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Evaporation and transpiration from forests in Central Europe – relevance of patch-level studies for spatial scaling

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With 7 Figures

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Summary

Spatial scaling from patch to the landscape level requires knowledge on the effects of vegetation structure on maximum surface conductances and evaporation rates. The following paper summarizes results on atmospheric, edaphic, and structural controls on forest evaporation and transpiration observed in stands of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*). Forest canopy transpiration (E_c) was determined by tree sapflow measurements scaled to the stand level. Estimates of understory transpiration and forest floor evaporation were derived from lysimeter and chamber measurements. Strong reduction of E_c due to soil drought was only observed at a Scots pine stand when soil water content dropped below 16% v/v. Although relative responses of E_c on atmospheric conditions were similar, daily maximum rates of E_c ($E_{c\max}$) could differ more than 100% between forest patches of different structure (1.5–3.0 mm d^{-1} and 2.6–6.4 mm d^{-1} for spruce and beech, respectively). A significant decrease of $E_{c\max}$ per leaf area index ($E_{c\max}$/LAI) with increasing stand age was found for monocultures of Norway spruce, whereas no pronounced changes in $E_{c\max}$/LAI were observed for beech stands. It is concluded that structural effects on $E_{c\max}$ can be specified and must be considered for spatial scaling from forest stands to landscapes. Hereby, in conjunction with LAI, age-related structural parameters are important for Norway spruce stands. Although compensating effects of tree canopy layers and understory on total evaporation of forests were observed, more information is needed to quantify structure-function relationships in forests of heterogenous structure.

1. Introduction

Evaporation from forests is studied within the research fields of forest hydrology, meteorology, and plant ecology. According to their specific objectives, information on evaporation and transpiration is provided on various temporal and spatial scales. Within the frame of Global Change research intensive efforts are made integrating hydrological and ecosystem processes to achieve a better understanding of physical and biological controls on hydrological cycles in a changing environment (cf. IGBP 1993; Tenhunen and Kabat, 1999). A network of forest studies was established by the European Community project EUROFLUX to investigate forest gas exchange and acclimation potential along climate gradients (Tenhunen et al., 1998). In combination with above canopy flux measurements, tree canopy transpiration is studied via sapflow methods in order to characterize functions of the dominating vegetation and to relate canopy water flux to forest structure.

Conceptual frameworks of evaporation processes regarding vegetation as a "big-leaf" are helpful to understand controls on evaporation and transpiration such as available energy, vapor pressure deficit of the air, aerodynamic and stomatal conductance (Monteith, 1965). However, the average stomatal conductance of a whole canopy (canopy conductance, g_c) is not easily determined, because it depends on species physiology, seasonal or site specific adaptations of the vegetation, distribution of nitrogen within the canopy, and the canopy structure (Field and Mooney, 1986; Shuttleworth, 1989; Monteith, 1995; Whitehead, 1998). Therefore, g_c is often empirically estimated from evaporation measurements (e.g., Kelliher et al., 1995). It is further questioned whether evaporation models suitable for spatial scaling (leaf-canopy-landscape) should include spatial information on leaf properties, physical properties of air and soil, etc. (e.g., Raupach and Finnigan, 1988; McNaughton and Jarvis, 1991; Rastetter et al., 1992). Hierachies of two- or three-dimensional, structure-dependent models were suggested in order to determine relevant aggregated parameters suitable for more simple models operating at larger scales (Tenhunen et al., 1999; 2001a). These modelling procedures along with long-term flux studies support the specification of functional units in landscapes linking vegetation structure with land-atmosphere exchange processes (cf. Valentini et al., 1999; Reynolds and Wu, 1999).

In contrast to previous findings (Roberts, 1983), a recent review on forest evaporation studies in Central Europe demonstrated large variation in annual evaporation components (total evaporation, transpiration, interception; Peck and Mayer, 1996). However, relationships between evaporation components and forest structure were difficult to establish. The authors especially complained the lack of detailed information on stand structural parameters and long-term measurements of water fluxes. These shortfalls may be overcome by interdisciplinary ecosystem research focussing on investigations of both plant and soil properties as well as on material fluxes between soil, vegetation and atmosphere (Tenhunen et al., 1998; 2001b). Ecosystem analysis begins at the plot or patch level signifying a homogenous unit of land, a specific biotic community or definable soil type. The size of the patch depends on the degree of detail specified (m^2–km^2; Woodmansee, 1988; Waring and Running, 1998).

Forest structure refers to the number and size of plant parts or individuals as well as to age and species composition (Oliver, 1992). In Central Europe, these factors are essentially determined by forest management practices. In Germany, the dominating tree species are Norway spruce (*Picea abies* L. [Karst.]), Scots pine (*Pinus sylvestris* L.), and European beech (*Fagus sylvatica* L.) covering 35%, 31%, and 25% of the forested area, respectively (Bundesministerium, 1993). Considering the present increase in average stand age reported from forest inventory (Krüger et al., 1994), effects of ageing may become important for the understanding of forest water fluxes at the stand and landscape level. In order to describe relationships between tree structure and tree water use, sapflow measurements became a key-instrument in forest ecosystem research bridging leaf- to stand-level processes and monitoring water fluxes through trees in the long-term (Granier et al., 1996a; Köstner et al., 1998b). It was shown that tree sapflow rates scaled to the stand level plus evapotranspiration from soil and understory agreed with water vapor fluxes measured above the forest canopy by eddy-correlation techniques (Diawara et al., 1991; Kelliher et al., 1992; Köstner et al., 1996b; Granier et al., 1996b). Therefore, sapflow techniques are combined with hydrological and meteorological methods to strengthen the analytical potential of water flux studies and to explain total flux rates from partial components.

The following paper reviews results on atmospheric, edaphic, and structural controls on forest water vapor fluxes observed from detailed patch-level studies in coniferous and broad-leaved stands. It aims at demonstrating the importance of quantifying forest structure to understand dynamics in long-term balances between vegetation and environment and potential variation in forest water vapor fluxes at the landscape level.

2. Determination of water vapor fluxes in forested areas

The following chapter provides a brief overview on methodological approaches estimating water flux components in forested areas at various temporal and spatial scales.

2.1 Sapflow measurements in trees

At the tree level water fluxes are determined by thermal sapflow measurements. Significant developments in sapflow techniques for trees have been made during the last decades (see Swanson, 1994). The sapflow data presented in this paper are based on both the tissue heat balance method according to Kucera et al. (1977) using the heat capacity of water to derive mass flow of water from a thermal signal, and on the method according to Granier (1987) using an empirical calibration to calculate water flux from a thermal signal in the tree stem. Both methods were proved to be comparable and applicable in forest stands (Köstner et al., 1996b; Köstner et al., 1998b). At appropriate time-scales (≥ 1 day) changes in tree water storage are low and water flux through the sapwood (water conducting tissue or xylem) equals tree canopy transpiration (cf. Schulze et al., 1985). Depending on the water conducting system of species and on forest structure, various approaches can be used to scale from individual measurements in trees to the stand. In most cases tree sapwood area, which is closest related to water transport in the tree, is used as a structural scaling factor. From sapflow density (flow rate per sapwood area) of individual sensors and the related sapwood area (A_s), canopy transpiration (E_c) is determined as follows:

$$E_c = J_{\text{mean}} * A_{s\text{-stand}}, \tag{1}$$

where J_{mean} = mean sapflow density of sample trees (kg m^{-2} s^{-1}) and $A_{s\text{-stand}}$ = cumulative sapwood area per ground area (m^2 m^{-2}).

In homogenous stands, the coefficient of variation (CV) for estimates of J_{mean} is usually less than 15% using ca. 10 sample trees (Köstner et al., 1996b) but variation may increase in older less homogenous stands requiring a larger number of sample trees (Köstner et al., 1998a). Estimates of $A_{s\text{-stand}}$ can be derived with relatively high accuracy from regression curves between stem diameter at breast height (dbh) and sapwood area of a subsample of trees applied to all trees within the patch (cf. Alsheimer et al., 1998). In forest stands composed of different canopy layers or tree species, E_c is summed up from several equations of type (1) representing different subsamples E_{ci} (i = layers, species, etc.) of the patch. Scaled sapflow rates provide an independent estimate of tree canopy transpiration as compared to total water vapor flux above the forest (Granier et al., 1996a, Köstner et al., 1998b).

The total water vapor transfer conductance (g_t) accounting for conductances from height of the "average" stomata in the tree canopy to the height of measurement of vapor pressure deficit of the air (D; Thom, 1972) can be estimated from E_c (Köstner et al., 1992):

$$g_t = E_c/D * \rho_w * G_v * T_K, \tag{2}$$

where E_c = canopy transpiration (mm s^{-1}); D = vapor pressure deficit of the air (kPa), ρ_w = density of water (998 kg m^{-3}), G_v = gas constant of water vapor (0.462 m^3 kPa kg^{-1} K^{-1}), T_K = air temperature (Kelvin).

The total conductance includes components of both stomatal (g_c) and aerodynamic conductance (leaf boundary layer and eddy diffusive conductance, g_a). Typically, g_a is more than an order of magnitude higher than g_c in rough forests where g_t approximates g_c $(1/g_t = 1/g_c + 1/g_a)$. Estimates of g_c derived from sapflow rates range within leaf-level estimates determined by porometer (Köstner et al., 1992) and are comparable to model-based estimates of g_c derived from canopy gas exchange (Köstner et al., 1998a).

2.2 Eddy-correlation technique

Considerable progress has been made using the eddy-correlation technique (Swinbank, 1951) to describe exchange processes between forest canopies and the atmosphere (e.g., Baldocchi et al., 1996; Aubinet et al., 2000). The method allows long-term monitoring (season, year) of energy and water vapor fluxes from forests beyond the spatial integration of scaled sapflow rates (> hectar). Total water vapor flux (E) includes soil and understory evapotranspiration as well as interception. It is determined from vertical wind speed (w) and atmospheric water vapor density (ρ_v) with the basic equation:

$$E = \rho_a \overline{(w' \rho_v')}, \tag{3}$$

where ρ_a is air density, primes indicate deviation from mean quantities, and the overbar signifies time average (e.g., Kelliher et al., 1992).

When interception is excluded, scaled sapflow rates (E_c) plus evapotranspiration from soil and understory (E_u) reached similar values compared to total forest evaporation determined by the eddy-correlation technique (e.g., Kelliher et al., 1992; Granier et al., 1996b). The combination of eddy-correlation measurements with studies of soil, understory and trees improves the interpretation of temporal and spatial variation in evaporation and makes it possible to relate flux components to specific ecosystem compartments.

2.3 Catchment water balance

The catchment water balance is the traditional approach to estimate total forest evaporation (e.g., Hewlett, 1982):

$$P = ET + I + R + \Delta S, \tag{4}$$

where P = bulk precipitation; ET = soil evaporation plus transpiration; I = interception; R = runoff; ΔS = change in water storage)

ET is calculated as the residual of Eq. (4), while I is estimated from P minus canopy throughfall. The water balance approach is suitable for estimates of $ET + I$ with high temporal (hydrological years) and spatial (catchment area) integration and is especially applied to investigate effects of forest manipulations (clearcutting, fertilization) on the catchment water balance (e.g., Bosch and Hewlett, 1992). Although estimates of ET depend on the accuracy of all other components in Eq. (4), the water balance approach has been the only spatially integrating method for a long time.

3. Controls on forest canopy transpiration

Within the frame of ecosystem studies in stands of Norway spruce (*Picea abies* [L.] Karst.), Scots pine (*Pinus sylvestris* L.), and European beech (*Fagus sylvatica* L.) in Germany, canopy transpiration (E_c) was estimated by monitoring tree sapflow rates (see Alsheimer et al., 1998; Sturm et al., 1998; Lischeid and Gerstberger, 1997 for detailed site descriptions). The investigations made it possible to analyze dependencies of E_c on atmospheric, edaphic, and structural factors independent of soil and understory evapotranspiration and interception. The following results demonstrate the range of responses observed for the coniferous and broad-leaved species.

3.1 Atmospheric factors

Canopy transpiration is controlled by atmospheric factors such as available energy, vapor pressure deficit of the air, and aerodynamic conductance coupling the leaf surface with the atmosphere above the canopy (e.g., Monteith, 1965; Shuttleworth, 1989). On a daily basis, a linear increase in E_c with increasing net radiation was observed both for spruce (Fig. 1A) and beech canopies (Fig. 1B). However, only 40–50% and 40–75% of net radiation was used for transpiration of spruce and beech, respectively indicating that available energy was generally not a limiting factor for transpiration. Highest daily transpiration rates of spruce occurred in a 40–60 year-old stand at 380 m a.s.l. (Hohe Warte, Bayreuth), whereas lowest rates were found in a 140-year-old stand at 790 m a.s.l. (Coulissenhieb, Fichtelgebirge). Within the mountainous sites, highest rates of E_c were observed at an uncleared boggy site (40-year-old, Schlöppner Brunnen) compared to a managed 40-year-old stand on drained soil (Weiden Brunnen). E_c of a small patch (250 m^2) of 90-year-old beech at Hohe Warte exceeded flux rates observed in a beech stand at the Steinkreuz catchment (Steigerwald, 440 m a.s.l.) (Fig. 1B). For example, at a daily R_n equal to 5 mm d^{-1} (ca. 12.3 MJ m^{-2} d^{-1}), E_c at Steinkreuz reached on average only 66% (= 2 mm d^{-1}) of E_c at Hohe Warte. This coincides with similarily reduced tree density and cumulative stem basal area (50%) at Steinkreuz compared to Hohe Warte.

The best single atmospheric predictor of daily E_c was found to be daily maximum D (D_{max}) or daily mean D (D_{mean} for daytime). However, canopy transpiration seemed to be confined to a specific maximum rate ($E_{c\mathrm{max}}$) which was reached at D_{max} of 20–25 hPa (ca. 15–18 hPa D_{mean}) in spruce stands (Fig. 1C) and at D_{max} of 25–30 hPa (ca. 18–22 hPa D_{mean}) in beech stands (Fig. 1D). Dependencies of E_c on D and R_n can be theoretically analysed by the canopy-atmosphere decoupling factor Ω (McNaughton and Jarvis, 1983). Typically, E_c is stronger controlled by R_n in dense grasslands ($\Omega \rightarrow 1$) while E_c of rough forests is stronger dependent on D ($\Omega \rightarrow 0$) (see Jarvis and McNaughton, 1986). In spruce stands of the Lehstenbach catchment, low values of Ω ($\Omega < 0.3$) indicated strong control of D on E_c (Köstner et al., 2001).

In principle, similar relationships between D and E_c were observed at various forest sites differing in species, forest structure and site conditions (Fig. 2). It is generally assumed that all

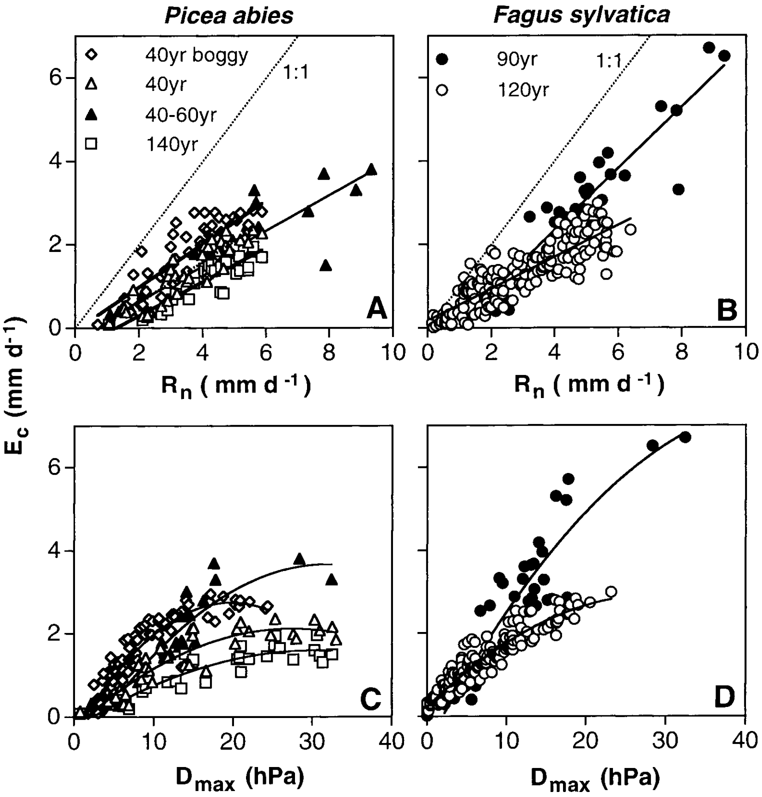

Fig. 1. Relationships between daily integrated net radiation (R_n, daytime values expressed in hydrological units, 1 mm $d^{-1} \approx 2.46$ MJ m^{-2} d^{-1}) and daily canopy transpiration (E_c) for *Picea abies* stands of different age in the Lehstenbach catchment/Fichtelgebirge (740–790 m a.s.l., open symbols) and at Hohe Warte near Bayreuth (380 m a.s.l., solid symbol) (**A**), as well as for *Fagus sylvatica* at Hohe Warte (solid symbol) and in the Steinkreuz catchment/Steigerwald (440 m a.s.l., open symbol) (**B**). For the same stands relationships are shown between daily half-hourly maximum of vapor pressure deficit of the air (D_{max}) and E_c for *Picea abies* (**C**), and *Fagus sylvatica* (**D**), respectively

Regression equations are as follows:

A:
40 yr boggy: $y = 0.519x - 0.057; r^2 = 0.699$
40 yr: $y = 0.493x - 0.384; r^2 = 0.801$
40–60 yr: $y = 0.425x - 0.218; r^2 = 0.789$
140 yr: $y = 0.409x - 0.528; r^2 = 0.775$

B:
90 yr: $y = 0.741x - 0.618; r^2 = 0.875$
120 yr: $y = 0.381x + 0.179; r^2 = 0.742$

C:
40 yr boggy: $y = -0.008x^2 + 0.320x - 0.410$
$r^2 = 0.857;$
40 yr: $y = -0.003x^2 - 0.174x - 0.271$
$r^2 = 0.837;$
40–60 yr: $y = -0.005x^2 - 0.295x - 0.997$
$r^2 = 0.867;$
140 yr: $y = -0.002x^2 - 0.123x - 0.283$
$r^2 = 0.819;$

D:
90 yr: $y = -0.004x^2 - 0.358x - 0.694$
$r^2 = 0.835;$
120 yr: $y = -0.003x^2 - 0.186x - 0.224$
$r^2 = 0.903$

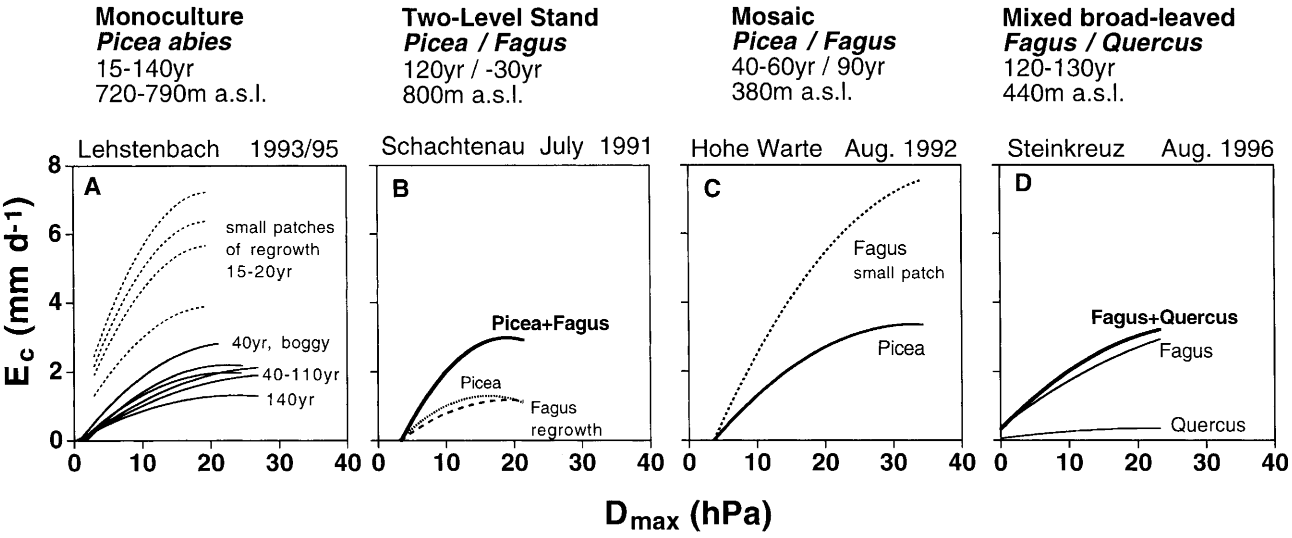

Fig. 2. Relationship between daily half-hourly maximum of vapor pressure deficit of the air ($D_{\max}$) and canopy transpiration (E_c) at various forest stands differing in species composition, structure and site conditions (A to D). Extremely high transpiration rates of small patches ($16\,\mathrm{m}^2$ and $250\,\mathrm{m}^2$ for natural regrowth of *Picea abies* (A) and *Fagus sylvatica* (C), respectively) could exceed available energy. Coefficients of determination range from $r^2 = 0.6$ for young spruce patches to $r^2 = 0.9$ for older stands. (Graphs include data from Alsheimer (1997); Poschenrieder (1992); Schäfer (1997); courtesy of meteorological data Dep. of Climatology, BITÖK and Chair of Bioclimatology, Munich)

transpiration rates presented in Fig. 2 were not affected by soil drought which would have resulted in significantly reduced rates of E_c independent of D. Highest flux rates were observed in small mosaic-like patches of spruce regrowth in the Lehstenbach catchment (Fig. 2A). But only about one third of the study area was covered by regrowth, while the remaining area consisted of grasses (*Deschampsia flexuosa, Calamagrostis villosa*), dwarf shrubs (*Vaccinium myrtillus*), and bare soil. Further studies are needed to assess the water vapor fluxes from the whole area and to compare it with older homogenous stands in the catchment.

Studies in a two-level stand of old spruce and regrowth of beech (Schachtenau, Bayerischer Wald) demonstrated that younger beech trees of the second canopy layer may contribute similar amounts to total E_c as old spruce trees forming the main canopy (Fig. 2B). $E_{c\max}$ of the 120-year-old spruce trees in the Bayerische Wald was comparable to $E_{c\max}$ of the 140-year-old spruce stand in the Fichtelgebirge (Fig. 2A). However, additional transpiration from young beech at the site Schachtenau resulted in much higher total rates of E_c exceeding those of younger monospecific spruce stands. At Hohe Warte, $E_{c\max}$ of a small patch of beech could exceed $E_{c\max}$ of the surrounding spruce stand by twofold (Fig. 2C). The small patch of beech was obviously functioning like an "oasis" within the coniferous forest. Highest transpiration rates of the beech patch could even exceed available energy. In contrast, typical rates of $E_{c\max}$ around 4–$5\,\mathrm{mm\,d}^{-1}$ were reported from large homogenous beech forests in eastern France as well as in northern and eastern Germany (Granier et al., 2000; Herbst et al., 1999; Heimann, pers. comm.). However, adjacent to the beech stand in northern Germany, $E_{c\max}$ rates up to $11\,\mathrm{mm\,d}^{-1}$ were observed in a belt of black alder (*Alnus glutinosa* (L.) Gaertn.) (Herbst et al., 1999).

Comparatively low canopy transpiration rates were observed in a mixed broad-leaved stand of the Steinkreuz catchment which was composed of European beech (67%) and of sessile oak (*Quercus petraea* [Matt.] Liebl.; 33%) (Fig. 2D). In the year of study, oak foliage was strongly reduced by caterpillars (*Tortrix viridana* L.) resulting in a very low leaf area index (LAI) of oak (projected LAI ca. 1). Obvioulsy, the reduced transpiration of oak was not compensated by increased transpiration of beech. Thus, total $E_{c\max}$ reached only around $3\,\mathrm{mm\,d^{-1}}$ at the site.

3.2 Soil factors

In most examples presented in this paper, frequent rainfalls during summer months precluded significant effects of soil drought on E_c. In spruce stands of the Fichtelgebirge, soil matrix potentials (Ψ_m) did not fall short of $-500\,\mathrm{hPa}$ in the main rooting zone (up to 0.90 m depth) and predawn leaf water potentials (Ψ_{leaf}) remained above $-0.5\,\mathrm{MPa}$ indicating no severe drought stress (Köstner et al., 1996a; Tenhunen et al., 2001a). Severe soil drought introduced artificially by a roof in a Norway spruce stand in the Vosges mountains was associated with predawn Ψ_{leaf} below $-1.2\,\mathrm{MPa}$ (Lu et al., 1995). At the Steinkreuz catchment, Ψ_m did not decline below $-450\,\mathrm{hPa}$ in 0.90 m depth and remained almost unchanged in 2.0 m depth during the year 1996 (Lischeid, pers. comm.). In an old beech stand in northern Germany, no restriction of E_c due to soil drought was observed throughout four years of study (Herbst et al., 1999). In a relatively dry year, the beech trees were able to exploit the soil water storage in more than 2 m depth. During three years of study, no drought stress was found in 15 stands of Norway spruce and Scots pine in Austria (Körner et al., 1989). Therefore, it seems to be a common phenomenon for Central Europe, that soil drought is confined to special site conditions and not a very frequent stress factor in many forest stands (cf. Körner, 1985).

Effects of severe soil drought could be studied in a 35-year-old Scots pine (*Pinus sylvestris* L.) stand growing on an old river terrace in the Upper Rhine valley near Hartheim (200 m a.s.l., precipitation $600\text{–}700\,\mathrm{mm\,yr^{-1}}$; see Sturm, 1998). The trees have no access to groundwater (groundwater level in 7 m depth; main rooting zone from 0–0.40 m depth) and frequent rainfalls are needed to maintain their physiological activity. On these conditions, E_c depends very much on soil water storage. Beyond a certain threshold of soil water content ($\theta_{\mathrm{soil}} = 16\%$ v/v in 0–0.40 m depth; field capacity 31% v/v) daily E_c dropped toward zero and predawn Ψ_{leaf} declined up to $-1.5\,\mathrm{MPa}$ independent of D (Fig. 3). Concurrently with soil drying, concentrations of abscisic acid (ABA) in the xylem sap increased from ca. 200 to $1900\,\mathrm{nmol\,l^{-1}}$ (Sturm et al., 1998). This underlies the function of ABA as a root-shoot signal (Davis and Zhang, 1991) during water shortage in Scots pine. Transpiration was less affected in July 1994 when θ_{soil} remained above 15% v/v. Accordingly, predawn Ψ_{leaf} maintained unstressed values ($>-0.6\,\mathrm{MPa}$) in 1994. More frequent drought stress of the trees is obviously avoided by the long-term balance between relatively low leaf area (projected LAI = 2.8) and soil water availability at the site. Soil drought also occurred in Scots pine stands in north-east Germany, where seasonal E_c determined by scaled sapflow measurements reached $82\text{–}113\,\mathrm{mm\,yr^{-1}}$ (Lüttschwager et al., 1999) compared to $200\,\mathrm{mm\,yr^{-1}}$ at Hartheim.

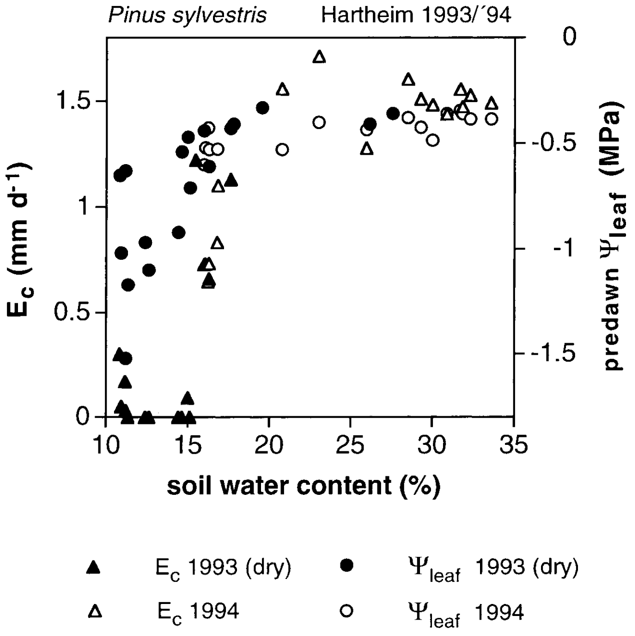

Fig. 3. Relationship of soil water content (% v/v) to canopy transpiration (E_c) and predawn leaf water potential (predawn Ψ_{leaf}) at the Hartheim Scots pine stand. Data are shown from the study year 1993 including a dry period in summer and from the study year 1994 with more frequent rainfall (data from Sturm, 1998)

3.3 Stand structure

The structure of a forest canopy affects canopy conductance and canopy transpiration (e.g., Shuttleworth, 1989). However, the conventional view of a forest canopy as a "big-leaf" has detracted attention from effects of spatial structure. Typical parameters used for structural information refer to

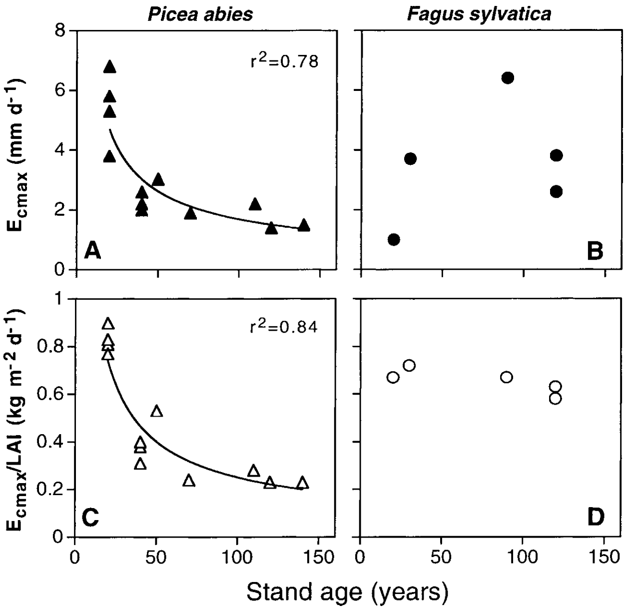

Fig. 4. Relationship between stand age and maximum daily canopy transpiration rate (E_{cmax}, determined at $D = 25$ hPa according to non-linear regressions in Fig. 2) for different sites of *Picea abies* ($y = 31.46x^{-0.635}$; **A**) and *Fagus sylvatica* (**B**) as well as between stand age and E_{cmax} per projected leaf area index (E_{cmax}/LAI) for *Picea* ($y = 5.61x^{-0.675}$; **C**) and *Fagus* (**D**). Graphs include results from a 30- and a 120-year-old beech stand in France (Granier et al., 2000). Information on leaf area of beech was partly provided by S. Fleck and M. Schmidt (unpubl.)

species, age, stem and leaf area index, stem and leaf area density, canopy height or biomass.

Functional relationships between stand age and E_{cmax} are shown in Fig. 4. Both E_{cmax} and canopy transpiration per leaf area (E_{cmax}/LAI) decreased significantly from small patches of natural regrowth (10–20 yr) to oldest stands (140 yr) of Norway spruce (range of LAI 5.3–8.4; Fig. 4A, C). A positive relationship is observed when canopy transpiration is related to tree density (Alsheimer et al., 1998; Köstner et al., 2001). Stand age and density are negatively correlated in managed stands. In conjunction with increasing stand age and decreasing tree density, the spatial distribution of leaf area becomes more aggregated and clustered in the canopy. Changes in light interception with increased needle aggregation (Niinemets and Kull, 1995; Cescatti, 1998) could be simulated by a three-dimensional, structure-dependent light interception model which was applied to predict gas exchange and canopy conductance of six spruce stands (40–140 yr) in the Lehstenbach catchment (Falge et al., 1997; Falge et al., 2000). Compared to scaled sapflow measurements, a similar reduction in canopy transpiration with stand age could be predicted by the model (Falge et al., 2000; Tenhunen et al., 2001a). The overall agreement between scaled sapflow measurements and the simulation was about 80% for daily transpiration rates using the same physiological parameterization for the "average needle" in all stands. Previous analyses from gas exchange measurements demonstrated similar response potentials of stomatal conductance for 40- and 120-year-old spruce trees (Falge et al., 1996). This differs from observations in 15- to 60-year-old Scots pine stands, where no changes in light interception per leaf area but an increase in hydraulic resistances with increasing stand age was found (Mencuccini and Grace, 1996). Further studies are needed to assess changes in physiological and structural properties of different tree species with increasing stand age.

For the complete water balance of the Lehstenbach catchment (4 km^2) a simple regression model of the type $E_c = k * (a * D - b * D^2)$ was applied (cf. Fig. 1C), in order to estimate E_c for all stands in the catchment. The factor k denotes stand age and was used for spatial scaling (Ostendorf and Manderscheid, 1997; Ostendorf et al., 1999). For a simulation period of 5 years, on average 176, 91, 223, and 345 mm yr^{-1} were predicted for E_c, E_u, I, and R, respectively. Average bulk precipitation amounted 894 mm y^{-1} while 59 mm yr^{-1} remained unexplained.

Significant differences in the relationships between canopy transpiration and stand age were observed for beech stands (Fig. 4B, D). No correlation was found between E_{cmax} and stand age (15–120 years), while E_{cmax}/LAI remained almost constant over a wide range of LAI (1.5–9). This could confirm high functional optimization of leaf area within the canopy (Field and Mooney 1986; Hollinger, 1996). A high potential in functional adaptation of leaf and canopy structure to light climate is reported for beech (cf. Niinemets, 1995). The distribution of typical sun- and shade-leaves as well as the relatively homogenous distribution of leaves within individual crowns and forest canopies may result in more similar light-use efficiencies and maximum assimilation and transpiration rates at the stand level as compared to spruce stands. It could be followed that LAI is a

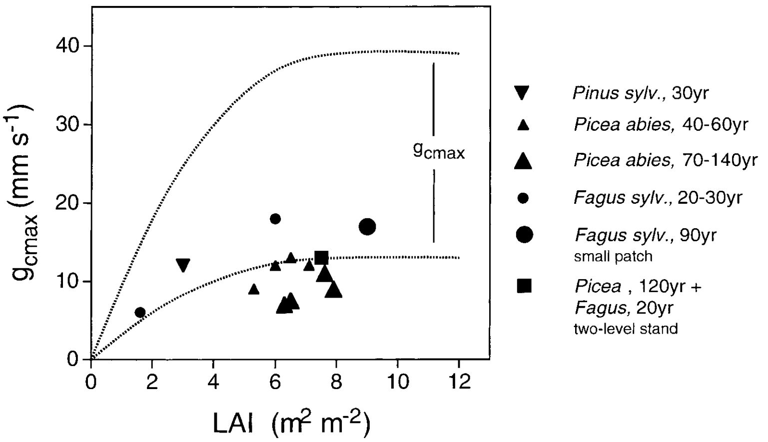

Fig. 5. Relationship between leaf area index (LAI, proj.) and maximum canopy conductance ($g_{c\max}$) derived from scaled xylem sapflow (symbols) for various coniferous and broad-leaved forest stands in Central Europe (including data from Granier et al., 2000). Further shown is the range of $g_{c\max}$ simulated by the Penman-Monteith equation and based on maximum leaf conductances determined by porometer measurements (Kelliher et al., 1995) (dotted line). This range comprises global vegetation types including fast growing fertilized crops

more suitable structural scaling factor for beech than for spruce stands. However, more investigatios in beech stands are necessary to confirm these findings.

Maximum leaf conductances ($g_{l\max}$) determined by porometer measurements in a variety of plants including tropical and crop species (reviewed by Körner, 1994) were used to predict their maximum canopy conductance, $g_{c\max}$ in relation to LAI (Kelliher et al., 1995; see also Schulze et al., 1994). The range of modelled $g_{c\max}$ agreed with the range of maximum surface conductances ($G_{s\max}$) determined from eddy-correlation measurements above corresponding vegetation types. This range was compared to $g_{c\max}$ derived from scaled sapflow measurements (Fig. 5). Values of $g_{c\max}$ from scaled sapflow were found to be within the lowest range of predicted values, but $g_{c\max}$ from old spruce canopies even fell short of this range. For modelled $g_{c\max}$ it was assumed that evapotranspiration from soil and understory does not contribute significantly to surface conductance for canopy LAI > 4. But this may be only true in young stands with homogenous distribution of canopy leaf area. It is shown below that in old stands with LAI > 6, understory vegetation can contribute significantly to canopy conductance at the whole stand level.

4. Comparison of evaporation components

4.1 Soil and understory evapotranspiration

Comparably few information on soil and understory evapotranspiration (E_u) is provided from forest evaporation studies (cf. Black and Kelliher, 1989) although, in pine stands water vapor fluxes from the understory may account for 30–70% of total transpiration (Roberts et al., 1980; Loustau and Cochard, 1991; Wedler et al., 1996a, Lüttschwager et al., 1999). At the Scots pine site near Hartheim, agreement between eddy-correlation estimates of water vapor fluxes and scaled sapflow measurements was only achieved when the water vapor flux from soil and understory was considered (Granier et al., 1996b; Bernhofer et al., 1996).

In dense spruce stands, litter evaporation is assumed to be less than 10% of total evaporation (e.g., Ellenberg et al., 1986). During studies of spruce stands in the Lehstenbach catchment it could be shown that in the oldest stand (LAI = 6.5), E_u reached 40–50% of total transpiration on summer days (Fig. 6). In the 40-year-old stands, E_u reached ca. 20% of total evaporation. Even at the uncleared boggy site with highest tree density (Schlöppner Brunnen), E_u (mostly from *Sphagnum* mosses) was similar to the 40-

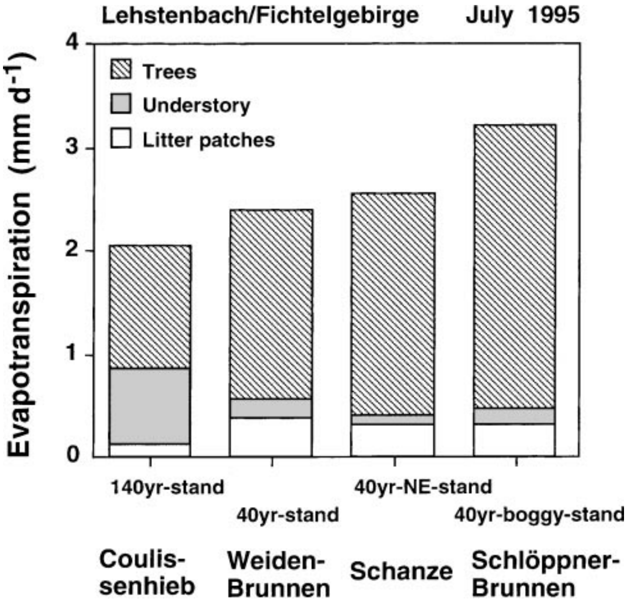

Fig. 6. Mean daily transpiration rate of tree canopy and understory as well as evaporation from litter patches during July 6–11, 1995 at four different Norway spruce stands within the Lehstenbach catchment (data by Wedler, Alsheimer, and Köstner; for description of methods see Wedler et al., 1996b; Köstner et al., 2001)

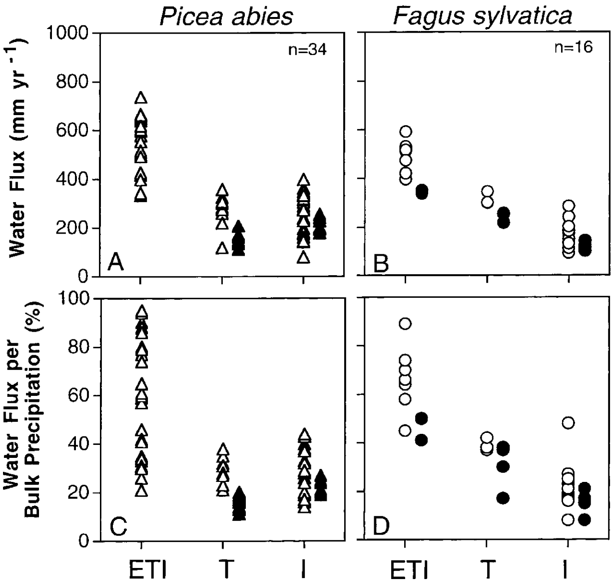

Fig. 7. Range of annual rates of water flux components (total evaporation *ETI*, transpiration *T*, and interception *I*) in spruce (**A**, **C**) and beech (**B**, **D**) forests according to literature reviewed by Peck and Mayer (1996) (open symbols; *n* refers to number of studies) and according to recent studies of tree sapflow and eddy-correlation (solid symbols). Data from Gülpen (1996) for *T*, Granier et al. (2000) for *ETI*, *T*, and *I*, as well as from Moritz et al. (1994) and Lischeid (unpubl.) for *I* were included. Ranges of absolute water flux rates (**A**, **B**) and rates per annual bulk precipitation (**C**, **D**) are shown

year-old stands on drained soils. For stands on drained soil (e.g., Coulissenhieb, Weiden Brunnen) no significant differences in total evapotranspiration occurred due to the compensating effect of E_u in the old stand. Further investigations are needed to confirm these results from lysimeter and chamber measurements during summer days. Although, a compensating effect of E_u on total stand evaporation was previously suggested, seasonal rates of evapotranspiration in spruce stands of the Lehstenbach catchment were more variable and significantly lower as reported by Roberts (1983).

4.2 Total evaporation, transpiration, and interception

Information on total evaporation is provided from micrometeorological measurements and forest catchment studies. Results on annual water flux rates (total evaporation *ETI*, transpiration *T*, interception *I*) mainly originating from forests in Central Europe were recently reviewed (Peck and Mayer, 1996). But only about 20% of the reviewed studies provided information on all flux components (*ETI*, *T*, and *I*). Similar ranges of *T* and *I* were observed for spruce reaching on average 30% of *ETI*. But absolute values differed more than 2-, 3-, and up to 5-fold for *ETI*, *T*, and *I*, respectively (Fig. 7A, C).

Water flux rates from beech forests remained within the range of spruce stands (Fig. 7B). However, a consistent higher portion of *T* on *ETI* (40% on average) compared to *I* on *ETI* (20% on average) was observed for beech (Fig. 7D). Variation in *ETI*, *T*, and *I* did not decrease when absolute water flux rates were related to annual bulk precipitation. Variation may decline when water vapor fluxes are related to seasonal instead of annual bulk precipitation, however this information was often not available. Recent data from long-term tree sapflow (*T*, solid symbols) and eddy-correlation studies (*ETI*, solid symbols) are relatively low compared to older studies (open symbols). More information is needed to clarify these differences. For a better understanding of the variation in water budgets, emphasis has to be put on tree and understory transpiration as well as on the spatial estimation of interception.

5. Conclusions

Scaled sapflow rates made it possible to investigate variation in forest canopy transpiration in relation to tree and canopy structure excluding other evaporating components. On similar environmental conditions, $E_{c\max}$ could differ more than twofold in neighbored spruce stands of different age. These differences could be predicted by a three-dimensional, structure-dependent (i.e., spatial distribution of leaf and stem area density) gas exchange model without changing needle physiology and response potential of stomatal conductance (Falge et al., 2000). It is therefore concluded, that variation in $E_{c\max}$ strongly depends on forest structure.

Only at a Scots pine site, where trees had no access to groundwater, effects of soil water restrictions on E_c were observed. In this case, effects of soil drought on E_c had to be considered for modelling (Sturm, 1998). More generally it can be concluded that for the forests under study, transpiration (and CO_2-uptake) was more frequently limited by low canopy conductance on days of high D than by periodical soil drought. Frequently drought-prone areas may be indicated by permanently low LAI. Although soil drought did not play a major role in our studies, the quantification of soil characteristics and rooting depth in georeferenced databases of landscape models has to be improved (Waring and Running, 1998).

The most prominent structural parameter of a plant canopy is leaf area index. At the patch level, LAI can be quite successfully determined from biomass harvests and optical measurements. For a coniferous canopy however, light interception per LAI may differ significantly due to the degree of needle clumping and mutual shading. Therefore, the relevance of LAI as a spatial scaling factor differs with tree species and canopy structure. Up to now the link between ground-based LAI and the measure of "vegetation greenness" derived from remotely sensed data i.e., the normalized digital vegetation index (NDVI) is difficult because NDVI is not well correlated with $\mathrm{LAI} > 4$ (Myneni et al., 1997). Accurate ground estimates of LAI including differentiation of LAI from understory and overstory plants are necessary to improve information from remote sensing (Waring and Running, 1998). While canopy LAI seemed to be a suitable predictor of $E_{c\max}$ in European beech ($E_{c\max}/\mathrm{LAI} \approx \mathrm{const.}$) independent of stand age, $E_{c\max}/\mathrm{LAI}$ decreased with increasing stand age in stands of Norway spruce. It is followed, that age and density-related structural information should be provided by GIS-based data. Promising results on density-related information of forest overstory were reported from evaluations of Landsat data (Olsson, 1994; Cohen et al., 1995). But various data sources had to be combined and structural information must be verified by ground-based measurements.

It was further shown, that the forest floor and understory or a second canopy level in the overstory can contribute significantly to total evapotranspiration of the system compensating for relatively reduced water flux rates from the main tree canopy. At one hand, this compensation could facilitate the estimation of total evaporation. On the other hand, variation in total annual forest evaporation (up to 200%) remained high compared to annual forest transpiration (up to 300%). Thus, forest structure may still explain a significant part of the remaining variation in *ETI*. More data are needed to valuate relatively low absolute water flux rates derived from scaled sapflow or eddy-correlation as compared to older data from literature often determined indirectly by the water balance equation of catchments or the soil water budget. At least the range of "typical" E_c (or T) as cited in the literature (e.g., 300–400 $\mathrm{mm\,yr^{-1}}$) has to be revised when compared with data from scaled sapflow measurements (110–260 $\mathrm{mm\,yr^{-1}}$) in this work.

Proceeding from a vertical view of vegetation-atmosphere exchange processes to a spatial view, patch-level studies are relevant to identify and quantify the role of vegetation and to define functional units of the landscape. Future research has to include more mixed forest stands varying in species and age as well as "untypical" or disturbed vegetation of high structural heterogeneity to represent the landscape mosaic of forest stands in Central Europe.

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