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Original article

Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany

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Abstract – Tree transpiration was observed with sapflow methods in six Norway spruce (*Picea abies*) stands located in the Lehstenbach catchment, Fichtelgebirge, Germany, differing in age (40 years up to 140 years), structure, exposition and soil characteristics. The seasonal pattern in tree canopy transpiration, with the highest transpiration rates in July, was very similar among the stands. However, young dense stands had higher transpiration compared to older less dense stands. Because of forest management practices, stand density decreases with increasing stand age and provides the best predictor of canopy water use. Measured xylem sapflux density did not differ significantly among stands, e.g. vary in correlation with stand density. Thus, differences in canopy transpiration were related to differences in cumulative sapwood area, which decreases with age and at lower tree density. While both total sapwood area and individual tree sapwood area decrease in older less dense stands, leaf area index of the stands remains high. Thus, transpiration or physiological activity of the average individual needle must decrease. Simulations with a three-dimensional stand model suggest that stand structural changes influence light climate and reduce the activity of the average needle in the stands. Nevertheless, age and nutrition must be considered with respect to additional direct effects on canopy transpiration. (© Inra/Elsevier, Paris.)

transpiration / canopy conductance / sapwood area / stand age / stand density / *Picea abies*

Résumé – Variations spatiotemporelles de la transpiration de peuplements d'épicéas dans un bassin-versant du Fichtelgebirge (Allemagne). La transpiration des arbres a été évaluée au moyen de méthodes de mesure du flux de sève dans six peuplements d'épicéas (*Picea abies*), situés dans le bassin-versant du Lehstenbach, Fichtelgebirge (Allemagne), qui différaient en âge (40 à 140 ans), structure, exposition, et en caractéristiques de sol. L'allure des variations saisonnières

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de la transpiration des arbres, avec notamment un maximum en juillet, était très similaire entre ces peuplements. Néanmoins, les jeunes peuplements denses ont montré une plus forte transpiration que les peuplements âgés et moins denses. La densité du peuplement s'est avérée être la meilleure variable explicative de la transpiration, car les pratiques sylvicoles réduisent la densité des peuplements en fonction de l'âge. La densité de flux de sève n'a pas montré de différences significatives entre les peuplements. Ainsi, les différences de transpiration étaient seulement dues aux différences de surface de bois d'aubier, qui diminue avec l'âge et la densité. Alors que la surface de bois d'aubier à l'échelle du peuplement comme à celle de l'arbre diminuaient dans les peuplements âgés et peu denses, l'indice foliaire de tous les peuplements étudiés restait élevé. Ainsi, il est probable que la transpiration ou l'activité physiologique des aiguilles diminuent avec l'âge des arbres. Des simulations réalisées au moyen d'un modèle de couvert 3D suggèrent que les modifications de structure des peuplements influencent le microclimat lumineux et réduisent l'activité foliaire. Malgré tout, l'âge et la nutrition doivent être pris en compte dans leurs effets sur la transpiration des arbres. (© Inra/Elsevier, Paris.)

transpiration, conductance du couvert, surface de bois d'aubier, âge, densité, *Picea abies*

1. INTRODUCTION

Norway spruce (*Picea abies* (L.) Karst.), because of its importance in timber production, is one of the most widely studied forest trees of Europe. The empirically derived yield tables for Norway spruce demonstrate that substantial differences in stand development and productivity occur regionally within Germany [3, 30, 54, 56, 73] and between neighboring countries (Austria in Marschall [44]; Slovakia in Halaj [26]; Switzerland in Badoux [5]). Observations and reconstructions of height growth and wood volume increment for Norway spruce at long-term sites demonstrate 1) a rapid increase in growth and production followed by growth decline after approximately 80–100 years [12, 57], 2) a clear differentiation in development due to climate and soils [30, 54] and 3) a recent trend for growth stimulation even in older stands due, among other factors, to high nitrogen deposition [16, 17, 54]. An evaluation of the relative importance of long-term changes in site climate (temperature, precipitation and atmospheric CO_2), site quality (also as affected by atmospheric nitrogen deposition), and tree physiology on forest growth requires both an improved analysis of heterogeneity in structure and function of spruce stands within landscapes and along chronosequences and new analytic capabilities to separate the complex effects of multiple factors on carbon fluxes, i.e. potentials for comparison of sites as may be achieved with process-oriented simulation models.

Landscape heterogeneity in transpiration occurs as a result of the presence of different species, variation in site quality, local climate gradients, the spatial mosaic in stand age as well as stand density, and silvicultural treatment. Heterogeneity in transpiration potential is accompanied by shifts in foliage mass to sapwood area ratios [43]. Espinosa-Bancalari et al. [13] found that variations in foliage area to sapwood area ratios are strongly correlated with mean annual ring width of the sapwood, implying that growth potential is an important component in the dynamic maintenance of xylem water supply capacity. Sapwood permeability is directly proportional to tree growth rate [74].

Greater latent heat exchange and CO_2 fixation in young as compared to old stands of *Pinus banksiana* were observed in northern Canada [63]. Decreases in canopy transpiration of 35 % with aging of Norway spruce were reported by Schubert (in [37]) in a comparison of 40- and 100-year-old stands. Yoder et al. [75] found that photosynthetic rates decreased in old trees of *Pinus ponderosa*, suggesting that canopy gas exchange is reduced in old stands as growth potential decreases. Falge et al. [14] reported in *Picea abies*, that the observed data were compatible with an unaltered mesophyll photosynthetic capacity but a greater stomatal limitation as trees aged.

In the present study, tree canopy transpiration was simultaneously examined along a chronosequence of *Picea abies* stands growing in relatively close proximity within a forested catchment of the Fichtelgebirge, Germany. Our purpose was to determine whether regulation of the transpiration flux differed, and if so, potential causes of this variation, i.e. potential differences in microclimate, in canopy structure and light interception, in site quality and tree nutrition, or in water supply capacity as reflected in the foliage area to sapwood area ratio. While tree canopy transpiration can be measured or estimated via micrometerological methods, homogeneous areas lend themselves best to interpretation with these methods and large fetch distances are required. Measurements of water flux at the leaf or shoot level are limited due to problems encountered in a direct scaling-up of rates to the stand level [39]. Thus, xylem sapflow measurements were used in our study and are viewed as the most appropriate method for obtaining coupled information about the physiology of individual trees, tree structural development, and site factors as they affect water relations.

2. MATERIALS AND METHODS

The experimental sites are located within the Lehstenbach catchment, Fichtelgebirge, northeastern Bavaria, Germany at an altitude of approximately 750–800 m. More than 90 % of the catchment is covered with Norway spruce [*Picea abies* [L.] Karst.]. The exposed substrates are mainly phyllite and gneiss and the most common soils are brown earths and podsols. Where ground water is near the surface, local boggy organic layers form. The mean annual air temperature is approximately 5.8 °C (at an altitude of 780 m) and mean annual precipitation is 1 000–1 200 mm. There is also a high occurrence of fog (100–200 d per year) and only a short growing season (100–130 d per year).

Six spruce stands differing either in age and structure, in exposition, or in soil characteristics were chosen for study. Three of the stands were of approximately the same age (40 years). The stand Schlöppner Brunnen compared to the other stands is growing on very wet and boggy soil (subsequently: 40-year boggy stand), while the stands Weiden Brunnen (subsequently: 40-year stand) and Schanze are located on moderately moist to moist soils. The stand Schanze has a north-east exposition (subsequently: 40-year NE stand) while all other stands occur on south-facing (south-east to south-west) slopes. In addition to these three stands of the same age, the 70-year old stand Süßer Schlag (subsequently: 70-year stand), the 110-year old stand Gemös (subsequently: 110-year-stand) and the 140-year-old stand Coulissenhieb (subsequently: 140-year stand) located on drained but moist soils were investigated. Tree density of the stands decreases with age owing to thinning and removal of wood in forest management. Stand characteristics are summarized in *table I*.

Investigations were carried out primarily in the year 1995 from the middle of April to the middle of November (preliminary experiments with fewer stands were conducted during 1994 as described below). Air temperature, relative humidity and net radiation or global radiation were recorded automatically at meteorological stations above the canopy at the 40-year boggy, the 40-year NE and the 140-year stand as well as for several weeks in autumn at the 40-year stand. Vapor pressure deficit (D) was calculated from temperature and relative humidity measurements at the first three sites. The remaining sites were considered most similar to the 140-year stand and transpiration at these sites was related to D at the 140-year stand. Precipitation was measured in an open field near the 140-year stand. At the 140-year stand, rainfall, throughfall and windspeed as well as soil temperature were

Table I. Characteristics of the experimental stands of *Picea abies* in the Lehstenbach catchment.

	Weiden Brunnen	Schlöppner Brunnen	Schanze	Süßer Schlag	Gemös	Coulissenhieb
Stand age (years)	40	40	ca 40	70	110	140
Exposition facing	south-west	south	north-east	south-east	south	south-west
Soil conditions	moist	boggy	moderately moist	moist to very moist	moderately moist	moist
Tree density (trees ha^{-1})	1007	1678	1006	504	446	322
Mean stand height (m)	16.1	14.7	17.8	24.1	25.7	25.2
Mean stem diameter (cm)	19.1	16.1	21.1	34.6	34.3	36.6
Cum. basal area (m^2 ha^{-1})	30.9	39.5	37.8	48.8	42.4	35.3
Cum. sapwood area (m^2 ha^{-1})	20.3	23.1	26.5	20	18.8	13.6
Needle biomass (t ha^{-1})	12.3	11.7	16.6	15.6	17.9	13.2
Leaf area index (projected basis)	5.3	6.5	7.1	7.9	7.6	6.5
Mean needle loss* (%)	32	19	21	31	20	26

* According to the Bayerische Forstliche Versuchs- und Forschungsanstalt ranking system, see [71]. Stand mean needle loss was determined from 35–40 trees per stand.

additionally recorded. Soil matrix potentials were measured with self-recording tensiometers [42], which were installed at 35 and 90 cm deep at the 40-year stand, the 40-year boggy stand and the 140-year stand, and with manually recorded tensiometers at 20 cm deep at the 40-year NE stand, the 70-year stand and the 110-year stand. Predawn water potentials of small twigs of the trees at the 140-year, 40-year, 40-year boggy and 40-year NE stand were measured every 2 weeks from the end of June to the middle of August, using a pressure chamber [58].

Sapflow installations were made in mid-April in three stands but were delayed until middle of May at the 40-year NE stand and until beginning of June at the 70-year and 110-year stands. Within all stands, transpiration was monitored on ten trees except in the case of the 140-year-old stand where 12–13 trees were examined. Two methods for measuring xylem sapflow were used: thermal flowmeters constructed according to Granier [19, 20] and the steady-state, null-balance method of Kucera et al. [36] Cermák et al. [9] and Schulze et al. [60]. With the Granier methods applied in all stands, 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 [19]. The steady-state, null-balance instrumentation was used to compare methods on the same trees within the 40-year stand. A constant temperature difference of 3 K was maintained between a sapwood reference point and a heated stem section. The mass flow of water through the xylem of the heated area is proportional to the energy required in heating. Additionally, both methods were used (on separate trees) to estimate transpiration in the 140-year stand.

Total sapflow per tree was obtained by multiplying sap flux density by the cross-sectional area of sapwood at the level of observation. Sapwood area of sample trees was estimated from regressions relating GBH (girth at breast height) to sapwood area determined either with an increment borer, by computer tomography [25], or from stem disks of harvested trees. Since no correlation was found between tree size and sap flux density except at the 40-year NE stand, stand transpiration (mm d^{-1}) was estimated (except at the 40-year NE stand) by multiplying mean flux density of all sample trees by total cross-sectional sapwood area of the stand and dividing by stand ground surface. At the 40-year NE stand where flux density was correlated with tree size, tree transpiration was extrapolated to stand transpiration according to the frequency of occurrence of trees in different size classes. For days with missing data owing to technical failures as well as for the early season before sensors could be installed in some stands, canopy daily transpiration sums were estimated from correlations established between the measured daily transpiration and daily maximum vapor pressure deficit (D_{max}, cf. *figure 4*).

From tree canopy hourly transpiration rates and hourly average D measured above the canopy, values of total canopy conductance (G_t) were derived. The time courses for measured sap flow were shifted by 0.5–1.5 h until compatability between morning increases in photosynthetic photon flux density and estimated tree canopy transpiration were achieved. Thus, our analysis assumes that a linear shift compensates for the capacitive delay in flow detection at breast height as compared to crown level transpiration. Further details regarding the estimate of G_t as dependent on shifted tree canopy transpiration and on D are given by Köstner et al. [32, 34] and Granier et al. [22]. Tree canopy conductance was calculated according to the following formula:

$$g_c = k\,(E_c / D) \quad \text{and} \quad k = G_v\,T_k$$

where g_c is tree canopy conductance (mm s^{-1}), E_c is tree canopy transpiration (kg H_2O m^{-2} h^{-1}), D is vapour pressure deficit (hPa), G_v is gas constant (0.462 m^3 kPa kg^{-1} K^{-1}), T_k is air temperature (Kelvin).

Needle nutrient content was measured for twig samples collected in July in the sun crown of five harvested trees at the 70-year and at the 110-year stands and at the end of October 1994 from five trees of the 40-year, the 40-year boggy and the 40-year NE stand. Nutrient content of the needles of the 140-year stand was determined in October 1992 and in October 1995.

Needle biomass of five individual trees per site, selected over the GBH distribution (girth at breast height), was determined by applying the 'main axis cutting method' of Chiba [10]. Needle area/needle biomass was determined for sub-samples taken from the lower-, mid-, and upper-third of the canopy with a Delta-T image analyzer (DIAS). Regression equations relating total needle surface area for trees to GBH were used to sum leaf area for trees in the stand and to estimate LAI. Harvest results indicated that trees from 40-year stands were of similar structure and these data were pooled for needle surface area regressions. For the older stands, LAI estimates are based on five trees per stand. Cross-sectional sapwood area of stands was estimated from regressions relating GBH to sapwood area determined either with an increment borer, by computer tomography [25], or from stem disks of harvested trees (cf. *figure 9*).

3. RESULTS

3.1. Stand climate and water supply

During the intensive measurement phase, which was carried out from the middle of April to the beginning of November 1995, a pronounced period of cloudy and rainy weather occurred in June, with sunny warm weather in early and mid summer, and cool clear weather in fall. Monthly changes in climate factors are given in *table II*. T_{max} and, thus, D_{max} were consistently lower (ca 15 %) at the 40-year NE stand as compared to the 40-year and 140-year stand which were adjacent on the northern divide of the watershed. The lowest D_{max} (20 % less than 40-year stand owing to evaporation from standing water and mosses in the understory) was found in the 40-year boggy stand. In mid-July and in August, moderate drying of the surface soil layers occurred. However,

Table II. Characteristics of stand climate and minimum matrix potential (mean of five tensiometers at 20 cm depth) during the months April to October 1995 measured at the 140-year stand stand or the adjacent 40-year stand.

	April	May	June	July	August	September	October
Maximum PPFD integ. (mol m^{-2} d^{-1})	*	47.7	53.6	53.2	45.5	31.8	21.9
Average PPFD integ. (mol m^{-2} d^{-1})	*	26.1	26.6	35.7	28.9	15.0	12.1
Precipitation total (mm)	101	53	165	158	121	124	17
Number of days with precipitation > 1 mm	16	6	18	10	10	14	6
T_{max} (°C)	18.7	22.7	23.6	28.3	25.4	19.2	20.0
T mean (°C)	4.3	8.6	11.3	17.8	15.7	9.2	9.0
T_{min} (°C)	–3.8	–0.8	4.4	8.7	4.3	0.6	–1.9
D_{max} (hPa)	14.9	16.8	18.3	26.9	24.4	11.4	10.2
Average daily D_{max} (hPa)	4.2	8.0	5.9	14.4	11.2	4.3	4.1
Minimum matrix potential at Coulissenhieb (hPa)	*	–170	–110	–230	–440	–90	–130

* No measurements available.

the lowest recorded soil matrix potentials at the 110-year-stand (ca –550 hPa at 20 cm soil depth) do not indicate that the trees were subjected to water stress. Tensiometer values from other stands fluctuated within the same range as observed in the 110-year stand. Lowest predawn water potentials of the trees measured at the 40-year stand during the end of June to the middle of August fluctuated only between –0.4 and –0.5 MPa.

3.2. Needle nutrient concentration

Needle analysis of twig samples showed that there are differences in needle nutrient concentration among stands. Mg^{2+}-concentration (± standard deviation), for example, is highest at the 110-year stand (1.12 ± 0.21 mg g^{-1}, 1-year-old needles) and is also high at the 40-year boggy stand (0.83 ± 0.12 mg g^{-1}, 1-year-old needles), while at the other stands the Mg^{2+}-concentration in the needles of this age class ranges between 0.25 ± 0.09 mg g^{-1} (40-year NE stand) and 0.63 ± 0.39 mg g^{-1} (70-year stand). Therefore, these other stands show values far below the limit of adequate mineral nutrient concentration for optimal growth according to Bergmann [6]. The Mg^{2+}-concentrations of the 40-year boggy stand and the 110-year stand are significantly different ($P < 0.05$) from the Mg^{2+}-concentrations of the 40-year-stand, the 40-year NE stand and the 140-year stand.

Differences between stands were also found in the Ca^{2+}-concentration of the needles. Lowest Ca^{2+}-concentration in 1-year-old needles was measured at the 40-year NE stand (1.41 ± 0.32 mg g^{-1}). A concentration of 2.46 ± 0.78 mg Ca^{2+} per g dry weight was found at the 40-year-stand. The 40-year boggy stand, the 70-year stand and the 140-year stand had almost the same relatively high Ca^{2+}-concentration in the needles (4.28 ± 1.21 mg g^{-1}, 4.28 ± 2.34 mg g^{-1} and 4.29 ± 1.42 mg g^{-1}, respectively). Highest Ca^{2+}-concentration was observed at 110-year stand (7.38 ± 1.52 mg g^{-1}).

The mean K^+-concentration of the 1-year-old needles reached higher values in the 40-year-old stands (5.97 ± 0.52 mg g^{-1}, 6.59 ± 1.11 mg g^{-1} and 6.34 ± 0.93 mg g^{-1} at the 40-year stand, the 40-year boggy stand and the 40-year NE stand, respectively) than in older stands (4.97 ± 0.52 mg g^{-1} and 5.53 ± 0.45 mg g^{-1} at the 70-year stand and the 140-year stand). The lowest K^+-concentration (3.46 ± 0.480 mg g^{-1}) was measured in 1-year-old needles of the 110-year stand, which was significantly different from the K^+-concentration of the needles of the other stands.

The needle nitrogen concentration is higher in the 40-year-old stands (3-year-old needles; 40-year stand: 15.1 ± 1.5 mg g^{-1}; 40-year boggy stand: 15.5 ± 1.7 mg g^{-1}; 40-year NE stand: 13.7 ± 0.6 mg g^{-1}) than in the 70-year stand (3-year-old needles: 12.5 ± 0.8 mg g^{-1}), the 110-year-stand (3-year-old needles: 11.8 ± 1.4 mg g^{-1}) and the 140-year stand (3-year-old needles: 11.7 ± 1.0 mg g^{-1}). Therefore two of the 40-year-old stands (40-year stand and 40-year boggy stand) and the three older stands were, concerning the nitrogen concentration of the 3-year-old needles, significantly different ($P < 0.05$) and also the differences between the 40-year NE stand and the 140-year stand were significant.

3.3. Tree canopy transpiration

A comparison of the estimated daily water transpired by six trees of the 40-year stand Weiden Brunnen when measured with the 'Granier' and 'Cermák/Schulze' methods is illustrated in *figure 1*. On an individual tree basis, there are systematic differences observed in transpiration estimates (average sapflux density) which depend on instrumentation specificities, local variation in wood structure, etc. However, with a sufficiently large number of installations (estimated requirement of 8–10 [35]), which are carried out in consistent fashion (in our study ten per stand), flux rates observed with both sys-

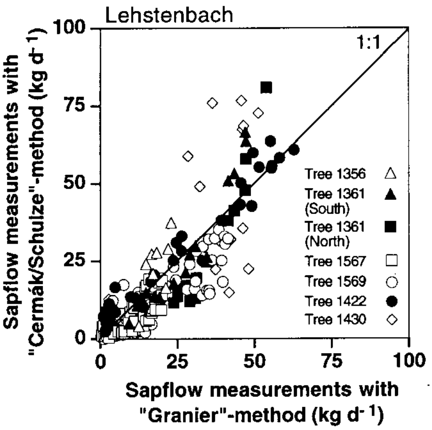

Figure 1. Comparison of diurnal integrated transpiration rates obtained by xylem sapflow measurements in the Weiden Brunnen 40-year stand according to the constant heating method ('Granier' method) and those results obtained by measurements on the same trees at the same time according to the steady-state, null-balance method ('Cermák/Schulze' method). At tree 1 361, two different measurement systems according to the 'Cermák/Schulze' method were installed at different stem height, one exposed to the south and one to the north, and compared to 'Granier' Installations at each height.

tems agree well. Studies by Köstner et al. [33] and Granier et al. [22], which have compared the two methods of sapflow measurements within the old spruce stand Coulissenhieb and in the case of *Pinus sylvestris*, also indicate that similar estimates of transpiration flux are obtained. The 'Cermák-Schulze' system should integrate over any changes in flux density that may occur with depth in the trunk and provide a direct measurement of total flow as long as the electrodes span the entire conducting sapwood. Given the good agreement found for these methods at the Weiden Brunnen site, we feel confident that the calibration factors provided by Granier [19] function well in estimating tree transpiration of spruce, at least when there is no apparent water stress. Thus, the 'Granier' method provides a useful and appropriate means for comparing transpiration rates and water use in the six selected experimental stands.

The average estimated half-hourly water use in transpiration of all six stands is shown for two clear summer days having different time course patterns in vapor pressure deficit (D) in *figure 2*. The simi-

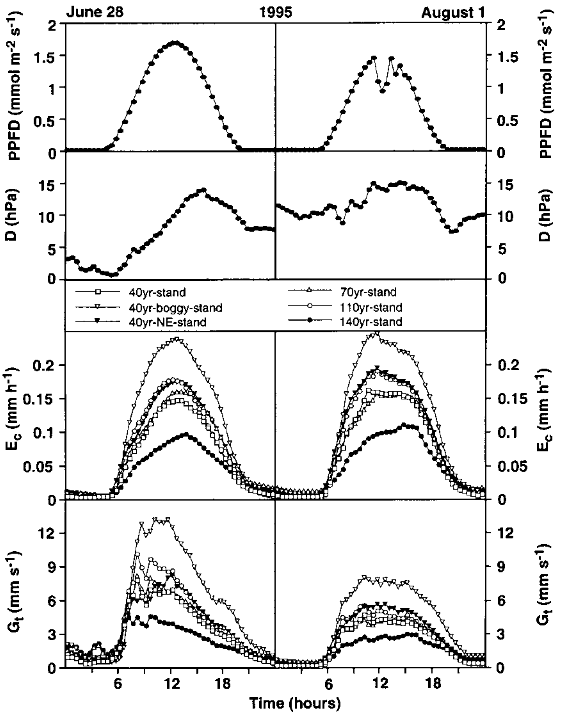

Figure 2. Half-hourly average values of photosynthetic photon flux density (PPFD), vapor pressure deficit (D) measured above the canopy at the 140-year stand, tree canopy transpiration of *Picea abies* (E_c) at six experimental sites determined from xylem sapflow, and total tree canopy water vapor transfer conductance (G_t) on 28 June and 1 August 1995. The time courses for sap flow rate were adjusted by 0.5–1.5 h (to achieve compatability between morning increases in PPFD and E_c) to compensate for the capacitive delay in flow detection at breast height as compared to crown level transpiration. G_t was estimated from shifted E_c and D as described by Köstner et al. [32].

larity at all locations in the diurnal pattern of water use is quite striking and the importance of variation in PPFD is obvious. On these days, the highest maximum hourly transpiration rates of ca 0.25 mm h^{-1} were observed for the 40-year boggy spruce stand, while the lowest hourly rates of only 0.11 mm h^{-1} were found for the 140-year stand. On 28 June, D increased continuously and rapidly for a long period until ca 14 hPa was reached in the afternoon, and then D decreased during the late afternoon hours. On 1 August, a similar maximum in D was achieved (ca 15 hPa), but D was already large during the previous night owing to warm air temperatures and increases in D occurring during the day were very gradual. A close comparison of the estimated time courses of transpiration illustrates that the actual rate occurring at 15 hPa D on these two days depends on the time course of change in conditions. Maximum values of G_t were depressed in August at all sites by ca 40 %, when D remained high during the night. Thus, canopy conductance is affected simultaneously by light and D, but also by endogenous factors related to water storage, hormonal regulation, and further as yet unexplained variables.

To obtain an impression of the overall influence of light and D on regulation of water loss from the spruce stands, the daytime half-hour values of stand conductance (G_t in *figure 2*) over the entire season were examined for agreement with several simple models. We hypothesized that stand conductance should increase with increasing PPFD incident on the canopy and then saturate at sufficiently high light when stomata are open in all canopy layers. We expected that increasing D would impose an additional linear restriction on the maximum stomatal conductance attained in each canopy layer. The data were separated into classes with differing ranges of D (0–5, 5–10, 10–15, 15–20 and > 25 hPa) and fit with non-linear regression techniques. An example of the general results is shown for the 40-year stand in *figure 3*. An equation in which conductance saturates with increasing light pro-

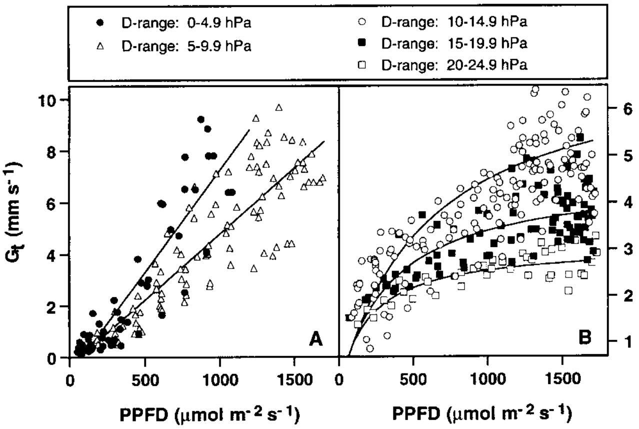

Figure 3. Analysis of the influence of photon flux density (PPFD) and vapor pressure deficit (D) on total tree canopy water vapor conductance (G_t) with the aid of non-linear regression techniques at the 40-year stand. At low D (up to 10 hPa) G_t was linearly correlated to incident PPFD (A), while at higher D G_t saturates with increasing PPFD (B). The solid lines indicate the linear regressions and the results of the non-linear model (equation of form: $G_t = 1/(a^*(1/\text{PAR}) + b^*D)$.

vided a good explanation of observations when D was greater than 10 hPa. At lower D, saturation did not occur and G_t was linearly related to incident PPFD. A simple model combining PPFD and D effects over the entire range of observations, cf. Lu et al. [41], resulted in an increasing stimulation of conductance with increasing PPFD at low D and, thus, was not further developed as a practical description. Time-dependent endogenous effects such as discussed above, time lags in sap flow response that we attempted to correct in relation to above canopy conditions, and potential measurements errors at low vapor pressure deficit contribute to the derived description of conductance behavior and may cause difficulties in these simple empirical models.

Daily transpiration has been linearly related to vapor pressure deficit measured at various times of day in a number of simplified hydrological models. In Germany, the time of observation at standard weather stations is used as the critical input variable [1, 27]. Integrated daily tree canopy transpiration in our study increased curvilinearly with daily maximum D, and the maximum capacity for transpiration in all stands saturated at D_{max} values of ca 20 hPa *(figure 4)*. Daily maximum G_t decreased strongly with increasing D_{max} *(figure 5)*. Thus, stomatal regulation with respect to D plays an important role in determining stand maximum transpiration rate. While linear approximations to the dependencies shown in *figure 4* may be useful for coarse estimates of water balances, the variation in response shown and these stomatal regulatory phenomena suggest that models such as Haude [27] should be applied with appropriate caution. While daily integrated tree canopy transpiration was correlated with daily maximum D, transpiration rates in late September and October seemed to be influenced by the previous night minimum air temperature.

Maximum rates of daily tree canopy transpiration at our sites increased from 2.4 mm d^{-1} in May to 2.8 mm d^{-1} in July at the the 40-year boggy stand, at which time the highest water use was measured, and decreased from 2.6 mm d^{-1} in August to 1.2 mm d^{-1} in October. As would be expected from the results shown in *figures 2* and *4*, this seasonal pattern in tree canopy transpiration was found in all six investigated stands *(figure 6)* and system-

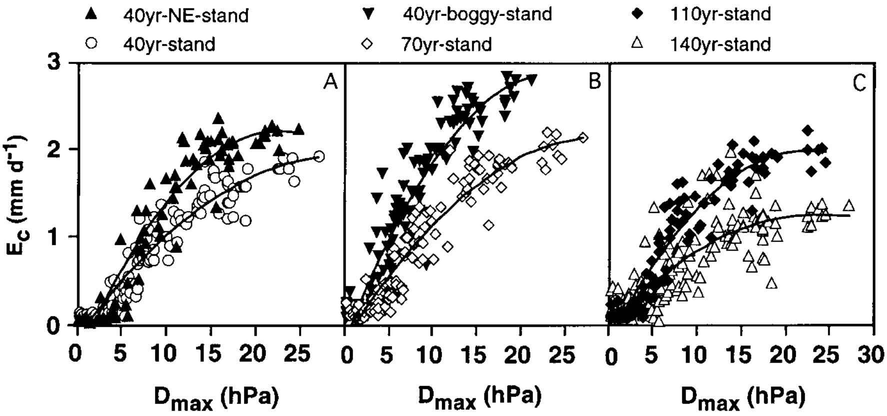

Figure 4. Relation of diurnal integrated tree canopy transpiration (E_c) to the daily maximum half-hourly value of vapor pressure deficit (D_{max}) during the measurement period in 1995 at the six investigated spruce stands.

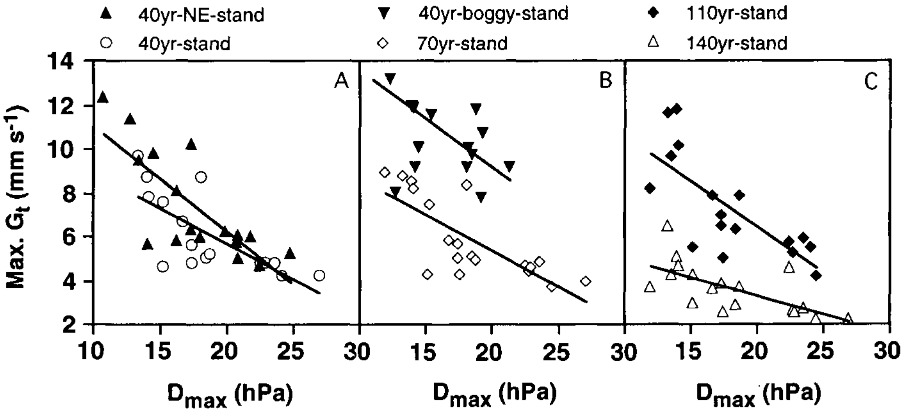

Figure 5. Relation of maximum total tree canopy water vapor transfer conductance (G_t) to the daily maximum half-hourly value of vapor pressure deficit (D_{max}) on sunny days during the period from the end of June to end of August in 1995 at the six investigated spruce stands.

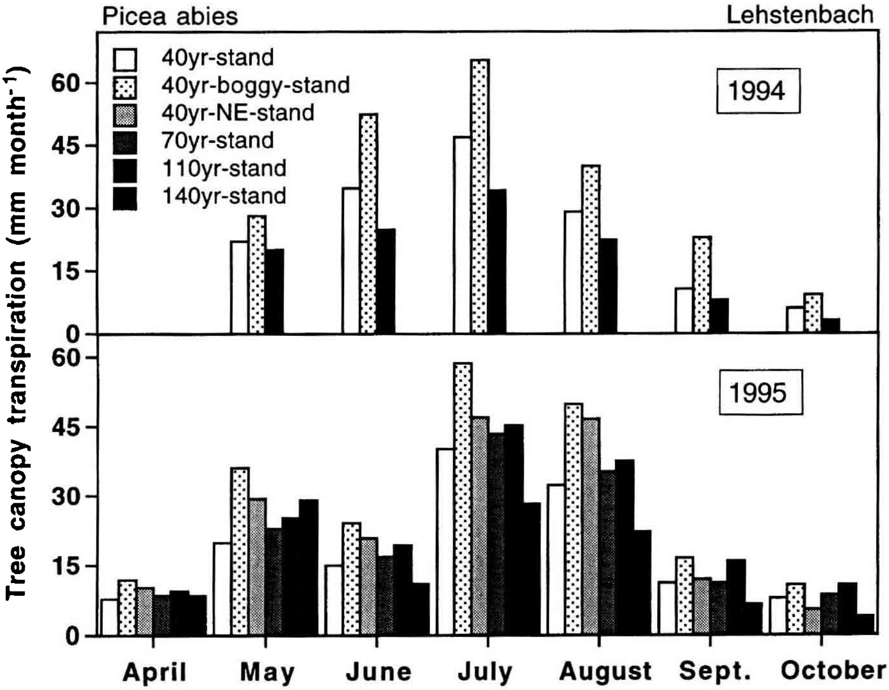

Figure 6. Seasonal variation during summer 1994 and 1995 in the monthly sum of tree canopy transpiration measured by xylem sapflow measurements at the experimental spruce sites at the Lehstenbach catchment. In 1994 measurements only took place at three of the six experimental sites and an estimation of transpiration rates in April was not possible.

atic differences between stands occur. Similar magnitudes in water use and differences between stands were observed during 1994, when tree transpiration was measured in only three of the stands. The daily sum of tree canopy transpiration was reduced by approximately 50 % during periods of overcast skies, and to essentially zero when overcast and rain occurred. In June 1995, these factors reduced the monthly sum of canopy transpiration by approximately 60 % in comparison to July 1995 and by approximately 50 % in comparison to June 1994 (half as many 'bad weather' days; *figure 6*).

Seasonal total overstory transpiration in the two 40-year-old stands on drained soil differed in proportion to stand leaf area indices, 134 mm at the 40-year stand Weiden Brunnen and 171 mm at the 40-year NE stand Schanze. T_{max} and, thus, D_{max} are consistently lower at Schanze as compared to Weiden Brunnen. LAI appears to increase in north-exposed stands, tending to maintain a similar stand water balance as discussed by Miller et al. [47]. Seasonal canopy transpiration, even after adjusting for LAI and despite the lowest D_{max} (due to evaporation from standing water and mosses in the understory), was greater at the 40-year boggy stand Schloeppner Brunnen (208 mm total). Comparative analyses of needles at the sites indicated a significantly higher Mg content at the 40-year boggy stand which may be related either to delivery in flowing water or better retention of Mg due to retarded transport away from the tree roots. Further experiments must be carried out in order to determine whether this change in nutrient status is causally related to the higher level of physiological activity of the 40-year boggy stand.

Transpiration of the oldest stand is much lower than in the young stands (*figure 6*; e.g. in 1995 transpiration of the 140-year-stand was only 81 % of the 40-year stand and only 52 % of the 40-year boggy stand), despite having greater or equal LAI. Seasonal transpiration from the older stands (147, 163 and 109 mm in the 70-, 110- and 140-year-old stands on a ground area basis, respectively) was similar after standardizing for LAI (*figure 7*). Current management practices in the Fichtelgebirge, result in decreases in stand density

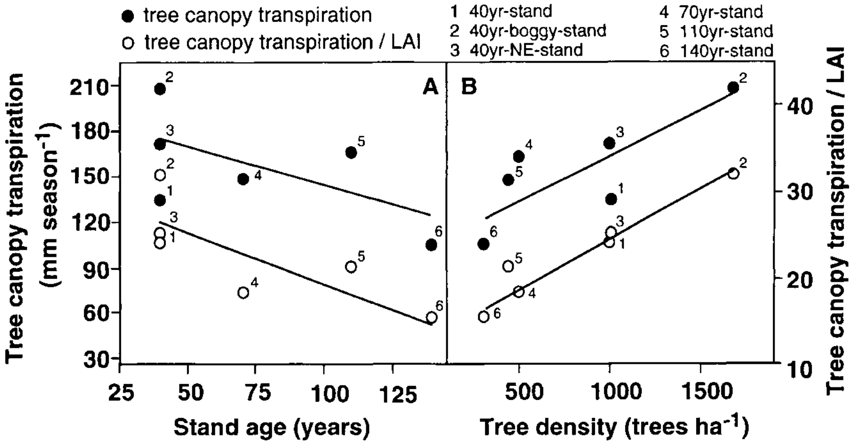

Figure 7. Correlation between stand age and tree density of the six investigated stands and seasonal total of tree canopy transpiration (absolute values as well as standardized on the basis of projected stand leaf area index).

that are correlated with stand aging. As illustrated in *figure 7*, stand density was found to be the best predictor of seasonal transpiration, even better than stand age. Differences in transpiration among the 40-year-old stands as a group and the older stands as a group could also reflect the influences of increasing N deposition in recent decades and early tree development under differing nutrient regimes.

Sapflux density in July for all trees varied between 0.017 kg d^{-1} cm^{-2} and 0.147 kg d^{-1} cm^{-2}. Although large differences in overstory transpiration occurred, measured xylem sapflux density did not differ significantly among stands, i.e. vary in correlation with stand density *(figure 8)*. Thus, differences in canopy transpiration were related to differences in cumulative sapwood area, which decreases with age and at lower tree density *(figure 8)*. To obtain greater confidence in our estimations of the cumulative sapwood area of the stands, sapwood area of individual trees was measured by different methods at the 40-year stand Weiden Brunnen. The same results were obtained either by measurement of sapwood area from stem disks of harvested trees, from stem cores, or from measurements with computer tomography *(figure 9A)*. The overall comparison of stands *(figure 8)* is based on coring and stem disk analysis. If the data from young (40-year stands) and old stands (> 40 years) are compared *(figure 9B)*, then it is quite clear that there is a shift in sapwood area relationships on an individual tree basis, the amount of sapwood area for similar size trees decreasing in older stands.

While both total sapwood area and individual tree sapwood area decreases in older less dense stands, leaf area index of the stands remains high *(table I)*. Thus, the needle area which must be supported by a specific sapwood area increases *(figure 10)*. With the same sapflux density, transpiration or physiological activity of the average needle must decrease. This was found independently for Norway

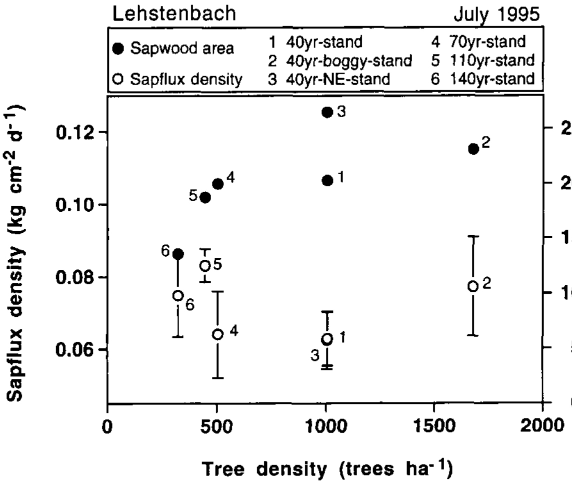

Figure 8. Mean sapflux density (transpiration per sapwood area; open circles) of 10–12 individual trees in each stand and cumulative sapwood area at breast height (solid circles) related to stand tree density (error bars: standard error). The values shown for sapflux density are averages for July 1995.

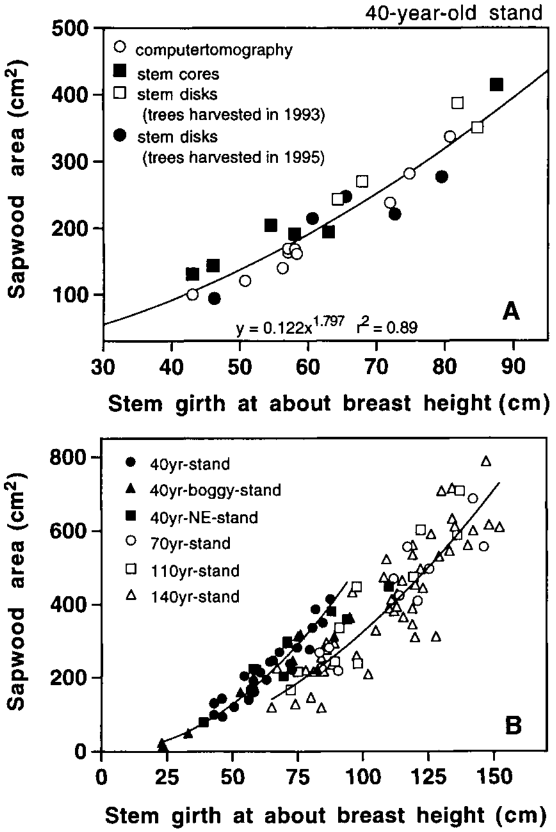

Figure 9. A: Correlation between stem girth at ca breast height and cross-sectional sapwood area at the same height determined either by measurements of sapwood from stem disks of harvested trees or with stem cores or by computer tomography at the 40-year stand (data of the trees harvested in 1995 were obtained by M. Mund; unpublished). B: Correlation between stem girth at ca breast height and cross-sectional sapwood area at the same height determined at the three 40-year-old stand and in the older stands.

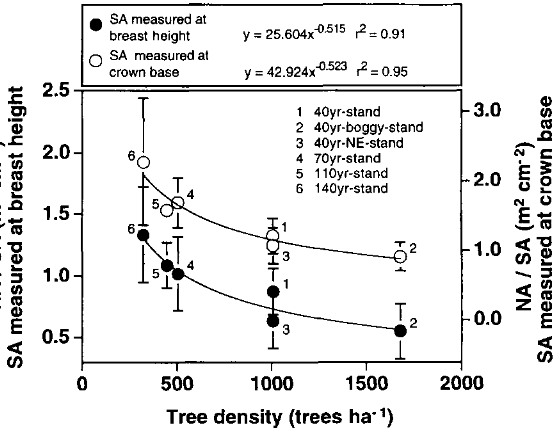

Figure 10. Relationship between tree density and the mean ratio of needle area (NA) to sapwood area (SA) of the harvested trees from each of the investigated spruce stands (error bars: standard error). Relationship is shown for SA measured at breast height and at crown base.

spruce on the basis of cuvette gas exchange measurements [14]. Given the limited water supply to needles in older stands and the greater stomatal restriction of needle gas exchange, total transpiration of older less dense stands is greatly reduced.

4. DISCUSSION

The influence of light and vapor pressure deficit on tree canopy transpiration was similar among the stands investigated, which resulted in a similar overall pattern in seasonal water use resembling that reported for *Picea abies* by Ladefoged [37] and for Douglas-fir by Granier [21]. Relatively low canopy transpiration rates in June 1995 *(figure 6)* were due to high precipitation during this month. As found by Graham and Running [18] for *Pinus contorta*, conductance during warm spring and summer periods was mainly determined by vapor pressure deficit of the air, while under cooler conditions (in our case in October and in their case during spring) conductance was correlated with previous night minimum air temperature.

The absolute values of maximum hourly transpiration rates in spruce stands of the Fichtelgebirge (from 0.11 mm h^{-1} at the 140-year stand up to 0.25 mm h^{-1} at the 40-year boggy stand; 1.4 mm d^{-1} in July at the 140-year stand up to 2.8 mm d^{-1} in July at the 40-year boggy stand) are relatively low for coniferous forests [62]. Similar low rates of maximum transpiration (0.15 mm h^{-1}) were found for a 120-year-old spruce stand in the Bayerische Wald (700 m NN; [51]) and low annual transpiration (145 mm in a 35- to 55-year-old and 137 mm in a 100-year-old spruce stand, respectively) was measured by Gülpen [24] in the Black Forest of Germany. The seasonal totals for canopy transpiration found in our studies (109–208 mm $year^{-1}$) are within the range of values (90–300 mm $year^{-1}$) reported by Cermak [50], who derived these values from xylem sap flow measurements of *Picea abies* at various sites.

Values between 0.25 and 0.7 mm h^{-1} were reported for *Picea abies* by Ladefoged ([37]; 2.6–3.8 mm d^{-1}) and McNaughton and Jarvis [46] and similar high rates for *Pseudotsuga menziesii* by Granier [21]. Tajchman [67] and Brechtel [7] determined water use by Norway spruce at two sites in Germany of 360 and 280 mm $year^{-1}$, respectively. Heimann [28] reported annual transpiration for a 40-year-old spruce stand located at the Harz, Germany, of 292 mm (± 97 mm, standard deviation). Roberts [55] summarized studies by Calder [8] indicating 290, 330 and 340 mm $year^{-1}$ transpiration for spruce sites in the United Kingdom.

Explanation of these apparent regional flux differences requires a better understanding of differences in site quality and the relative importance of simultaneous variations in climate, canopy LAI and the understory contribution to evapotranspiration. In some cases, the transpiration estimates have been derived from hydrological or meteorological measurements, assuming a negligible understory flux. Transpiration from the understory can be large and its relative contribution to total evapotranspiration may be underestimated [72]. Stand transpiration and conductance of coniferous stands are reduced strongly under conditions of limited soil water availability [11, 31, 66]. Water supply limitations may be ruled out in terms of explaining the low rates observed in the Fichtelgebirge. Measurements of soil matrix potentials indicate that trees were not exposed to water stress during the growing season of 1995. This is supported by the relatively high predawn water potentials (–0.4 up to –0.5 MPa) measured in twig samples. Gross and Pham-Nguyen [23] found for spruce trees that moderate restriction in water supply was associated with predawn water potentials in the range of –0.7 to –0.8 MPa, while trees exposed to strong water stress exhibited predawn water potentials of –1.2 to –1.4 MPa.

On the other hand, low Mg^{2+}-concentration in needles is typical for this region where the forest stands grow on acidified soils poor in cations [38, 61]. Not only were Mg^{2+}-concentrations very low at the 40-year- and the 40-year NE stand, but also the Ca^{2+}-concentration was lowest in these two young stands. The highest needle yellowing and needle loss (*table I*, needle loss) was also recorded for the 40-year stand, along with the lowest transpiration rates among the 40-year-old stands. Locally high water tables occur which seem to result in improved nutrition (sufficient nutrient supply at the 40-year boggy stand, especially magnesium) either due to supplemental delivery of nutrients in flowing water or due in some manner to better nutrient retention. Direct measurements which might determine whether higher gas exchange capacity is found in needles from the 40-year boggy stand must be undertaken. Higher magnesium concentrations in the needles were also found at the 110-year stand, which was fertilized with magnesium in 1983. It is interesting that water use by the 110-year stand was low despite fertilization. Differences between the 40-year-old stands as a group and the older stands as a group were found in needle nitrogen concentration. Increased N-deposition in recent decades, as it possibly affects the growth patterns, 3-D tree structure and stand light climate, as well as needle physiology are further factors that may contribute to the differences observed in canopy transpiration of different aged stands.

Site fertility is known to influence the leaf area/sapwood area ratio, which in turn affects growth rates, hydraulic conductivity of trees and stand transpiration [13, 40]. Our measurements showed that variation in sap flux density among the stands is small but that differences in cumulative sapwood area are extremely important (*figure 8*). While the total sapwood area and individual tree sapwood area decreases in older, less dense stands, leaf area index of the stands remain high and the needle area which must be supported by a particular sapwood area increases. A similar effect of stand age on the leaf area/sapwood area ratio of stands was reported by Albrektson [2], while Aussenac and Granier [4] showed that this ratio is influenced by tree density and, therefore, by thinning practices. Changes within stands seem to be related to the response to light climate [64]. Thinning results in large changes in tree density at the sites investigated and on the leaf area/sapwood area ratio (*figure 10*). This means that the amount of needles supported by a sapwood element increases as tree density of the stands decreases (as described in [65] or [29]) and as stand age increases. Therefore, with the same sapflux density average transpiration of the average needle must decrease.

Pothier et al. [52] found that sapwood permeability increases with increasing age, which is partly due to an increase in tracheid length. Pothier et al. [53] concluded that: '...tracheid length and sapwood relative water content are the two most important characteristics of sapwood with which we can explain the variation of sapwood permeability with stand development'. Water conductance is influenced by sapwood permeability, by sapwood area and by the length of the pathway. Pothier et al. [52] found with jack pine (*Pinus banksiana* Lamb.) at good quality sites that sapwood conductance decreases with age. Mattson-Djos [45] also reported a decrease with age in conductance for the entire pathway between roots and foliage of *P. sylvestris*. One reason for this decrease in sapwood conductance may be the increased resistance to water flow in minor branches compared to the main stem

([68, 69, 70, 76] all in Pothier [52]) and greater biomass distribution to minor branches in older trees. At the spruce sites investigated in the Fichtelgebirge, shifts in individual tree function apparently occur that allow a degree of equilibration to thinning practices and xylem sapflux density that remains within a restricted relatively constant range. Since spruce canopies are quite dense, mechanisms involved in growth and which affect canopy form and needle clumping may provide an additional means for trees to maintain the balance between xylem water supply and canopy water demand.

Correlation was found between stand age and tree canopy transpiration at sites within the Lehstenbach catchment. Age dependencies of transpiration rates were reported by Schubert (in Ladefoged [37])

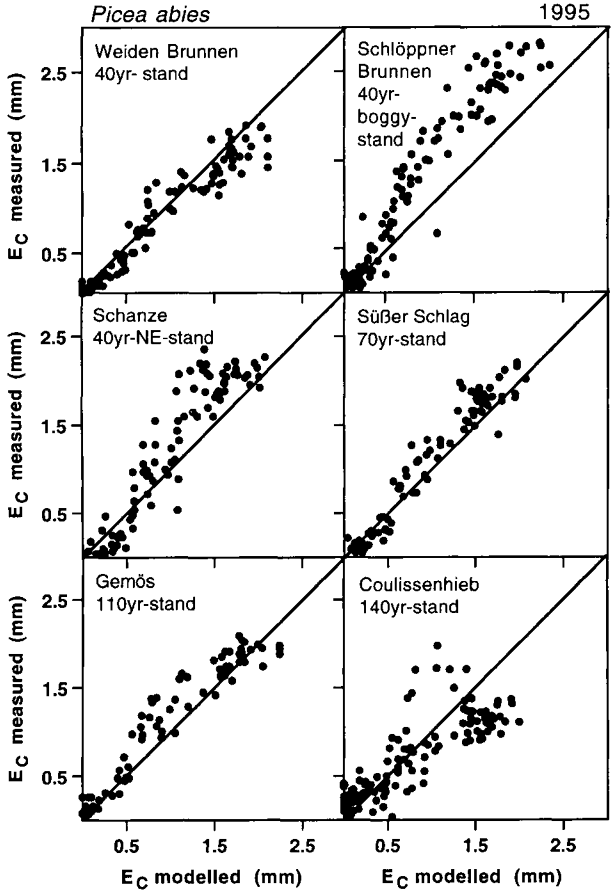

Figure 11. Comparison of measured and simulated daily integrated tree canopy transpiration rates for the six experimental spruce stands studied in 1995 in the Lehstenbach catchment. The assumptions of the model (STANDFLUX, [15]) include a single needle physiology, a single average tree structure defined for each stand, and variation among stands due to tree density (overall $r^2 = 0.82$).

who found a decrease in transpiration of ca 35 % in 100-year-old spruce trees in comparison to 40-year-old trees. Yoder et al. [75] reported differences in net photosynthesis between 45-year-old and 250-year-old pine trees (*P. ponderosa* and *P. contorta*) of approximately 14–30 % with the interpretation that the changes are not due to changes in mesophyll photosynthetic capacity but are related to decreased hydraulic conductivity in larger trees and decreased stomatal conductance in the old trees. At our sites, tree density decreases with age and is a better predictor of transpiration than age *(figure 7B)*. The lower canopy transpiration in old versus young stands is clearly related to differences in average physiological activity of the needles. The hypothesis that the observed differences in tree canopy transpiration between stands can be explained by changes in average structure and spacing of individual trees, was tested with the aid of the forest canopy light interception and gas exchange model STANDFLUX [15]. Using only a single average tree type and the same physiology for all needles, model estimates of water use are very similar to measured tree canopy transpiration rates *(figure 11)*. When all data are pooled, 80 % of the variation in daily water flux is explained. In some stands (40-year boggy stand and 40-year NE stand), transpiration rates were underestimated, suggesting greater average physiological activity at these sites. Thus, this preliminary scaling-up of cuvette gas exchange measurements with the 3-D model STANDFLUX independently suggests that a large portion of the observed variation in tree canopy transpiration is due to changes in intercepted photon flux. A large mass of needles in the shade crown of older stands may not contribute greatly to photosynthetic carbon gain. In simulations, the photosynthetic rate and water use efficiency of the older conifer stands are low compared to the younger stands. On the other hand, substantial variation in response remains to be explained. More work is required to examine the degree to which model predictions might be improved if physiological differences of needles due to needle age [38] and tree age [75], due to differing nutrition, or due to acclimation along light gradients within the canopy [48, 49] and if the distribution of tree structures within stands are considered.

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