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ORIGINAL PAPER

Transpiration of forest trees and stands at different altitude: consistencies rather than contrasts?

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Abstract Compared to lowland trees and forests, evidence on water relations at mountainous and sub-alpine sites with their climatic and topographic peculiarities is scarce. On such limited grounds, the outcome of three pilot studies is reviewed, intended to launch working hypotheses for initiating integrative research across the altitudinal gradient of the European Alps. Highlighted are tree transpiration and structural differentiation as well as stand water balance of mono-specific and/or mixed forests with *Picea abies*, *Pinus cembra*, *Larix decidua* and *Fagus sylvatica* at sub-alpine (timberline ecotone), mountainous and colline elevation. Given the preliminary evidence, tree-allometric structures of relevancy for water transport appeared to be independent of elevation and forest type, although timberline trees under open-canopy conditions did not buffer transpiration by internal water storage and had enhanced foliage/sapwood area ratios. Transpiration appeared to depend on site conditions rather than site-dependent adaptation. Canopy transpiration approached 20% of the high seasonal precipitation at the mountainous site, with about 60% being ascribed to run-off, whereas the water budget of the colline site was balanced during summer. The water balance of the subalpine site resembled, at lower precipitation, that of the mountainous site. The derived hypotheses focus on mixed-stand transpiration under altitude-specific topography and moisture regimes, hydraulic adaptation and water demand versus uptake capacity, as this latter ratio is crucial at high altitude in view of expected warming. The clarification of consistencies relative to contrasts indicated by the pilot studies will be challenging across altitudes in view of tree species, forest types and topography.

Keywords High altitude · Water balance · Tree/stand transpiration · Canopy structure · Tree allometry

Introduction

Given the wealth of information on the transpiration and water balance of forest trees and stands at low-altitudinal sites (e.g. Alsheimer 1997; Köstner 1999; Tenhunen et al. 1998), corresponding knowledge is scarce about mountainous and sub-alpine locations (Kräuchi et al. 2000). This deficit is remarkable, as such forests have been recognized for their high potential in timber production (Innes 1991; Graumlich 1991; Wuebbles et al. 1999; Grace et al. 2002), and even more importantly, their prominent function in landscape protection (Ammer et al. 1996). The lack of quantitative knowledge on water balances at high altitude represents a major limitation on modelling water budgets of mountainous forests with their climatic and topographic peculiarities and, as a consequence, risks of natural hazards (e.g. by avalanches, landslides or flooding; Ammer et al.

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1996; Bader and Kunz 1998) at the regional scale (Aulitzky 1994, 1996). Such risks may be exacerbated in populated landscapes, if protective functions of forests in mountainous regions are compromised (Veit 2002). This latter issue has gained attention in view of “global change” (Schlesinger 1997), as high-altitudinal sites are regarded as sensitive indicators of altered environmental impact (Körner 2003). As in other areas of ecological field analysis, the functional characteristics of the extremes of ecological gradients—here, high altitude—demand for particular clarification to ensure adequate coverage by modelling and scenario simulations (Tenhunen et al. 1998; Hofmann et al. 2009; Stumpp et al. 2009; Engelhardt et al. 2009).

The following account will review, therefore, the outcome of three individual pilot studies in relation to the scarce available evidence. These independent pilot studies (i.e. not being interrelated through a joint experimental design) are to provide orientation about peculiarities in tree and stand water relations at different altitude, and about the respective relevance of tree species and forest types. It is intended to derive research questions and hypotheses to guide required integrative experimentation and analysis along altitudinal gradients in the European Alps. To this end, hydraulically relevant tree allometry will be exemplified along with tree and stand transpiration in southern Central Europe at subalpine (1,950 m a.s.l.), mountainous (1,220 m a.s.l.) and colline elevation each (485 m a.s.l.). Water balances will be viewed at given stand structure, topography and edaphic and climatic conditions prevailing each, and being widely common, at the three selected altitudes. Norway spruce (*Picea abies*) was examined in all three pilot studies. This evergreen conifer will be highlighted in relation to European beech (*Fagus sylvatica*) at the mountainous and colline, and European larch (*Larix decidua*) at the subalpine site, both species contrasting by their deciduous habit. As broad-leaved beech can be a climax species across the colline and submountainous range in Central Europe and represents a competitor of spruce at mountainous elevation, coniferous larch is a pioneer of the timberline ecotone at sub-alpine sites (Ellenberg 1996; Tranquillini 1979). Evergreen cembran pine (*Pinus cembra*) will be included as the climax species of the timberline in the central European Alps.

Mixed forests are of interest, in particular, at the mountainous range of the Northern Alps (Ellenberg 1996), as beech together with spruce (and other broadleaf and coniferous tree species) rather than spruce monocultures constitute the autochthonous tree vegetation, and because beech is increasingly favoured in reconstructing mixed forests (Dertz 1996; Rennenberg et al. 2004; Ammer et al. 2005). Water relations of mixed stands are a key issue, as canopy transpiration (Ec) is determined by the interspecific differences in crown architecture and foliage habit (Mackey et al. 2003; Schume et al. 2003), and since, in these latter terms, spruce and beech (as well as larch and cembran pine) represent contrasting extremes within the tree vegetation of Central Europe (Schulze 1982; Matyssek 1986; Reiter et al. 2005). Ec may substantially vary in such stands, mediated through heterogeneity in canopy structure (Köstner 2001; Zirlewagen and von Wilpert 2001), and leading to local constraints in soil water supply (Zierl 2001; Schume et al. 2003).

The pilot studies still used one common methodology, i.e. the heat balance approach (Cermak et al. 1973; Sakuratani 1981; Granier 1985), to assess the sap mass flow through the trunk xylem. This approach provides crown transpiration, fed by the sap flow through tree trunks, as both parameters match each other on a daily and seasonal basis in the absence of severe drought (e.g. Schulze et al. 1985), as typically is the case at mountainous and sub-alpine elevation in Central Europe. High time resolution (cf. Finnigan and Raupach 1987; Hollinger et al. 1994; Schulze 1994) and direct sap flow assessment through the tree compartment are advantageous over hydrological or meteorological approaches, the latter being restricted to stand-level analysis or limited by non-ideal topographic conditions (cf. Benecke and Van de Ploeg 1976; Jarvis et al. 1976). Such latter limitation is typical at mountainous and sub-alpine sites with steep slope inclination. The sap flow approach, in addition, distinguishes the tree-internal water storage capacitance (Tyree and Zimmermann 2002) that, depending on tree allometry, determines transpiration (Meinzer et al. 2006; Whitehead 1998). Being a basic tool in experimental and diagnostic plant ecology (e.g. Werk et al. 1988; Matyssek et al. 1991, 2004; Cermák and Kucera 1993; Wieser et al. 2003; Köstner et al. 2008), the sap flow approach allows for scaling transpiration from the tree to the stand canopy level (Cermák 1989; Köstner et al. 1992; Arenth et al. 1996).

On these grounds, transpiration will be elucidated in relation to prevailing site and tree features, including foliage type and stand structure. Upon an overview on site conditions and methodology, tree and stand transpiration will be introduced each at the mountainous elevation, before viewing “downwards” to the colline and “upwards” to the subalpine site. Although the presented evidence is preliminary, given the pilot character of the three referred studies, comparisons will be made with the available knowledge on high-altitudinal forests. The account will conclude by deriving research questions and hypotheses to initiate integrative research on tree and stand water relations across the altitudinal gradient of the European Alps.

Materials and methods

Study sites were typical in terms of tree species and climate at each elevation, including the open stand structure at the timberline ecotone as opposed to the closed canopy and lower tree density at the other two sites, and the steep slope inclination of the mountainous forest. Given the orientational character of each individual pilot study, the plot number was restricted in total—i.e. one in a mixed stand at the subalpine, one each in a monoculture and mixed stand at the mountainous, and one in a mixed stand at the colline elevation. Hence, a comparative statistical analysis across the altitudinal gradient is not intentional in this account and, therefore, omitted. Site and plot features were in detail:

Sites of the three pilot studies

Mountainous elevation

This study site was located at 1,220–1,260 m a.s.l. at the northern edge of the Bavarian Alps in the forest district of Oberammergau/Wildsteig (about 60 km SW of Munich/Germany) and belonged to the watershed of Sperrgraben (1.1 km^2; 47°37′33″N, 10°56′51″E), which is a mountainous side valley (extending across a height gradient of 600 m) that feeds the Halbammer river as part of the Ammer river system. The cool-temperate climate at the site was characterized by a mean annual air temperature of 6.3°C, annual precipitation of up to 1,620 mm and snow cover from November through May. Two neighbouring plots (at a distance of 200 m) were selected at the upper southern edge of the Sperrgraben watershed, one carrying a monoculture of Norway spruce (*P. abies*), the other one a mixed culture of Norway spruce and European beech (*F. sylvatica*).

The about 80-year-old managed spruce monoculture with up to 31 m high tree individuals was NE-exposed (slope inclination 25° at 1,260 m a.s.l.) and formed a closed canopy, LAI (projected needle area) was 6.8 $m^2\ m^{-2}$. The projected area of the plot was 3,066 m^2 (440 trees ha^{-1}). The soil had developed above clayey-marly Flysch into a Luvisol (Pseudogley) with mold as the main humus form. Under the high precipitation regime, the pH ($CaCl_2$) ranged within the uppermost 30 cm between 3.2 and 3.4 but increased towards 3.9 at 90 cm soil depth (Huwe, personal communication). The ground coverage of the understorey vegetation, consisting of mosses, spruce saplings and *Oxalis acetosella*, was less than 5%. Also the mixed forest was managed (51% *P. abies*, 49% *F. sylvatica*), about 80 years old and formed a closed canopy (LAI = 6.6 $m^2\ m^{-2}$), with the spruce and beech individuals reaching heights of up to 28 and 22 m, respectively (at 1,220 m a.s.l.). The projected area of this plot was 3,897 m^2 (559 trees ha^{-1}), although the NE exposure had an inclination of 55°. Again, Luvisol (Pseudogley) with mold (underneath spruce) and mull (underneath beech) as humus forms had developed from clayey-marly Flysch, with pH ($CaCl_2$) of 4.0 (uppermost 30 cm) and 4.5 (at 90 cm soil depth; Huwe, personal communication). The ground coverage by the understorey was about 5%, mainly consisting of mosses as well as *Lysimachia nemorum* and *Homogyne alpina.* Selection of study trees for sap flow assessment was oriented at the "social dominance" of individuals within the stand according to the 5-grade "Kraft classes" system (Kraft 1884, as defined, in the present study, by tree height and trunk diameter at breast height, DBH), covering the range between highest (class 1) and lowest (class 5) tree vigour. The number of selected trees per Kraft class reflected the respective proportion within the tree population of each species at the site (*n* = 1–5; cf. Reiter et al. 2005) during the study period (1999 through 2001).

Colline elevation

The study site Kranzberg Forest was located at 490 m a.s.l. near Freising/Germany (48°25′08″N, 11°39′41″E, about 30 km N of Munich) and represented a managed mixed forest of European beech (54% *F. sylvatica* L.) and Norway spruce [46% *P. abies* (L.) KARST; plot size 5,312 m^2, 776 trees ha^{-1}, N-exposed inclination of 1.8°; Pretzsch et al. 1998]. At the time of investigation (1999 through 2001), spruce individuals were about 50 years old, whereas beech trees were 7 years older, according to common silvicultural planting practices (Hehn 1997). Trees were up to 27 m high and formed a closed canopy, LAI (projected leaf area) was 6.0 $m^2\ m^{-2}$. Scaffolding and a canopy crane allowed access to individual tree crowns (see Nunn et al. 2002; Häberle et al. 2003). Long-term means of annual air temperature and precipitation were 7.8°C and 786 mm, respectively. Soil had developed from loess above tertiary sands into a Luvisol (Pseudogley and Pseudogley–Parabrown earth) that allowed a rooting depth of about 1 m. Water and nutrient availability were apparently not limiting (the latter being higher under beech than spruce), given the high stand productivity in the absence of respective decline symptoms (Pretzsch et al. 1998), as pH ($CaCl_2$) ranged within the uppermost 30 cm between 3 and 4 and reached >4 at about 90 cm soil depth. An understorey of *Rubus fruticosa agg.* L., *Oxalis acetosella* L. and mosses (ground coverage of 5–15%, according to Reichelt and Wilmanns 1973and Braun-Blanquet 1928) was present only under spruce. Selection of study trees for sap flow assessment followed same principles as at the mountainous site (*n* = 3–5 per Kraft class; see above).

Subalpine elevation

This study site was located at the alpine timberline at 1,950 m a.s.l. on a NW-exposed slope of 5° inclination near the Klimahaus Research Station on Mt Patscherkofel (47°12′37″N, 11°27′07″E) south of Innsbruck/Austria, being characterized by an open subalpine mixed forest (Larici-Pinetum Cembrae) of cembran pine (*P. cembra* L.), European larch (*L. decidua* Mill.), and Norway spruce [*P. abies* (L.) Karst.]. At the time of the study (1997–1998), the trees were 70–90 years old and their height ranged between 9 and 14 m. The number of individuals was 1,038 ha^{-1} (84% *P. cembra*, 7%, *P. abies*, 9% *L. decidua*; Wieser and Stöhr 2005), with a basal area in total of 47.6 m^2 ha^{-1}. LAI was 3.9 m^2 m^{-2} on a projected needle area basis. Cool subalpine climate with low temperatures prevailed at the site (continuous snow cover from October through May), with a chance of frost during each summer month. According to a 40-year record of a weather station nearby the mean annual air temperature was 2.4°C with summer maxima of up to 32°C and winter minima down to −28°C. The mean annual precipitation was 950 mm, mainly falling during May through October, and the 10-year mean of annual soil temperature ranged between 2.6 and 5.7°C at 5 cm soil depth (summer maxima up to 15°C, winter minima down to −6.5°C).

The geology of the Mt Patscherkofel region (Tuxer Alps as part of the Central Tyrolean Alps) is dominated by gneisses and schist. According to the World Base for Soil Resources (FAO–ISRIC–ISSS 1998), a Haplic Podzol (Wieser 2004) typical for the Central Austrian Alps (Neuwinger 1970, 1980) prevailed at the study site, carrying a 20–30 cm thick layer of raw humus (L, F, H) on the top of the mineral E, B_1, and B_2 horizons. Mineral horizons at 30–60 cm soil depth were dominated by sand (47–58%) and silt (35–46%), with variable clay content (6–11%). pH (determined in 1n KCl) ranged between 2.9 and 4.2 across the soil horizons. The volumetric soil water content averaged 72 ± 3 and 54 ± 6 m^3 m^{-3} in the humus layer and the mineral horizons, respectively. Due to frequent summer precipitation, soil moisture rarely dropped to below 20% (approximating soil water potentials of greater than −0.01 MPa, including the summer drought of 2003; cf. Ciais et al. 2005).

Six tree individuals (i.e. two each of *P. cembra*, *P. abies* and *L. decidua*) were selected for sap flow assessment in 1997 and 1998. Based on height and crown area, the study trees were canopy dominants or co-dominants (corresponding to Kraft class 1 at lower elevation sites). Stem diameter at breast height ranged between 20.0 and 37.7 cm.

Assessment of whole-tree transpiration

At each altitude, mass flow of xylem sap through tree trunks was measured at breast height by means of the "tissue heat balance" approach (THB) according to Granier (1985), providing crown transpiration on a daily and seasonal basis (e.g. Schulze et al. 1985). At Kranzberg Forest, sensors were installed into N and S-facing sides of trunks, whereas steep slope inclination allowed access only to S-facing sides at Sperrgraben, preventing however, sun exposure of the sensors. At the subalpine site, sensors were installed into the N-facing sides and shielded through a thermally isolating styrofoam cover as done at the other sites.

Results and discussion

Structural and ecophysiological tree features

Mountainous and colline elevation

Viewing tree performance at different elevation, the hypothesis may arise that structural and functional differentiation varies with altitude (Körner 2003). One common allometric measure used in silviculture is the relationship between trunk diameter at breast height (DBH) and tree height (Fig. 1). In beech and spruce, this relationship was similar at mountainous and colline elevation (given some scatter in the limited sample sizes), irrespective of the forest type (spruce monoculture or beech/spruce mixed stand). The relationship also covered, in each species, datasets assessed by Burger (1941, 1950, 1953) at different locations. DBH related closely also to the projected foliage area, again regardless of elevation and in consistency with Burger's previous assessments (Fig. 2a, b).

The correlation between DBH and cross-sectional sapwood area (SA) relates tree allometry to water transport. SA increased exponentially with DBH in beech and spruce at the mountainous and colline site, with similar slopes across sites and species, although beech tended at mountainous elevation towards enhanced thickness at given SA (Fig. 2d, e). Also, when relating foliage area (A_F) to sapwood area (A_S) in each tree individual (A_F/A_S, adapted from the reciprocal "Huber value", Huber 1928, 1956; Tyree and Ewers 1991; Tyree and Zimmermann 2002; Fig. 3) and averaging, irrespective of species, across the tree individuals per study site, stand-level ratios were similar in the spruce monoculture and mixed beech/spruce stand of the mountainous site to those of the mixed stand at low elevation. A_F/A_S reflecting the long-term adjustment between water demand of the foliage and water supply through the trunk (Tyree and Zimmermann 2002) is an expression of hydraulic whole-tree functionality, which appears, given the preliminary dataset, to be hardly affected by elevation and stand type.

The water transport capacity typically declines centripetally within sapwood depth, as recently formed annual rings have the highest sap flow density (Cermak et al.

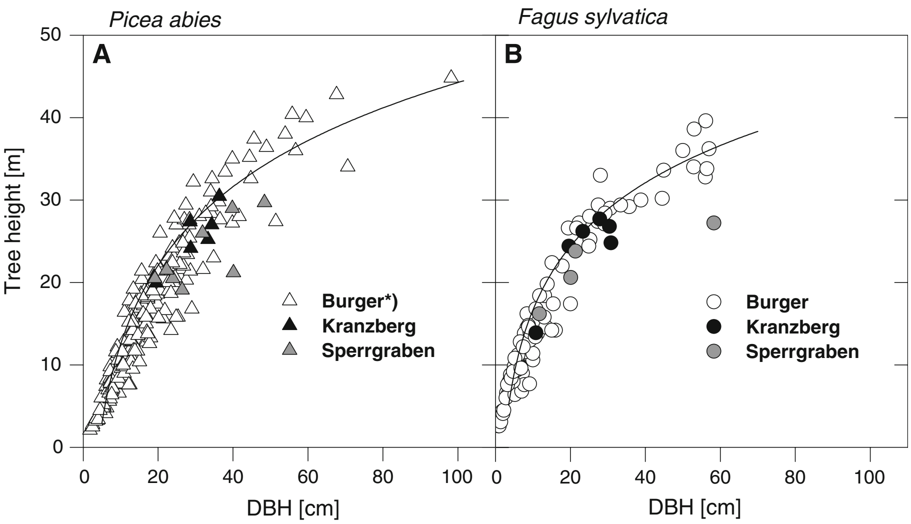


Fig. 1 The relationship between tree height and stem diameter at breast height (DBH) in *Picea abies* (**a**) and *Fagus sylvatica* (**b**) at the colline (Kranzberg) and the montane (Sperrgraben) study site as compared to findings by Burger (1953). Fitted functions in (**a**) are $y = -4.153 + 8.838 \ln x$, $r^2 = 0.86$ (*Picea abies*), and in (**b**) $y = -4.456 + 9.069 \ln x$, $r^2 = 0.87$ (*Fagus sylvatica*)

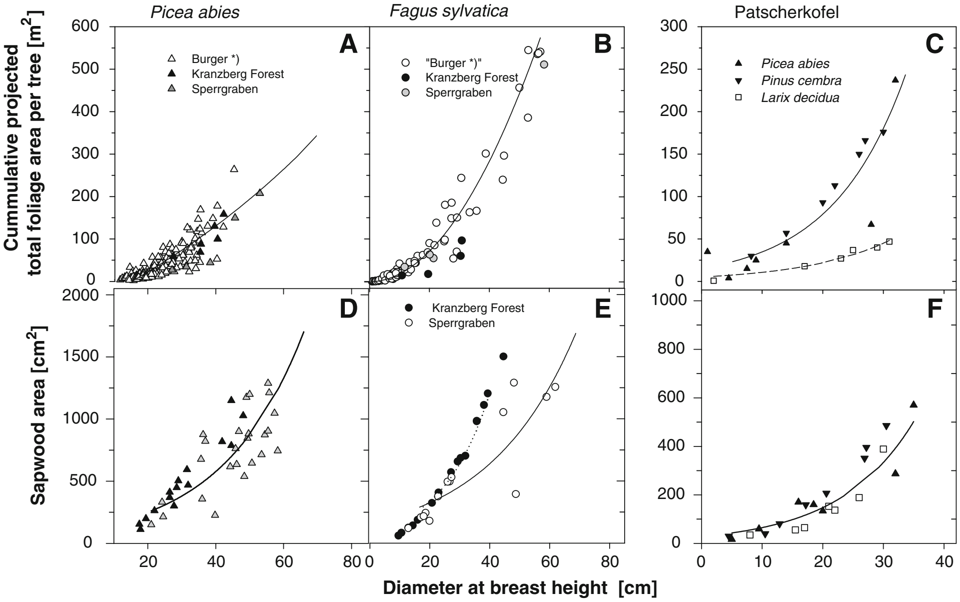


Fig. 2 The relationship between cumulative projected foliage area and stem diameter at breast height (DBH) in *Picea abies* (**a**) and *Fagus sylvatica* (**b**) at the colline (Kranzberg) and the montane (Sperrgraben) study site as compared to findings by Burger (1953), as well as respective relationships (**c**) in *Picea abies*, *Pinus cembra* and *Larix decidua* at the subalpine site (Patscherkofel). Accordingly related to stem diameter at DBH is cross-sectional sapwood area in **d**–**f**, regarding tree species and sites. Note the different scaling factors of the *X* and the *Y*-axis in **a** and **b** vs. **c**, and **d** and **e** vs. **f**. Fitted functions in **a** are $y = 23.667e^{0.0418x}$, $r^2 = 0{,}6308$; **b** $y = 4.7833e^{0.1009x}$, $r^2 = 0.8075$; **c** $y = 11.155e^{0.093x}$, $r^2 = 0.7056$ for spruce and cembran pine, and $y = 0.8828e^{0.1406x}$, $r^2 = 0.93$ for larch; **d** $y = 93.255e^{0.0436x}$, $r^2 = 0.6674$; **e** $y = 39.962e^{0.0894x}$, $r^2 = 0.9545$ for Kranzberg Forest, and $y = 104.92e^{0.0433x}$, $r^2 = 0.7827$ for Sperrgraben; **f** $y = 14.387e^{0.1122x}$, $r^2 = 0.8866$

1992). This was the case at low elevation (Fig. 4), where spruce displayed lower flow density than beech within the peripheral sapwood. At the mountainous site, sap flow density of both tree species did not display a consistent profile across sapwood depth (not shown), perhaps indicating harsh environmental impact during wood formation (cf. Cermák and Nadezhidina 1998; Jiménez et al. 2000). Conversely, beech and spruce resembled at both altitudes in using and refilling the internal water storage capacitance in the morning and at night, respectively, as exemplified in Fig. 5 for low elevation by proportional diurnal courses of leaf transpiration and sap flow at DBH (maximum rates set as 100% each). The sap flow setting in during sunny days with delay of 3–4 h relative to incipient leaf transpiration at sunrise indicates the drain of the tree-internal water storage (Schulze et al. 1985; Köstner et al. 1998a, b). Also at the mountainous site, such a time delay occurred in beech and spruce irrespective of the stand type (not shown). At both

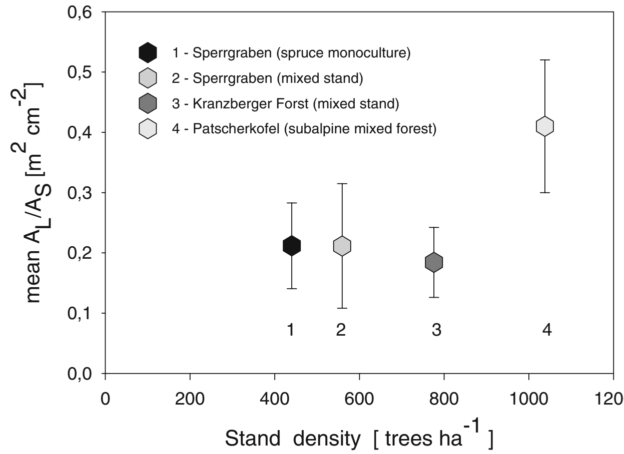


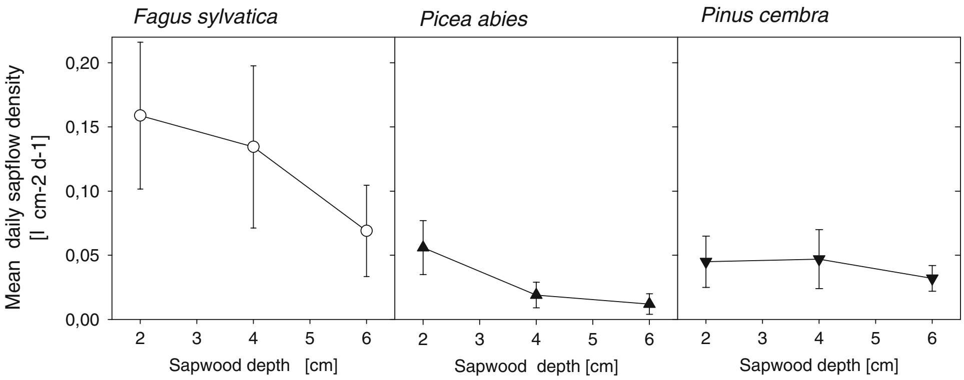
Fig. 3 The relationship between foliage area versus sapwood area (A_F/A_S) and ground area-related number of trees at the three study sites

altitudes, utilization of water storage was not detectable during overcast and rainy days, when transpiration was low. In total, site-dependent influences seem to hardly affect hydraulic tree differentiation at mountainous and colline elevation, given the current evidence from the respective pilot studies.

Subalpine elevation

At the timberline ecotone, projected foliage area also increased exponentially with DBH (Fig. 2c), with similar slopes in cembran pine and spruce (of all three elevations). However, the slope was lowered in larch, as this light-demanding pioneer carries fewer branches per unit of stem length as compared to the other tree species. Regarding SA, the exponential relationship with DBH did not vary between cembran pine, spruce and larch (Fig. 2f), and at the timberline the slope approached, within the actual DBH range, that of spruce and beech at lower elevations (within the scatter in the relationships; cf. Fig. 2d, e). Enhanced light availability due to the open-canopy structure, driving water demand, rather than retarded heartwood formation, may determine the dimension of SA at the timberline. In consistency with the light demand of larch, respective water demand appeared to be reflected by low A_F/A_S (0.38 m^2 cm^{-2} relative to 0.45–0.50 m^2 cm^{-2} in cembran pine and spruce at the timberline), although scaling to the stand level, comprising all three tree species, yielded 0.45 ± 0.19 m^2 cm^{-2}, which was higher than at lower elevations (Fig. 3). The high A_F/A_S ratio of the mixed timberline stand pretending reduced water demand relative to lower elevations appears to conflict with the water demand of an open-canopy structure. What cannot be clarified in this context and must be left for further research, however, is the issue of the hydraulic SA conductance at the timberline. If high water demand of the open stand is met by enhanced hydraulic conductance, then the A_F/A_S ratio may stay high. High conductance may result also in response to enhanced water viscosity at low temperatures, the latter being a typical feature of the timberline environment. Given remaining uncertainties, further arguments in favour of high water demand at the timberline, nevertheless, are the short growing seasons that require high daily carbon gains and, hence, high water consumption (Tranquillini 1979; Wieser and Tausz 2007), as well as, the open stand structure that allows for higher coupling of gas exchange to the atmosphere relative to the closed-canopy conditions at lower elevations (Wieser and Tausz 2007). Perhaps, high water demand also led to the even flow density across sapwood depth (as e.g. in cembran pine, Fig. 4). Contrasting with the trees at lower elevation, however, temporary decoupling of transpiration from water uptake was not detectable at the timberline, as exemplified for cembran pine in Fig. 5. This finding is attributed to the foliation of the timberline trees extending in the open stand along the entire stem length down to 50 cm aboveground. As a consequence, transpiration and, hence, drain of water set in simultaneously along the entire stem at sunrise. At the lower elevations, closed canopies favoured the formation of leafless trunks up to about 15 m in height, by this, enabling apparently for a water storage that was not evenly drained after sunrise, and hence, allowed for buffering the

Fig. 4 The dependence of sapflow density on sapwood depth in *Picea abies* and *Fagus sylvatica* at the colline study site (Kranzberg), and in *Pinus cembra* at the subalpine study site (Patscherkofel)



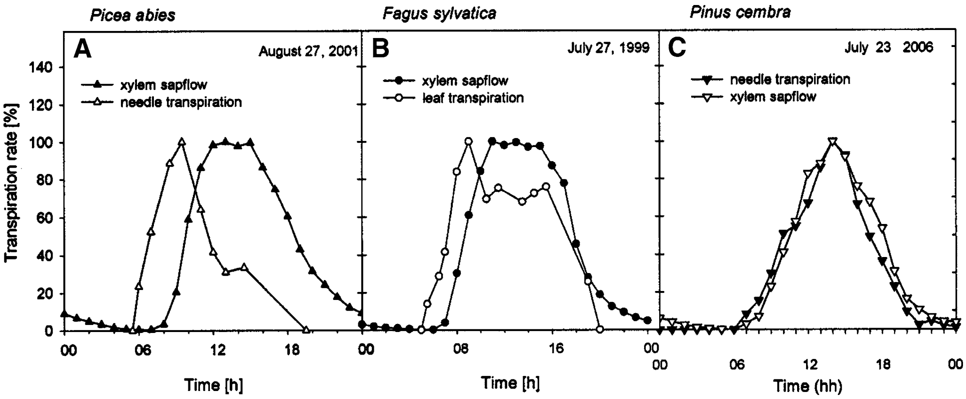


Fig. 5 Daily course of leaf transpiration in sun-exposed crown parts obtained from gas exchange measurements and xylem water flow through the trunk in *Picea abies* (**a**) and *Fagus sylvatica* (**b**) at the colline site (Kranzberg) and in *Pinus cembra* (**c**) at the subalpine timberline study site (Patscherkofel)

water demand in the foliated upper stem during the morning hours.

Seasonal whole-tree transpiration

Mountainous elevation

At the mountainous site, weather conditions were rather uniform across the growing seasons of the three study years, as reflected by the seasonal light sum as well as mean air temperature and VPD that ranged between 2,900 and 3,100 mol photons m^{-2}, 12.0–12.7°C, and 0.70–0.74 kPa, respectively. Insolation was constrained by the N exposure of the study site. Courses of insolation were similar during each growing season, with daily light sums reaching maxima in June/July of about 35 mol photons m^{-2} that contrasted with frequently occurring levels of less than 5 mol photons m^{-2}. Low levels resulted from foggy or overcast conditions, typically associated at this altitude of the northern Alps with ample precipitation. The inter-annual variation of precipitation during growing seasons was larger than in radiation, temperature and air humidity, as rainfall amounted to about 620 mm in 2000 but about 1,000 mm each in 1999 and 2001.

The daily crown transpiration of individual trees was driven by the daily light sum (Fig. 6). Scatter in crown transpiration was high, as daily means comprised all trees in a Kraft class, irrespective of individual crown size and extent of mutual shading. The slope of relationships declined from dominant towards suppressed trees (Fig. 6), irrespective of stand type (i.e. mixed stand or monoculture). In beech, crown transpiration of Kraft class 3 individuals hardly depended on insolation. The trends of 1999 exemplified in Fig. 6 were representative for 2000 and 2001 (not shown).

Daily crown transpiration was condensed into weekly means as shown in Fig. 7 for the seasonal course of 1999 per tree species, Kraft class and forest type. In spruce, crown transpiration of dominant individuals tended to be lower in monoculture than under mixed-stand conditions. Transpiration of spruce in the mixed stand was probably favoured by the less evenly structured canopy in the presence of beech, allowing for enhanced light penetration (cf. Beyschlag 2001). Within the mixed stand, dominant spruce individuals reached daily crown transpiration similar to that of dominant beech (Fig. 7).

Colline elevation

Although the growing season was longer by 2 months at the low elevation, seasonal light sums ranged across the study years between about 6,700 and 8,200 mol photons m^{-2}, being more than proportionally higher than those at the N-exposed mountainous site, which had a higher degree of cloudiness (cf. Ellenberg 1996). In addition, insolation varied at low elevation between years with the highest seasonal light sum occurring in 2000. Also at low elevation, variation in daily insolation was due to overcast conditions around 5 mol photons m^{-2} day^{-1}, often associated with rainfall. However, seasonal precipitation was lower than at the mountainous site of the northern Alps, ranging between about 500 and 620 mm during the longer growing seasons at low elevation. At higher insolation, both mean seasonal air temperature (13.1–14.1°C) and VPD (0.82–1.05 kPa) were higher by about 1°C and 0.2 kPa, respectively, than at the mountainous site.

Relationships between mean daily crown transpiration and light sum resembled, at low elevation, those of the mountainous site (Fig. 6), although in the mixed stand at low elevation, beech had higher weekly crown transpiration than spruce (Fig. 7). Also at low elevation, crown transpiration declined towards suppressed tree individuals.

Subalpine elevation

Weather conditions during the study years were representative at the timberline site of Mt. Patscherkofel, with growing seasons extending on average from mid-May

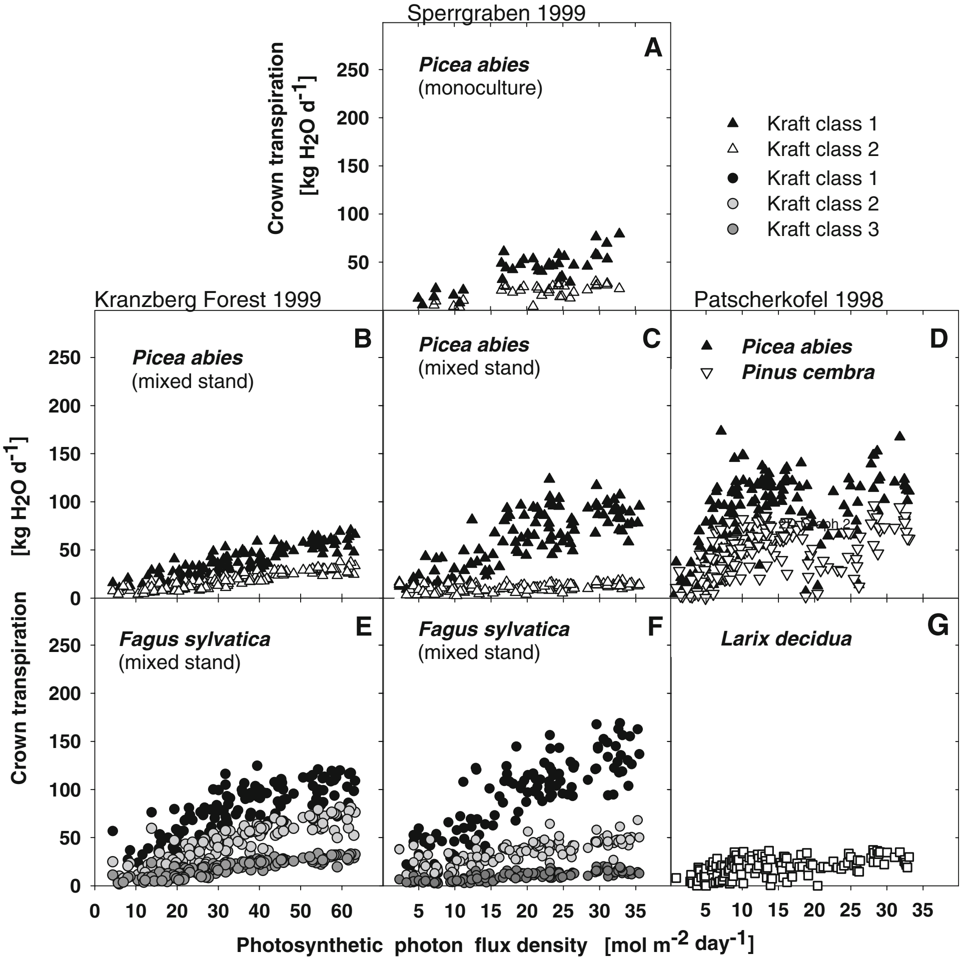


Fig. 6 Mean daily crown transpiration as a function of daily photosynthetic photon flux density (PPFD) in *Picea abies* and *Fagus sylvatica* varying with respect to Kraft class at the montane study site (Sperrgraben, *left*), the colline study site (Kranzberg Forest, *middle*), and in *Picea abies*, *Pinus cembra*, and *Larix decidua* at the subalpine timberline study site (Patscherkofel, *right*)

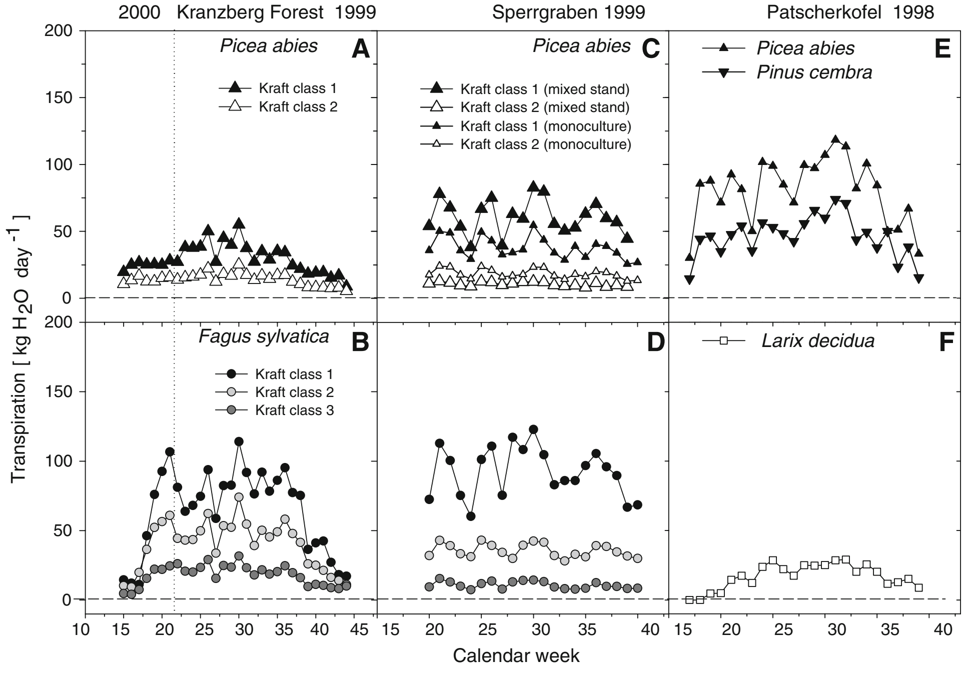


Fig. 7 Weekly mean crown transpiration of *Picea abies* and *Fagus sylvatica* varying with respect to Kraft class and at the colline study site (Kranzberg Forest, *left*) and at the mountainous study site (Sperrgraben, *middle*) during the growing season of 1999, and of *Picea abies*, *Pinus cembra*, and *Larix decidua* at the subalpine timberline study site (Patscherkofel) during the growing season of 1998 (*right*). Note that at the colline site transpiration of weeks 14 through 21 is shown from the respective period in 2000 (*left of vertical line*) for reasons of demonstration, given the delayed beginning of data recording in 1999

through the end of October (Havranek and Tranquillini 1995; Wieser 2004). Light sums ranged between 1,320 and 1,874 mol m^{-2} in 1997 and 1998, respectively (May 15 through September 15, as at lower elevations) and were low because of NW exposure. Mean air temperature and VPD ranged between 8.2 and 8.9°C and 0.24 and 0.26 kPa, respectively, and precipitation was 496 mm in 1997 and 625 mm in 1998. Frequent rainfalls enabled soil water holding capacity to stay above 21% volume (45% vol. on average).

Although daily crown transpiration of individual trees was driven by daily light sum (Fig. 6, exemplifying 1998), contrasting with the lower elevations a plateau was reached at high insolation, being an effect of the open stand structure (cf. Larcher 2001). Weekly transpiration means were highest in spruce and lowest in larch (Fig. 7), positively correlating with the foliage area of the tree species at the timberline site (Wieser et al. 2003).

Seasonal stand transpiration

Mountainous elevation

The relationship between the daily mass flow of xylem sap through tree trunks (equalling single-tree transpiration) and the corresponding trunk diameter at DBH allowed for tree-to-stand scaling of transpiration (Granier et al. 1996; Wullschleger et al. 2001; Ewers et al. 2001; Zimmermann et al. 2000), being performed separately per Kraft class in each species upon DBH assessment of all trees per study plot. Stand transpiration was expressed on a ground area basis, either per unit of the slope-parallel area of the study plot (intrinsically conveying slope inclination), or per unit of the projected ground area for reasons of standardization. Per unit of slope-parallel area, maximum daily stand transpiration ranged between 1.5 and about 2 mm in the spruce monoculture of the mountainous site, but stayed close to 1.5 mm in the neighbouring mixed culture with beech (Fig. 8, closed-canopy conditions each). Nevertheless, the daily transpiration became similar in both stand types during overcast days. Across entire growing seasons, higher water demand was reflected by the spruce monoculture than mixed stand ($P < 0.05$, each in study year), which was consistent with a slightly higher ground area based number of individuals in the spruce monoculture, when expressed per unit of slope-parallel area (Table 1).

The difference in individual number was reversed, however, when relating trees to the projected ground area (Table 1), and consistently, so was the seasonal transpiration ratio between mixed stand and monoculture (Table 2). Projected ground area as reference made the seasonal stand transpiration of the spruce monoculture appear lower relative to the mixed-stand transpiration (164–172 and 198–202 mm, respectively). Conversely, the mixed stand conveyed lower transpiration in relation to the spruce monoculture on a slope-parallel stand area basis (113–119 and 148–155 mm, respectively). Either way, the difference in transpiration between stands was about 15–20% (in proportion of the higher transpiration each). One needs to be aware, though, that such percentages fall within the reported range of tree-to-stand scaling accuracy (Köstner 1999). Nevertheless, expressing stand transpiration on a slope-parallel area basis is compelling in view of high slope inclination, as typically encountered at mountainous forest site conditions.

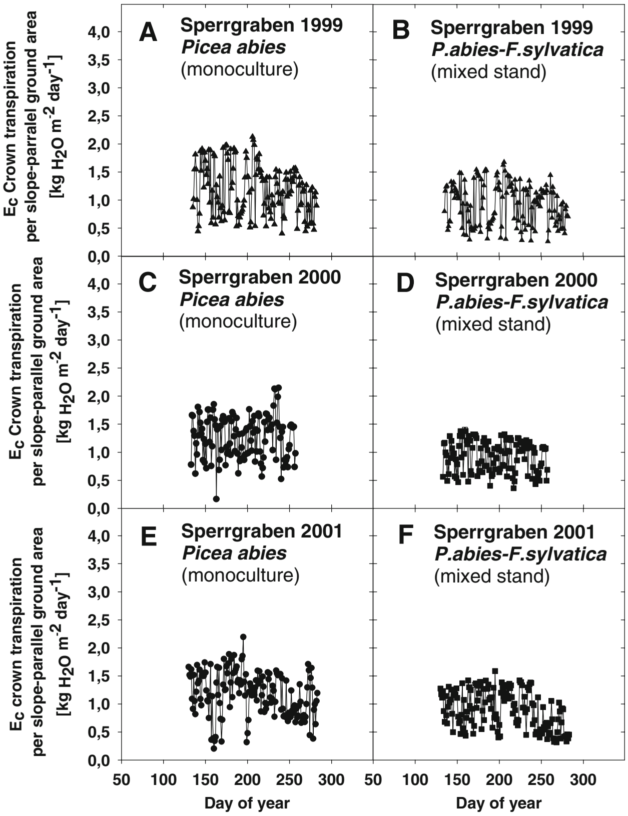


Fig. 8 Seasonal course of daily canopy transpiration of a *Picea abies* stand and a neighbouring mixed stand of *P. abies* and *Fagus sylvatica* at the montane study site (Sperrgraben) during the growing seasons of 1999, 2000 and 2001

Transpiration as based on SA (assessed through coring) at DBH relates water demand to transport capacity in view of the hydraulic architecture of trees and the "pipe model theory" of internal long-distance water transport (Tyree and Zimmermann 2002). The ratio was higher in the mixed stand by about 30–40% in beech than spruce, when relating the proportion of seasonal stand transpiration in each species to the cumulative sapwood area of respective tree individuals at the study plot (Table 1). However, the ratio was similar in spruce irrespective of the stand type.

Table 1 Number of trees at Sperrgraben, Kranzberg Forest and the subalpine site which were assessed for trunk diameter at breast height (DBH; by W. Faltin, J. Tenhunen, R. Grote and H. Pretzsch); number of trees expressed per unit of projected or slope-parallel ground area, and cumulative sapwood area assessed for spruce and beech each at Sperrgraben und Kranzberg Forest. For each site and forest type, stand transpiration is shown during the same time period (May 15 through September 15) within the growing seasons of 1997–2001 (sap flow gauges in operation at Kranzberg Forest only since June 1999)

	Beech/spruce mixed forest **Sperrgraben**			Spruce monoculture **Sperrgraben**	Beech/spuce mixed forest **Kranzberg**			Mixed *P. cembra* forest mixed forest **subalpine site**			
Trees per ground area (projected ground area basis) [trees ha^{-1}]	559			440	776			1058			
Trees per ground area (slope-parallel area basis) [trees ha^{-1}]	320			397	775			1038			
Stand transpiration per unit of cumulative sapwood area [t m^{-2}]: May 15 through Sept. 15 of	Beech/spruce mixed forest	Proportion of spruce	Proportion of beech	Spruce monoculture	Beech/spruce mixed forest	Proportion of spruce	Proportion of beech	Mixed forest	Proportion of Larch	Proportion of spruce	Proportion of pine
1997								71.3	87.0	130.0	79.0
1998								111.9	131.0	202.0	126.0
1999	78.9	70.7	92.3	57.2							
2000	75.0	58.3	102.6	58.1	86.1	69.2	126.4				
2001	77.9	63.0	103.0	55.8	76.5	61.5	105.9				

Table 2 Stand transpiration at the subalpine site, at Sperrgraben and Kranzberg Forest during May 15 through September 15 between 1997 and 2001 each (sap flow gauges in operation at Kranzberg Forest only since June 1999)

	Stand transpiration, based on projected ground area [mm]			Stand transpiration, based on slope-parallel ground area [mm]		
	1997	1998		1997	1998	
Subalpine site						
Mixed Pinus cembra forest	246	431		224	392	
	1999	2000	2001	1999	2000	2001
Sperrgraben						
Spruce monoculture	168	172	164	153	155	148
Beech/spruce mixed forest	202	192	198	119	113	117
	1999	2000	2001	1999	2000	2001
Kranzberg Forest						
Beech/spruce mixed forest		277	246		277	246

Colline elevation

Tree-to-stand scaling was performed as pointed out above, however, given the minor slope inclination of the mixed forest at low elevation, transpiration was only expressed on a projected ground area basis. Calculated for same time periods and given similar LAI and closed-canopy conditions in both cases, stand transpiration was higher by about 33% at low elevation (compared with the mountainous mixed forest on a projected ground area basis, Table 2). Ratios of transpiration to cumulative SA were similar in spruce and beech of mixed stands at the low-altitudinal and mountainous site (Table 1). Being aware of the statistical constraints, the similarities perhaps indicate absence of adaptation in tree hydraulics to altitude.

Subalpine elevation

Given the substantial slope inclination at the subalpine site, the mixed-stand transpiration was expressed per unit of slope-parallel ground area. In consistency with the mixed-stand features at the timberline (open canopy, high density, Tables 1, 2), seasonal transpiration was about 1.6–3 times higher than of the mixed forests at the mountainous and colline sites (Table 2). The reduced stand transpiration at the timberline during the growing season of 1997 is attributed to lower irradiance, evaporative demand and precipitation relative to long-term averages (cf. "Sites of the three pilot studies"), and consequently lowered soil water content (from 45 to 40%) that favoured stomatal closure (Havranek and Benecke 1978; Wieser and Kronfuß 1997; Kronfuss et al. 1998). Total transpiration per unit of cumulative SA of the mixed spruce/pine/larch stand ranged between 85 t m^{-2} in 1997 and 134 t m^{-2} in (humid) 1998, and tended to be higher than ratios of the spruce/beech mixed stands at the mountainous and colline sites (Table 1).

Seasonal stand water balance

Mountainous elevation

Seasonal stand water balances were determined for the time period of May 15 through September 15 of each study year, according to the equation

$$B = P - T - I,$$

where B is the stand water balance as resulting from P as precipitation (set as 100% each year), T as stand transpiration, and I as interception (calculated as the difference between the above and below-canopy precipitation). Below-canopy P was corrected, in the mixed stand, for the separately assessed stem flow of beech with its smooth

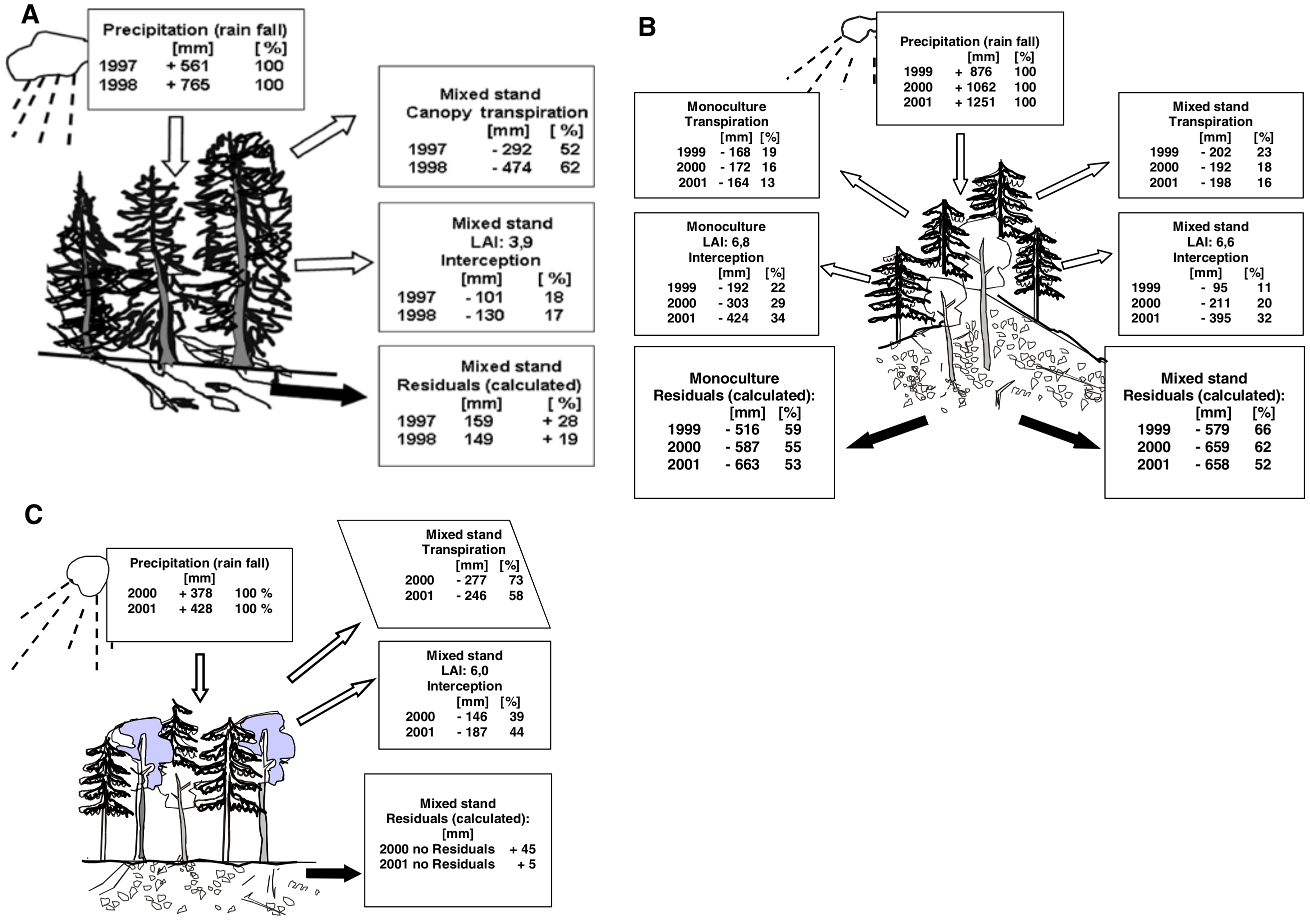


Fig. 9 Seasonal water balances at the subalpine (**a**), montane (**b**) and colline study site (**c**) during 15 May through 15 September of the study years depicted

trunk and branch periderm surfaces and steep-angled branch orientation. The equation was expressed on a projected ground area basis to ensure comparability across sites and plots. In the spruce monoculture, *I* amounted to 22–34% of *P* across the three study years (Fig. 9), while *T* ranged between 13 and 19%. The remaining amount of water, i.e. *B*, amounted to 53–59% (termed as "residuals" in Fig. 9) of *P*. At similar LAI, *I* of the mixed beech/spruce stand was more variable but similar to that of the spruce monoculture, ranging between 11 and 34% of *P* (Fig. 9). Beech stem flow was about 5% of *P* in the mixed stand (not shown), while *T* amounted to 16–23%, reflecting a range similar again to that of the spruce monoculture. As a consequence, also *B*—being 52–66% in the mixed stand—was similar in both stand types. The high proportion of *B* in both stands resulted from the high seasonal *P* and rather low *T* and *I* under the high-humidity conditions of the mountainous range in the Northern Alps (cf. Ellenberg 1996). *B* is concluded to be subject to run-off rather than evaporation under the closed canopies or water storage in soil and plants, given the steep slope inclination of the study sites.

Colline elevation

Calculation of *B* was restricted in the mixed beech/spruce stand to 2000 and 2001 (Fig. 9). At similar LAI, *I* approaching 39–44% of *P* as well as stem flow of beech (13%, not shown) tended to be higher at the low than mountainous elevation. Also *T* ranging between 58 and 73% of *P* was higher at the colline site (Fig. 9). As a result, *B* approached zero, which is mainly attributed to *P* being about 50% of that at the mountainous site (assuming marginal effects of run-off at the colline site, and again, of evaporation under the closed canopy or water storage). As *P* is consumed by *T* and *I* during the growing season, soil moisture is concluded to be fuelled by *P* during the remainder of the year.

Subalpine elevation

At the subalpine site, *B* was assessed for the same reporting period (May 15 through September 15) as at the lower elevations. Given the lower LAI of the mixed forest with open canopy, *T* amounted to 52–62% of *P* (Fig. 9) and,

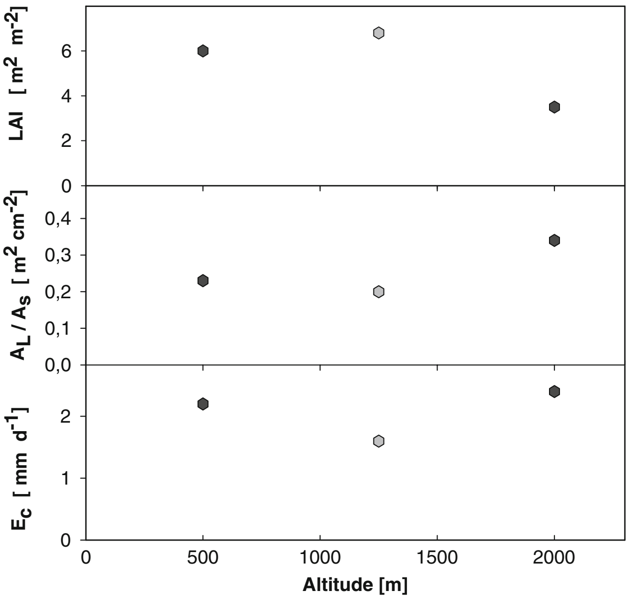


Fig. 10 Daily mean canopy transpiration during the period 15 May to 15 September, proportion of foliage area to sapwood area (A_F/A_S) and leaf area index (LAI) in mixed stands of Kranzberg Forest, Sperrgraben and Patscherkofel with respect to elevation in the European Alps between 485 and 1,950 m a.s.l.

therefore, was higher in proportion than at the mountainous but similar to the colline site. The higher proportion of *T* at the subalpine site appears to be plausible in relation to the high-humidity conditions of the mountainous elevation that lower *T*, whereas the open canopy at the timberline may have favoured *T* at *P* similar to that of the colline site. Evaporation from the forest floor was negligible at the subalpine site, given the dense cover of needle litter on the soil (Wieser 2004). Markart (2000) calculated soil evaporation in a 35-year-old cembran pine afforestation to account for only 1.6% of *P* during the growing season. Assuming *I* as 1.5 mm per precipitation event (cf. Waring and Running 1998), I accounted for roughly 18% of *P*, this percentage being within the range reported for open cembran pine stands by Aulitzky et al. (1982). Still, this proportion was lower than suggested for low-altitudinal forests (cf. Waring and Schlesinger 1985; Larcher 2001) and found indeed at the low-elevation study site. B indicated run-off of about 19–28% of *P* at the subalpine site, in the absence of significant differences in soil water content between the beginning and the end of the growing season, and was lower than at the mountainous site due to lower *P* and slope inclination.

Summarizing evaluation and conclusion

Given the limitation in datasets, the preliminary evidence available from the three pilot studies suggests the seasonal daily mean of canopy transpiration (Ec) to average, in mixed forest, about 2 mm day^{-1} along the altitudinal profile, although enhancement is indicated at the timberline, and reduction at the mountainous elevation (range of 1.6–2.4 mm day^{-1}, Fig. 10). Such indications may be supported by the absence of periodic soil drought at the timberline (Tranquillini 1979; Wieser and Havranek 1995, 1996), contrasting with low elevation (Löw et al. 2006), and ample rainfalls associated with high air humidity and low irradiance that dampen Ec at the mountainous range of the Northern Alps (Ellenberg 1996). Tendencies in Ec resembled those of the A_F/A_S ratio, irrespective of tree species involvement (Fig. 10). Conversely, LAI was lowest at the timberline with its typically open stand structure as compared to closed canopies at lower elevation (Fig. 10). As a consequence of decreasing LAI and, hence, increasing wind velocity in timberline stands, aerodynamic and boundary layer conductances are higher than in closed-canopy forests (Jarvis et al. 1976). In addition, open forests heat up to a larger extent which promotes evapotranspiration (Palladry et al. 1995). Therefore, conifers of the timberline ecotone typically exhibit higher transpiration rates than at lower altitudes (Wieser and Havranek 1995, 1996; Wieser et al. 2000). Such phenomena are consistent only with the increased A_F/A_S ratio at the timberline, if the hydraulic conductance of the sapwood increases under the enhanced water demand (see "Structural and ecophysiological tree features"), and such a need may even be promoted, as radial stem growth is constrained by climatic limitation (Loris 1981). The hydraulic conductance may have been higher also at the whole-tree level, as the distance of water transport from soil to crowns is shorter because of the lower stem heights of timberline trees as compared, at similar age, with trees at lower elevation (14 m height vs. up to 30 m, respectively, in these pilot studies). Integrative research along altitudinal gradients needs to clarify, if Ec of 2 mm day^{-1} indeed represents a reliable seasonal mean, irrespective of elevation and site conditions (cf. Fig. 10). One needs to be aware, though, that Ec can reach 2.5–6 mm day^{-1} during clear days, both under closed-canopy and open conditions at low elevation and at the timberline. It is remarkable, at least, that the mean Ec of the studied mixed forests was similar to that of various grassland ecosystems in the Central Austrian Alps (between 580 and 2,530 m a.s.l), displaying 2.3 mm day^{-1} independent of elevation and LAI (Wieser et al. 2008, cf. also Körner 1999).

Working hypotheses and perspectives

Based on the outcome of the above introduced pilot studies, the following three working hypotheses are derived, intended to guide upcoming integrative research along the altitudinal gradient of the European Alps:

Working hypothesis I (WH I) states that mixed stands have enhanced transpiration due to high light penetration into canopies, but that stand water demand is lower, in general, at the humid and cloudy mountainous range than at low-elevation and sub-alpine sites with higher evaporative demand.

Working hypothesis II (WH II) claims transpiration to be determined by altitude-specific climatic site conditions rather than altitude-specific ecophysiological tree features.

Working hypothesis III (WH III) postulates limited soil water availability upon warming to endanger trees through water imbalances, in particular, at their upper distribution limit.

Arguments for hypotheses and needs in examination

Tree transpiration varied to an extent within Kraft classes at the mountainous site of the Northern Alps so that substantial overlap occurred in the dependence of Ec on irradiance between classes, tree species and stand types (i.e. mixed vs. spruce monoculture). Integrated research related to WH I with a study design that allows comparative statistical analysis across elevations and stand types, must clarify as to whether stand transpiration differs between mixed and monocultures at mountainous altitude as well as in relation to colline sites, given closed-canopy conditions and similarity in LAI and ground area-based number of individuals. Care must be taken also of similar edaphic conditions (Watta et al. 2006). High soil moisture may reduce variation in Ec, regardless of canopy shape and size (Pereira et al. 2006), so that in beech stands variation in Ec may become smaller, in proportion, than in precipitation (Schipka et al. 2005). The extent to which foliage type (evergreen vs. deciduous) and its proportion in mixed stands govern water demand, irrespective of altitude, has to be clarified. The marked physiological differences, including water demand, between evergreen and deciduous leaf organs (cf. Matyssek 1986; Stitt and Schulze 1994) apparently vanish at the tree (Reiter et al. 2005) and apparently also the stand level. Somewhat higher water demand of spruce in mixture may relate to stimulation in productivity under such growth conditions (Pretzsch 2003), an effect typically mediated through enhanced light penetration within the heterogeneously structured canopy of mixed forests (Styles et al. 2002; Beyschlag 2001).

The extent is unclear to which Ec is affected by downhill water flow along steep slopes as typically encountered at mountainous sites. In such a context, the comparison of stand transpiration, either expressed per unit of projected ground or slope-parallel area, illustrated the relevance in choosing reference areas. This choice made the direction of the difference in Ec change between the spruce monoculture and spruce/beech mixed stand at the mountainous site, although differences were small and close to the range of methodological resolution. As projected area ensures standardized comparability between sites and studies, topographic effects on Ec are neglected. Conversely, the slope-parallel area intrinsically accentuates inclination effects on Ec (cf. Körner 1998). Apparently, slope inclination affects the degree of tree crown exposure to irradiance which is a driving force for transpiration. Also, water run-off from the site is affected, which is relevant for stand water balances, as indicated in the comparison between the mountainous and colline site. Slope inclination and light exposure increasingly determine tree performance towards the sub-alpine elevation (Tranquillini 1979; Häsler 1982; Herzog et al. 1998). Within the timberline ecotone, run-off along slopes increases from forest towards dwarf shrub and grassland systems (Kronfuss 1997; Guggenberger 1980; Wieser et al. 2008), which—in particular, if originating from anthropogenic impact—may become starting points of soil erosion (cf. Wieser and Tausz 2007). As changes in high-altitudinal vegetation sensitively affect the regional water balance (Körner et al. 1989), stand transpiration and run-off must be assessed as intrinsic components of mountainous water relations. Viewing topography-driven effects on Ec, the slope-parallel rather than projected ground area may be chosen as an appropriate reference.

Environmental harshness exacerbates in terms of reduced growing seasons and lowered temperature regimes towards the timberline ecotone (Grill et al. 1999; Tranquillini 1979; Körner 1998; Wieser and Tausz 2007). Besides disrupted production, hydraulic conductance of shoot axes is low in winter because of frost-induced cavitation (Cochard et al. 2001). Such inhibitions persist until snow melt in late spring (Styles et al. 2002), but frost may occur also during the growing season (Ellenberg 1996). Irregularities may result in wood formation and the radial sap flow profile (cf. Cermák and Nadezhidina 1998; Jiménez et al. 2000) as observed in the tree trunks of the mountainous site, but not so at low elevation (cf. Granier et al. 2000; Köstner et al. 1998a, b). Also these are issues relating to WH I. In addition, mountainous forests are expected to have lower water consumption than subalpine ones in the Central Alps, as leaf conductance increases towards subalpine elevation (Wieser and Havranek 1996). This tendency (of relevance for the second part of WH I) appears to be backed at the latter sites by the ample precipitation and high insolation during summer (because of reduced cloudiness), although in spring and fall low air and soil temperature limits water uptake and transpiration (Hadley and Smith 1987; cf. Goldstein et al. 1985;

Zimmermann 1964; Wieser et al. 2000). Obviously, site-ecological specificities along the altitudinal gradient will provide a crucial context in evaluating WH I.

In view of WH II, the sapwood area-related crown transpiration of beech and spruce each appeared to be similar during growing seasons at comparable age, irrespective of altitude (cf. Table 1; cf. Schipka et al. 2005; Zimmermann et al. 2000), this ratio reflecting whole-tree integration of crown water demand versus supply capacity through trunks. Another argument in favour of WH II is that, at colline and mountainous altitudes, beech and spruce resembled in using the internal water storage for tree transpiration (Tyree and Zimmermann 2002). In analogy to findings about photosynthesis and carbon gains of trees along altitudinal gradients (Benecke et al. 1981; Havranek and Matyssek 2005), the pilot studies also suggested the water demand to be determined by the length of the growing season rather than by specific ecophysiological adaptations to the climatic and/or edaphic peculiarities at different elevation. In addition, hydraulic tree architecture, as reflected by high correlation between SA at DBH and crown transpiration, was similar at both altitudes in both tree species, which provided the basis for tree-to-stand scaling of transpiration (cf. Granier et al. 1996; Wullschleger et al. 2001; Ewers et al. 2001; Zimmermann et al. 2000). Such correlations reflecting whole-tree functionality of internal long-distance water transport (Tyree and Zimmermann 2002) appeared, within the scope of the pilot studies, to be independent of elevation and investigation (Burger 1941, 1950, 1953). Research related to WH II should focus, therefore, at different altitude also on the relevancy of whole-tree allometry for water transport.

In relation to WH III, subalpine forest ecosystems at the timberline are expected to undergo significant alterations within the next century (Walther et al. 2005) due to climate change (cf. Wieser and Tausz 2007). Limited soil water availability upon warming may endanger timberline trees through water imbalances, in particular, at the upper distribution limit, where tree habit becomes stunted and deformed to "*krummholz*", in the "*kampfzone*" (Tranquillini 1979; Holtmeier 2000; Wieser and Tausz 2007). The latter zone already today is affected by temporary soil drought at wind-exposed ridges and leeward sun-exposed slopes with thin soil layer (Aulitzky 1963, 1984). As in the timberline ecotone effects of slope inclination and, as a consequence, solar radiation as well as wind velocity and direction are by far more important than in the closed forests below (Wieser 2007), research related to WH III should not only be directed to elevational gradients within the ecotone ("*kampfzone*" vs. mountainous range), but also focus on micro-scale effects on tree water relations. This is because water balance, besides a positive annual carbon gain, is crucial for seedling establishment and successful re-afforestation, warranting high-elevational protection forests to counteract the increasing risks of future hazards in the populated landscapes of the European Alps.

On the grounds of WH I, II and III, it is postulated, therefore, that up-coming research along the altitudinal gradient of the Alps, pursuing one joint study design across sites, is to integrate structural and functional differentiation and spatio-temporal process scaling of relevancy for tree and stand water balance (e.g. by combining concepts as pursued in this study with such as employed by Hofmann et al. 2009, Stumpp et al. 2009; Engelhardt et al. 2009). The promising challenge will be the clarification of the extent to which spatio-temporal consistencies indicated in the pilot studies outweigh contrasts along the altitudinal profile, irrespective of tree species, forest types and topography.

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