Water use in neighbouring stands of beech (Fagus sylvatica L.) and black alder (Alnus glutinosa (L.) Gaertn.)

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Original article

Water use in neighbouring stands of beech (*Fagus sylvatica* L.) and black alder (*Alnus glutinosa* (L.) Gaertn.)

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Abstract – In neighbouring stands of beech and black alder in northern Germany, transpiration, soil evaporation and interception evaporation were estimated for four meteorologically different years. By means of standard weather data a two-layer evaporation model of the Shuttleworth–Wallace type was applied. In the 105-year-old beech forest (tree height 29 m, maximum leaf area index 4.5), annual transpiration (Tr) varied between 326 and 421 mm (mean 389 mm or 50 % of gross precipitation, P_G) and annual evapotranspiration (ET) between 567 and 665 mm (mean 617 mm or 79 % of P_G). In the 60-year-old alder stand (tree height 18 m, maximum leaf area index 4.8) the respective values were 375 and 658 mm (mean 538 mm or 69 % of P_G) for Tr and 612 and 884 mm (mean 768 mm or 99 % of P_G, for ET. In years with high radiation input, ET in the alder stand (along a lake shore with unlimited water availability) exceeded both P_G and net radiation. The higher inter-annual, weather-dependent variation of transpiration in alder corresponds to a lower capacity of stomatal regulation in alder if compared with beech. (© Inra/Elsevier, Paris.)

forest / beech / black alder / evaporation / transpiration

Résumé – Utilisation de l'eau dans deux peuplements de hêtre (*Fagus sylvatica* L.) et d'aulne (*Alnus glutinosa* (L.) Gaertn.) juxtaposés. Dans une hêtraie et une aulnaie voisines, au nord de l'Allemagne, la transpiration, l'évaporation du sol et l'évaporation de l'eau interceptée ont été éstimées pour quatre années présentant des conditions météorologiques différentes. Basé sur des données météorologiques standard, un modèle à deux couches a été appliqué. Pour la hêtraie, âgée de 105 ans (hauteur des arbres 29 m, indice de surface foliaire maximal 4,5), la transpiration annuelle (Tr) varie entre 326 et 421 mm (moyenne 389 mm ou 50 % des précipitations, P_G) et l'évapotranspiration annuelle (ET) entre 567 et 665 mm (moyenne 617 mm ou 79 % des P_G). Pour l'aulnaie, âgée de 60 ans (hauteur des arbres 18 m, indice de surface foliaire maximal 4,8), les valeurs respectives sont de 375 et 658 mm (moyenne 538 mm ou 69 % des P_G) pour Tr et de 612 et 884 mm (moyenne 768 mm ou 99 % des P_G) pour ET. Pour l'aulnaie, située au bord d'un lac (à disponibilité en eau illimitée), ET dépasse P_G ainsi que le rayonnement net dans les années à fort ensoleillement. La variation interannuelle de la transpiration, dépendante des conditions météorologiques, est plus élevée pour l'aulnaie, ce qui est dû à une capacité moindre de régulation des stomates. (© Inra/Elsevier, Paris.)

forêt / hêtre / aulne / évaporation / transpiration

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1. INTRODUCTION

Beech (*Fagus sylvatica* L.) and black alder (*Alnus glutinosa* (L.) Gaertn.) belong to the most widespread tree species of mid-European broadleaved forests, but represent very different habitats: Whilst the shade-tolerant and highly competitive beech is the dominating species at mesic sites, the more light-demanding, fast-growing and flooding-tolerant black alder is restricted to moderately to extremely wet sites [6]. In this study we ask how this separation between different habitats corresponds to the water consumption of the two species and their ability to regulate the stand water balance. How strong is the influence of weather pattern, water availability and stomatal control on the water turnover rates? What are the feedbacks between water consumption and groundwater level and/or site microclimate? Roberts [32] and Peck and Mayer [30] reviewed several case studies regarding certain aspects of beech water balance, but many of them are not fully comprehensive, and as yet no data about alder are available. We will address the questions outlined above by a model study, which results from a comprehensive synopsis of previous studies on single components of the water balance of neighbouring stands of beech and black alder at the Bornhöved site in northern Germany [7–9, 12–14, 18]. An analysis for representative, sufficiently long time periods was possible only by modelling, because continuous long-term measurements of stand water fluxes were not possible at the investigated site (see later). However, standard meteorological data from a nearby weather station were available over several, meteorologically different annual courses. For the parameterisation of the two-layer evaporation model we used results from intensive measurement campaigns in the two forests during 1992 to 1995. As the neighbouring stands were exposed to an identical mesoclimate, our study allows an interesting comparison between beech and alder with respect to the influence of tree physiology on stand water balance.

2. MATERIALS AND METHODS

2.1. The site

The research site is located in the Bornhöved lakes region, about 30 km south of Kiel, at 54°06'N and 10°15'E, in an area with maritime, humid temperate climate. Annual mean temperature is 8.1 °C and annual precipitation 697 mm (means 1951 to 1980). Typical wind speeds are in the order of 3 $m \cdot s^{-1}$. Some climatic characteristics for the period of investigations are given in *table I*. The years 1992 and 1995 were characterised by relatively sunny and dry weather, whereas 1993 was cool and wet and 1994 warm and wet. The research site includes a great variety of aquatic and terrestrial ecosystems and is highly representative of the eastern Schleswig-Holstein landscape. Therefore, it was chosen by the Ecosystem Research Center of Kiel University to investigate some fundamental processes of mass and energy transfer in and between ecosystems. An overview about properties of the Bornhöved site is given in *figure 1*.

2.2. The beech forest

The even-aged, 105-year-old beech (*Fagus sylvatica* L.) forest covers almost 50 ha of nearly flat terrain and is surrounded by other forest plantations to the west and east and by small plots of agricultural land separated by hedgerows to the north and south. Average tree height is 29 m, tree density 150 $stems \cdot ha^{-1}$. The crowns of the trees have an average length of 19 m, which means that the lowest branches are found about 10 m above the ground. The forest soil is covered by a sparse herb layer with *Milium effusum* being dominant. The trees grow on a typical mesotropic Cambisol associated with typical oligotrophic Cambisol, developed on loamy to silty moraine sand over fluvioglacial sand [35]. The field capacity is 170 mm in 0–1 m depth and 260 mm in 0–2 m depth. The wilting point (pF = 4.2) is reached at

Table I. Meteorological data for the period of field investigations compared to long-term means.

	Mean 1951–1980	1992	1993	1994	1995
Sunshine duration ($h \cdot a^{-1}$)	1 646	1 665	1 250	1 436	1 509
Mean temperature (°C)	8.1	9.6	7.8	8.6	8.0
Precipitation ($mm \cdot a^{-1}$)	697	756	838	977	687

Data from a weather station near the research site.

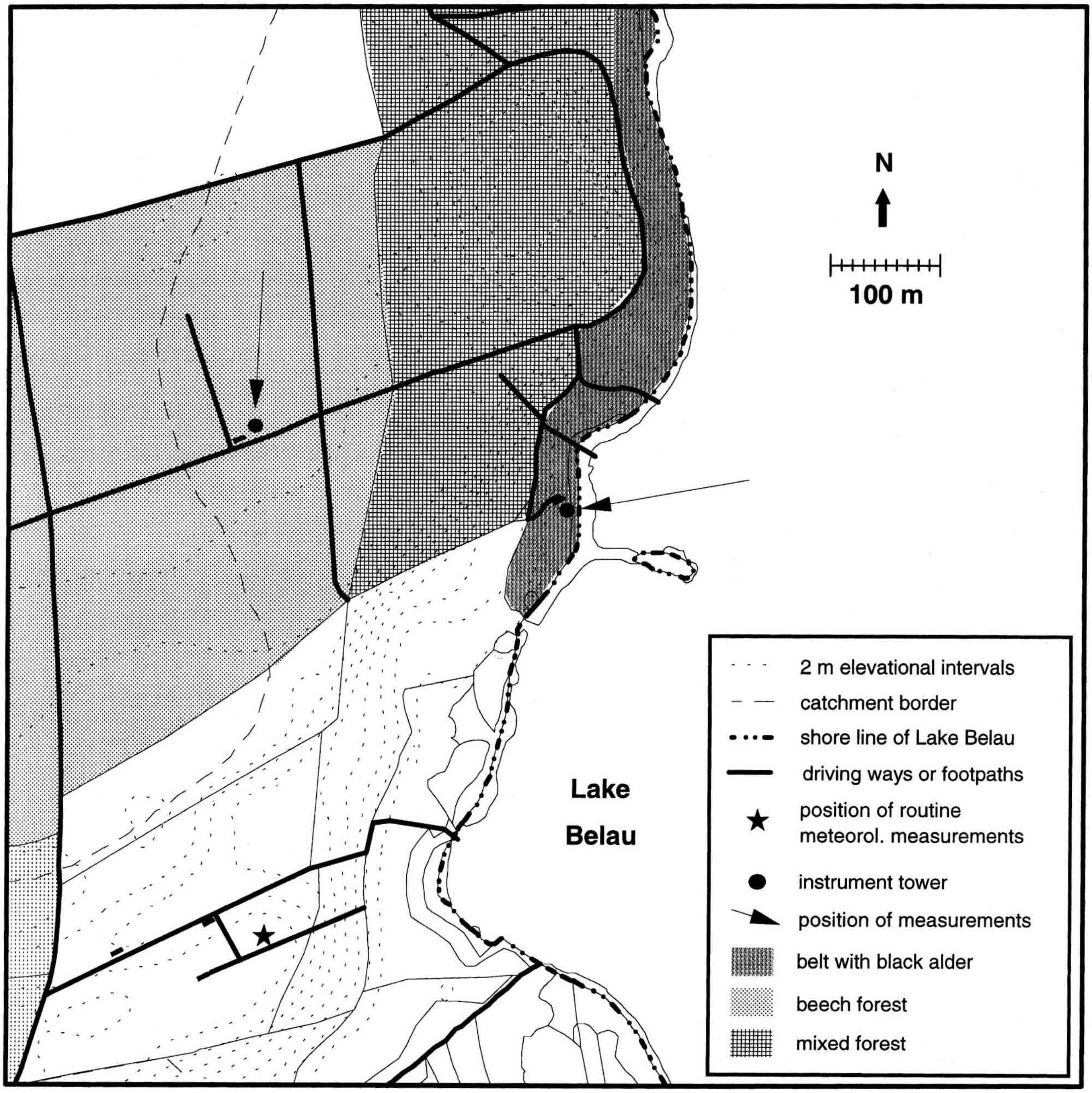

Figure 1. Map of the research site.

about one tenth of these values [1]. A scaffold tower of 36 m height is located in the eastern part of the beech forest. Air temperature, relative humidity and horizontal wind speed were measured continuously (recorded as hourly means) at 2, 12, 25, 30 and 36 m. Net radiation and wind direction were determined at 36 m, soil heat flux at –0.05 m. Gross precipitation and global radiation were measured 200 m outside the forest. Throughfall and stem flow in four representative areas of the forest were determined weekly as described by Hörmann et al. [18].

Measurements of stand evaporation of the beech forest by use of the Bowen ratio technique and the derivation of canopy conductance from these data were described in detail by Herbst [12]. Evaporation from the soil was measured with a weighing lysimeter and additionally with a Bowen ratio system placed 1 m above the ground [13].

2.3. The alder stand

The alder stand (*Alnus glutinosa* (L.) Gaertn.) is located about 300 m from the beech forest, on the shore of Lake Belau (see *figure 1*). The trees are about 60 years old and 18 m high. There is access to the canopy by a scaffold tower (18 m). The alder stand has a sparse understorey, mainly consisting of small *Prunus padus* trees. The stand forms a 30 m wide belt and grows on histosols developed from decomposed alder peat [35]. Microclimate in various positions of the canopy has been recorded during 1992 and 1996. Leaf transpiration was investigated continuously during the growing season at peripheral and inner parts of the crown [9]. Leaf area index (LAI) of different crown layers necessary to scale up porometer data was determined monthly by counting leaves and by measurements with an optical sensor [8]. A mathematical description of the seasonal course was obtained by fitting an optimum-typed curve to the measured data [7]. Stand scale measurements of gas exchange by micrometeorology were not possible at this site because of the narrow extension of the alder belt.

2.4. Evaporation modelling

Transpiration, interception evaporation and soil evaporation were modelled by use of a two-layer evaporation model that is based on the scheme of Shuttleworth and Wallace [36]. It uses the Penman–Monteith equation and a detailed network of canopy, soil surface and aerodynamic resistances to calculate the water vapour flux from hourly meteorological standard variables. Extending the original model, a formulation was introduced regarding the partitioning between transpiration and rainfall interception when the canopy is partially wet. Therefore, two values for canopy evapotranspiration were always calculated, using 1) the actual and 2) an infinite canopy conductance, representing 1) dry and 2) wet leaf surfaces. The 'true' evapotranspiration was considered to be between these two limits and to depend on the size of the wet fraction of the canopy, which can easily be calculated from rainfall data and the interception parameters given in *table II*. The structure of this two-layer model was described by Herbst and Kappen [15] in detail. Driving variables for the model runs were incoming solar radiation (R_G), air temperature (T), relative humidity (RH), wind speed (u) and gross precipitation (P_G) measured about 500 m south of the investigated tree stands (*figure 1*). Other radiation quantities necessary to run the model were estimated from these standard data as follows: Net radiation (R_N) above the forests could be related to R_G as $R_N = 0.68\ R_G - 40$ [13], and heat flux into the soil was neglected. Instead, heat flux into storage in the biomass and in the air between the trees was taken into account using a method used by Kiese [21], who developed a seasonal and diurnal dependent regression approach to calculate this component of the energy balance from R_N. Photosynthetic active radiation (PAR) measured above the alder stand on average was higher than PAR above the beech forest (55 and 50 %, respectively, of R_G recorded at the weather station 500 m south). This was explained by the reflection of radiation from the neighbouring lake surface to the alder belt. One $W{\cdot}m^{-2}$ (PAR) was considered to equal 4.5 $mmol{\cdot}m^{-2}{\cdot}s^{-1}$ (PPFD).

2.5. Model parameterisation

The parameterisation of the modified Shuttleworth–Wallace-model is based on the data analysis carried out in several previous studies which are listed in *table II*. Beech forest transpiration obtained from Bowen ratio measurements during time periods when leaves and soil surface were completely dry was used to calculate canopy conductance (g^c_s) by inverting the Penman–Monteith equation. Most of the observed variations of g^c_s could be explained from actual light and humidity conditions above the forest [12] using an equation given by Lohammar et al. [24]. Although an equation containing a linear light response function gave even a slightly better fit to the measured data, the more widely used Lohammar equation was applied because this facilitates the comparison of parameters with those reported for other European forest sites.

Leaf gas exchange and leaf conductance of peripheral and inner parts of an alder crown were investigated continuously during the growing season with leaf chambers [9]. Leaf conductance (g_l) was modelled by use of a function used by von Stamm [37] relating g_l to ambient photon flux density (PPFD) and vapour pressure deficit (VPD) [7] and was scaled up to g^c_s considering three crown layers with different light conditions [13].

The water vapour conductance of the soil surface (g^s_s) in the beech forest was calculated from measurements of soil evaporation and microclimate near the forest floor. It exhibited an exponential decrease with the time since the

Table II. Selected functions and parameter values for evaporation modelling (with references).

	Beech	Alder	Reference
α	0.69	0.66	[13]
z_0/h	0.1		[14, 18]
d/h	0.8		
S (summer)	1.28 mm		
S (winter)	0.84 mm		
S_t	0.09 mm		
p (summer)	0.25		
p (winter)	0.9		
p_t	0.05		
Function to calculate canopy conductance	$g_s^c = a \cdot \frac{PPFD}{PPFD + b} \cdot \frac{1}{1 + c \cdot VPD}$	$g_s = \left(\frac{b}{VPD} + c - d\right) \cdot \left(1 - e^{-\frac{a \cdot PPFD}{b/VPD + c - d}}\right) + d$	[7, 12]
Parameter a	$0.0965\ m \cdot s^{-1}$	outer part $2\ mmol \cdot \mu mol^{-1}$ inner part $3.5\ mmol \cdot \mu mol^{-1}$	
Parameter b	$559\ \mu mol \cdot m^{-2} \cdot s^{-1}$	$1\,000\ \mu mol\ m^{-2} \cdot s^{-1} \cdot mbar$	
Parameter c	$0.495\ mbar^{-1}$	$100\ mmol \cdot m^{-2} \cdot s^{-1}$	
Parameter d		$15\ mmol \cdot m^{-2} \cdot s^{-1}$	
Function to calculate soil surface conductance	$g^s_s = a\ b^t$		[13]
Parameters	$a = 0.0347\ m \cdot s^{-1}$ $b = -0.0797\ VPD + 0.8485$		

See text for further explanations.

last rainfall event. On average, the soil surface conductance was in the same order of magnitude as the canopy conductance. The transpiration of the sparse herb layer was measured by means of a leaf porometer, but was shown to be negligible for the forest water balance [13].

From measurements of gross precipitation, net precipitation and stem flow, interception storage capacities of the canopy and the stems were estimated by use of a method described by Gash and Morton [10]. On average, canopy capacity (S) is 1.28 mm in summer and 0.84 mm in winter, stem capacity (S_t) is 0.09 mm [14]. Hörmann et al. [18] demonstrated that, for particular rainfall events, these capacities depend strongly on wind speed. The coefficient of free throughfall (p) was estimated as 0.25 in summer and 0.9 in winter; 5 % of rainfall is diverted to the trunks (p_t).

All relevant equations and parameter values are summarised in *table I*. It was assumed, because of similarities in LAI and crown architecture, that rainfall interception and soil evaporation were the same in the black alder stand as in the beech stand and thus, could be modelled using the same functions as for beech. The relationships between stand height, zero plane displacement height and roughness length were taken from the literature [28] but were not experimentally verified.

3. RESULTS

3.1. Model validation

To validate the model with independent field data, measurements of stand evapotranspiration of the beech forest by use of the Bowen ratio energy balance method were available. The measurements worked reliably only when the leaf surfaces were dry, but not during periods with evaporation from the wet canopy when temperature and humidity gradients above the forest were often smaller than the resolution of the instruments. Data obtained in winter were not used for model validation because the vertical distance of 36 m between the sensors and the forest floor did not allow a representative measurement of soil evaporation. The data from 1992 could not be used for validation because they were the base for the parameterisation of canopy conductance (and therefore not 'independent'), and data from 1994 were also excluded because of long periods of sensor failures.

The remaining measured values of daily beech forest ET from 1993 and 1995 were plotted against simulated ET for the same days. *Figure 2* illustrates that the model predictions matched quite well the measured values. A slight, but obviously systematic overestimation for 1993 and underestimation for 1995 data remains unexplained. It cannot be excluded that either inter-annual variations in physiological behaviour of the beech trees or – more likely – uncertainties in LAI modelling may have caused these deviations: For instance, Breda and Granier [2] have shown for an oak forest a linear relationship between LAI and the ratio of stand transpiration versus potential evaporation.

For the alder stand on the shore of Lake Belau, a validation of modelled evaporation with stand scale measurements was not possible, but observations of the groundwater level in connection with water balance models for the lake shore region indicate that model results for alder are quite plausible (W. Kluge, personal communication). However, because only one tree could be investigated by porometry for practical reasons, an uncertainty of g^c_s values of up to one third must be considered if they are extrapolated from an individuum to the whole stand [23]. The procedure of scaling-up leaf conductance data to the canopy was already validated in a previous study [12] for the beech forest.

Rainfall interception in the beech forest measured as the difference between gross and net precipitation was 99 mm in 1992 and 126 mm in 1994. Taking a possible uncertainty of gross rainfall measurements of up to 40 mm a^{-1} into account [14], the correspondence between modelled and observed values is satisfying, and model results are plausible.

3.2. Model results

In all years under investigation leaf unfolding started earlier in black alder than in beech (*figure 3*, uppermost panel). The annual course of LAI did not reach a steady state. A maximal LAI of about 4.8 was observed in the alder stand always in late July. In the beech forest leaf unfolding started, depending on the weather, during late April and took place very rapidly. In general, the LAI remained at a constant value of about 4.5 from mid-May to late September.

To illustrate the differences in canopy conductance (g^c_s) between the two tree stands, midday values of g^c_s were chosen (from 1200 to 1300 hours). During this time the evaporative demand of the atmosphere is high and g^c_s influences the stand water balance most effectively. On average, g^c_s was significantly higher in alder than in beech. In both tree stands conductances were slightly higher in the darker and wetter years 1993 and 1994 than in the brighter and drier years 1992 and 1995. This suggests the general relevance of a VPD-dependent regulation of stomatal conductance in both species. However, during periods with the highest saturation deficits of the air (early summer 1992, mid-summer 1994 and 1995), g^c_s was reduced more in beech than in alder, which indicates that such a VPD regulation is more effective in beech.

The Omega factor [26] describes whether the transpiration of a plant stand is controlled merely by the energy input (leaves and atmosphere decoupled, Ω close to one) or by the stomata responses (leaves well-coupled to the atmosphere, Ω close to zero). Omega depends mainly on the ratio between canopy and aerodynamic resistances. Although both forest canopies are aerodynamically rough and well-ventilated, the beech forest was coupled more strongly to the atmosphere than the alder stand (*figure 3*, lowest panel). This can be explained by the lower canopy conductance of the beech stand. In both stands transpiratory water loss is controlled by the stomata more effectively than by the energy supply ($\Omega < 0.4$).

Daily sums of simulated transpiration, interception and soil evaporation for the whole 4-year period of investigations are presented in *figures 4* and *5*. In the beech forest (*figure 4*) transpiration reached maximum values of 5 mm·d^{-1} in 1992 and 1995 and of 4.5 mm·d^{-1} in 1993 and 1994. In spring 1992, transpiration increased very suddenly due to a fine weather period during the phase of rapid leaf unfolding in May. Most of the transpiration occurred during the first 2 months of the growing season, whereas in 1993 high transpiration rates were simulated only for single days; further periods of intensive transpiration were observed in July 1994 and July and August 1995. Soil evaporation was insignificant during summer but reached values between 1.5 and 2 mm·d^{-1} temporarily in spring prior to leaf unfolding. The peak values of daily interception evaporation in summer were in a similar range as transpiration.

As interception and soil evaporation were parameterised similarly for both tree stands, the daily sums modelled for alder (*figure 5*) were on the same order of magnitude as for beech. However, the different annual

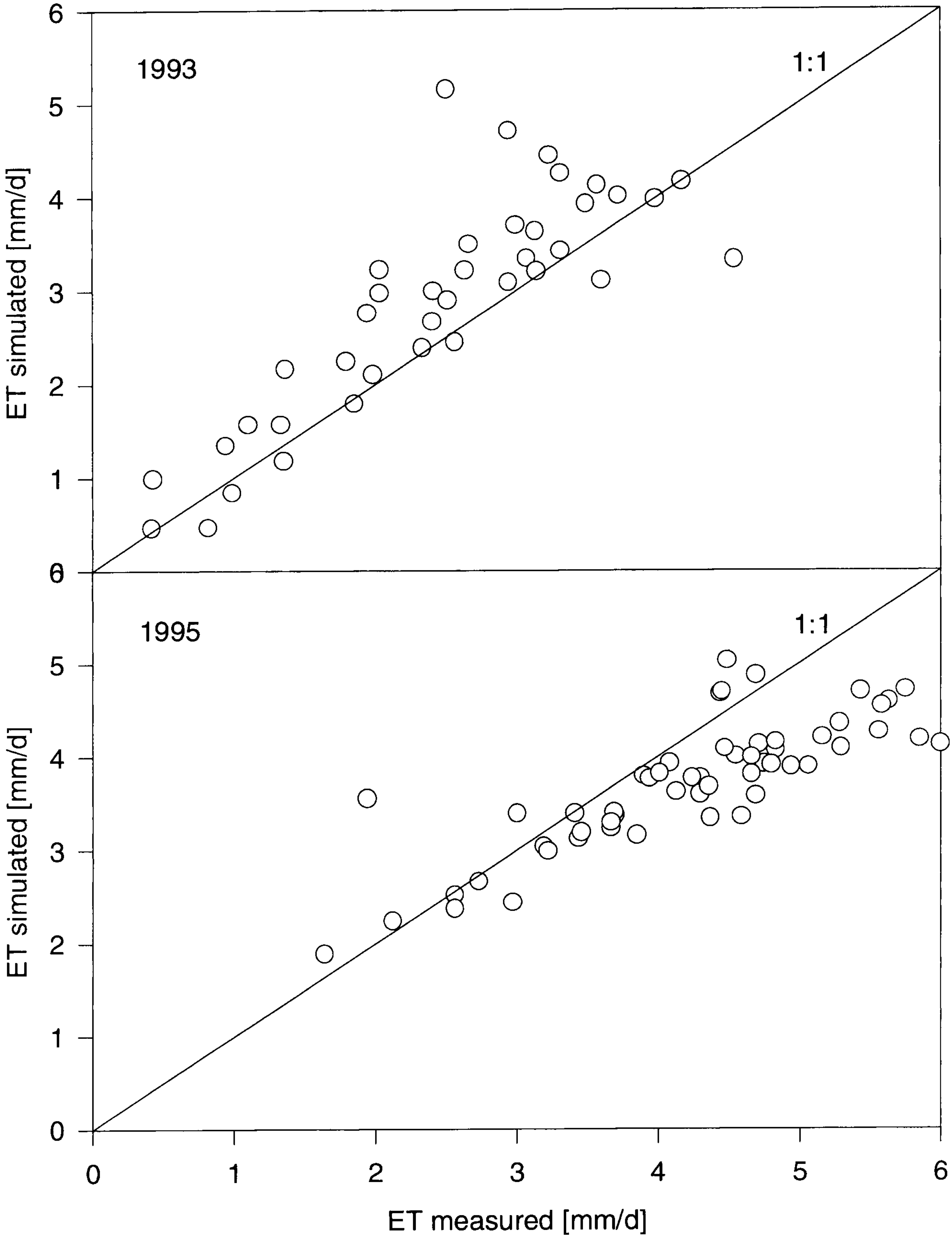

Figure 2. Measured versus modelled evapotranspiration (ET) of beech forest (daily sums) for selected days from two growing seasons.

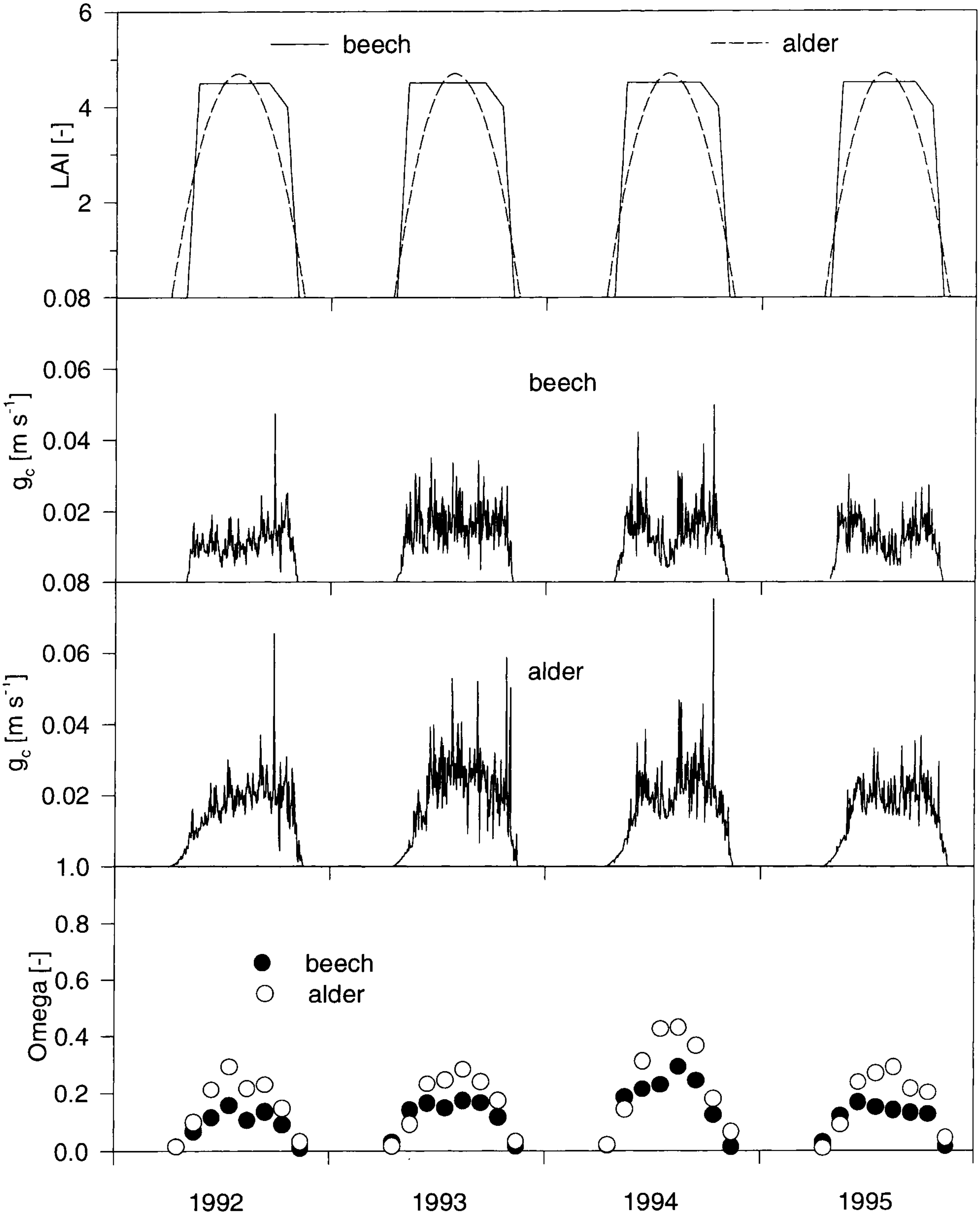

Figure 3. Modelled values of leaf area index (LAI), canopy conductance (g_c, midday values) and decoupling coefficient (Omega, monthly means) over 4 years.

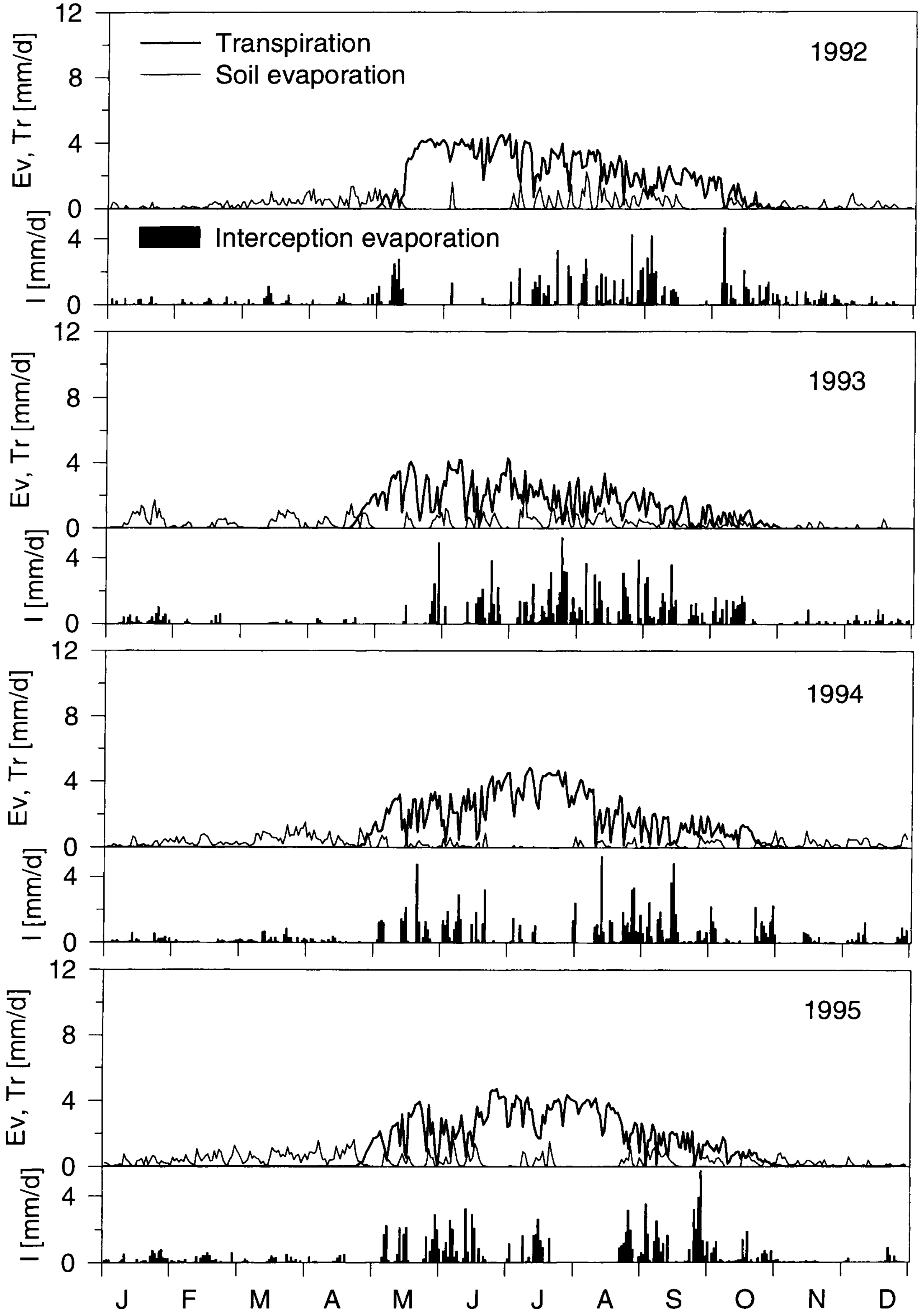

Figure 4. Modelled daily sums of transpiration (Tr), interception evaporation (I) and soil evaporation (Ev) for the Bornhöved beech forest from 1992 to 1995.

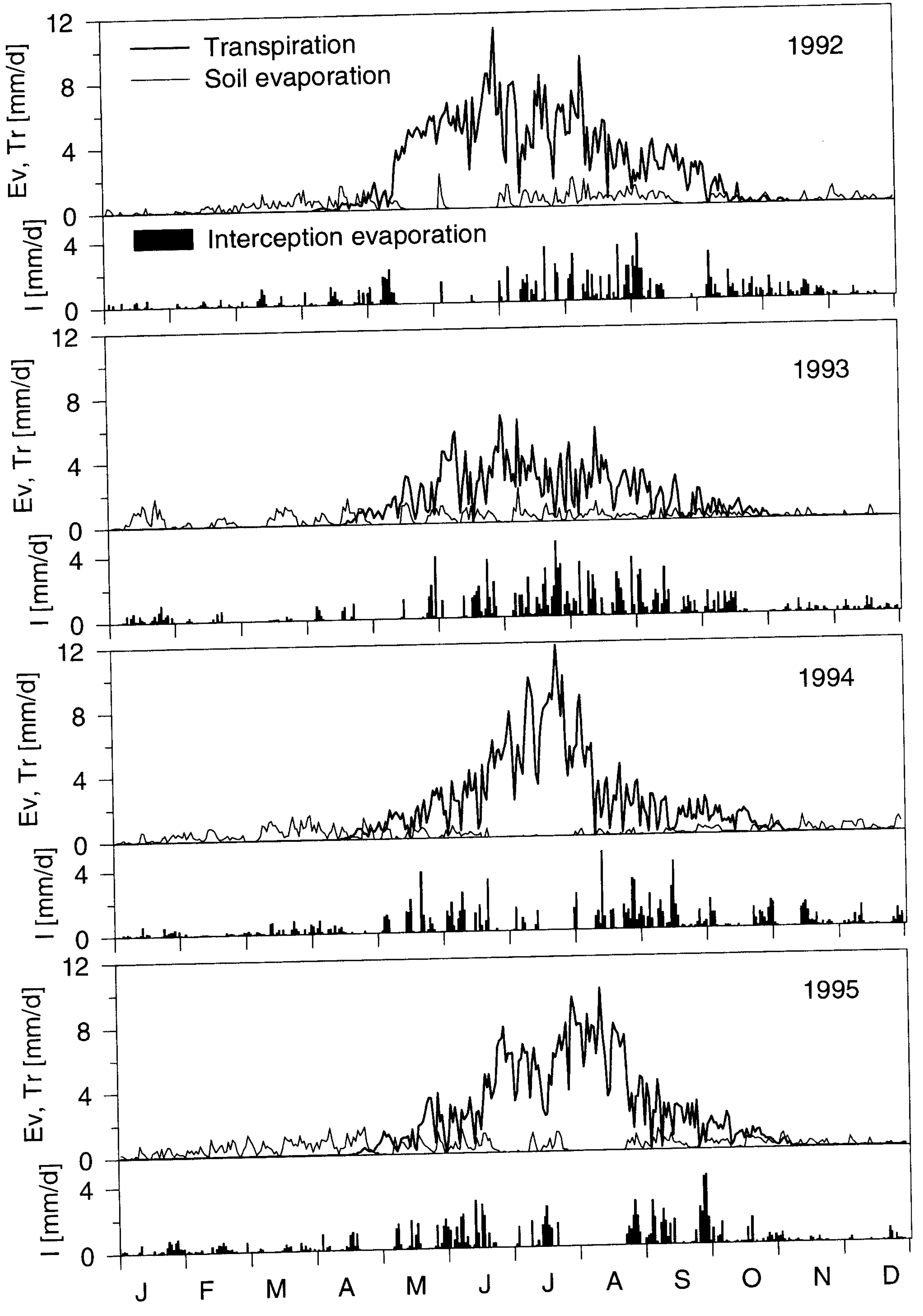

Figure 5. Same as in *figure 4* but for alder.

development of LAI caused the modelled interception evaporation for alder to be lower in spring and late summer than for beech. Transpiration was very different for alder and beech. The annual course of alder stand transpiration exhibited a higher amplitude because the sigmoidal LAI course coincided with the annual course of radiation. Therefore, the increase of transpiration in spring 1992 was more gradual in alder than in beech, and the annual course of transpiration during 1994 was very irregular due to the simultaneous occurrence of high irradiance and maximum LAI in July. The maximal transpiration rates were much higher for alder than for beech, and reached values beyond 10 $mm{\cdot}d^{-1}$. As the equivalent amount of net radiation even on sunny days was only around 6 $mm{\cdot}d^{-1}$, this extraordinarily high transpirational water loss can be explained only from a downward flux of sensible heat above the alder stand.

Considering the annual sums of evaporation components and total evaporation (ET), not only the absolute magnitude of Tr and ET but also the magnitude of the year-to-year variations of these quantities, are significantly higher in alder than in beech. Annual ET (mean 617 mm or 79 % of P_G), varied in beech by less than 100 mm even between climatically very different years, but ranged between 612 and 884 mm a^{-1} in alder depending on the weather conditions. It nearly equalled gross precipitation if the entire observation period of 4 years is considered. Soil evaporation in the beech forest was slightly more suppressed than in the alder stand as a consequence of stronger shading due to a more rapid leaf unfolding in spring, a later shedding of leaves and a slightly higher extinction coefficient (see *table II*) caused by a different leaf angle distribution. In both forests, annual interception evaporation was slightly higher than soil evaporation. In the beech forest annual ET was always lower than P_G and R_N. This applies to the alder stand only for the darker and wetter years, but not for 1992 and 1995 when ET exceeded both P_G and R_N.

4. DISCUSSION

4.1. A comparison with other forests

The canopy conductances we have modelled for the beech forest correspond well with data from other studies on broadleaved forests in temperate regions. In a review, Kelliher et al. [20] report maximum g^c_s values between 20 and 25 $mm{\cdot}s^{-1}$ for this type of vegetation. Most of our results (see *figure 3*) for midday (= maximum) conductances fall into this range as well. To our knowledge there are no comparable studies about alder stands in the literature, except for poplar, which is also a fast-growing species preferring wet soils: Dolman et al. [5] observed maximum g^c_s values of 55 $mm{\cdot}s^{-1}$, which was approximately twice as high as maximum g^c_s of other broadleaved forests.

Considering transpiration, Roberts [32] observed that mid-European forests transpire in a very 'conservative' range (mean 333 $mm{\cdot}a^{-1}$), independent of climate, species composition and forest structure. Our study indicates that this is not relevant to alder stands growing on wet soils. The extraordinarily high transpiration rates observed for this forest type exceed Roberts' value by more than 200 $mm{\cdot}a^{-1}$ on average (see *table III*). On the other hand, the modelled annual transpiration for the Bornhöved beech forest ranging from 326 to 421 $mm{\cdot}a^{-1}$ (mean 389 $mm{\cdot}a^{-1}$) is closer to Roberts' mean value and in the same range as those given in more recent studies [30, 33]. Peck and Mayer [30] reviewed nine studies of evaporation components of European beech forests, and found mean values of 363 $mm{\cdot}a^{-1}$ for transpiration (range 268 to 601 $mm{\cdot}a^{-1}$) and 561 $mm{\cdot}a^{-1}$ for evapotranspiration (range 396 to 937 $mm{\cdot}a^{-1}$. The sum of transpiration and interception evaporation (mean values of 389 + 128 = 517 $mm{\cdot}a^{-1}$) almost exactly equals the 529 $mm{\cdot}a^{-1}$ (288 + 241) found by Nizinski and Saugier

Table III. Modelled annual sums of evaporation components and total evapotranspiration (ET) for beech and alder forest compared to gross precipitation (P_G) and equivalent net radiation (R_N).

Year	Beech				Alder				P_G	R_N
	Tr	E_I	E_S	ET	Tr	E_I	E_S	ET		
1992	421	116	103	640	658	111	115	884	703	738
1993	326	141	100	567	375	133	104	612	827	638
1994	389	129	79	597	525	124	82	731	878	788
1995	419	126	120	665	596	115	135	846	698	797

All values in $mm{\cdot}y^{-1}$.

[29] for the oak forest of Fontainebleau with a similar LAI as the Bornhöved beech forest, but with an understorey of small beech trees and less availability of soil water.

The high transpiration rates of the alder stand seem to be unusual for forest canopies. It has been discussed [27] that estimates of forest transpiration from leaf conductance data may be too high if boundary layer conductances are low. However, this is clearly not the case in this study because we did not calculate Tr simply as a product of g^c_s and VPD [27], but applied a two-layer SVAT model taking aerodynamic resistances and evaporation partitioning into account. Other possible sources of error, such as a heterogeneous behaviour of the trees or uncertain measures of LAI or microclimate, are not likely to occur all in the same direction, from a statistical point of view. Therefore, they do not question the general reliability of the model results [16]. The canopy conductance in the Bornhöved alder stand was not higher than observed in poplar stands at other sites [5, 17]. Those stands transpired less than the alder stand because they were more strongly decoupled from the atmosphere (Ω up to 0.66, compared with a maximum of 0.4 in alder). Thus, the poplar stand transpiration was more strictly limited by the radiation input than alder stand transpiration.

With respect to interception evaporation, *figures 4* and *5* showed for both beech and alder forests, peak values for daily E_i equal to the maximal values of beech forest transpiration, although available energy on rainy days is clearly much lower than during phases of maximum transpiration. On 16 September 1994 for example (see peak in *figure 4*), the beech forest interception evaporation was 5 $mm \cdot d^{-1}$ according to our model and this value was three times as high as the equivalent net radiation on that day of 3.7 $MJ \cdot d^{-1}$. However, these values are plausible if compared with other findings [38, 39] that show a frequent occurrence of negative Bowen ratios above wet forest canopies, corresponding to downward fluxes of sensible heat and to evaporation rates that exceed net radiation severalfold. This corresponds also to the recent study of Martin et al. [25], who demonstrated that an infinite surface conductance (representing wet leaf surfaces) would increase forest evaporation severalfold under a given radiation input. The observed amount for E_i of 16 % of P_G for beech and alder forest is even lower than the 29 % reported by Nizinski and Saugier [29] for the above-mentioned oak forest of Fontainebleau, but matches a range that is typical for broadleaved forests in temperate regions [18, 30].

Evaporation from the forest floor is treated very differently in the literature. Whilst some authors explicitly set this component of the forest water balance to zero [29, 31, 42], others put emphasis on the significant amount of soil evaporation even under a closed forest canopy [41], especially under wet climatic conditions. Kelliher et al. [19] reported that 10–20 % of the total evaporation in a closed *Nothofagus* forest came from the soil surface. In a pine forest, Denmead [4] measured similar average values and even 40 % after rainfall events. In addition, Roberts et al. [34] emphasised the important role of rainfall interception in and evaporation from the litter layer. They observed mean evaporation rates of 0.3–0.6 $mm \cdot d^{-1}$ under a pine forest canopy. The modelled amount of E_s in the Bornhöved beech forest corresponds well to interception storage capacities of the litter layer on the order of 2.5–3 mm, measured by Thamm and Widmoser [40].

4.2. Hydrological consequences

The comparison of gross rainfall and total evaporation (*table III*) illustrates that the extraordinarily high water consumption in the alder belt can influence the groundwater level. In warm and dry years, ET was significantly higher than P_G. As ET of alder is also higher than equivalent net radiation, the missing energy necessary to evaporate the high amounts of water must have come from horizontal advection to the alder belt and/or from a downward flux of sensible heat. Such fluxes cause a cooling of the air in the lake shore region.

The transpiration of a beech forest could be simulated in our study satisfactorily by use of a model approach basing only on PPFD and VPD as driving variables for g^c_s. As this was also valid for the dry summer of 1995 (see *figure 2*), no extra effect of soil drought was necessary as a parameter, as for instance in the model approach by Granier and Breda [11] for oak forest transpiration. We conclude, therefore, that the beech trees either make use of sapwood storage in the trunks [3] or explore more soil water from deeper layers. Taking the latter into account we have to state that from late April to mid-August 1995 the total evaporation in the beech was 260 mm higher than gross rainfall. This amount equals the field capacity of the forest soil between 0 and 2 m depth. Thus, the roots should have reached layers deeper than 2 m. Alder is also known for a deep rooting system and therefore is also able to grow in temporarily dry sites [9].

The results of our study illustrate a difference between the strategies of water use of the two investigated tree species. Beech maintains a more constant water consumption than alder (see *figures 4* and *5*). Thus, it regulates its water use more strictly and is more 'conservative' with respect to amounts of evaporation [32], i.e.

less weather-dependent. This can be observed during fine weather periods in summer when the combined action of stomatal regulation and root growth or sapwood storage (or both) ensures that not more than 5 mm water per day is consumed, but that this amount is kept constant even during rainless periods of several weeks. This contrasts with more drought-tolerant tree species like oak, which exhibits a strong stomatal response to decreasing soil water content [11] and uses available water even more sparingly than beech. Alder, however, shows a much weaker regulation and exhibits no significant differences in transpiration behaviour between inner and outer parts of the crown or even between wet and dry sites [9]. By shedding leaves alder avoids rather than tolerates drought if water becomes short. Our results indicate that alder trees growing with unlimited water availability have a strongly varying water consumption depending on leaf area index, radiation input and the evaporative demand of the atmosphere. The very high g^c_s values found in alder also cause Ω to be higher than in beech. Water turnover rates in alder stands are generally much higher than in beech stands as long as water availability is unlimited.

The previously discussed differences in water use by the two species correspond to similar differences in the their carbon balance [22] and may characterise why alder is a representative of early successional forest phases, whereas beech is a typical late successional species.

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