half and xylem sapwood area to two thirds of that in 1993 *(table I)*, stand transpiration (rate of soil water extraction) in relation to soil moisture content below 16 volume percent was approximately the same during both years. Thus, individual trees appeared to conduct more water at this soil moisture level during 1994. It is not clear whether these observations are an artifact of the time sequence of change in conditions, internal regulatory phenomena, and hysteresis effects, or whether the trees have actually adjusted their response (greater conductance as shown in *figure 6*) to fully utilize the available water resource.

4. DISCUSSION AND CONCLUSIONS

The shape of stomatal response curves derived by analyzing the upper limits of scatter plots *(figure 1)* are consistent with results that have been obtained by other methods for pine and coniferous species. Granier and Lousteau [18] found that light saturation of stomatal conductance for *P. pinaster* occurred at 400 µmol m^{-2} s^{-1} PPFD. They estimated a maximum stomatal conductance of 12.9 mm s^{-1} based on projected leaf area, while we determined a value of 13.6 mm s^{-1} (280 mmol m^{-2} s^{-1}) for *P. sylvestris* in the Hartheim stand. Bernhofer et al. [8] and Granier et al. [19] reported a maximum conductance of 12.5 and 13 mm s^{-1} for a period in May 1992 at Hartheim. Slightly higher maximum conductances of ca 16 mm s^{-1} were reported by Beadle et al. [7] for *P. sylvestris* growing in Thetford Forest, UK and by Cienciala et al. [11] for a 50-year-old stand of *P. sylvestris* in central Sweden. Their measurements also support light saturation for stomatal conductance at approximately 500 µmol m^{-2} s^{-1}. A broader perspective on intersite variability in the absolute level of maximum conductance is needed for *P. sylvestris*, since even small differences cause large effects when incorporated into models that integrate water use over time.

While Beadle et al. [7] concluded that air saturation deficit was the primary environmental factor explaining time-dependent changes in stomatal conductance in Thetford Forest, it was not possible in our studies at Hartheim to identify one specific environmental driver that played a dominant role, rather temperature, saturation deficit and irradiance showed strong interactions in determining response. During periods of reduced soil water content, conductance was strongly coupled to the available soil water. Some stomatal models describe conductance as a product of individual correlation functions (e.g. [4, 34]). It is assumed in these that the shape of the response functions is invariable. However, the correlation between stomatal conductance and air temperature indicates that maximum conductance is reached at lower temperatures when illumination is low. Such important interactive effects must be included in stomatal models in order to avoid large prediction errors. An indirect means of including interactive effects on conductance is to describe interactive effects of environmental factors on photosynthesis and to exploit the correlative changes that occur in conductance and photosynthesis rate[6, 45].

A time lag of as much as 15 min was observed in the response of stomata of *P. sylvestris* to changes in irradiance. For this reason, good correlations between highly resolved stomatal conductance values and irradiance can only be expected with sufficient time for equilibration. A similar time lag was reported for *P. taeda* [50]. A longer period of adjustment of two hours or more was reported by Ng and Jarvis [38] for *P. sylvestris*. This could not be verified with our measurements because such long periods of constant illumination do not occur under field conditions. In any case, time-lag effects are included in the responses described in *figure 1*. Models based on these data may on averge perform well but fail when radiation fluctuates rapidly (cf. *figure 2*). At the stand level, time-lag effects in response to changing irradiance were not obvious. Self-shading and the integrated response of all shoots apparently determine response characteristics at this level, including hysteresis effects [38]. Whitehead and Teskey [50] concluded that hysteresis in shoot response has a great influence on stomatal behavior during short time periods but that the influence on daily transpirational sums is negligible. These conclusions are also supported by the Hartheim data.

Stand conductance values measured in 1993 and in 1994 show distinct differences. Thinning of the stand and frequent rain resulted in a filled water store into late June during 1994. Larger leaf level stomatal conductance values occurred during July and August 1994 and resulted in higher daily water use than during summer 1993. Under non-water-stressed conditions, Whitehead et al. [49] found that stand transpiration rates were significantly lower with lower tree density in a spacing experiment for *P. sylvestris* even several years after thinning. In contrast, Bréda et al. [9] found a significant decrease in stand transpiration of *Quercus petraea* in the first year after thinning but transpiration rates equal to the unthinned stand in the second year. The measurements reported here were only begun during 1993 after the soil dried. In order to consider the effects of thinning on gas exchange capacity, we must refer to the observations of Granier et al. [19] in this same stand during May 1992, where transpiration fluxes of 2–2.7 mm d^{-1} occurred with high available energy. Comparing May 1992 to June 1994, we can conclude that transpiration potential of the stand was reduced by thinning in approximate proportion to change in leaf area index and sapwood area. The low rates in fall of 1993 are the result of low available energy. Jackson et al. [22] found in two

P. sylvestris stands that xylem relative water content decreased after one cycle of drought as an effect of cavitation but that xylem water conductance and transpiration rate were not affected. Although drought was stronger at Hartheim, our results do not contradict this conclusion.

As previously reported for Mediterranean shrubs [46], *P. sylvestris* exhibits a sensitive response to soil drying and initial small changes in predawn water potential. With initial drying, roots in the upper soil layer appear to increase the concentration of xylem ABA to between 200 and 500 nmol L^{-1}, apparently as the root–shoot signal proposed by Davies and Zhang [12]. Thus, an immediate leaf-level reaction to the onset of summer weather conditions is observed, i.e. leaf conductance and water use decrease (cf. [43, 44, 46]). As drought continues and water potentials become more negative, a second phase in response is observed which is associated with very conservative water use and much higher levels of ABA. We hypothesize that ABA functions as a key control on water balance, transmitting information about soil water status and endogenously modifying canopy response, such that extensive cavitation damage is avoided in most years.

The intent of our simultaneous observations of leaf-, tree- and stand-level conductances throughout the course of two summer seasons at Hartheim was to characterize temporal changes and scale effects on water use by *P. sylvestris* at a site frequently subjected to low water availability, ideal with respect to fetch, and relatively homogeneous from the standpoint of stand structure. The site provides a natural laboratory useful for clarifying aspects of both plant–soil and plant–atmosphere coupling. The current observations with *P. sylvestris* permit us to view several aspects of response to drought in relation to one another. Porometery has allowed a determination of the shape of stomatal conductance response surfaces and a definition of the range in response as well as the identification of important time-dependent phenomena. Simultaneous observations of sap flow and estimation of stand water use and conductance has allowed us to examine the effects of leaf conductance on whole plant water use, while thinning during autumn 1993 revealed the effects of stand level phenomena on conductance regulation. The observations provide a framework within which existing model hierarchies [13, 14] may be used to quantify water use and carbon fixation of pine stands as well as to examine response in scenarios describing potential climate change. Long-term data records at the Hartheim site will in fact allow us to test such models for previous periods and to examine the relationship of fluctuating carbon budgets to growth and production.

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