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WATER USE OF FORESTS ALONG ELEVATION GRADIENTS IN THE BERCHTESGADEN NATIONAL PARK

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DANKSAGUNG

1. INTRODUCTION

1.1. General Theme

Mountain regions have long been a focus of attention in ecosystem research, but in the context of global change, they are becoming increasingly important. Mountain areas represent about 20% of the Earth's terrestrial surface, and they provide fresh water to at least half of humankind; most major river systems originate in such terrain (Price 2003; Reasoner 2002). Mountain areas also provide goods and services, including energy, minerals, food and forest products, and are centers for tourism and recreation. These regions are characterized by high biodiversity. Along elevation gradients climate, hydrological and ecological conditions change strongly, and fluctuations in these conditions have over the long-term continually promoted migration of species between high elevations and lowlands, and, thereby, speciation. Mountain environments, which are critical to the existence of the global ecosystem, are very sensitive to changes in the atmosphere, in deposition and in climate and are subject, thereby, to rapid degradation.

Climate change, increases in water and air pollution, and changes in land use represent environmental change that will modify fragile mountain ecosystems. With global warming, the frequency of occurrence of extreme events may shift, which may in turn lead to altered stability of mountain landscapes and to new requirements with respect to water resource management (Pahl-Wostl 2002). Temperature increase, changes in precipitation patterns and altered snow cover are expected to influence vegetation distribution and along with this, ecosystem functioning (ACE Information Programme; Körner 1999; UNFCCC [United Nations Framework Convention on Climate Change]). Scientists have already observed climate-induced changes in many physical processes and in biological communities (UNFCCC). Observations show that some plant species are moving up in the European Alps by one to four meters per decade and that some mountaintop species have already disappeared (UNFCCC).

Increases in air temperature will result in a decline in mountain glaciers and snow cover, and may cause an increase in erosion, changes in the hydrological system and modified vegetation characteristics. In mountain regions the hydrological regime depends on snowfall and snowmelt. An increase in air temperatures will result in a reduction in precipitation falling as snow and an increase in runoff and a greater probability of floods. This will have an influence on seasonal river flows and water supply (ACE Information Programme; Change; UNFCCC). In order to know how best to respond to changes such as those indicated in resource management measures, a well-founded and improved understanding of basic ecosystem processes is needed in mountain regions.

About two-thirds of solar radiation is used for water evaporation in latent heat flux. Global warming may cause an increase in surface temperatures and, thereby, evapotranspiration. An increase in the average temperature of the Earth's surface should cause a shift in the composition and functioning of forest ecosystems as they slowly adapt to the changes in environment. As major sources of water vapor to the atmosphere, forests have an important influence on both regional and global climate. They have an impact on ground temperature, albedo, surface roughness, cloud formation and precipitation. Thus, it is necessary to investigate the response to meteorological and environmental factors of forests ecosystems, which play a major role in flood protection and erosion control, above all in mountains regions.

Several techniques for better estimating whole-plant water use have been developed in recent years. To these methods belong weighing lysimeters, large-tree porometers, ventilated chambers, radioactive and stable isotope applications, thermal-based methods like energy-balance, heat dissipation balance, and heat pulse-techniques (Wullschleger et al. 1998). Sapflow measurements by thermal balance (Cermak 1984) and heat-dissipation methods (Granier 1985; 1987) are easy to use, suited to measure mass flow rate in large trees and relatively inexpensive. They can be used in forests, where one or two species typically dominate (Köstner et al. 1992), and can be utilized in complex mountain terrain.

In the 2002 growing season, the transpiration of three spruce stands, one beech stand, one larch stand and one dwarf-pine site, located from 630 m a.s.l. to the timberline at 1720 m in the Berchtesgaden National Park, was investigated. This area on the Watzmann Mountain in Berchtesgaden National Park was chosen because of the large gradients in climate conditions and elevation that occur in a comparatively small area, thus facilitating the maintenance of experimental studies along the elevation gradient. The heat-dissipation method was used to measure water use by individual trees (Granier 1985; 1987). To obtain canopy transpiration, sapflow rates were scaled to the stand level by multiplying sap flux density in different layers of the xylem by sapwood area (Köstner 1999a; Meinzer et al. 2001).

The collected climate data sets were subsequently used as input information for the GAS-FLUX canopy light interception and gas exchange model (Falge et al. 1996; 1997; Reichstein et al. 2003; Tenhunen et al. 1994b), in order to compare the observed behaviour of stand transpiration with simulated water use from the model. Model parameter values were modified to study potential reasons for differences in flux control at different elevations.

1.2. Goals of the Study

The objective of this study was to determine the dependence of forest stand transpiration with respect to meteorological conditions at a series of sites along an elevation gradient in the Alps. To this end, the following main points were examined:

- diurnal and seasonal changes in forest stand transpiration,
- the influence of climate conditions on tree transpiration,
- the relationship of forest stand transpiration to stand structure,

- the magnitude of water fluxes in forest stands along the elevation gradient in the National Park Berchtesgaden,
- the use of field data to estimate water fluxes in mountain regions with a stand level model in order to develop an extrapolation potential for other similar mountain locations.

1.3. Berchtesgaden National Park

Berchtesgaden National Park (210 km^2), established in 1978 by decree of the Bavarian government, is located in south-eastern Germany between 12°47’ and 13°05’ E and 47°27’ and 47°45 N and borders on Austria’s province of Salzburg (**Fig. 1.1**). In 1990, the park as a nearly natural alpine ecosystem became a UNESCO Biosphere Reserve. The Berchtesgaden National Park belongs to the oldest protected areas in the Alps, and it is the only alpine biosphere reserve in Germany. The park is situated in the Northern Limestone Alps, where huge mesozoic carbonate deposits are present. The dominant bedrock in this region is limestone. The landscape with steep valleys and moraines illustrates recent glacial recession. The altitudes in the Berchtesgaden National Park range from 603 m at the lowland lake Königssee to 2713 m at the summit of the towering Watzmann Mountain. The climate of the region is characterized by both Atlantic and continental influences. At high altitudes, typical mountain climate conditions prevail. The mean annual temperature ranges, depending on altitude, from +7°C (Königssee) to –2°C on the Watzmann summit (2713 m). Annual precipitation varies between 1500 and 2200 mm, while the mean annual precipitation in the region is ca. 1880 mm (Berchtesgaden National Park Administration).

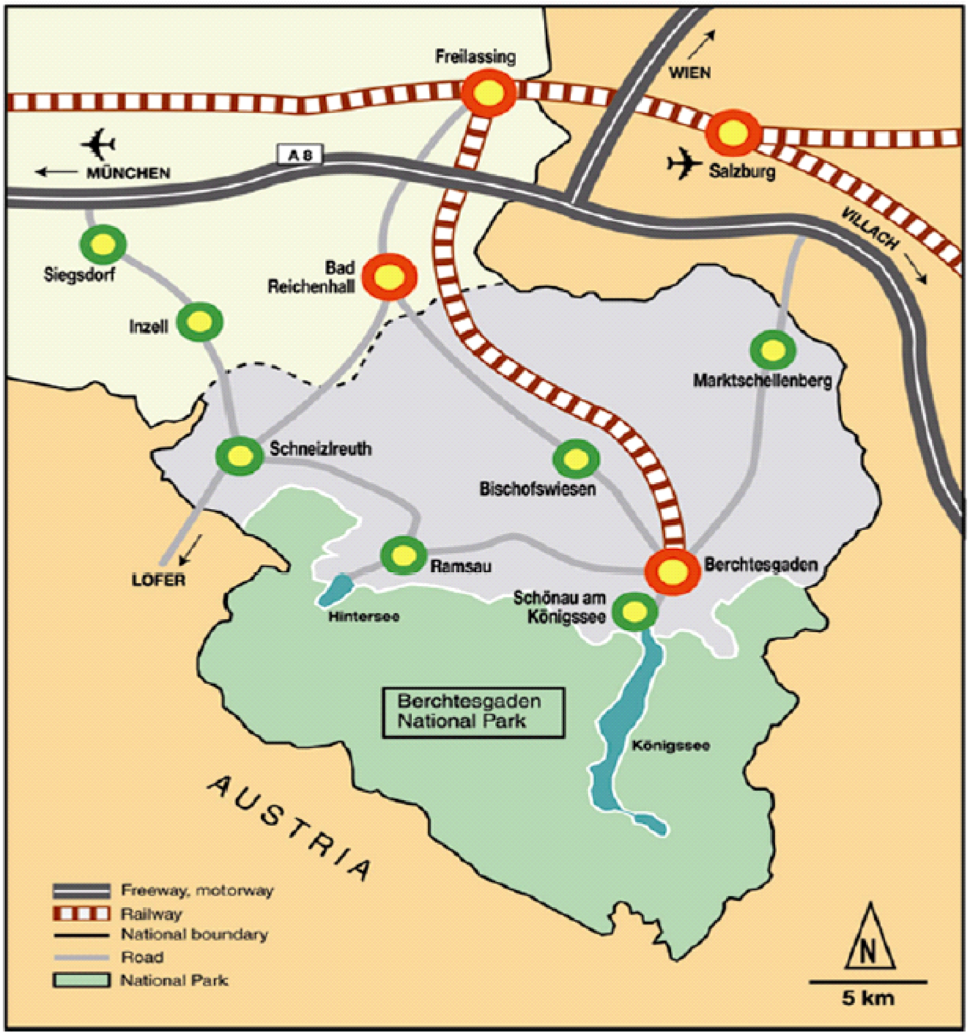


Fig. 1.1: Location of Berchtesgaden National Park.

Vegetation in the National Park Berchtesgaden is strongly affected by elevation gradients. The composition of forest species changes naturally with altitude, the proportion of conifers increasing in higher situated stands. The forested area and forests composition in the National Park Berchtesgaden have been also altered due to hundreds of years of human use. Through clear cutting and exploitation for building and heating, the proportion of forested area was heavily reduced. The changes in species composition increased with intensive salt mining in this region, which reached its maximum in the 16th century. Large quantities of wood were needed to evaporate water from the salt brine. Spruce was planted as the most desirable forest tree species because the boles float well, making their transport in rivers and on the Königssee easier. The intensive harvest of wood as well as high browsing damage and planting of spruce trees resulted in spruce dominated forests on sites between 900 and 1500 m a.s.l., where mixed stands would occur naturally. Within the boundaries of the park, near-natural forests are growing today only on the slopes of the valley adjacent to the Königssee and along rivers. This antropogenic impact has had the result that in many places where conifer forests dominate, and in the northern part of the park, deciduous forests and silver fir (*Abies alba*) are missing. Recently, programs have been implemented that attempt to restore the forest to a more natural state; a state found prior to clear-cutting practices.

1.4. Vegetation and the Tree Species Studied

The strongly shifting climate along elevation gradients results in zonation of the vegetation. Deciduous forest thrives below 700 m, mixed mountain forest reaches to 1400 m, and above that conifer forests occur. Wind-dwarfed bushes and alpine meadows dominate above 2000 m a.s.l. The dominant tree species in the submontane zone (700 m a.s.l.) is European beech (*Fagus sylvatica*); while within the beech forests *Fraxinus excelsior* and *Acer pseudoplatanus* also occur. In small areas, *Alnus incana*, *Tilia platyphyllos* and *Ulmus glabra* are locally distributed. In the montane zone, at elevations from 700 to 1400 m, mixed forests composed of *Fagus sylvatica*, *Acer platanoides*, *Picea abies* and *Abies alba* dominate. The subalpine zone, 1400 – 2000 m a.s.l., includes spruce-larch forests (*Picea abies* and *Larix decidua*). In the understory, numerous mosses, ferns and dwarf shrubs are found. In small areas of the Berchtesgaden National Park larch-alpine pine forest also occurs. In the alpine zone – above 2000 m a.s.l. - wind-dwarfed pines (*Pinus mugo*) and alpine meadows prevail. Very commonly one finds stands of *Alnus viridis, Rhododendron hirsutum* and *Rhododendron ferrugineum*.

Based on the vegetation zonation, the following species were chosen for study along the elevation gradient in the park:

Norway spruce (*Picea abies* (L.) Karst.) is the European forest tree species of greatest dominance (Bauer et al. 1997; Department of Communications) and greatest economic importance (Commission of the European Communities 2002). Spruce forests are naturally distributed from the Pyrenees, Alps and Balkans through Germany to Scandinavia and eastwards to western Russia. In the 1500s, it was introduced to Ireland and Britain. Also in Germany, Norway spruce is one of the most important tree species with cover of ca. 33% of all forested area (Bundesministerium für Ernährung, Landwirtschaft und Forsten 2002).

Norway spruce achieves 30 to 50 m height in Europe (Kremer 1996) and 0.6 m maximum diameter. It is adapted to temperate and cool climates, grows at high altitudes (800 to 2500 m), and is most productive with moist soils rich in humus. *Picea abies* has a shallow root system. Spruce in monocultures adds to soil acidification.

European beech (*Fagus sylvatica* L.) is a native European large tree, reaching 30 m. Beech forests extend from Italy to southern Scandinavia and from northern Spain, France and southern England to Poland and Romania in the east. Beech prefers moist, well drained slightly acid soils, but also grows well in sandy, basic soils. It has a shallow root system and is sensitive to drought. It is the best adapted tree species to environmental conditions in Central Europe (Kremer 1996). The beech forest as the natural climax vegetation was dominant in many parts of Germany before clearing of the forest by man.

European larch (*Larix decidua* (Mill.) belongs to the deciduous conifers. It grows to a height of 24 to 30 m (Kremer 1996), prefers high altitudes and cool temperate climate conditions. European larch is native to Europe; primarily occurring only in mountain regions: in the Alps, Carpathian and Sudety Mountains. Recently, it is very common also in lower regions as a plantation tree. Larch forests occur at elevations from 1000 to 3000 m, where it often forms the timberline. *Larix decidua* grows well in slightly acidic to neutral and well-drained soils; it tolerates wet sites.

Dwarf-pine (*Pinus mugo* Turr.) is a 1 to 5 m tall shrub (rarely a tree), usually with one or more curved trunks and long, prostrate branches (Christensen 1987). It is naturally distributed in central and southeastern European mountain regions. Dwarf-pine grows at high altitudes (1400 to 2500 m), mostly in the high subalpine zone and above the timberline. Dwarf-pine can also grow at lower altitudes in peat bogs, frost hollows and along river courses, when propagules are transported from higher altitude. It prefers a moist loam soil. *Pinus mugo* plays an important role in erosion control and in avalanche protection. For these reason, it is protected by law in some countries (Poland, Croatia).

2. LITERATURE REVIEW

In this study sapflow measurements and modelling were used to estimate the daily and seasonal changes in forest stand water loss along elevation gradients. The stand structure, sap flux densities and meteorological conditions were investigated to understand the reasons for different transpiration rates between Norway spruce stands occurring at different elevations and between species at the same altitude. The comparison of field data from the stands with different climate conditions and a stand level model can be used for an extrapolation to other similar mountain locations and for prediction of response to changes in environment.

The heat-dissipation method according to Granier (1985; 1987) was chosen, because it is suited to use in mountain terrain. The sapflow may be measured by the thermal balance method (Cermak 1984), which could also be used on mountain slopes, but is more destructive. With the eddy covariance system, the canopy gas-exchange, evapotranspiration and understory transpiration can be investigated. This method allows the measurements of both the water vapor and the carbon dioxide fluxes in forests, grasslands and agricultural ecosystems (Falge et al. 2002; Grace et al. 1995; Gu et al. 2003; Reichstein et al. 2002; Thalmann et al. 2002), however, it can not be used in complex mountain regions.

In many studies, the variations in season length and in plant productivity with increasing altitude, have been observed, which is linked with different climate conditions (Bassman et al. 2003; Smith et al. 2003; Tranquillini 1979). Photosynthetic primary production of trees decreases with increasing elevation because the available time for photosynthesis at high altitudes is drastically shortened. The growing season length declines with increasing altitude by about 3 – 4 days per 100 m (with 0.6 °C decreasing temperature) (Tenhunen 2000). At higher altitudes, bud break, extension of twigs, and leaf-out occur later. Friedel (1967) reported that the period during which larch bears green needles at the bottom of the Ötztal (700 m) was 94 days longer than at the timberline (2100 m). The length of photosynthesis period is linked with a shift in initiation of shoot activity, which can be observed along the elevation gradients.

With increasing altitude, stand density, basal area, LAI, carbon gain capacity and water flux decrease (Tenhunen 2000). The air temperature seems to be a key factor limiting vegetative growth of trees at high elevations (Smith et al. 2003). For *Picea abies* and *Larix decidua* trees at 1900 m a.s.l. (tree line), 50 % reduction of growth in comparison to trees occurring at 1300 m a.s.l. was observed. Similar decrease was reported for the Japanese beech at elevations 500 – 1600 m a.s.l. (Maruyama 1971). James et al. (1994) investigated growth and photosynthesis of *Pinus sylvestris* L. along an altitudinal gradient in the Cairngorm Mountains, Scotland. The authors observed a decrease in shoot length, needle length and needle number with altitude. Significant decline in plant production occurs above tree line, because of high precipitation, low air and soil temperatures and short growing season.

Low temperatures at high altitudes have an effect on photosynthesis (Neilson et al. 1972; Pharis et al. 1967; Willstätter and Stoll 1918). Because of cold stress, carbon assimilation decreases along an elevation gradient and the optimum photosynthesis occurs at lower temperatures compared with trees at lower elevations. Decrease in optimum photosynthesis temperature with elevation for *Abies balsamea* was demonstrated by Fryer and Ledig (1972). Slatyer and Morrow (1977) measured in *Eucalyptus pauciflora* a strong correlation between photosynthetic capacity and mean maximum temperature of the 10-day period before the measurement. Under near natural conditions at optimum temperature, the decline in photosynthesis from 18 mg CO_2 dm^{-2} h^{-1} at 915 m to 14 mg CO_2 dm^{-2} h^{-1} at 1645 m was observed. The low total seasonal CO_2 uptake at high elevations was caused by the slow increase in photosynthetic rates at the beginning of summer and their rapid decrease at the end of summer. Rook (1969) observed in seedlings of *Pinus radiata* a significant decrease in photosynthetic capacity when the day/night temperature changed from 33/28 °C to 15/10 °C, which in turn caused a clear increase in the respiration rate. Neuwirth et al. (1966) measured the differences in gas-exchange in *Picea abies* and *Abies alba* along an altitudinal gradient (at 1320, 1600, 2000 m a.s.l.) in the Rila Mountains, Bulgaria. In sun-shoots at timberline (2000 m), the assimilation was 25% less than at 1600 m and 1320 m, even though the trees at timberline received more radiation. At similar radiation level, the photosynthetic performance at 2000 m was 50% lower than at 1320 m. Similar results were described by Winkler (1957). The annual photosynthesis for *Picea abies* in the valley was 3.9 CO_2 g^{-1} d.w. $year^{-1}$, whereas at timberline only 1.8 CO_2 g^{-1} d.w. $year^{-1}$. A decrease in photosynthetic capacity with increasing altitude was observed also in laboratory experiments in which the gas exchange of branches and seedlings from different altitudes were studied. The photosynthesis of *Fagus crenata* was measured along an elevation gradient on Mount Ninohji, Japan (Maruyama and Yamada 1968). The authors found a decline in duration of photosynthetic capacity with altitude between 500 and 1350 m, in contrast to the maximum rates of photosynthesis, which increase with increasing elevation. The impact of air temperature, radiation and water availability on photosynthetic carbon gain in seedlings of *Abies lasio-carpa* and *Picea engelmannii* at a forest site and at timberline was investigated in the Rocky Mountains in Wyoming, USA (Johnson et al. 2004). At timberline the mean daily photosynthesis in seedlings of both species was less than at a lower forest site (19 and 29% for subalpine fir and Engelmann spruce, respectively). The night time temperatures below 2 degrees were associated with reduced maximum photosynthesis rates on the following day. Gieger and Leuschner (2004) investigated the differences in needle water status, stomatal conductance, carbon isotope signature, and foliar nitrogen concentration along an elevation gradient from 1600 m (upper montane forest) to 2100 m the (timberline) in mature trees of *Pinus canariensis*. The measurements were carried out during wet and early dry seasons on Mt. Teide, Tenerife, Canary Islands. The daily maximal stomatal conductance of pine needles decreased significantly with increasing elevation. During the dry season, an increase in minimum needle water potential along the elevation gradients (from -1.0 to -1.5 MPa at 1600 m to -2.0 to -2.5 MPa at 1800 and 2100 m) were measured. Results from this study suggest that the mature *P. canariensis* trees at the timberline are seasonally affected by edaphic and probably climatic drought.

According to Benecke (1972) there was a significant difference between seedlings from 1950 m and lower elevations (650 and 1300 m) placed in the same locality. These altitudinal changes in photosynthetic capacity may be partially explained by genetics. The reduction in photosynthesis depends on plant species, i.e. for *Picea abies* a decline of 61% at 1950 m in comparison to 650 m was measured. Körner (1999) demonstrated for non-tree species an increase in photosynthetic capacity with elevation to compensate the low CO_2 concentrations in the atmosphere.

The decrease in air temperature with increasing elevation influences gas exchange physiology. The reduction in net photosynthesis and an increase in dark respiration along the elevation gradients were described in many studies (Bassman et al. 2003; Mclaughlin et al. 1993; Pisek and Winkler 1958). On the contrary, stem respiration decreases with increasing altitude (Tranquillini and Schütz 1970). Respiration rates are higher in spring in new leaves and then decrease during summer (Falge 1997; Häsler 1991). In the extreme upper limits, reduction in photosynthesis in *Alnus virdis* was related to reduction in the chlorophyll content (Benecke 1972). In spruce seedlings both the reduction in chlorophyll content and radiation damage were observed. Gansert et al. (2002) described no significant differences in respiratory behaviour between *Betula ermanii* at treeline and the montane *Fagus crenata*.

At lower elevations, higher soil and air temperatures, and higher vapor pressure deficits occur than at higher altitudes, which causes differences in water availability between ecosystems (Bassman et al. 2003). “Water balance per se and transport potentials are a function of landscape and topography, being influenced by the spatial distribution of the vegetation canopy conductance, by topographic effects on energy input, by groundwater distribution and availability to plants, and spatial aspects of boundary layer climate” (BAHC 1993). Kubota et al. (2005) examined the influences of meteorological parameters and soil moisture on transpiration rates in *Fagus crenata* with increasing elevation. The observations were carried out in the Naeba Mountains, Japan at elevations of 550, 900 and 1500 m. The water fluxes were also measured in *Pinus ponderosa* in the Sierra Nevada Mountains using a combination of sap flow and eddy covariance techniques, and then modelled with a biophysical model FORFLUX (Kurpius et al. 2003). Many authors (Kirby et al. 1991; Liebscher 1972; Liebscher and Wilke 1981) described a reduction in evapotranspiration rates and increased discharge in nonforested (grass cover) versus forested areas, and gradual maximization of annual stand evapotranspiartion with canopy closure (Mcculloch and Robinson 1993). The water fluxes depend also strongly on species physiology (Whitehead and Calder 1993).

The differences in transpiration rates between stands located at different elevations above sea level (from 300 to 500 m) were examined in Steigerwald, Germany (Köstner et al. 2004). The daily maximum transpiration rates for a beech site on a plateau were higher (1.82 mm) than for beech site on a slope (1.35 mm). However, the seasonal transpiration measured at the lower situated site was higher ca. 61 mm higher than at higher elevation. Havranek (1972b) obtained a reduction in transpiration of 20% in young larch trees (*Larix decidua*) and spruce (*Picea abies*) when soil tempereture fell from 25 to 15°C. Neuwirth et al. (1966) measured a decrease in transpiration rates along an elevation gradient in *Picea abies* and *Abies alba* in the Rila Mountains, Bulgaria. In August, the rates at 1600 m were 49% and at 2000 m 39% of the rates at 1320 m a.s.l. Mooney et al. (1968) investigated the transpiration of plants growing at elevations from 1500 to 3600 m in the White Mountains, California. The plants in the subalpine and alpine zones used less water. At timberline, trees are not forced to restrict water loss (*Pinus mugo*, *P. cembra*), or if so, then only very temporarily (*Larix decidua* and *Picea abies*), whereas in the valley drastic reductions of transpiration frequently occur (Berger-Landefeldt 1936; Pisek and Cartellieri 1939).

The annual vapor loss at 14 grassland sites in the central Alps drops from nearly 700 mm at low altitude near Innsbruck to 210 – 250 mm at the upper limit of the alpine grassland belt. The elevational reduction of transpiration may be explained by the altitudinal decline of season length (Körner 1999). On a typical bright day the author reported vapor losses from 3.7 to 4.5 mm d^{-1} for high and low altitude, respectively. The evapotranspiration of upland (open bedrock/jack pine forest) and lowland (aspen/willow forest) sites in a boreal forest drainage basin in southeastern Manitoba, Canada, was measured with meteorological techniques (Amiro and Wuschke 1987). Net radiation (R_n) and ground heat flux (H) were measured directly using an energy balance method, and the sensible heat flux was measured by the eddy correlation. The mean daily value of R_n - H at the higher located site was 0.57 times the value at the lower elevation. The mean ratio of daily H/ R_n was 0.6 for the upland site and 0.4 for the lowland site. Zimmermann et al. (1999) observed the evapotranspiration in two small forested watersheds situated at two different elevations. The experimental catchments were located at 323 – 424 m a.s.l and 675 – 750 m a.s.l. The investigations were carried out in the Eastern Ore Mountains, where large areas at the ridge are deforested mainly due to high atmospheric sulphur dioxide deposition. In humid climates, interception is a major part of forest evapotranspiration due to their low aerodynamic resistances. The evapotranspiration in summer reached upto 51% of open-field precipitation at the lower elevation and 28% at the higher situated site. The major source for evapotranspiration at the ridge watershed was fog interception. Rada et al. (1999) observed gas exchange in four *Adesmia* species at different altitudes in order to understand the variability in water relation parameters, which occur under low water availability conditions. The measurements were carried out in the north-central Chilean Andes for *A. hystrix* (3300 m), *A. aegiceras* (3300 and 3750 m), *A. echinus* (4200 m) and *A. subterranea* (3750 and 4200 m). All *Adesmia* species show important stomatal control during most of the day linked to low soil water content. *A. aegiceras*, at both altitudes, exhibits maximum assimilation rates (6-8 µm mol m^{-2} s^{-1}) compared to the other three species (2-6 µm mol m^{-2} s^{-1}). Only by *A. hystrix* at 3300 m and *A. aegiceras* at 3750 m did turgor loss during the daily courses occur. Maximum CO_2 assimilation rates were lower in comparison to other species from mid-latitude high mountains. Carbon isotope analysis in a pinyon-juniper woodland (Lajtha and Getz 1993) showed that experimental species (*Juniperus monosperma* and *Pinus edulis*) had higher water-use efficiency (WUE) at the lowest, and presumably driest, sites. In the drought-tolerant juniper, positive carbon gain at lower predawn xylem pressure potentials than in pinyon was observed, whereas the WUE was not significantly greater than in pinyon. The responses of organic matter production to climate change, and therefore water use must be accounted for in ecosystem modelling.

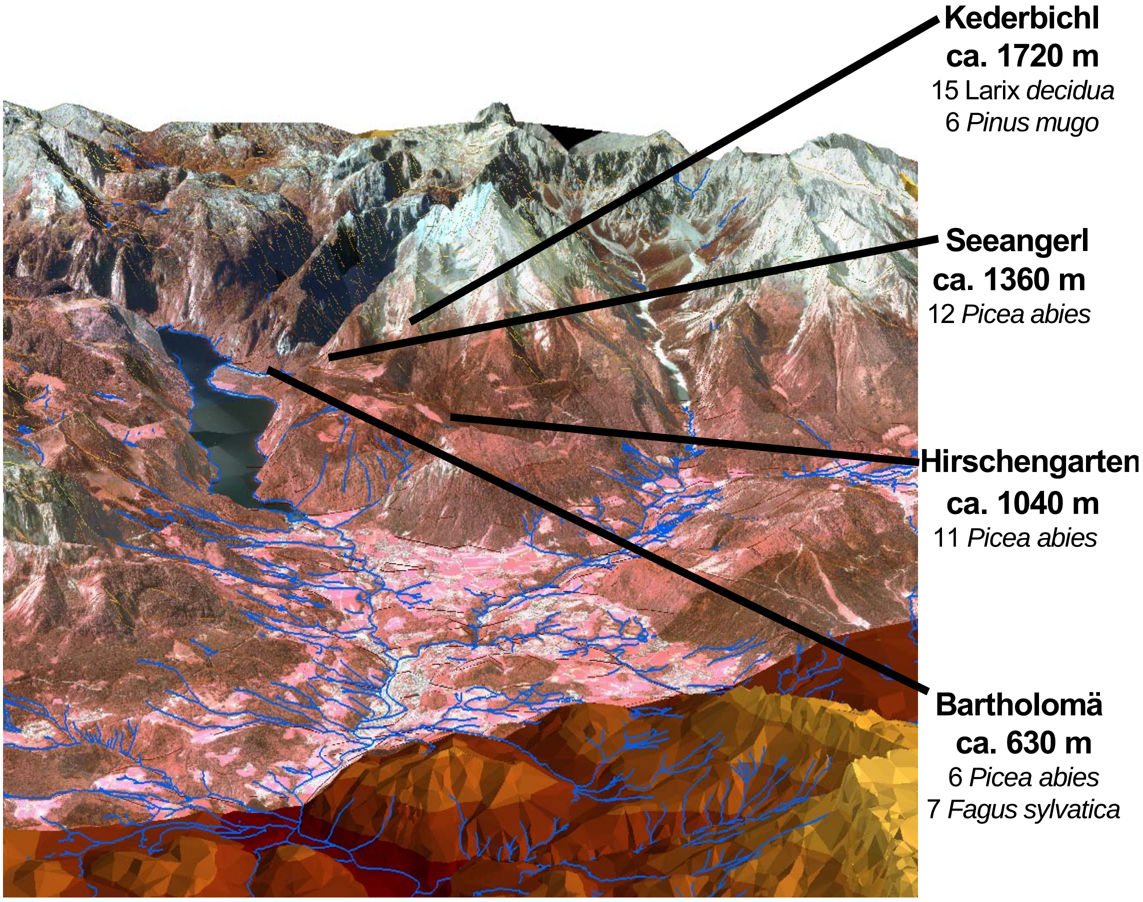
For a better understanding of the changes in forest ecosystems and to simulate gas exchange processes at the stand level, models have been developed (Falge et al. 1997; Wedler et al. 1996a; Wedler et al. 1996b; Whitehead and Hinckley 1991). The models have been used to estimate the tree and stand gas exchange and water use, because there are not always direct methods for measurements. The simulations may be used as a basis for transfer of knowledge and comparative applications of techniques in other forest ecosystems. “The models provide also a link to ecosystem theory, which attempts to examine and establish principles of overall system behaviour” (Falge 1997). Sala and Tenhunen (1996) combined a mechanistically based C-3 leaf photosynthesis model with an empirical stomatal model and a canopy model of light interception and microclimate for a simulation of net photosynthesis and transpiration in *Quercus ilex* stands in the l'Avic watershed, Spain. The measurements and then estimation were carried out for two locations within the watershed along an elevation gradient on clear, overcast and variable days during the year. For total annual net photosynthesis only small differences between the two sites were found, despite large differences in soil water content. The estimated annual canopy water loss was similar to estimated evapotranspiration using the hydrological input/output method. A stand level model based on field data of needle gas exchange was used to estimate water fluxes in two mountain spruce stands Davos (1660 m a.s.l.) and Stegerwald (1380 m a.s.l.) (Falge 1997).

Methods that have been used for estimation of photosynthesis and canopy transpiration are important for understanding of influences of climate change on ecosystems. After modification and modulation they can be also applied for similar forest sites or ecosystem types.

3. MATERIALS AND METHODS

3.1. Study sites

The study was carried out from the beginning of May to the end of September 2002 in Berchtesgaden National Park at altitudes from 630 to 1720 m (**Fig. 3.1**).



Kederbichl
ca. 1720 m
15 Larix *decidua*
6 *Pinus mugo*

Seeangerl
ca. 1360 m
12 *Picea abies*

Hirschengarten
ca. 1040 m
11 *Picea abies*

Bartholomä
ca. 630 m
6 *Picea abies*
7 *Fagus sylvatica*

Fig. 3.1: Location of sapflow measurement sites along an elevation gradient in the National Park Berchtesgaden in 2002. The view shown looks towards the south; the sites are exposed to the east on the Watzmann Mountain. Also indicated are the number and species of trees instrumented at each location. Graphics produced by H. Franz, Berchtesgaden National Park Administration.

For investigation of water use of forests along elevation gradients, three spruce stands with similar exposition, inclination and soil characteristics, but situated at different elevations of 630, 1040, and 1360 m above sea level, were chosen. Also, transpiration of one beech site at an elevation of 630 m, and one

European larch together with a dwarf-pine site at elevation 1720 m a.s.l. were studied. The overall characteristics of the stands are summarized in **Tab. 3.1**.

Tab. 3.1: Characteristics of the forest stands situated in the Berchtesgaden National Park.

Stand	Bartholomä		Hirschen-garten	Seeangerl	Kederbichl	
	Spruce	Beech	Spruce	Spruce	Larch	Dwarf-pine
Elevation a.s.l. (m)	630	630	1040	1360	1720	1720
Inclination (°)	30	26	26	32	32	34
Exposition	NO	O	NO	O	NO	NO
Tree density (n ha^{-1})	1490	800	690	1090	170	20
Mean stand height (m)	15	15	30	25	20	-
Plot area (ha)	0.04	0.05	0.1	0.1	0.3	-
Basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$)	40.4	27	51	60	22	-

Long-term records of the National Park indicate that mean annual temperature for Bartholomä (630 m) is approximately 5 to 6 C°, for Hirschengarten (1040 m) and Seeangerl (1360 m) 3 to 4 C° and at Kederbichl (1720 m) 1 to 2 C°. The estimated meteorological situations are derived from the park network of weather stations. The monthly mean temperatures are shown in **Tab. 3.2**.

Tab. 3.2: Mean air temperature at different elevations a.s.l. in Berchtesgaden National Park. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl, KB = Kederbichl (Konnert 2001).

Mean air temperature	BA (630 m)	HG (1040 m)	SA (1360 m)	KB (1720 m)
January	-2 – 0	1 – 2	1 – 2	-4 – (-3)
May	11 – 12	7– 8	5 – 6	3 – 4
July	13 – 14	11– 12	9 – 10	3 – 4
Year	5 – 6	3 – 4	3 – 4	1 – 2

The four investigated stands have different growing season lengths (days with temperature equal or higher than 5°C). At 630 m a.s.l., the growing season starts about 15 April and ends ca. 25 October (190 days). At 1040 m a.s.l., the growing season continues from 18 April to 20 October (183 days), at 1360 m a.s.l. from 25 April to 18 October (158 days), and at 1720 m a.s.l from 6 May to 16 October (143 days) (Konnert 2001). The number of days with average temperature above 10°C, is at Bartholomä ca. 151, at Hirschengarten 112, at Seeangerl 71 and at Kederbichl 47.

The mean annual precipitation at the lowest situated stand is ca. 1600 and at the highest situated stand 2100 mm (**Tab. 3.3**). From May to October the precipitation is 1000 mm in Bartholomä and Hirschengarten, 1100 mm in Seeangerl and 1200 mm in Kederbichl. Lower precipitation occurs during the winter period.

Tab. 3.3: Mean precipitation at different elevations a.s.l. in Berchtesgaden National Park. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl, KB = Kederbichl (Konnert 2001).

Mean precipitation	BA (630 m)	HG (1040 m)	SA (1360 m)	KB (1720 m)
May – October	1000	1000	1100	1200
November – April	600	800	900	900
Year	1600	1800	2000	2100

At the 630 m site snow melt occurred at the end of April, at the 1040 m and 1360 m sites at the beginning of May and at 1720 m site at the end of May in 2002.

The soil profiles in each investigated site were poorly formed (20-30 cm). Under a thin organic layer, layers with a significant percentage of large to very large stones are found. The spruce and beech forests at 630 m a.s.l. occur on shallow stony loams with a moder layer. The spruce stands Hirschengarten and Seeangerl are located on soils with a shallow tangel layer (kalkrohhumus; on weathered solid rocks) (Konnert 2001). The substrate groups at the 1720 m site were identified as moderately deep tangel layer on rocks.

3.2. Structure of the Studied Forest Stands

3.2.1. Mapped Tree Locations

Tree position and tree height was measured with a Forest-Laser (Criterion 400 Survey Laser Instrument, Laser Technology Inc., Englewood, USA). The 630 m site is located on a northeast facing mountain slope near to the Eisbach River. Spruce and beech forests grow there adjacent to each other. Tree density in this spruce stand was ca. 1490 trees ha^{-1} and was greater than in the two other stands occurring at higher elevations. The mean stand height was approximately 15 m (**Tab. 3.1**). Individual young *Acer pseudoplatanus*, *Fagus sylvatica* and *Fraxinus excelsior* trees were also found within the investigated spruce stands (see **Fig. 3.2**, **3.3**). The density in the beech stand was ca. 800 trees ha^{-1}, mean tree height was 15 m. The tree distribution within the stand is shown in **Fig 3.2** and **Fig. 3.4**.

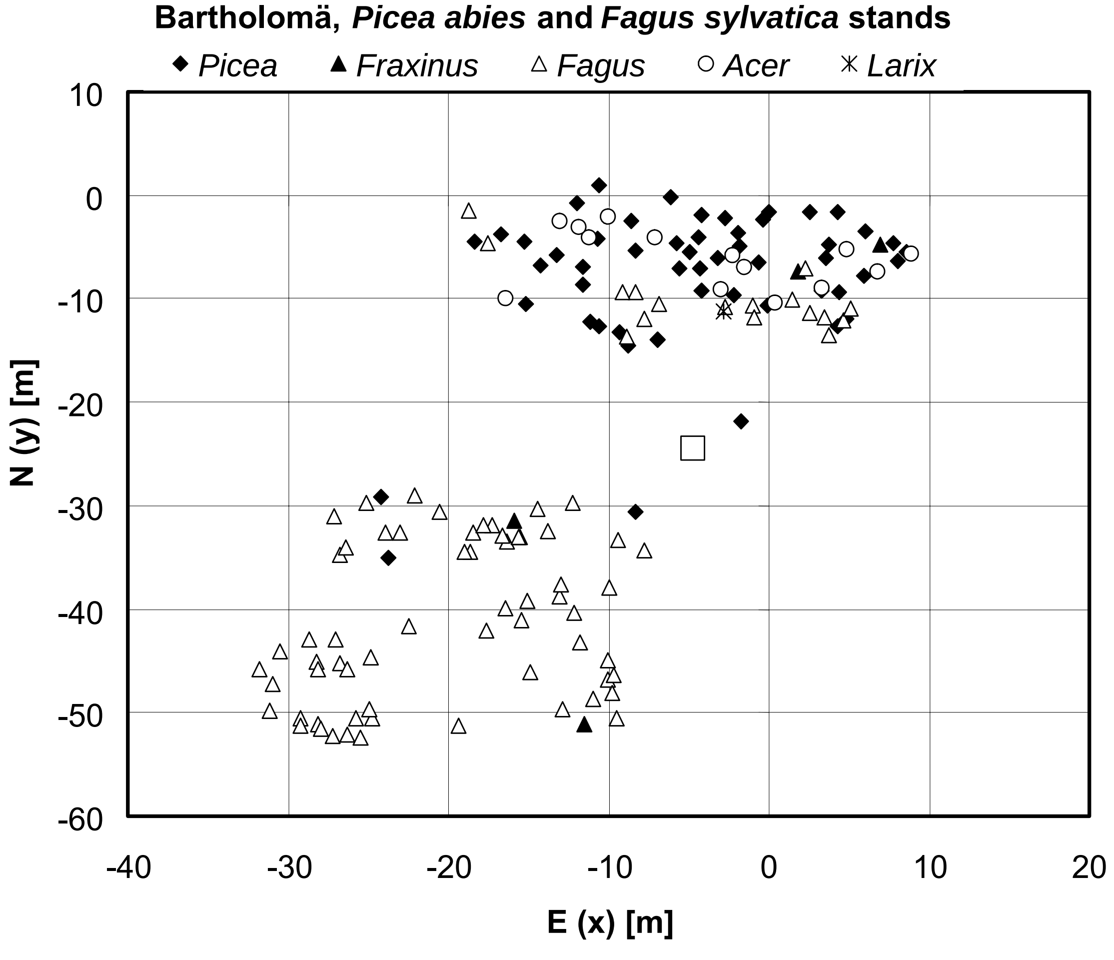


Fig. 3.2: Tree distribution in the mapped areas of investigated *Picea abies* and *Fagus sylvatica* stands at Bartholomä (630 m a.s.l.) in Berchtesgaden National Park. Species identification is indicated. The square indicates the approximate location of the data logger between the stands.

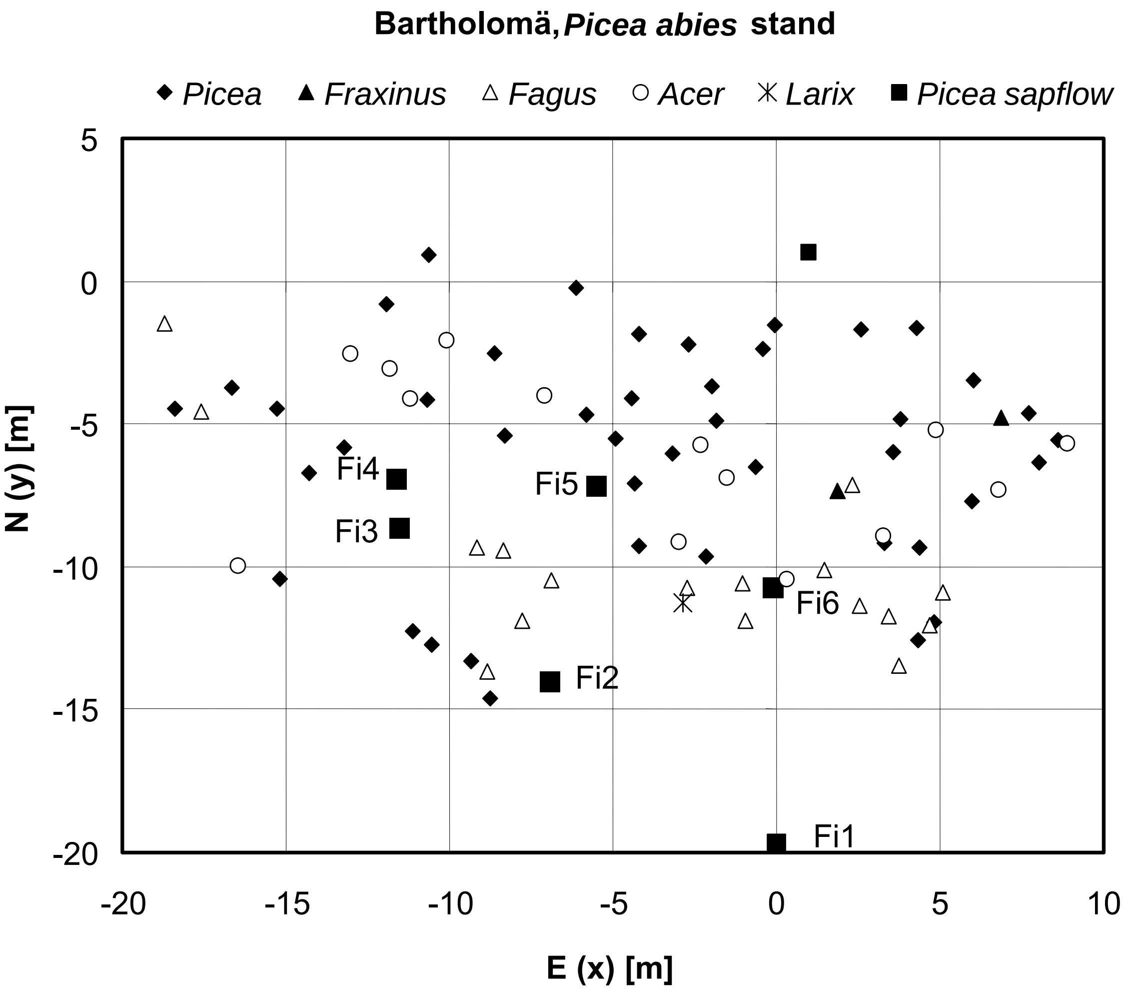


Fig. 3.3: Tree distribution in the investigated *Picea abies* stand at Bartholomä (630 m a.s.l.) in Berchtesgaden National Park. The sapflow trees are indicated with numbers.

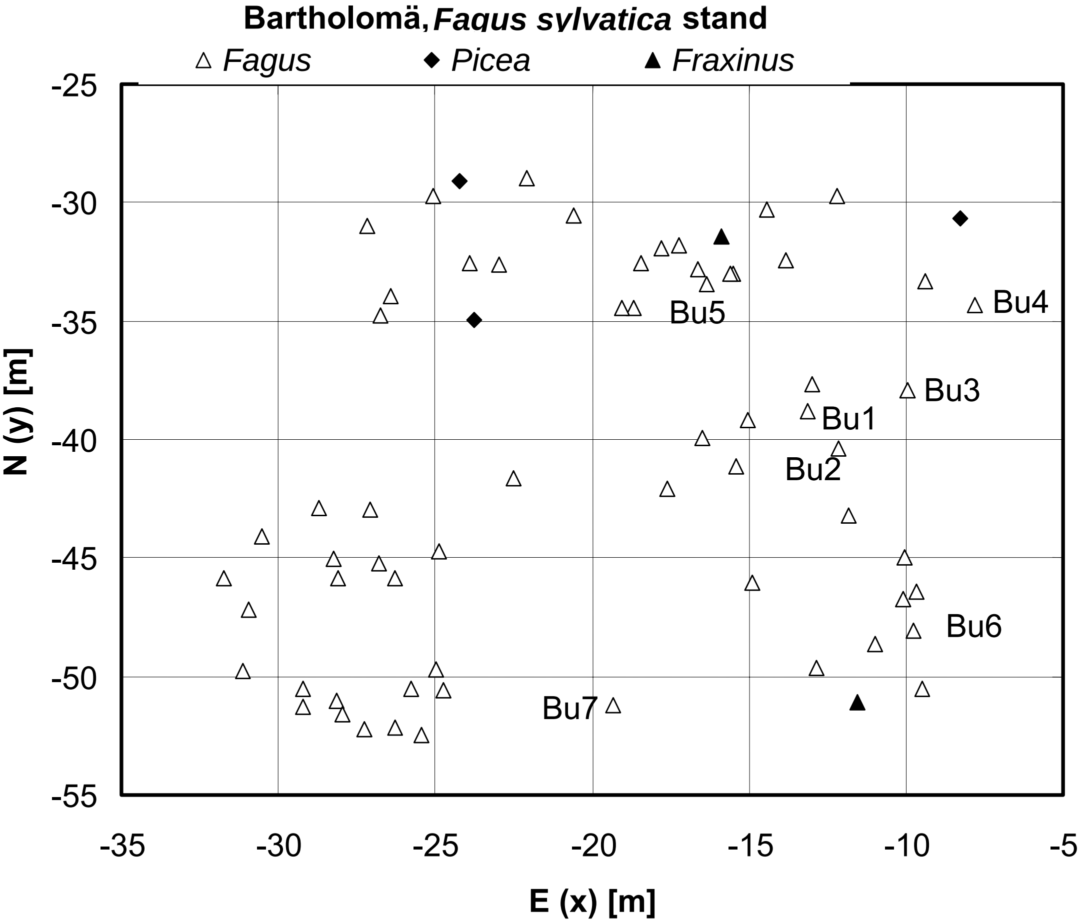


Fig. 3.4: Tree distribution in the investigated *Fagus sylvatica* stand at Bartholomä (630 m a.s.l.) in Berchtesgaden National Park. The sapflow trees are indicated with numbers.

The 1040 m and 1360 m sites are located on northeast and east facing slopes. In these two stands, the canopies are dominated by *Picea abies* with occasional occurrence of *Acer pseudoplatanus*, and in Hirschengarten (1040 m a.s.l.) also *Fraxinus excelsior* trees (**Fig. 3.5**, **3.6**). Mean tree height of the investigated stands reached 30 and 25 m for Hirschengarten and Seeangerl, respectively. At Hirschengarten, tree density was lower in comparison to Seeangerl (**Tab. 3.1**).

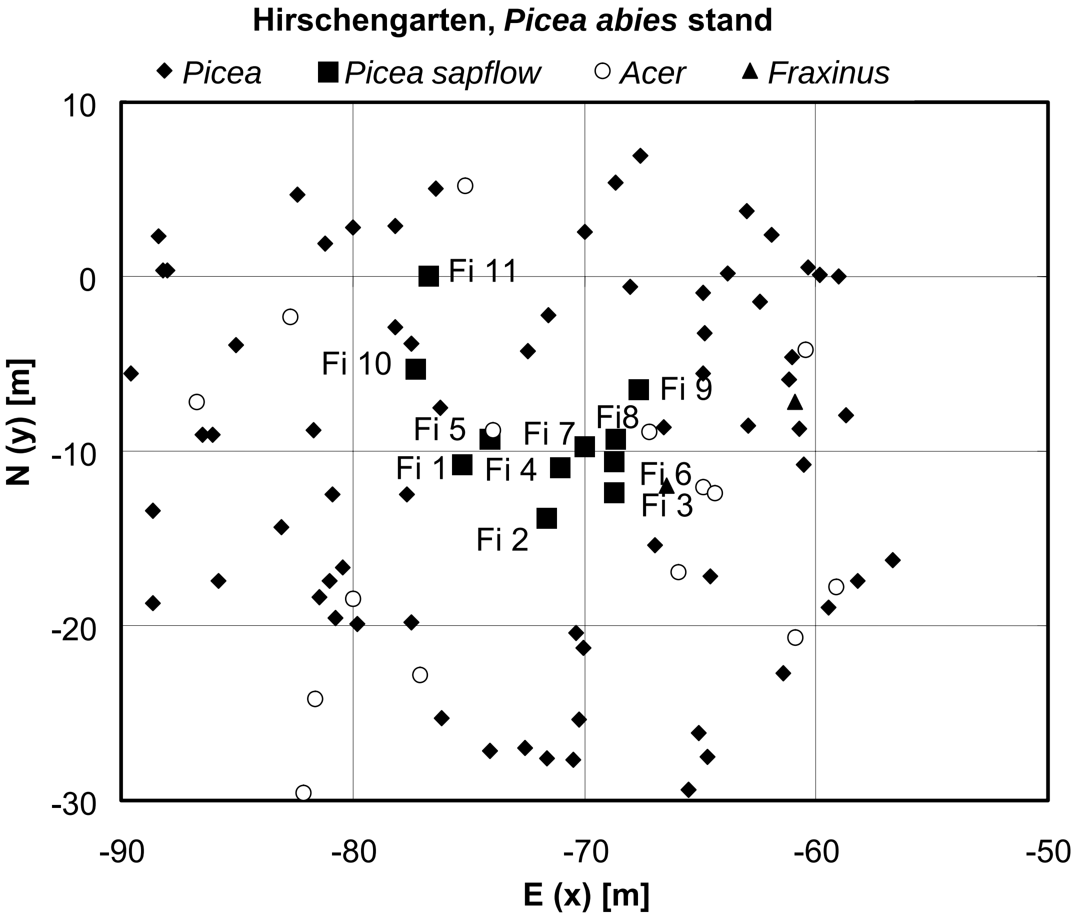


Fig. 3.5: Tree distribution in the investigated *Picea abies* stand at Hirschengarten (1040 m a.s.l.) in the Berchtesgaden National Park. The sapflow trees are indicated with numbers. Species identification for other elements in the stand is also given.

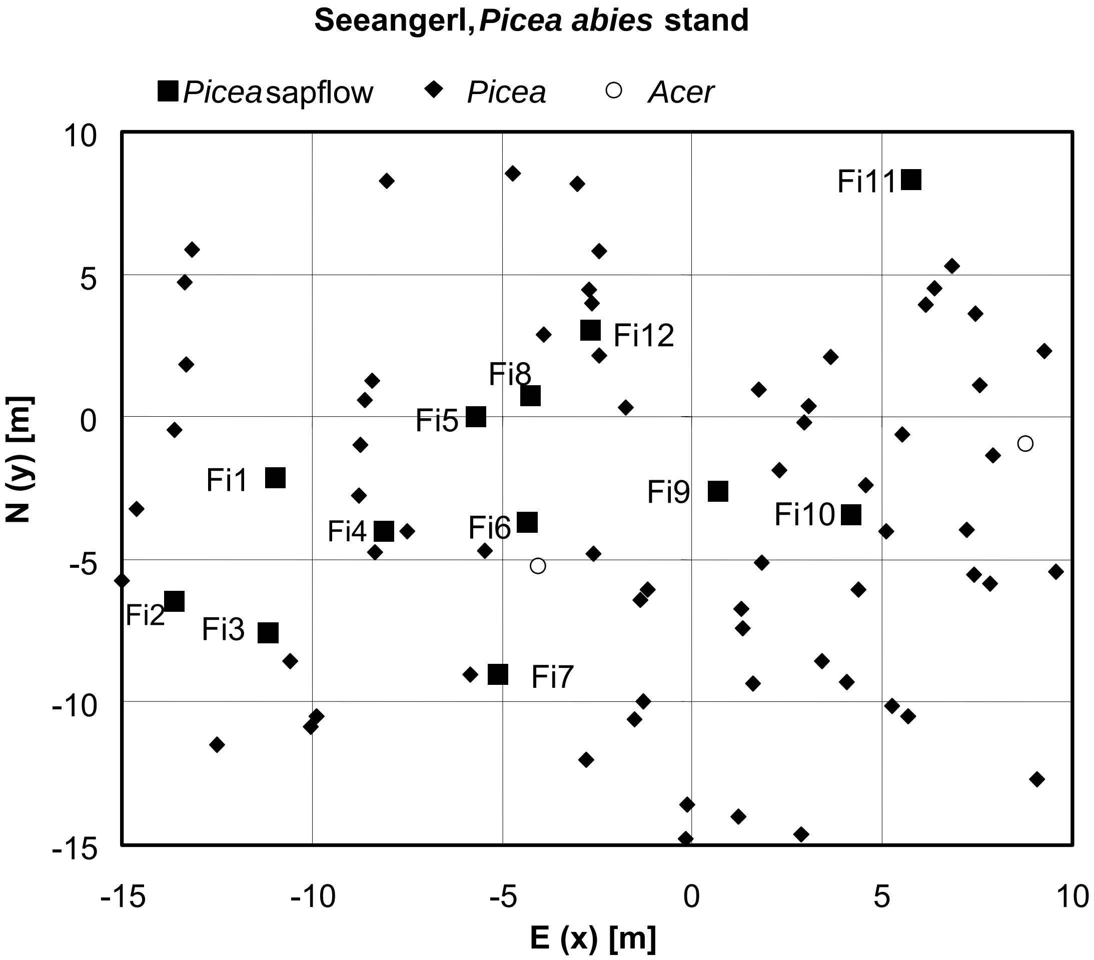


Fig. 3.6: Tree distribution in the investigated Picea abies and stand at Seeangerl (1360 m a.s.l) in the Berchtesgaden National Park. The sapflow trees were indicated with numbers. Individual Acer trees are also indicated.

The *Larix decidua* and *Pinus mugo* site is situated at the elevation 1720 m a.s.l, on a north-east facing mountain slope (**Tab. 3.1**). The tree position in the experimental stand is shown in **Fig. 3.7**. Tree density reached 170 trees ha^{-1}, the mean tree height approximately 20 m. At this site, three vegetation types occur: high montane - subalpine larch forest, dwarf mountain pine-scrub and subalpine dwarf-shrub heath. Grass stands, herbs and alpine shrubs grow under and between the trees. *Vaccinium myrrtillus*, *Rhododendron hirsutum* and *Calamagrostis villosa* occur in patches. Individual *Sorbus aucuparia* and *Alnus virdis* trees were also found within the investigated larch stand. All species occurring at the Kederbichl site are listed in Appendix 1 (Tenhunen, B. personal communication).

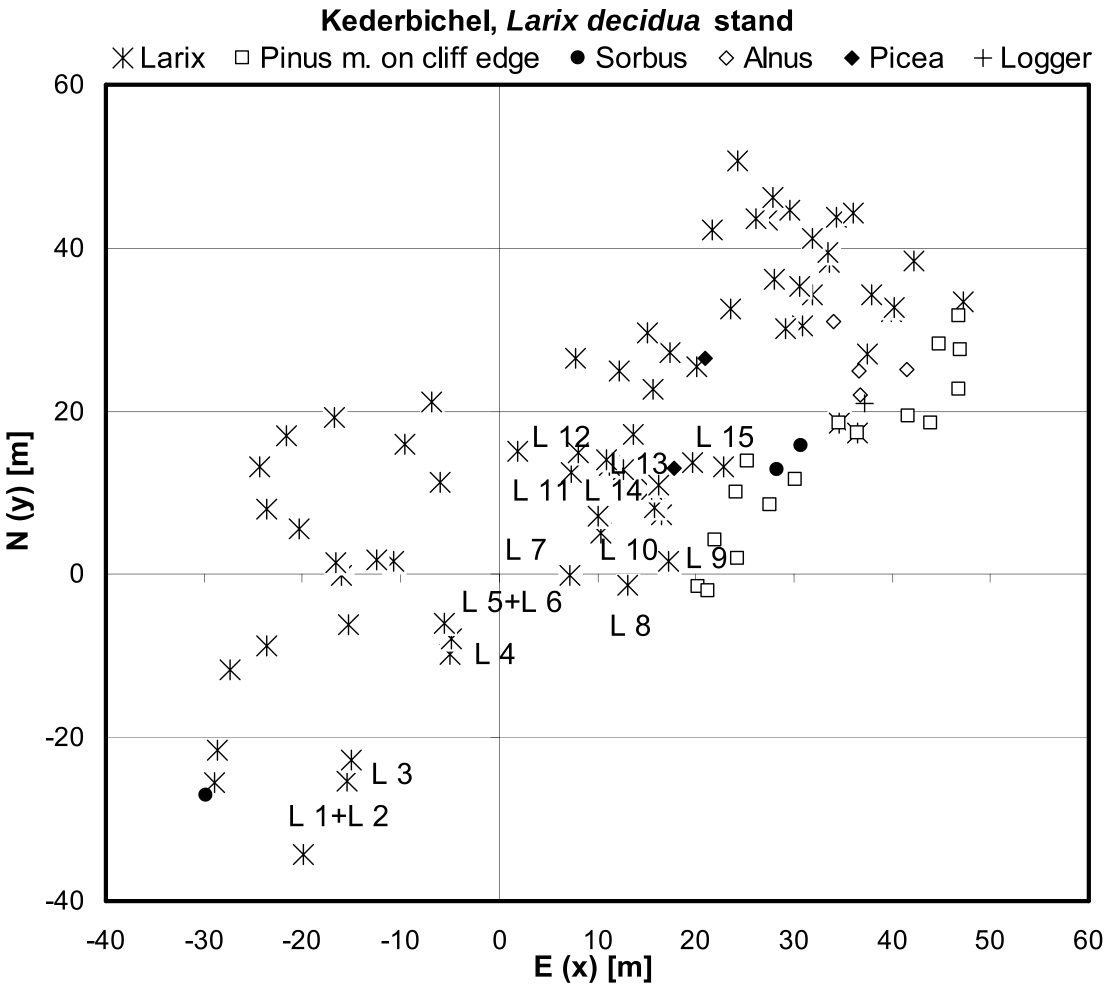


Fig. 3.7: Tree distribution in the investigated *Larix decidua* and *Pinus mugo* stands at Kederbichl (1720 m a.s.l.) in the Berchtesgaden National Park. The sapflow trees were indicated with numbers.

3.2.2. Characteristics of Individual Trees

The frequency distribution of tree circumference at breast height (CBH measured at 1.35 m) was measured for 39 spruce trees in Bartholomä, 82 in Hirschengarten and 102 at Seeangerl. At the 630 m, 1040 m and 1360 m sites, the range in circumference at breast height was 15 to 112 cm, 22 to 171 cm, and 10 to 196 cm respectively (see **Tab. 4.1 – 4.3**). Mean circumference at breast height was 53.4 cm at Bartholomä, 89.9 cm at Hirschengarten and 66.5 cm at Seeangerl. In comparison to Bartholomä and Seeangerl, the site Hirschengarten was characterized by the tallest trees, the largest average tree circumference, lowest stand density and greatest basal area (**Tab. 3.1**).

The same measurements were done for 51 beech trees (see **Tab. 4.1**) at the 630 m site. In the European beech stand, the circumference at breast height ranged between 9 and 200 cm. Mean CBH was approximately 42.6 cm.

The frequency distribution of CBH was measured for 73 larch trees at the 1720-m site. The larch stand Kederbichl is very sparse, the *Larix decidua* trees are growing individually and do not form a closed canopy. Tree density was ca. 170 trees per ha. Mean tree height was approximately 20 m. The circumference at breast height ranged between 85 and 199 cm, and mean CBH was 136 cm (see **Tab. 4.4**).

At elevation 1720 m, *Pinus mugo* shrubs are growing near to the larch stand and near to open avalanche channels. Because the dwarf-pine site was approximately 2 m high, the CBH could not be measured, rather the circumference of individual “sapflow branches” was measured at the point of emergence from the ground. Mean circumference of dwarf-pine branches reached ca. 24 cm (see **Tab. 4.4**). The diameters of dwarf pine branches at their emergence at ground level were in the range of 4.6 to 8 cm.

The sapwood depth and the stand age at each location were estimated with fresh cores. At each site, 9 to 11 cores were sampled at breast height with an increment borer. The 5 mm diameter cores were drilled to the center of trees and the annual growth rings were counted.

3.2.3. Tree Size Distribution and Selection of Measurement Trees

From the circumference at the breast height, the stem diameters (DBH) were estimated. The frequencies of DBH-classes are shown for each Norway spruce stand in **Fig. 3.8**. At the 630 m and 1360 m site, smaller trees are most frequent that belong to 5 to 30 cm DBH-class. In each stand, six to twelve trees – representing three different DBH classes – were selected for sapflow measurements in order to include potential variation in sap flux densities among trees of different sizes (Köstner 1999a).

The experimental trees were chosen for three size classes:

- Bartholomä I) 5 to 25 cm (32 trees), II) 25 to 30 cm (5 trees) and III) >30 cm (2 trees).
- Hirschengarten I) 5 to 25 cm (31 trees), II) 25 to 40 cm (39 trees) and III) >40 cm (12 trees).
- Seeangerl I) 5 to 30 cm (85 trees), II) 30 to 40 cm (13 trees) and III) >40 cm (4 trees).

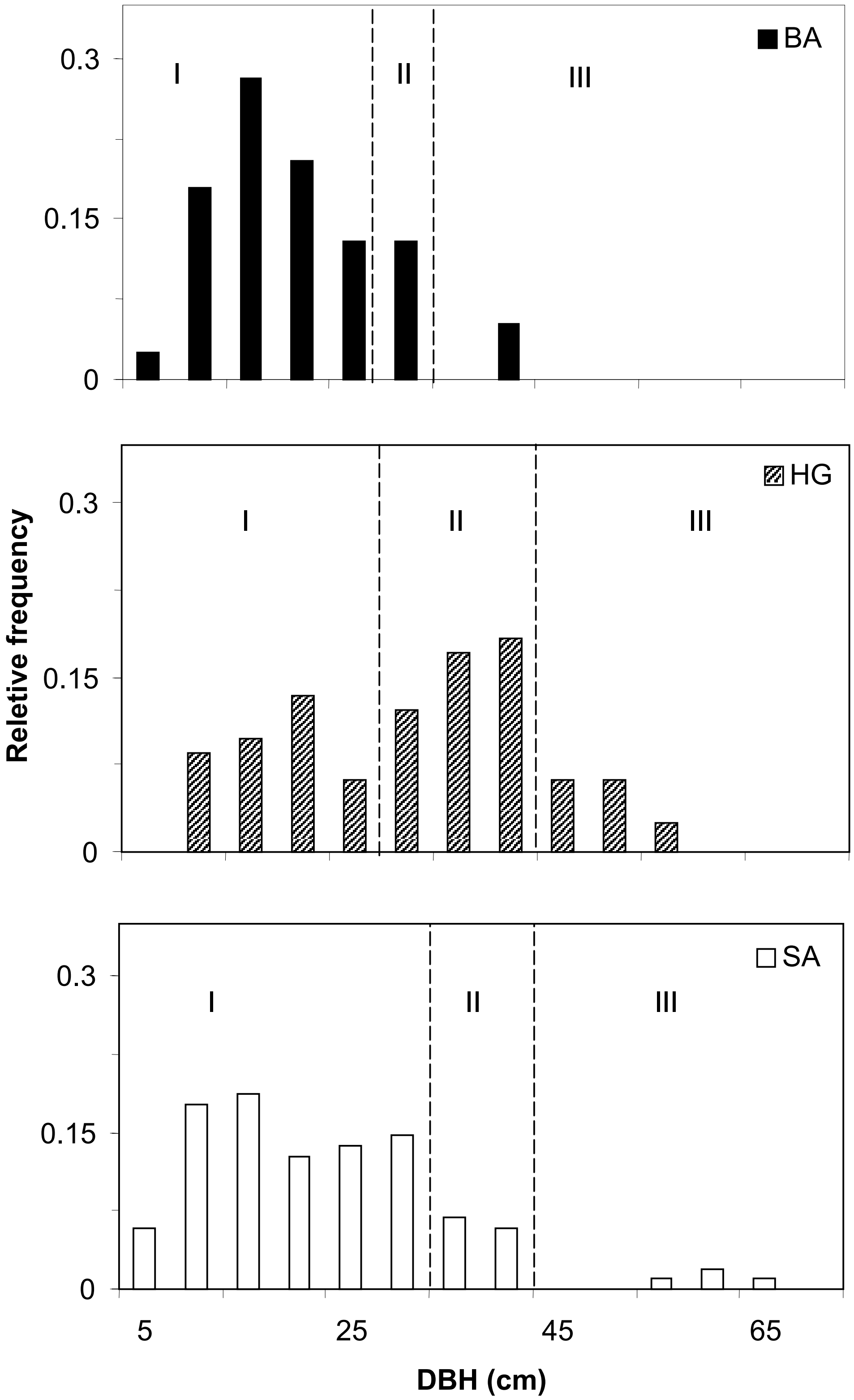


Fig. 3.8: Frequency distribution of tree diameters at breast height in three measuring plots in Berchtesgaden National Park as described in the text. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl. I,II,III = DBH classes.

In the European beech stand, small trees, which belong to the 5 to 20 cm DBH-class dominate. The frequency of DBH classes is shown in **Fig. 3.9**. For sapflow measurements, 7 trees – with different DBH – were selected. The experimental trees were again chosen for three size classes: I) 5 to 15 (34 trees), II) 15 to 25 (14 trees) and III) >25 cm (3 trees).

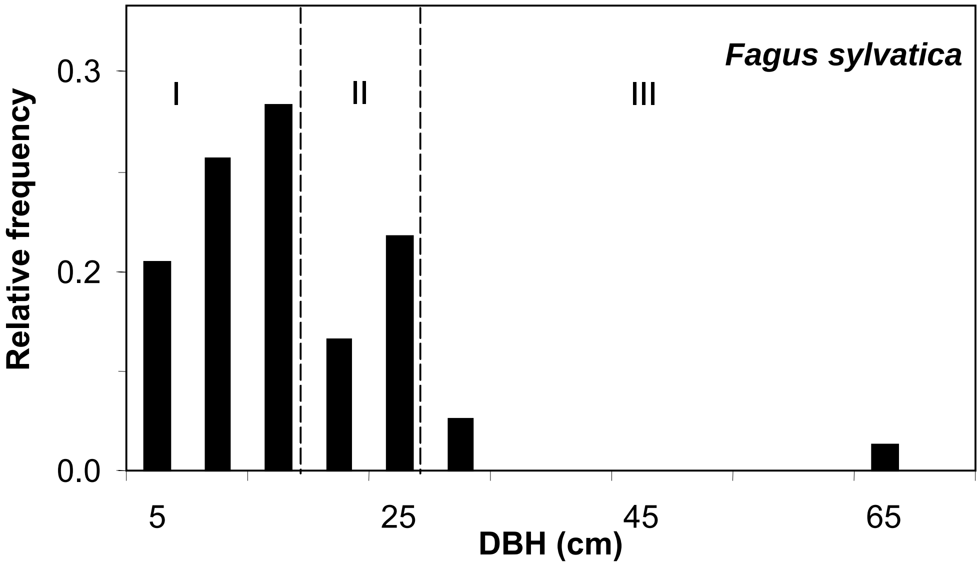


Fig. 3.9: Frequency distribution of tree diameters at breast height in *Fagus sylvatica* measuring plot in Berchtesgaden National Park. I,II,III = DBH classes.

The frequency distribution of tree diameter at the breast height in the European Larch stand is shown in **Fig. 3.10**. Because very similar sapwood depth was found to occur, the trees selected for transpiration measurements were not selected according to DBH-classes, but rather from practical considerations related to the proximity with respect to the central logger and power supply.

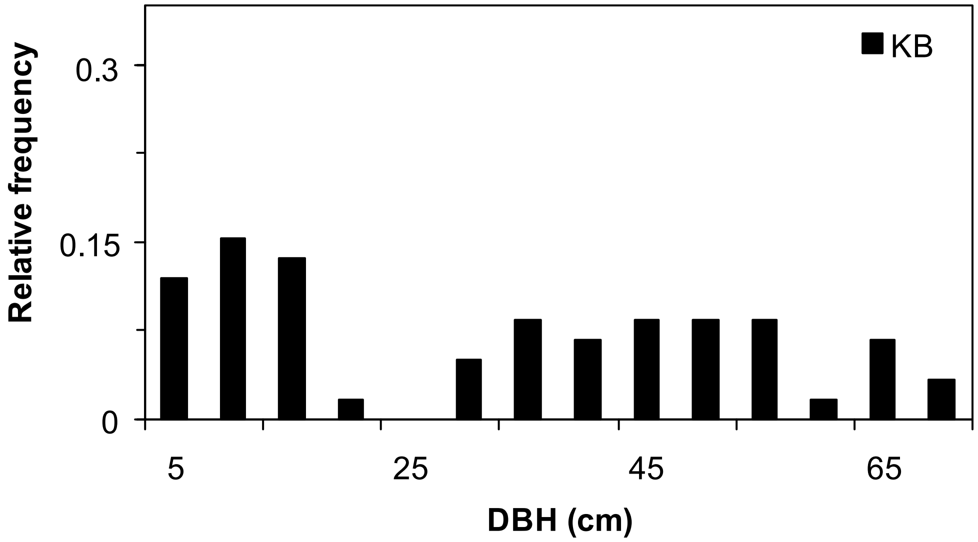


Fig. 3.10: Frequency distribution of tree diameters at breast height in the *Larix decidua* measuring plot in the Berchtesgaden National Park.

3.2.4. Leaf area index (LAI)

Important ecosystem processes acting at the interface between the land surface and the atmosphere, such as photosynthesis (Bonan 1993), respiration, transpiration, litter fall and energy balance (Running 1992, Bobeva 2003) are primarily determined by the canopy structure of the vegetation. Leaf area index provides important information related to a variety of plant canopy processes, and is a value required when including the above ecosystem processes into quantitative descriptions, i.e. into ecosystem models. LAI can be measured or derived by different methods: by harvesting, by collection and weighing of total leaf litter, by allometry of trees with up-scaling to stand level, and by indirect optical or light interception approaches (hemispherical photography, sunfleck ceptometers, tracing radiation and architecture of canopies (TRAC), optical instruments – LAI-2000, LI-COR; see (Chen and Cihlar 1995)). Direct measurements of canopy structure are difficult, destructive and expensive. Therefore, other methods such as the use of allometric relationships that relate tree size to leaf area, or satellite remote sensing – must be used to obtain LAI over large areas. In this study, the LAI for spruce and beech sites was estimated with allometric functions. Due to lack of information from harvests, LAI measurements in the experimental larch stand were estimated with a canopy analyzer (light interception method). Leaf area index of *Pinus mugo* was estimated by direct harvest of stands adjacent to the measurement branches.

3.2.4.1. *Picea abies* sites

For estimating the leaf area index in the three investigated spruce stands, an allometric function was applied based on tree harvests by Alsheimer (1997), Burger (1939; 1942; 1953), and Faltin (unpublished). The equation derived is as follows:

$$LA = 0.1\ CBH^{1.72} \qquad \textbf{Eq. 3.1},$$

where CBH is circumference at the breast height (1.35 m) and LA is the total surface leaf area of individual trees. The LAI of the spruce stand was calculated as the sum of LA for all individual trees growing in the investigated plot and by dividing by plot area:

$$LAI_{stand} = \Sigma\ LA_{tree}/\ (PA*2.57)\ (m^2\ m^{-2}) \qquad \textbf{Eq. 3.2},$$

where LAI_{tree} is the total leaf area of individual trees ($m^2\ m^{-2}$), PA is the plot area (m^2), and 2.57 is the conversion factor for estimating projected leaf area from total surface area (Alsheimer 1997; Oren et al. 1986). Total plot area was determined from the mapping of trees as described in section 3.2.1. The plot boundaries were set at the mid-point between included and adjacent trees as shown in **Fig. 3.11**.

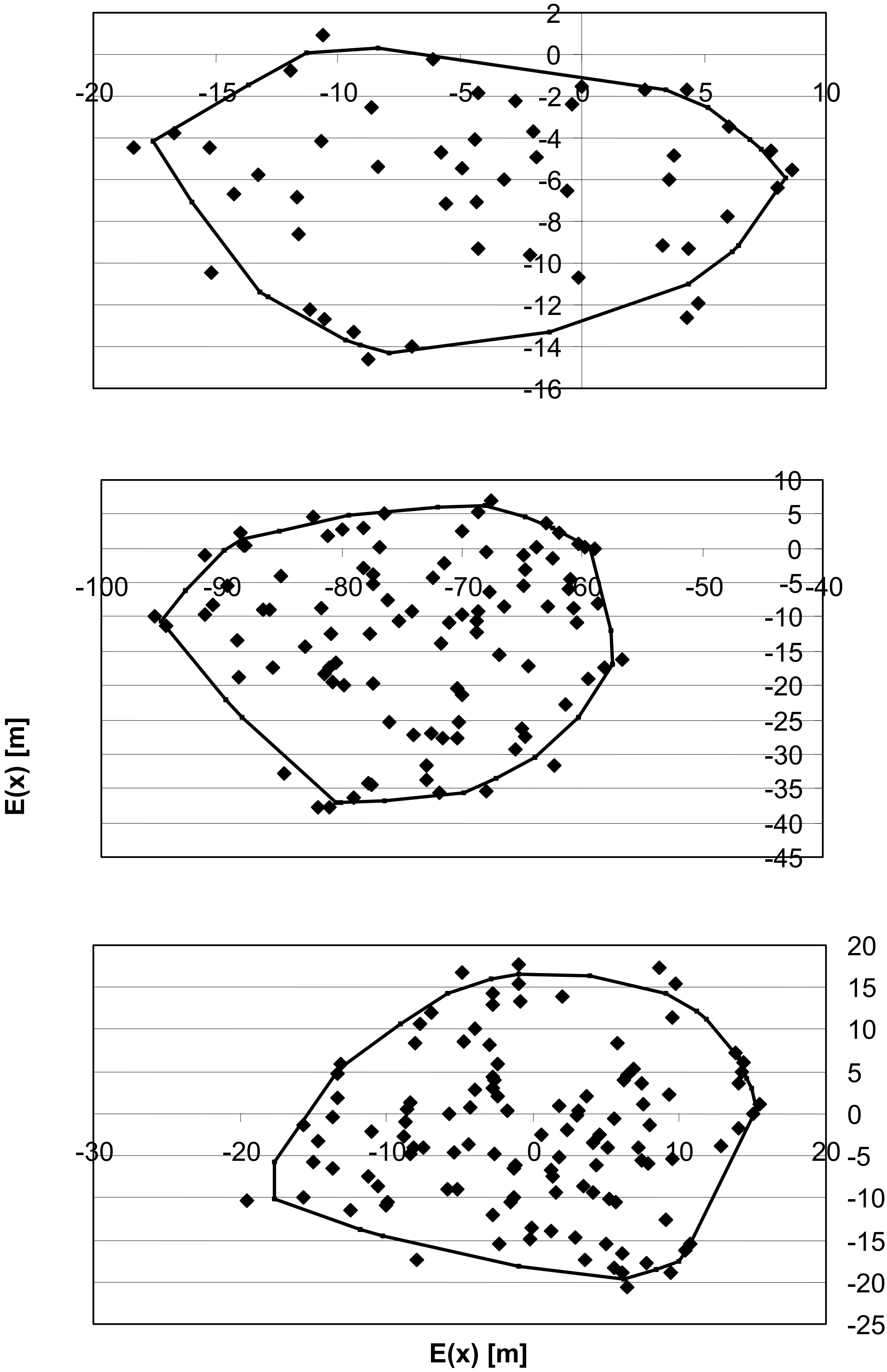


Fig. 3.11: Determination of plot boundaries at mid-points between included trees and adjacent trees at three spruce sites in Berchtesgaden National Park. Leaf area was determined for all included trees and set in relation to the surface area within the circumscribed polygon. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl.

3.2.4.2. *Fagus sylvatica* site

To estimate leaf area index of the experimental European beech stand, an allometric function was similarly based on harvest data (Bartelnik 1997; Burger 1945; Pellinen 1986). The equation is as follows:

$$LA_{tree} = 0.118\ CBH^{1.565} \qquad \textbf{Eq. 3.3},$$

where CBH is circumference at the breast height (1.35 m) and LA is the projected leaf area of individual trees.

The leaf area index of the site was calculated as the sum of LA for all individual trees growing in the investigated plot divided by plot area:

$$LAI_{stand} = \Sigma\ LA_{tree}/\ PA\ (m^2/\ m^2) \qquad \textbf{Eq. 3.4},$$

,

where LA_{tree} is the leaf area of individual trees and PA is the plot area (m^2). The plot boundaries were set at the mid-point between included and adjacent trees as shown in **Fig. 3.12**.

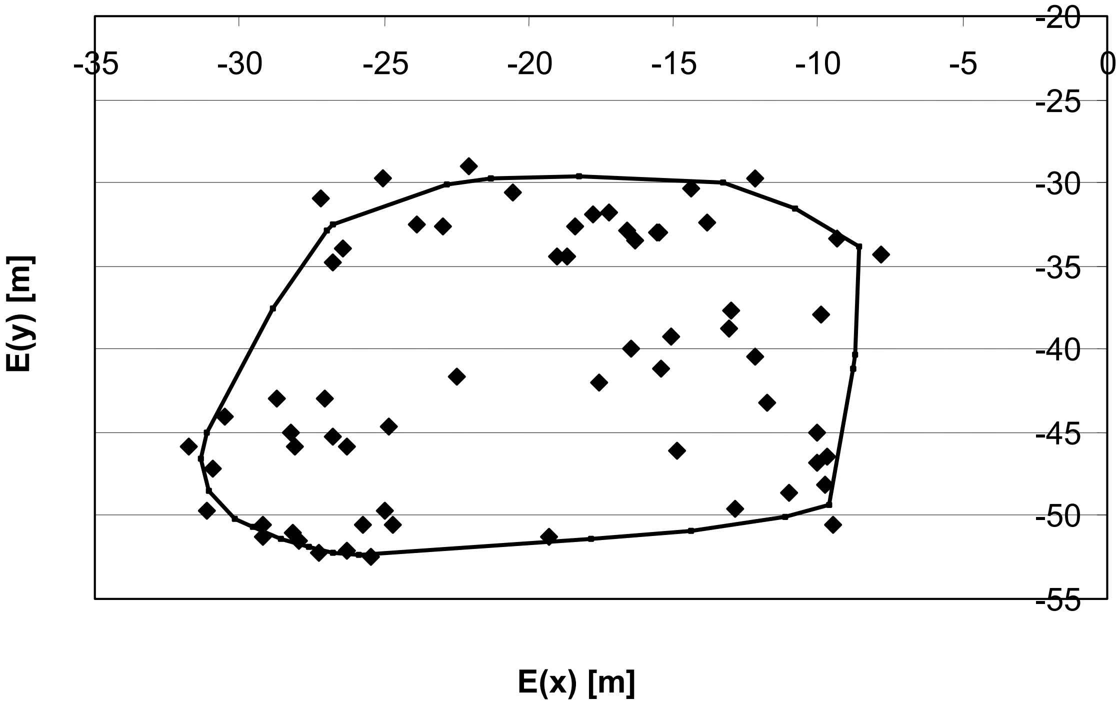


Fig. 3.12: Determination of plot boundaries at mid-points between included trees and adjacent trees at the beech site in Berchtesgaden National Park. Leaf area was determined for all included trees and set in relation to the surface area within the circumscribed polygon.

3.2.4.3. *Larix decidua* and *Pinus mugo* sites

The measurements of larch leaf area index (LAI) were carried out in 2001 with the Plant Canopy Analyzer LAI2000, LI-COR Inc., Lincoln, USA. The LAI-2000 measures the effective LAI from canopy gap fraction recorded for different solid angles. It is an optical instrument equipped with five detectors monitoring a series of concentric rings. Detector 1 measures radiation directly overhead (0-13° from vertical), while detector 5 measures incoming radiation of a ring between 61° and 74° from vertical. Two instruments are used, one underneath the forest canopy and the second mounted in a nearby open clearing to provide open-sky reference of radiation conditions. This instrument is designed to be used in diffuse light conditions.

In the context of considering water use by the entire stand, the well-developed understory is an important component. Thus, in 2002, maximum biomass and

LAI of the herbaceous and understory vegetation were estimated by harvesting during mid-July.

Leaf area index, i.e., development of stands of *Pinus mugo*, appears to be highly variable depending on disturbance, soil depth and exposition. Thus, it was only possible to make some coarse estimates of LAI for this species near to the measurement installations in two different ways. First, the LAI of actual measurement branches was estimated by measuring the total length of needled branchlets. Needle area per length of branchlet was quantified previously at the site by harvesting, removing needles and measuring needle projected area with a leaf area meter (CI-202, CID, Camas, WA). With the estimates of needle area per branch, the measured data for the branch which had needles at all levels within the stand could be expressed as an average flux per needle projected surface area. The plot boundaries were set at the mid-point between included and adjacent trees as shown in **Fig. 3.13**.

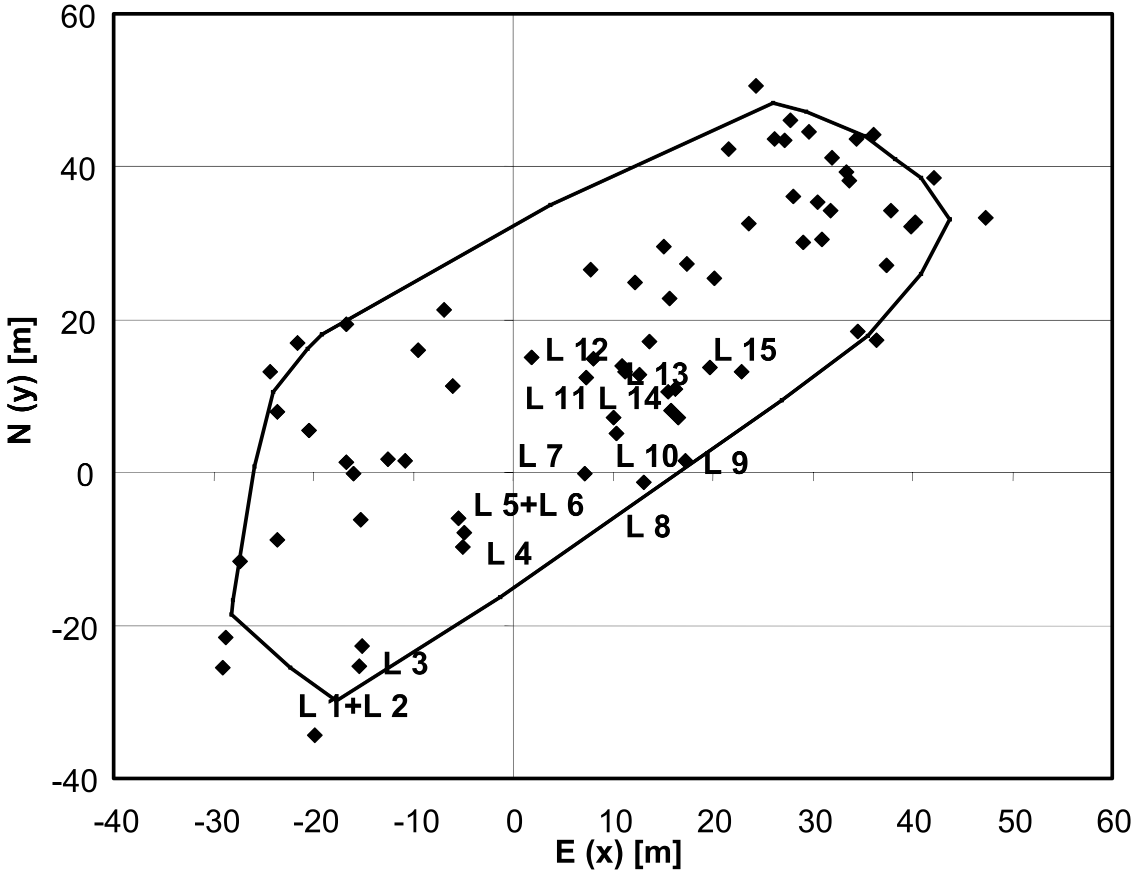


Fig. 3.13: Determination of plot boundaries at mid-points between included trees and adjacent trees at the larch site in Berchtesgaden National Park. Leaf area was determined for all included trees and set in relation to the surface area within the circumscribed polygon.

In addition, a 2 x 2 meter plot was established adjacent to the measurement site at the end of the season and all biomass was harvested in a series of layers between the top of the stand and the ground surface. The material was separated into branches, needles and cones. Fresh weights for each component were determined and sub-samples were taken for needle surface area determination and for oven drying in Bayreuth. From the sub-samples, total LAI and total biomass of the aboveground components was determined. For the estimation of total LAI for *Pinus mugo*, the leaf area (LA) of needles from different layers was measured, summed and divided by ground area. After harvesting of *Pinus mugo*, the biomass and leaf area of understory herbaceous plants and grasses was also measured.

3.3. Needle nutrient concentration

The nutrient concentration of needles may possibly be indicative of photosynthetic capacity, which in turn may be correlated with stomatal conductance and, thereby, with transpiration. In order to obtain information on potential physiological differences, the nutrient concentrations in spruce needles were investigated in July 2003 at four spruce stands situated at different elevations above sea level. At three of these sites, sapflow was measured during 2002, while additional samples were collected from small spruce trees found together with larch at tree line. From 16 to 18 July 2003, spruce branches were cut and current- and 1 year-old needles separated in order to examine possible translocation of nitrogen from older to younger needles and to examine possible changes in leaf nitrogen and carbon content along the altitudinal gradient. In each investigated stand, sunlit-shoots of 5 spruce trees were cut using a 4-m pruning pole. Samples were placed in plastic bags and stored in an ice chest. The 0 and 1 year-old needle samples were taken to the laboratory, detached from shoots, oven-dried for 24 hours at 85 °C, ground in a ball mill and then stored in a desiccator. In the stand Seeangerl, only one year-old needles were used for nutrient concentration analysis due to infection of the current year needles by *Chrysomyxa rhododendri* (which was not present in 2002).

Carbon isotope concentration provides information about water use efficiency (Farquhar et al. 1989). For isotope analysis, the ground needle samples were prepared with the Dumas method. The samples (ca 4.5 mg) were weighed into tin pans and were completely combusted at 1020 °C in the presence of pure O_2 (99.9%) and the catalysts chromium (III) oxide and silver cobaltous (II/III) oxide. Helium was used as carrier gas. The combustion products were H_2O, CO_2, NO_x, N_2, SO_2 and He. Water vapor, oxygen and carbon dioxide were removed from the resulting gas stream by a series of thermoelectric coolers and chemical sorbents. NO_x was reduced to N_2 when passed through a reduction column that is packed with hot copper (650°C). The resulting N_2, CO_2 and H_2O gases were separated and analyzed with a mass spectrometer (delta S finnigan MAT, EA 1108 Elemental Analyzer, Fisions Instruments). For the determination of C and N concentration, acetanilide (C-content 71.09 %, N-content 10.36 %) was used.

The elements Zn, Ca, K, Mg, P, S, Al, Fe, Mn were decomposed with the 8-hour pressure pulping with 65% nitric acid at 170 °C. For the measurements of the element concentrations the Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP–AES, VISTA-PRO, VARIAN, Melbourne) was used. The element contents were verified by NBS standards (National Bureau of Standards and Technology). The element concentrations were analyzed in BITÖK (Bayreuther Institut für Terrestrische Ökosystemforschung).

3.4. Meteorology

Meteorological variables were measured at Bartholomä, Hirschengarten and Seeangerl from the beginning of May to end of September in the investigated spruce and beech stands. At the 1720 m site Kederbichl, the measurements were started later (at the beginning of June) due to bad weather and difficulty with installation of the instruments. The measurements of radiation and relative humidity were conducted in open areas near the sites. At three experimental sites, at elevations 630, 1040, 1360 m a.s.l., photosynthetic photon flux density (PPFD) was measured with LI-190 quantum sensors (LiCor, Lincoln, Nebraska) and at the Kederbichl site (1720 m a.s.l) with a BF2 sensor (Delta-T Devices, Burwell, England). The BF2 sensor measures direct and diffuse components of incident PPFD, and provides a measure of sunshine hours. In order to fill data gaps in radiation records, total photosynthetically-active radiation (PAR) at the measurement sites was also estimated with a radiation model that extrapolated from observations near Schönau and accounted for topographic and atmospheric composition effects (Wang et al. 2004).

Relative humidity was measured with Fischer 431402 temperature/humidity sensors. Vapor pressure deficit was calculated from ambient temperature and relative humidity. For soil moisture measurements, Theta probes (type ML 2x, Delta-T-Devices, Cambridge, England) were installed at 5, 20 and 50 cm below the ground surface. At the site Bartholomä, soil moisture was measured only at a 5 cm depth because of the occurrence of large stones in the soil profile. The air and soil temperature were measured with thermistors (Thermistor M841, Siemens Germany). The air and soil temperature for spruce and beech sites in the stand Bartholomä were measured independently. Air temperature was measured at a height of 200 and 10 cm above the ground surface. For soil temperature measurements, the thermistors were installed at –2, –5, –10 and –20 cm depth. Half-hourly mean values of these meteorological parameters were stored by data logger (DL2 and DL2e, Delta-T Devices, Burwell, England). In three investigated stands – Bartholomä, Hirschengarten and Seeangerl – precipitation was collected in rain gauges and its sum was read every three weeks. At the site Kederbichel, precipitation was recorded continuously with a tipping bucket gauge (ARG100, Environmental Measurements Ltd., Sunderland UK).

3.5. Sapflow measurements

At all investigated sites xylem sapflow was measured by the constant heating method according to Granier (1985; 1987). Two cylindrical probes, 2 or 4 cm length depending on sapwood depth, and 2 mm diameter were inserted into the trunks. For a better thermal conduction, sensor needles were greased with silicon gel and inserted into aluminium tubes (Phillips et al. 1997). The upper probe, installed 10 cm above the lower, was heated with constant power (0.2 Watt). Each of the sensor needles contained a copper-constantan thermocouple, which were connected together in opposition. The voltage measured across the copper leads represents the temperature difference between these two probes. The temperature differences, between the two sensor needles, depend on sap flux density around the upper probe. The highest temperature differences can be observed when no flux occurs, such as at night or during rain events, because the upper probe is not cooled by flowing sap. The flowmeters in spruce, beech and larch trees were installed under bark at breast height and at azimuth north. The sensors were thermally insulated with white styrofoam covers and were sealed with silicone to eliminate rain water flow. The temperature difference between two sensors was measured and half-hourly mean values were recorded by data loggers (DL2 and DL2e, Delta-T Devices, Burwell, England). The power supply was provided from lead-acid batteries recharged by solar panels.

Granier (1985) established a relationship between sap flux density and flow index K:

$$K = T_{\Delta M} - T_{\Delta a} / T_{\Delta a}, \qquad \textbf{Eq. 3.5},$$

where $T_{\Delta M}$ is the temperature difference for no flow and $T_{\Delta a}$ is the current temperature difference.
The sap flux density was calculated from the equation:

$$u = 119 * 10^{-6} K^{1.231} \quad (\mathrm{m\ s^{-1}}) \qquad \textbf{Eq. 3.6},$$

Total sapflow per tree (E_{tree}) was estimated from the relationship between sap flux density (u) and the ratio of temperature differences (K) (Granier 1985; 1987; Köstner 1999b) :

$$E_{tree} = 0.119 * ((\Delta T_{max} - \Delta T) / \Delta T)^{1.23} * S_A \qquad (\mathrm{m^3\ s^{-1}}), \qquad \textbf{Eq. 3.7},$$

where ΔT_{max} and ΔT are the temperature differences between heated and reference sensor and S_A is the cross-sectional sapwood area at the heated thermocouple (m^2).

The sapflow measurements in each site started shortly after snowmelt. Sapflow was estimated by the method of Granier (1985; 1987) in 6 to 12 trees per site, in 2, 4 and 6 cm xylem depth, depending on sapwood thickness. The sap flux was measured in small trees with one sensor in 0 – 2 cm, in middle-sized trees with two sensors in 0 to 2 cm and 2 to 4 cm, and in the largest trees with three sensors in 0 to 2, 2 to 4 and 4 to 6 cm xylem depth (**Fig. 3.14**). The sensors were removed at three spruce and one beech sites at the end of September and in the larch and dwarf-pine site at the beginning of October.

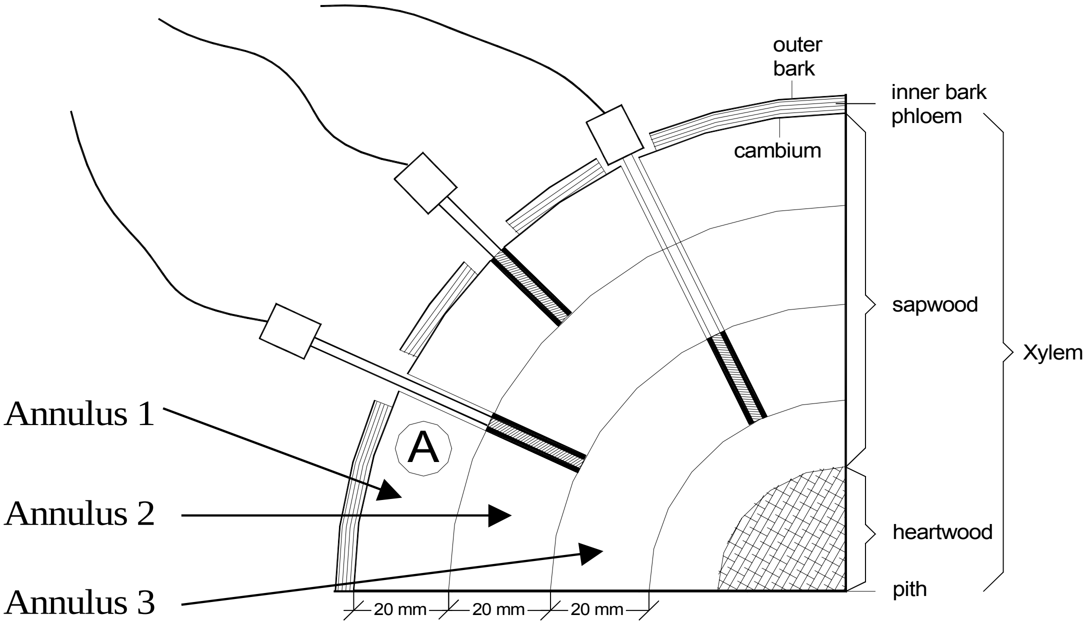


Fig. 3.14: Sensor installation in different sapwood depths. Graphics produced by M. Schmidt.

Sapwood depth was estimated at breast height (1.35 m) by fresh cores. An increment borer was drilled to the centre of tree and the xylem depth was measured on the basis of differences in color of sapwood and heartwood. In some investigated trees, there were no visible difference between sapwood and heartwood. In this case, the dye bromocresol green was applied. After spraying the cores with bromocresol green, the hardwood and sapwood were distinguishable through color changes due to differences in water content (Fischer et al. 2002). In trees in which two or three flowmeters were used, the total tree water flux was calculated as the sum of fluxes in all investigated sapwood rings. The sap flux density in each individual ring was multiplied by its sapwood area. Thereafter the sum of fluxes in two or three sapwood layers was divided by the sum of their sapwood area. For up-scaling to the stand level see Section **3.6**.

In all larch trees, the "Granier sensors" were installed at 2 cm xylem depth. Because of the thin active sapwood ring (less than 2 cm in depth), a correction of sap flux data was necessary to eliminate an error in estimation of tree total water use. When the sapwood depth was less than 2 cm, the total sapwood area over which to integrate sap flux density was that determined by sapwood depth rather than sensor length.

In dwarf-pine shrubs the sap flux was measured with sensors installed at 0 – 2 cm sapwood depth which was greater than half the radius of the branches. Because of curved and prostrate branches, the sensors were installed on their upper surface and covered with styrofoam.

3.6. Canopy transpiration and conductance

The control of gas exchange by the stomatal regulation is well known (Köstner et al. 1992), but can be difficult to estimate at plant and canopy scale. In this study, canopy conductance (gt) was estimated from canopy transpiration (Köstner 1999a):

$$g_t = E_c / VPD * k, \text{ and} \qquad \textbf{Eq. 3.8},$$

$$k = \rho_w * G_v * T_k \qquad \textbf{Eq. 3.9},$$

where: E_c is canopy transpiration (mm s^{-1}), VPD is vapor pressure deficit of the air (kPa), ρw is the density of water (998 kg m^{-3}), G_v is the gas constant of water vapor (0.462 m^3 kPa/ g*K), and T_k is air temperature (Kelvin).

The canopy conductance, gt, derived from xylem flow rates and vapor pressure deficit in the air, includes aerodynamic (g_a) and stomatal conductance (g_c) and represent total vapor transfer conductance via the “average” stomata in the tree canopy with respect to the measurement of VPD (Köstner 1999a).

For each investigated spruce and beech stand, the canopy transpiration was estimated as (Köstner 1999a):

$$E_c = \Sigma\, J_{mean} * S_{A\text{-}class} \qquad \textbf{Eq. 3.10},$$

where J_{mean} is the mean sapflow density of DBH-class (kg m^2 s^{-1}), and $S_{A\text{-}class}$ is the cumulative sapwood area per ground area for each class (m^2 m^{-2}).

For calculation of the canopy conductance (g_t) only data from clear days between 7 and 14 hour, were used. The night, early morning and late afternoon data and days when rainfall occurred were eliminated. During periods with low radiation and low air vapor pressure deficit in the air, sapflow declines close to zero, which results in large uncertainties in the canopy conductance calculation (Granier et al. 1996a).

3.7. Lysimeter measurements

In the sparse, young and open forest stands, the evaporation from the understory may be larger than tree water loss (Black and Kelliher 1989). To estimate total evapotranspiration within the *Larix decidua* stand, both the sapflow in trees and water loss from understory vegetation were measured. The understory water vapor flux was derived from small weighing lysimeters (13 cm in diameter and 10 cm depth), randomly installed in the soil within the investigated larch stand, and the water loss was scaled-up to the stand level. Eleven monoliths with grass were cut from the ground and placed into lysimeters. The lysimeter had a mesh bottom to allow contact with the soil below. The lysimeters were weighed every two hours, i.e., three to seven times a day.

3.8. Model

For examination of controls on spruce forest transpiration that were found along the elevation gradient (see **4.6**), the GAS-FLUX model was used (Falge et al. 2003; Reichstein 2001). Originally this model was used for estimating leaf gas exchange in mediterranean ecosystems (Caldwell et al. 1986). It has been subsequently developed, modified and applied for other ecosystem types (Falge et al. 2003; Sala and Tenhunen 1996; Tenhunen et al. 1994a). The GAS-FLUX model integrates information about stand structure, light interception and microclimate. The canopy is assumed to be horizontally homogeneous but heterogeneous in the vertical profile.

The GAS-FLUX model allows the estimation of photosynthesis, transpiration and respiration. It provides information at both leaf and canopy level – the single-leaf photosynthesis and transpiration rates are evaluated for sunlit and shaded leaves weighted by the respective sunlit and shaded fractions and leaf area of each layer and summed over all layers in the canopy. The leaf energy balance includes absorption and emission of radiation, convective heat loss, and latent heat loss (transpiration). The photosynthetic assimilation is calculated using the Farquhar - von Caemmerer model (Farquhar et al. 1980; Farquhar and von Caemmerer 1982). The gas exchange of foliage elements is based on the enzyme kinetics of Ribulose-1,5-biphosphate-carboxylase-oxygenase (Rubisco) and on the light dependence of electron transport capacity.

The canopy transpiration is calculated under the assumption that the relationship between stomatal conductance (g_s) and photosynthetic assimilation is the following (Ball et al. 1987):

$$g_s = g_{\min} + g_{fac} \cdot \frac{P \cdot rh_s}{c_s} \quad (\text{mmol m}^{-2}\ \text{s}^{-1}) \qquad \textbf{Eq. 3.11},$$

where g_s is stomatal conductance, g_{min} is conductance of the leaf with closed stomata, g_{fac} is the Ball-Berry proportionality determined between stomatal conductance and net photosynthesis rate, P is the photosynthetic assimilation, rh_s is relative humidity, and c_s is CO_2 concentration on the leaf surface.

At the leaf level, transpiration is calculated by multiplying leaf conductance by the difference between vapor pressure at the leaf surface and the vapor pressure in the surrounding air divided by air pressure.

$$tr = \frac{VPD \cdot g_l}{P} \qquad \text{(mmol m}^{-2}\text{ s}^{-1}\text{)} \qquad \textbf{Eq. 3.12},$$

where tr is the transpiration rate, VPD is vapor pressure deficit, g_l is leaf conductance and P is air pressure.

Leaf conductance is calculated as:

$$g_l = \frac{1}{\frac{1}{g_b} + \frac{1}{g_s}} \qquad \text{(mmol m}^{-2}\text{ s}^{-1}\text{)} \qquad \textbf{Eq. 3.13},$$

where g_b is boundary layer conductance and g_s is stomatal conductance.

At the canopy level the transpiration is estimated by summing up the leaf transpiration in all layers, taking into account the leaf area in each layer.

For calculation of photosynthesis and transpiration, the meteorological parameters radiation, air temperature, relative humidity, wind speed, and barometric pressure are required as input.

3.8.1. Parameterisation:

Input parameters used in this model are optical (absorptance, reflectance, transmittance of PAR and total short wave radiation) and vegetation parameters (vegetation type, LAI, canopy structure). All parameters used for modelling are shown in **Tab**. **3.4 – 3.6**.

The comparison of forest water use (measurements vs. modelled) was conducted only for clear days with high transpiration or where radiation input could be reliably estimated on clear days with data gaps according to Wang et al. (2004). Air temperature, soil temperature, and relative humidity were measured with automated weather stations at the three measuring sites (see chapter **3.4**). Because no measurements of wind speed were available, a value of 1.5 m s^{-1} was assumed in the model. The soil albedo for each spruce stand was set to 0.12.

Elevational differences in carbon dioxide concentration in the air and barometric pressure were considered, because carbon dioxide concentration in the air and barometric pressure decrease with increasing elevation. Carbon dioxide concentration was set to 342, 330 and 321 ppm for Bartholomä (630 m a.s.l.), Hirschengarten (1040 m a.s.l.) and Seeangerl (1360 m a.s.l.), respectively. The calculated values of barometric pressure were 949, 908 and 875 hPa for the 630, 1040 and 1360 m spruce stands.

Because physiological parameters for Norway spruce were not measured in the Berchtesgaden National Park, the initial leaf parameters were based on data measured in a Norway spruce forest in Davos (1660 m a.s.l.) (Falge 1997). In this study, all leaf parameters were assumed to be uniform throughout the canopy. The vegetation parameters, vegetation type, canopy layers, number of species, leaf area index, stem area index and leaf width were set to the values indicated in **Tab. 3.4**. Optical properties of leaves were assumed to be uniform throughout the canopy (Sala and Tenhunen 1996). Absorptance, reflectance and transmittance for 400 – 700 nm were chosen according to values reported by Wedler (1991), the value of the absorptance of infrared radiation was set according to Gates (1980).

Tab. 3.4: Parameters of the GAS-FLUX model independent of canopy layer, which were used in this study based on Falge (1997).

Parameter	Value	Unit
Vegetation type	conifers	-
Canopy layers	14	-
Leaf area index	7 (canopy), 0.5 (per layer)	$m^2 m^{-2}$
Leaf width	0.15	cm
Converting factor for leaf surface area to projected area of intact twig	0.3	-
Converting factor for projected bare twig to projected area of intact twig	6.749	-
Absorptance of PAR	0.8	-
Transmittance of PAR	0.06	-
Reflectance of PAR	0.14	-
Absorptance,	0.5	-
Reflectance,	0.5	
Transmittance of total short-wave light	0.0	
Stem area index	1.4 (total) 0.1 (per layer)	$m^2 m^{-2}$
Absorptance of infrared	0.975	-

The projected leaf area index for each spruce stand was set at 7 (close to the values calculated with allometrics (see section 3.2.4.1), the stem area index was assumed to be 20% of LAI based on harvests in the Fichtelgebirge (Falge 1997). In each of the three investigated spruce stands, the canopies were divided into 14 layers. The leaf area and stem area, which play an important role in light interception (Reynolds et al. 1996), were assumed to be identical for each canopy layer, implying different layer heights. For each canopy layer the LAI was assumed as 0.5 m^2 m^{-2} and the SAI as 0.1 m^2 m^{-2}. Parameters dependent on canopy layer used in GAS-FLUX in this study are shown in **Tab. 3.5**.

Tab. 3.5: Parameters dependent on canopy layer used in GAS-FLUX in this study.

Layer no.	Leaf angle	Stem inclination angle
	°	
1 (top)	60	45
2	60	45
3	47	30
4	30	20
5	30	20
6	40	10
7	47	2
8	34	5
9	34	12
10	34	20
11	20	20
12	20	12
13	20	5
14 (bottom)	5	5

In this exploratory study, two tests were carried out. In the first, the changes in transpiration rates between stands were examined as influenced by possible changes in leaf physiological capacities along an elevation gradient as well as in response to local environmental factors. The levels for carboxylation, RuBP reduction and respiration capacities of leaves from Davos were adjusted along the elevation gradient, while the response or sensitivity of leaf physiological parameters to environmental factors was not modified (except for a slight initial change to account for an apparent difference in optimum temperature compared to Davos (Falge 1997); see **Tab. 3.6**). In testing a second hypothesis, the differences in transpiration rates were considered to be explained by differences in stomatal patchy closure along with local environmental factors, i.e., considering that water supply to the crown could differ in the stands. In these simulations, the carboxylation, RuBP reduction and respiration capacities for each stand were assumed to be the same, and the portion of leaves that is active in gas exchange was changed along the elevation gradient. The modelled water use was compared with estimates derived only from sapflow measurements.

Tab. 3.6: Constants and scaling factors used in the GAS-FLUX model for three investigated Norway spruce stands in the Berchtesgaden National Park. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl (Falge 1997). * For c and fvc see Tab. 3.19.

Parameter		Value	Unit
Electron transport capacity	ΔH_a (Pml)	70000	J mol^{-1}
	ΔH_d (Pml)	243000	J mol^{-1}
	ΔS (Pml)	823	J mol^{-1} K^{-1}
	C (Pml)	*	µmol m^{-2}s^{-1}
Dark respiration	E	88500	J mol^{-1}
	D	0.290	µmol m^{-2}s^{-1}
	RDFAC	0.5	-
Enzyme specificity	$f(\tau)$	2339.53	-
	$Ea(\tau)$	-28990	J mol^{-1}
Oxygenation kinetic	$E_a(K_O)$	36000	J mol^{-1}
	$f(K_O)$	159.597	ml l^{-1}
Carboxylation kinetic	$E_a(K_C)$	65000	J mol^{-1}
	$f(K_C)$	299.469	µmol l^{-1}
Carboxylation capacity	$\Delta E_a(Vc_{max})$	70000	J mol^{-1}
	$\Delta H_d(Vc_{max})$	243000	J mol^{-1}
	$\Delta S(Vc_{max})$	823	J mol^{-1} K^{-1}
	$fvc(Vc_{max})$	*	µmol m^{-2}s^{-1}
Quantum use efficiency	α	0.08	µmol CO_2 mol quantum^{-1}
Stomatal conductance	g_{min}	0	mmol m^{-2}s^{-1}
	g_{max}	640	mmol m^{-2}s^{-1}
	gfac	10	-

Model validation was based on the correlation between modelled and observed data as measured by Willmott's Index of agreement (IA) (Willmott 1981; Willmott et al. 1985):

$$IA = 1 - \frac{\sum_{i=1}^{N} \left(O_i - P_i\right)^2}{\sum_{i=1}^{N} \left(\left|O_i - \overline{O}\right| + \left|P_i - \overline{O}\right|\right)^2}$$

Eq. 3.14,

where N is the number of half-hourly or daily values, P_i are the model results, and O_i the observed values, and overbars indicate the mean of all values of the given time period.

4. RESULTS

4.1. Sapwood depth, sapwood area and annual growth

Norway spruce: The average sapwood thickness of sampled trees was approximately 73.6 mm, 52.6 mm and 62.9 mm for Bartholomä, Hirschengarten and Seeangerl, respectively (**Tab. 4.1 – 4.3**). From the counting of annual rings, the mean age of spruce trees at the three experimental sites were ca. 40, 60 and 50 years for Bartholomä, Hirschengarten and Seeangerl. Coring also allowed measurement of the bark thickness. Along the elevation gradient, an increase in mean bark thickness was measured: the mean bark thickness was 0.55 cm at 630 m, 0.65 cm at 1040 m and 0.72 cm at the 1360 m sites (**Tab. 4.1 – 4.3**). The sapwood area of experimental *Picea abies* trees at the site Bartholomä ranged from 128 to 625 cm^2, at site Hirschengarten from 52 to 194 cm^2 and at Seeangerl from 56 to 178 cm^2 (**Tab. 4.1 – 4.3**).

Tab. 4.1: Biometric parameters of individual trees at the site Bartholomä. Numbers of trees correspond to the trees identified in Figs. 3.3 to 3.4.

Tree number	CBH (cm)	DBH (cm)	Bark thickness (mm)	Sapwood depth (cm)	Sapwood area (cm^2)
Fi1*	75	21.3	5	7.9	401
Fi2*	100	31.8	6.5	7.7	606
Fi3*	101.1	32.2	7	7.9	626
Fi4*	82.1	26.1	6	12.4	529
Fi5*	69.5	22.1	4.5	7.2	342
Fi6*	85	27.1	5.5	10.5	548
Fi7	70	22.3	5.9	5.9	313
Fi23	58	18.5	6.2	6.2	243
Fi40	80	25.5	5.15	5.2	345
Fi13	47	15.0	3.25	3.3	127
Bu1*	66.8	21.3	4	6.9	318
Bu2*	71.5	22.8	2.5	7.5	373
Bu3*	70.8	22.5	5	10.3	393
Bu4*	68.5	21.8	4.5	8.5	360
Bu5*	86.5	27.5	4	8.5	521
Bu6*	53.5	17.0	3.5	4.4	183
Bu7*	225	71.6	-	-	-
Bu14*	39.0	12.4	2.5	4.5	114
Bu15*	45.4	14.5	2.5	4.1	139

Fi = Norway spruce, Bu = European beech, CBH = circumference at the breast height, DBH = tree diameter, *sapflow trees

Tab. 4.2: Biometric parameters of individual trees at the site Hirschengarten. Numbers of trees correspond to the trees identified in Fig. 3.5.

Tree number	CBH (cm)	DBH (cm)	Bark thickness (mm)	Sapwood depth (cm)	Sapwood area (cm^2)
Fi1*	132.1	42.0	8.1	8.2	887.5
Fi2*	95.1	30.3	7.2	5.2	436.8
Fi3*	98.8	31.4	8	5.8	494.2
Fi4*	58.6	18.7	5.9	4.2	212.5
Fi5*	81.6	26.0	6.1	3.1	244.3
Fi6*	62.8	20.0	4.1	2.7	165.4
Fi7*	52	16.6	4.4	1.5	85.4
Fi8*	87.2	27.8	9	4.4	361.5
Fi9*	193.7	45.7	7.2	5.4	1212.6
Fi10*	109.4	34.8	7.4	8.3	719.4
Fi11*	145	46.2	7.8	9.1	1065.7

Fi = Norway spruce, CBH = circumference at the breast height, DBH = tree diameter, *sapflow trees

Tab. 4.3: Biometric parameters of individual trees at the site Seeangerl. Numbers of trees correspond to the trees identified in Fig. 3.6.

Tree number	CBH (cm)	DBH (cm)	Bark thickness (mm)	Sapwood depth (cm)	Sapwood area (cm^2)
Fi1*	93	29.6	5	5.1	417.8
Fi2*	107.3	34.2	6.1	7.1	642.9
Fi3*	85.5	27.2	8.4	4.8	371.4
Fi4*	74	23.6	6.2	6.3	357.7
Fi5*	99	31.5	6	6.6	540.0
Fi6*	72.5	23.1	9.5	5.4	323.8
Fi7*	80.5	25.6	8.2	6.2	389.4
Fi8*	77	24.5	8	5.2	345.0
Fi9*	64	20.4	6.1	6.0	278.5
Fi10*	56	17.8	6.7	6.2	228.1
Fi11*	178	56.7	11.2	7.8	1323.2
Fi12*	56.5	18.0	5	4.3	144.9

Fi = Norway spruce, CBH = circumference at the breast height, DBH = tree diameter, *sapflow trees

With an increase of tree circumference, a linear increase in sapwood area was determined:

$$S_A = 8.66\ \mathrm{CBH} - 304; \qquad r^2 = 0.94 \qquad \textbf{Eq. 4.1},$$

where CBH is the stem circumference in cm at the breast height (1.35 m). The correlation between cross-sectional sapwood area and stem girth at breast height is shown in **Fig. 4.1**:

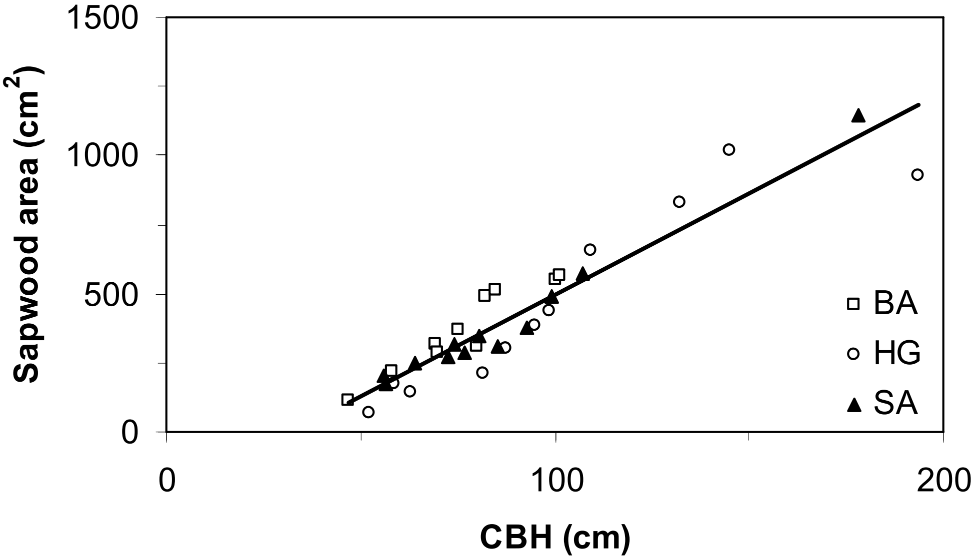


Fig. 4.1: Correlation between stem circumference at breast height and cross–sectional sapwood area at the same height in three Picea abies stands in National Park Berchtesgaden. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl.

The stand level cumulative cross-sectional sapwood area estimated from all trees was calculated from CBH of individual trees (**Eq. 4.1**). For two experimental spruce sites – Bartholomä (630 m a.s.l.) and Seeangerl (1360 m a.s.l.) – similar cumulative cross-sectional sapwood areas at breast height were estimated, while sapwood area in Hirschengarten was only slightly lower. The highest value was found for Bartholomä 28.9 m^{-2} ha^{-1}. At Seeangerl and Hirschengarten the total cross-sectional sapwood area was 28.5 and 27.2 m^{-2} ha^{-1}, respectively.

A decrease in growth along the elevation gradient was observed. The highest mean annual diameter increment occurred at the Bartholomä site – the mean stem growth based on sapwood rings reached 0.31 cm year^{-1} at Bartholomä; was lower at Hirschengarten (0.26 cm year^{-1}) and lowest at Seeangerl (0.25 cm year^{-1}). In comparison, the values of annual growth based on forest inventory (Konnert 2001) suggest a different pattern. Contrary to the fresh core measurements, the highest annual increment is recorded in the analysis of Konnert (2001) at the site Hirschengarten (7 – 8 m^3 $ha^{-1}year^{-1}$), lower values were found at Seeangerl (5 – 6 m^3 $year^{-1}$ ha^{-1}) and the lowest growth was indicated to occur at Bartholomä (4 – 5 m^3 $year^{-1}$ ha^{-1}).

European beech: The measurements of sapwood depth and bark thickness were also carried out via coring with *Fagus sylvatica* trees. The mean age of beech trees estimated from fresh cores was 40 years, but several very old trees were scattered within the stand. Annual growth of beech trees estimated with fresh cores approximated 0.26 cm a year and was lower than annual growth of spruce trees (0.31 cm) in the adjacent stand.

Visual distinction between sapwood and heartwood in beech trees is very difficult (Granier et al. 2000). In experimental trees, in which the sapwood and heartwood was impossible to identify visually, bromocresol green was applied to the cores. After atomizing with bromocresol green, the hardwood and sapwood take on different color depending on water content (Fischer et al. 2002). Based on the best estimates with dying as necessary, the sapwood depth in investigated beech trees ranged from 3.2 to 12.3 cm with an average of 7.1 cm. Sapwood area in 10 investigated trees ranged from 114 to 522 cm^2, while the sapwood area of sapflow measurement trees was in the range of 183 to 522 cm^2 (**Tab. 4.1**). The mean bark thickness in beech trees (0.56 cm) was similar to the bark depth of spruce trees (0.55 cm) occurring at the same elevation a.s.l.

With an increase in tree circumference, a strong increase in sapwood area was observed (**Fig. 4.2**).

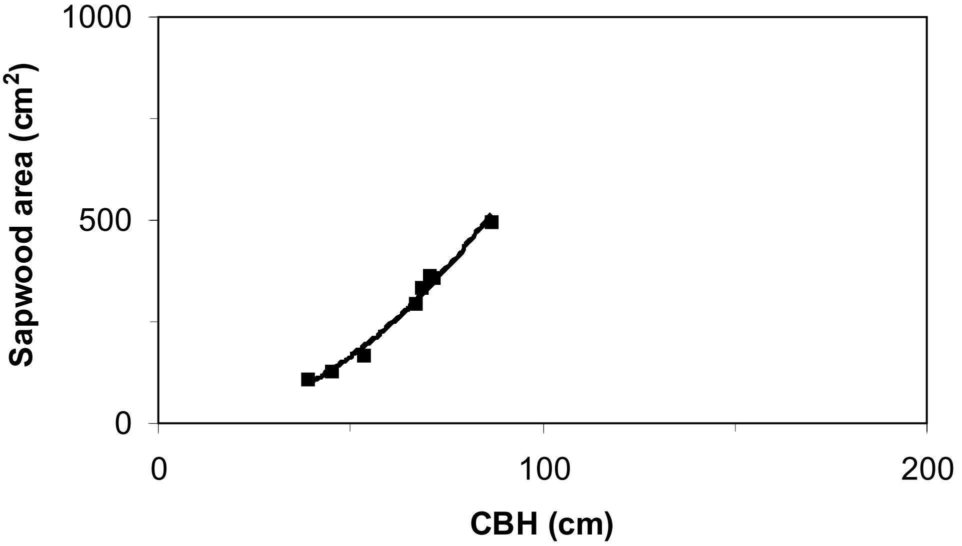


Fig. 4.2: Correlation between stem circumference at breast height and cross–sectional sapwood area at the same height in the investigated *Fagus sylvatica* stand in National Park Berchtesgaden.

The following correlation was found to describe the relationship between cross-sectional sapwood area and the CBH of individual trees at breast height:

$$S_A = 0.049 \text{ CBH}^{2.078}; \qquad r^2 = 0.98, \qquad \textbf{Eq. 4.2},$$

where CBH is the stem girth in cm at breast height (1.35 m). The cumulative cross-sectional sapwood area at the beech site estimated from CBH and sapwood depth was approximately 14.1 m^2 ha^{-1}, which can indicate higher sapflow densities.

European larch and dwarf-pine: The annual diameter increment in larch was very low and estimation of tree age and annual growth was very difficult. Mean age determined for three larch trees with the best recognizable rings was 190 years. The stems of *Larix decidua* trees have a thick bark layer. In experimental trees the bark depths ranged from 0.2 to 3.0 cm, with a mean of 1.1 cm. The larch trees have only a thin sapwood layer. In 15 measured trees, sapwood depth was in the range of 1.0 to 3.2 cm. The mean sapwood depth was approximately 1.8 cm. The sapwood area in individual trees, in which sap flux was measured, ranged between 143 – 611 cm^2 (**Tab. 4.4**). Although high variability occurred, the sapwood area appeared to increase with increasing circumference at breast height (**Fig. 4.3**).

Tab. 4.4: Biometric parameters of individual trees at the Kederbichl site. Numbers of trees correspond to the trees identified in Fig. 3.7.

Tree number	CBH (cm)	DBH (cm)	Bark thickness (mm)	Sapwood depth (cm)	Sapwood area (cm^2)
La1*	85	27.1	5	1.4	143
La2*	122	38.8	8	1.2	216
La3*	174	55.4	7	3.2	611
La4*	116	36.9	20	2.5	422
La5*	135	43.0	13	1.2	290
La6*	135	43.0	5	2.0	307
La7*	199	63.3	2.3	1.0	233
La8*	94	29.9	8	2.3	249
La9*	176	56.0	31	2.0	339
La10*	133	42.3	18	2.7	497
La11*	166	52.8	6	2.3	439
La12*	131	41.7	9.3	2.1	349
La13*	95	30.2	5.5	1.6	181
La14*	140	44.6	18.5	1.0	332
La15*	135	43.0	6	1.5	257
P1	31.5	10.4	8	5	45
P2	23.9	7.6	6	3.8	337
P3	19.5	6.2	6.1	3.1	23
P4	28.5	9.1	8	4.5	39
P5	22.3	7.1	6.6	3.5	28
P6	15.8	5.0	4.6	2.5	15

La = Larch, P = *Pinus mugo,* CBH = circumference at the breast height, DBH = tree diameter, *sapflow trees, **circumference

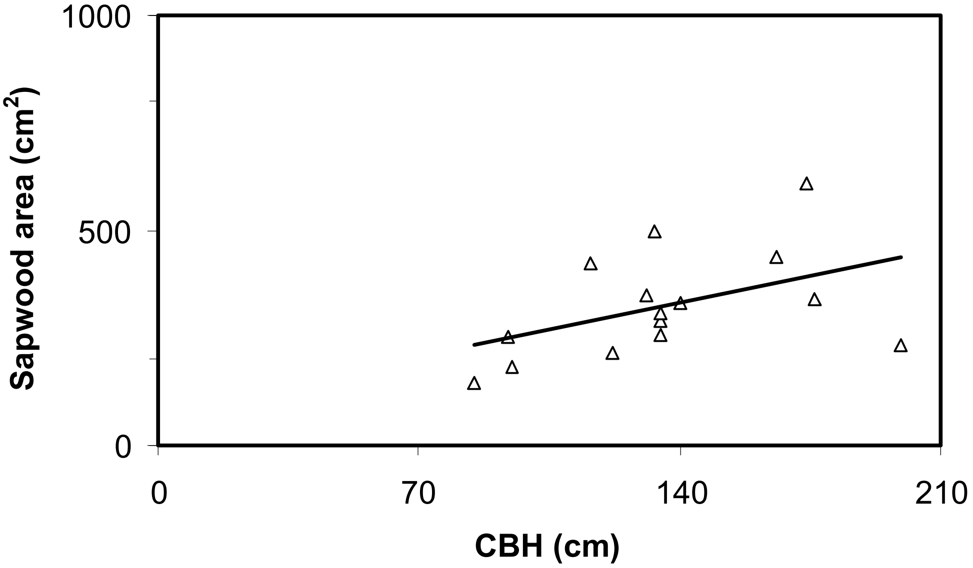


Fig. 4.3: Correlation between stem circumference at breast height and cross–sectional sapwood area at the same height in the *Larix decidua* stand in National Park Berchtesgaden.

The relationship between cross-sectional sapwood area and stem girth at breast height may be expressed as:

$$S_A = 1.815\ \mathrm{CBH} + 78.151;\ r^2 = 0.22 \qquad \textbf{Eq. 4.3},$$

where CBH is the stem girth in cm at breast height (1.35 m). The cumulative cross-sectional sapwood area at the larch site estimated from CBH and sapwood depth was approximately 3.9 m^2 ha^{-1}.

In *Pinus mugo* branches, heartwood was not present. The sapwood depth was equal to the radius of branches and reached 2.5 to 5 cm. In measurement dwarf-pines, the xylem area was in the range of 15 to 45 cm^2. The mean bark thickness measured in dwarf-pine reached ca. 0.3 cm.

4.2. Leaf area index

Leaf area index estimated with allometrics (see **3.2.4.1**) for the three experimental spruce stands was very similar and typical for Norway spruce, ranging from 6.1 to 7.0 m^2 m^{-2} (**Tab. 4.5**). The leaf area index estimated for the beech stand, 6.4 m^2 m^{-2}, was similar to LAI of spruce at the same elevation. The measured leaf area index of European larch at Kederbichl was low: 1.5 m^2 m^{-2} (considering only the trees), and LAI of dwarf-pine was ca. 5.0 m^2 m^{-2}. The LAI values for patches of understory plants - herbs, grass and shrubs - growing at the Kederbichl site are shown in **Tab. 4.6**. The highest LAI was observed for grasses growing under and between larch trees and for *Pinus mugo* shrubs, and the lowest for *Vaccinum myrtillus*.

Tab. 4.5: Leaf area index (LAI) of the tree layer in forest stands studied in the Berchtesgaden National Park

Stand	Bartholomä		Hirchengarten	Seeangerl	Kederbichl	
	Spruce	Beech	Spruce	Spruce	Larch	Dwarf-pine
LAI m^2 m^{-2}	6.1	6.4	6.7	7.0	1.5	5.0

Tab. 4.6: Leaf area index (LAI) of different understory vegetation types („patches“) at the Kederbichl site (1670 to 1720 m a.s.l.) determined by harvesting. Values for *Pinus mugo* are first for the pine and in parentheses including the additional LAI of *Vaccinium mytillus* below the pine.

	Grasses under/between *L. decidua*	*Rhododendron hirsutum*- “patch”	*Vaccinium myrtillus* “patch”	*Pinus mugo* (with *Vaccinium myrtillus* - understory)
LAI m^2 m^{-2}	5.0	2.0	1.6	5.0 (6.2)

4.3. Needle nutrient concentrations

The highest average nitrogen concentration was observed in current-year needles at Bartholomä (630 m a.s.l.) (**Tab. 4.7**, **Fig. 4.4**).

Tab. 4.7: Mean nitrogen and carbon content, mean total nitrogen and carbon concentrations, mean $\delta^{15}N$ and $\delta^{13}C$ ratios and mean C/N ratios in 0 and 1-year-old needles sampled in July 2003 in four investigated spruce stands in Berchtesgaden National Park. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl, FL = forest limit.

	N Sample (%)	Total N (mmol g dw^{-1})	$\delta^{15}N$ (‰)	C Sample (%)	Total C (mmol g dw^{-1})	$\delta^{13}C$ (‰)	C/N
0-year-old							
BA	1.46	1.04	-5.64	48.85	40.71	-27.12	34.10
HG	1.10	0.79	-3.80	50.17	41.81	-26.14	45.83
SA	-	-	-	-	-	-	-
FL	1.21	0.87	-3.70	49.48	41.23	-26.23	40.94
1-year-old							
BA	1.28	0.92	-6.03	50.16	41.80	-27.92	39.42
HG	1.14	0.82	-4.35	50.62	42.18	-26.83	44.91
SA	1.33	0.95	-4.42	50.31	41.92	-28.06	37.88
FL	1.26	0.90	-3.94	51.42	42.85	-26.39	41.12

The differences in N concentration between Bartholomä, Hirschengarten and the stand at forest limit were statistically significant (P = 0.04 and 0.02, respectively), while no significant difference in nitrogen concentration between Hirschengarten and the stand at forest limit was observed (P = 0.81). There were also no significant differences in N concentration in one-year-old needles, except for Hirschengarten and Seeangerl (P = 0.002).

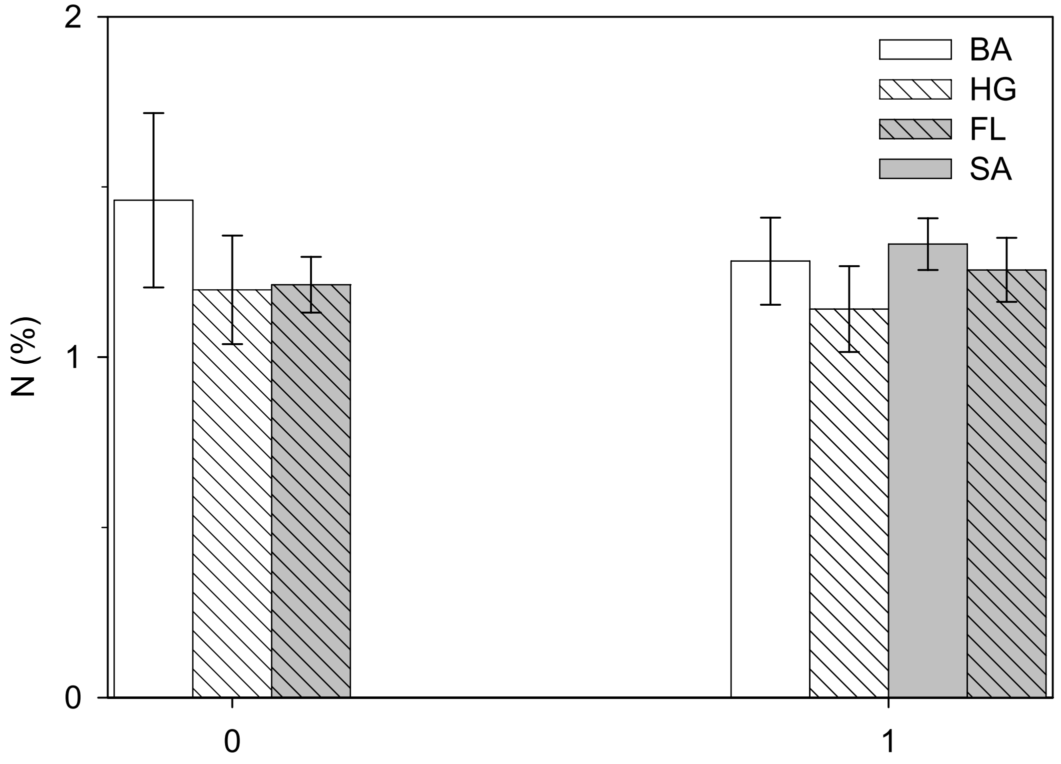


Fig. 4.4: Nitrogen content of current- and one-year-old Picea abies needles in four investigated stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

Total nitrogen concentrations in current and 1-year-old needles are shown in **Fig. 4.5**. The differences in total nitrogen concentration in 0-year-old needles between spruce stands along the elevation gradient were statistically significant (P = 0.004, 0.02, 0.03 between Bartholomä and Hirschengarten, Bartholomä and Seeangerl and Hirschengarten and Seeangerl, respectively). For 1-year-old needles statistically significant differences were found only between Bartholomä and the stand at forest limit (P = 0.01) and Hirschengarten and the stand at forest limit (P =0.006).

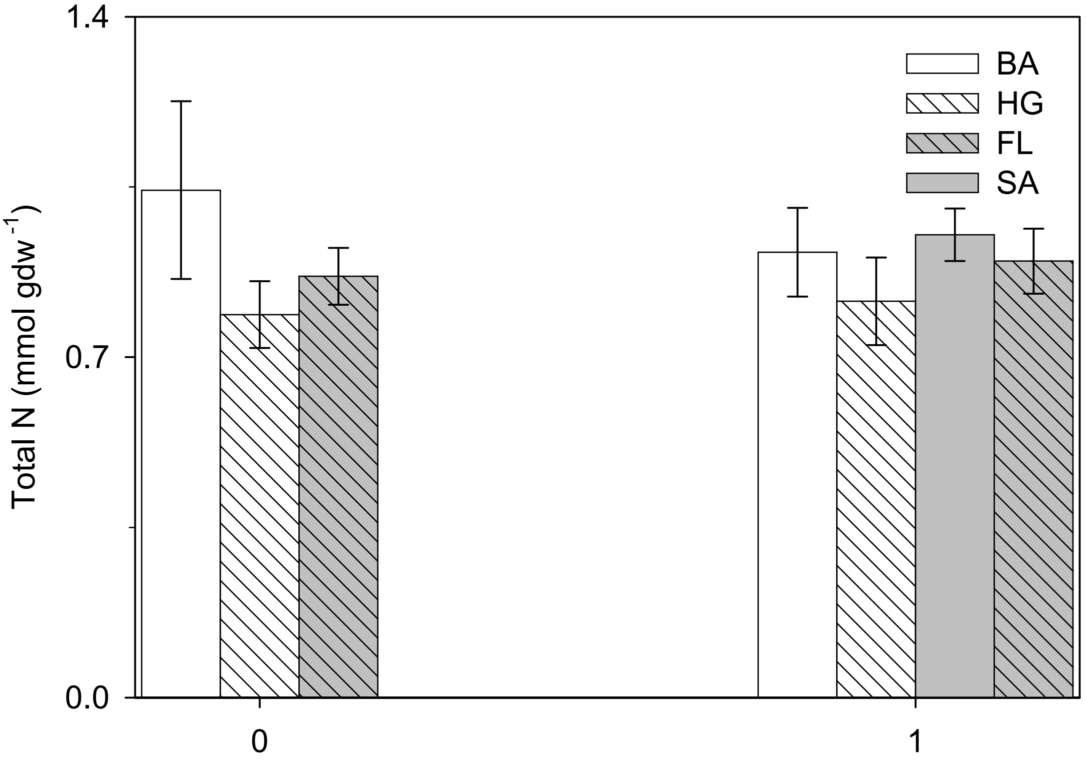


Fig. 4.5: Nitrogen concentration in current- and one-year-old *Picea abies* needles in four investigated stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

Along the elevation gradient, an increase in foliar δ^{15}N ratio was observed (**Tab. 4.7**). The lowest δ^{15}N values in current-year needles were measured at Bartholomä (-5.64 ± 0.67 ‰) and the highest at the tree line (-3.7 ± 0.61 ‰) (see **Fig. 4.6**). This pattern was also observed in 1-year-old needles -6.03 ± 0.72 ‰ and -3.94 ± 0.41 ‰ for the lowest and highest situated sites, respectively.

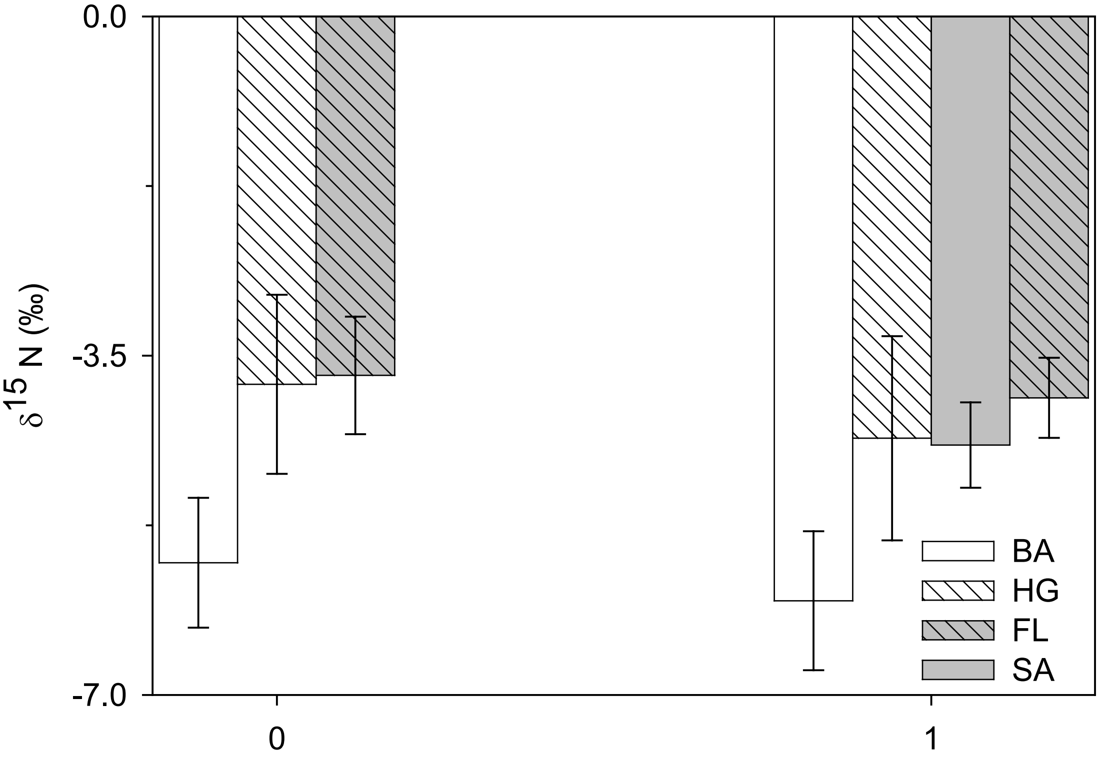


Fig. 4.6: δ^{15}N of current- and one-year-old *Picea abies* needles in four stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

In contrast to the δ^{15}N ratio, there were no significant differences in δ^{13}C observed in Norway spruce needles along the elevation transect (**Fig. 4.7**). The highest δ^{13}C values –27.12 ± 1.02 ‰ were measured at elevation 630 m a.s.l (**Tab. 4.7**).

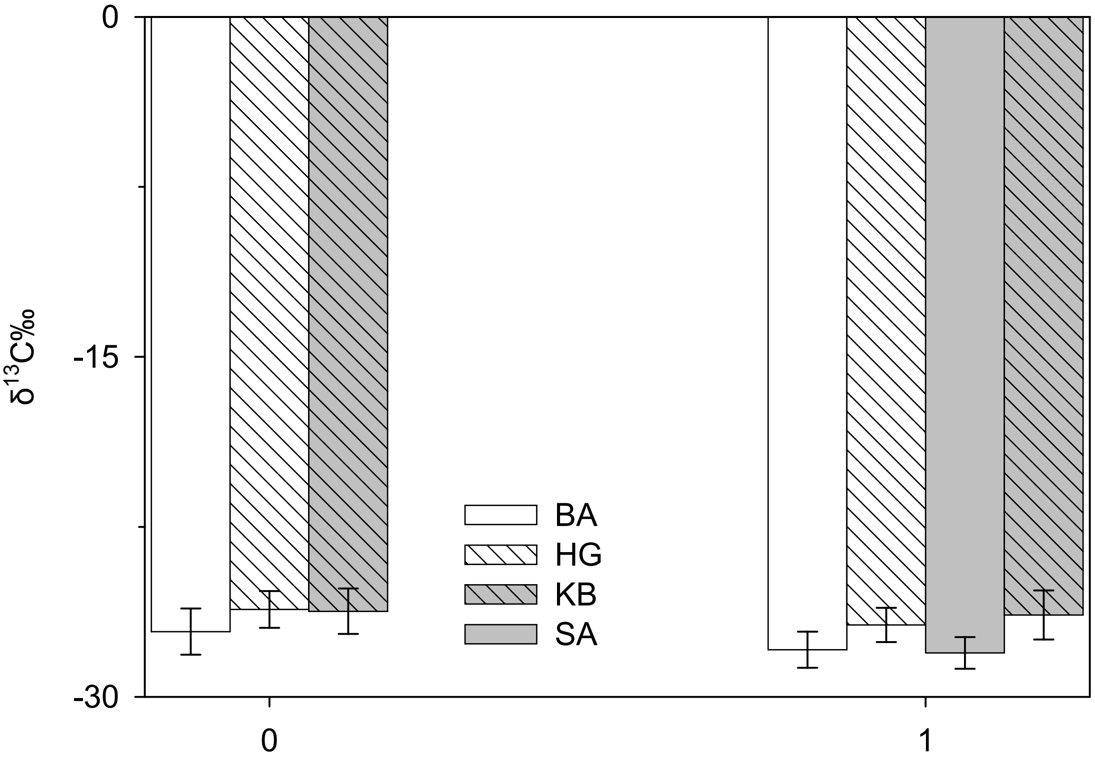


Fig. 4.7: δ^{13}C of current- and one-year-old *Picea abies* needles in four *Picea abies* stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

The carbon content and total carbon concentrations per gram dry weight in needles at the four investigated sites were the same (**Fig. 4.8**, **Fig. 4.9**). The mean carbon content in current-year needles ranged between 48.8% at Bartholomä and 50.2% at Hirschengarten. C/N ratio varied between investigated spruce stands (**Tab. 4.7**), but neither relationships between C/N ratio and altitude nor between C/N ratio and needles age were found.

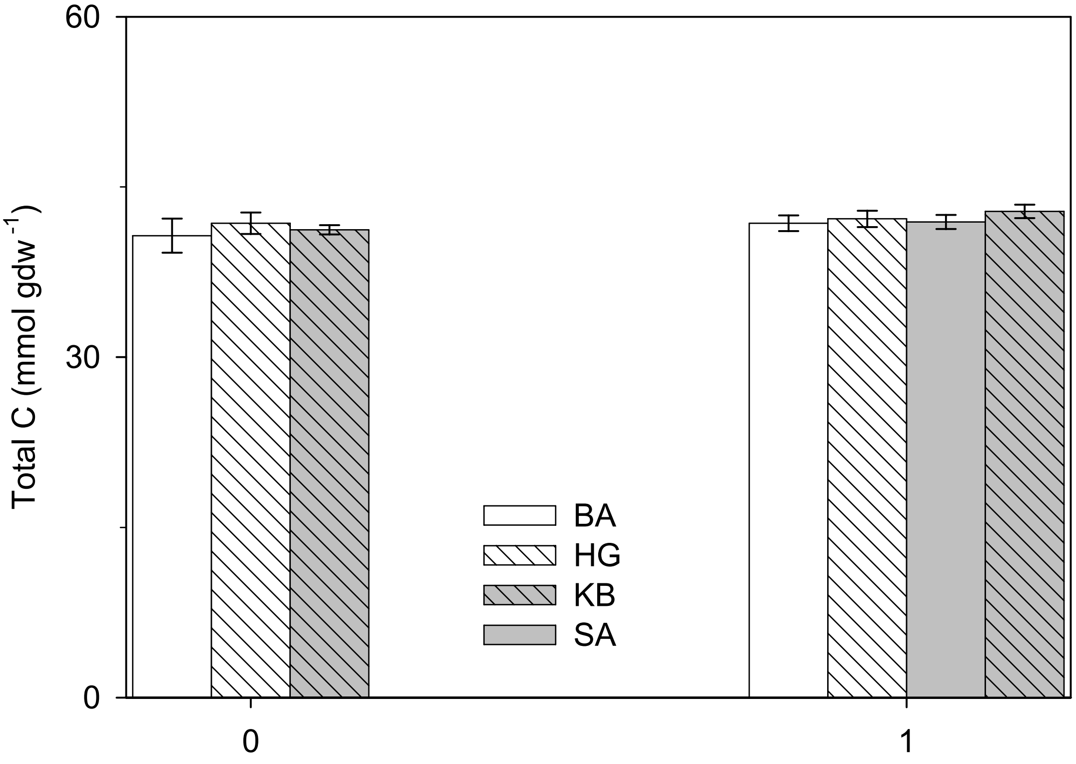


Fig. 4.8: Carbon concentrations in current- and one-year-old *Picea abies* needles in four investigated stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

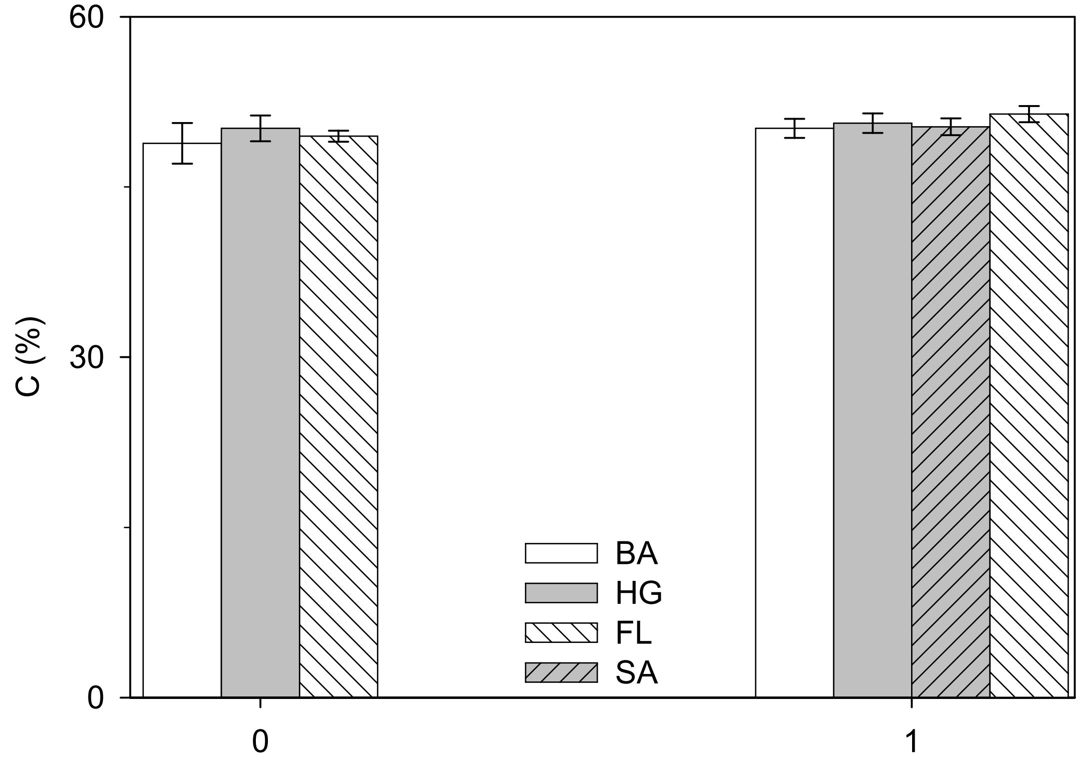


Fig. 4.9: Carbon content of current- and one-year-old Picea abies needles in four investigated stands in Berchtesgaden National Park. 0= current year needles, 1= one-year-old needles. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

The analyses of nutrient concentrations in spruce needles suggest differences in nutrient supply between stands. The highest magnesium content in the spruce needles was measured at the Bartholomä site (see **Tab. 4.8**). At two others sites, the mean Mg^{2+} concentrations had a similar value. For the 630 m and 1360 m sites, the magnesium concentrations in 1-year-old needles were slightly higher than in current-year needles. The highest mean Ca^{2+} concentration in 0-year needles (4.60±1.77 mg g^{-1} dw) was observed at the site Hirschengarten, the lowest (4.20±1.94 mg g^{-1} dw) at Bartholomä. In 1-year-old needles, no correlation with calcium concentration and elevation a.s.l. was observed. At two sites, Hirschengarten and at the spruce forest limit, the mean contents were similar and higher than at the two other sites. The Ca^{2+} contents in older needles were ca. 1.6 to 1.7 times higher than that from needles of the current year. In contrast to the results with Mg^{2+} and Ca^{2+} content, the mean K^+

concentration in 0-year-old spruce needles decreased with increasing elevation a.s.l., and the concentrations were 1.2 to 1.7 times higher than in 1-year-old needles.

Tab. 4.8: Mean nutrient concentrations in 0- and 1-year-old spruce needles in the experimental sites at the National Park Berchtesgaden.

	Nutrient concentration (mg g^{-1} dw)			
	Bartholomä (630m)	Hirschengarten (1040m)	Seeangerl (1360m)	Forest limit (1600m)
Magnesium				
0-year-old needles	1.04±0.10	0.94±0.15	-	0.96±0.08
1-year-old needles	1.07±0.17	0.86±0.13	1.01±0.26	0.97±0.07
Calcium				
0-year-old needles	4.20±1.94	4.60±1.77	-	4.50±1.08
1-year-old needles	6.64±2.73	7.56±2.11	5.76±2.50	7.58±1.63
Potassium				
0-year-old needles	8.34±1.91	6.85±0.82	-	6.43±1.35
1-year-old needles	5.03±1.73	5.51±1.04	5.72±1.61	3.99±1.33
Phosphorus				
0-year-old needles	0.95±0.78	0.88±0.48	-	1.37±0.35
1-year-old needles	0.53±0.23	0.79±0.10	0.93±0.07	0.86±0.10
Sulfur				
0-year-old needles	1.01±0.19	0.75±0.08	-	0.91±0.07
1-year-old needles	0.89±0.13	0.77±0.08	1.03±0.13	0.98±0.13
Manganese				
0-year-old needles	0.05±0.01	0.12±0.02	-	0.14±0.05
1-year-old needles	0.07±0.02	0.20±0.05	0.30±0.16	0.25±0.08
Iron				
0-year-old needles	0.03±0.0004	0.02±0.002	-	0.03±0.004
1-year-old needles	0.05±0.02	0.03±0.005	0.05±0.01	0.04±0.004
Zink				
0-year-old needles	0.05±0.01	0.05±0.05	-	0.05±0.004
1-year-old needles	0.05±0.04	0.04±0.01	0.04±0.02	0.05±0.01
Aluminium	0.03±0.01	0.03±0.01	-	0.02±0.01
0-year-old needles	0.04±0.01	0.03±0.003	0.06±0.01	0.04±0.01
1-year-old needles				

A strong increase in the mean phosphorus content with increasing elevation was observed in 1-year-old needles. The lowest concentration in current year needles (0.88±0.48mg g^{-1} dw) was measured at Hirschengarten, the highest (1.37±0.35 mg g^{-1} dw) at the forest limit. The mean P concentrations in 1-year-old needles were significantly lower than in 0-year-old, the lowest content was measured at Bartholomä (0.53±0.23 mg g^{-1} dw) and the highest at Seeangerl (0.93±0.07). The mean P concentration in 1-year-old needles at the forest limit was lower than at the 1360 m site.

No significant differences in sulfur content with needle age or with altitude were found. The highest mean S concentration in current year needles was measured at Bartholomä (1.0±0.19 mg g^{-1} dw), and in 1-year-old needles at Seeangerl (1.03±0.13 mg g^{-1} dw). The mean manganese concentration also increased strongly with increasing elevation a.s.l. The highest mean Mn content in 0-year-old needles was measured at the forest limit (0.14±0.05) and in 1-year-old needles at Seeangerl (0.30±0.16 mg g^{-1} dw). In the investigated stands, the mean Mn concentrations in 1-year-old needles were 1.4 to 1.7 times higher than in needles from current year. The mean manganese concentration, like the phosphorus concentration, in 1-year-old needles at the forest limit were lower than at the 1360 m site.

The mean iron concentration in current year needles at the Bartholomä site (0.03±0.004 mg g^{-1} dw) was higher than at two other sites (0.02±0.002 mg g^{-1} dw and 0.03±0.004 mg g^{-1} dw for Hirschengarten and the forest limit respectively). The lowest mean Fe^{2+} concentrations in 0- and 1-year-old needles were measured at Hirschengarten. The mean iron concentrations in the needles change with needle age; in older needles the Fe^{2+} content was 1.3 to 1.7 times higher than in 0-year-old needles. No correlation between Fe^{2+} content and elevation was found. The mean zinc concentrations do not differ strongly among the stands studied. In 0- and 1-year-old needles the highest concentrations were measured at Bartholomä. The mean Zn^{2+} concentration in current-year needles were slightly higher than in the older needles. In 0-year-old needles the mean Al^{3+} concentration decreased with increasing elevation. The highest mean aluminium concentration was measured at Bartholomä

(0.03±0.01), the lowest at the treeline (0.02±0.01 mg g^{-1} dw). Higher aluminium concentration was observed in 1-year-old needles in comparison to current year needles. Very high mean Al^{3+} concentration occurred in the spruce needles at the site Seeangerl (0.06±0.02 mg g^{-1} dw).

Both the nutrient concentrations and the relations between nutrients are important for the growth and development of plants. The K/Ca relations in the spruce needles were low (see **Tab 4.9**). The soils in the Berchtesgaden National Park are rich in cations Ca^{2+} that react antagonistically with cations K^{+}. At all experimental sites the K/Ca ratios were significantly higher in current year needles than in 1-year-old needles. The mean K/Ca ratios in 0-year-old needles decreased with altitude. The same pattern was observed in 1-year-old needles except at the site Seeangerl, where the K/Ca had the highest value (1.12±0.49). Because of magnesium deficiency in spruce needles, the K/Mg and Ca/Mg relations were relatively high. While in current year needles the K/Mg ratio decreased with increasing altitude, this correlation was not observed in 1-year-old needles.

Tab. 4.9: Nutrient ratios in 0- and 1-year-old spruce needles sampled in the Berchtesgaden National Park in 2003. BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, FL = forest limit.

		Mean and standard deviation			
		BA	HG	SA	FL
K/Ca	0-year-old	2.50±1.64	1.60±0.48	-	1.53±0.61
	1-year-old	0.91±0.55	0.78±0.22	1.12±0.49	0.57±0.38
K/Mg	0-year-old	8.21±2.75	7.38±1.26	-	6.72±0.94
	1-year-old	4.86±2.14	6.39±0.69	6.50±3.84	4.14±1.37
Ca/Mg	0-year-old	3.99±1.72	4.88±1.19	-	4.73±1.17
	1-year-old	6.34±2.76	8.72±1.79	5.86±1.49	7.84±1.66
N/K	0-year-old	1.77±0.13	1.62±0.19	-	1.91±0.20
	1-year-old	2.70±0.60	2.11±0.21	2.72±0.86	3.39±0.80
N/P	0-year-old	30.08±26.50	28.19±31.71	-	9.28±2.19
	1-year-old	28.14±12.13	14.57±1.92	14.75±1.25	14.86±1.93
N/S	0-year-old	14.56±1.10	14.83±1.09	-	13.35±0.61
	1-year-old	14.51±1.04	14.90±1.08	13.09±1.28	12.96±1.44
N/Mg	0-year-old	14.35±4.06	11.86±1.67	-	12.77±0.71
	1-year-old	12.25±2.33	13.34±1.22	14.20±5.06	13.05±1.45

The mean N/K ratios in the spruce needles were low (1.62 – 3.39) because of relatively low nitrogen concentrations. Higher nitrogen/potassium ratios were found in 1-year-old needles. The mean N/P ratios varied strongly between stands from 9.3 to 30. The highest nitrogen/phosphorus ratios were measured in lower situated stands. Also higher N/S ratios were found at Bartholomä and Hirschengarten. The nitrogen/sulfur ratios were similar in the current-year and 1-year-old needles. N/Mg ratios were generally higher in 1-year-old needles. Only at the site Bartholomä was the nitrogen/magnesium proportion higher in current-year needles. The mean N/Mg values ranged from 11.9 to 14.4.

4.4. Microclimate Conditions

During the season, some difficulties occurred in meteorological measurements linked to the different local situation of radiation sensors in relation to the investigated trees. During some periods, the observed radiation was influenced by local factors, resulting in shading of the instruments and stands to an unequal degree. At the Bartholomä site, the radiation sensor was shaded by Watzmann Mountain in the afternoon, earlier than the tree canopy. At Hirschengarten, the agreement between the radiation measurement and radiation input to the stand was better than at the 630 m site, but in the afternoon, shading was also not the same on the stand and sensor. At Seeangerl the radiation sensor, installed in a deep and narrow meadow surrounded by trees, was shaded longer in the morning and earlier in the afternoon than the experimental site. At the Kederbichl site, the radiation sensor was well-exposed and recorded the same radiation as experienced by the investigated trees.

Also, vapor pressure deficits observed in open areas located near to the experimental sites were most probably different from those within the stands, depending on air circulation and dew evaporation from the surroundings at the stations and the stands. On sunny days within the forest stands, cooler air temperatures occur than in neighbouring open areas. At night the thermal situation is opposite, the temperatures within the forest are higher in comparison to the non-forested areas because the emission of long-wave radiation from soil and plants is slowed down by branches and leaves (Bac et al. 1993).

Within the dense forest stands, the flows and exchanges of air masses are also slowed. Near the soil surface almost no air flow could be measured with the equipment used. Weak air exchange and lower temperature result in higher air humidity within forests stands than in the open areas. Nevertheless, most of the transpiration of the trees occurs in the sun crowns. During periods of the day when both the meteorological sites and sun crowns are well ventilated, and when radiation measurements are also undisturbed by the surroundings, we can assume a good correlation between meteorological conditions at the monitoring sites and for the stands in general. Except for early and late in the day, this should be the case and the measured conditions should relate well to overall water use by the forest stands.

Seasonal trends in the observed microclimate conditions along elevation gradients are, thus, shown for the Norway spruce stands in **Fig. 4.10** and are described in **Tab. 4.10**. At the three investigated spruce sites, the highest radiation input (PPFD integrated over the day) was measured from June to August. The highest mean air temperatures of 16.3, 14.5, and 12.2 °C were observed in June at Bartholomä, Hirschengarten and Seeangerl, respectively. The lowest air temperatures were measured at Bartholomä in May and at the two other stands in September. The lowest maximum air temperatures during the measurement period were observed at the highest situated site. However, at lower sites, the t_{max} values were similar. The differences in minimum temperature among the 630 m site, 1040 m and 1360 m sites were large. From May to October the largest VPD_{max} usually occurred at Bartholomä and VPD_{max} decreased with altitude. Nevertheless, on some days with valley fog, higher sites experienced drier conditions.

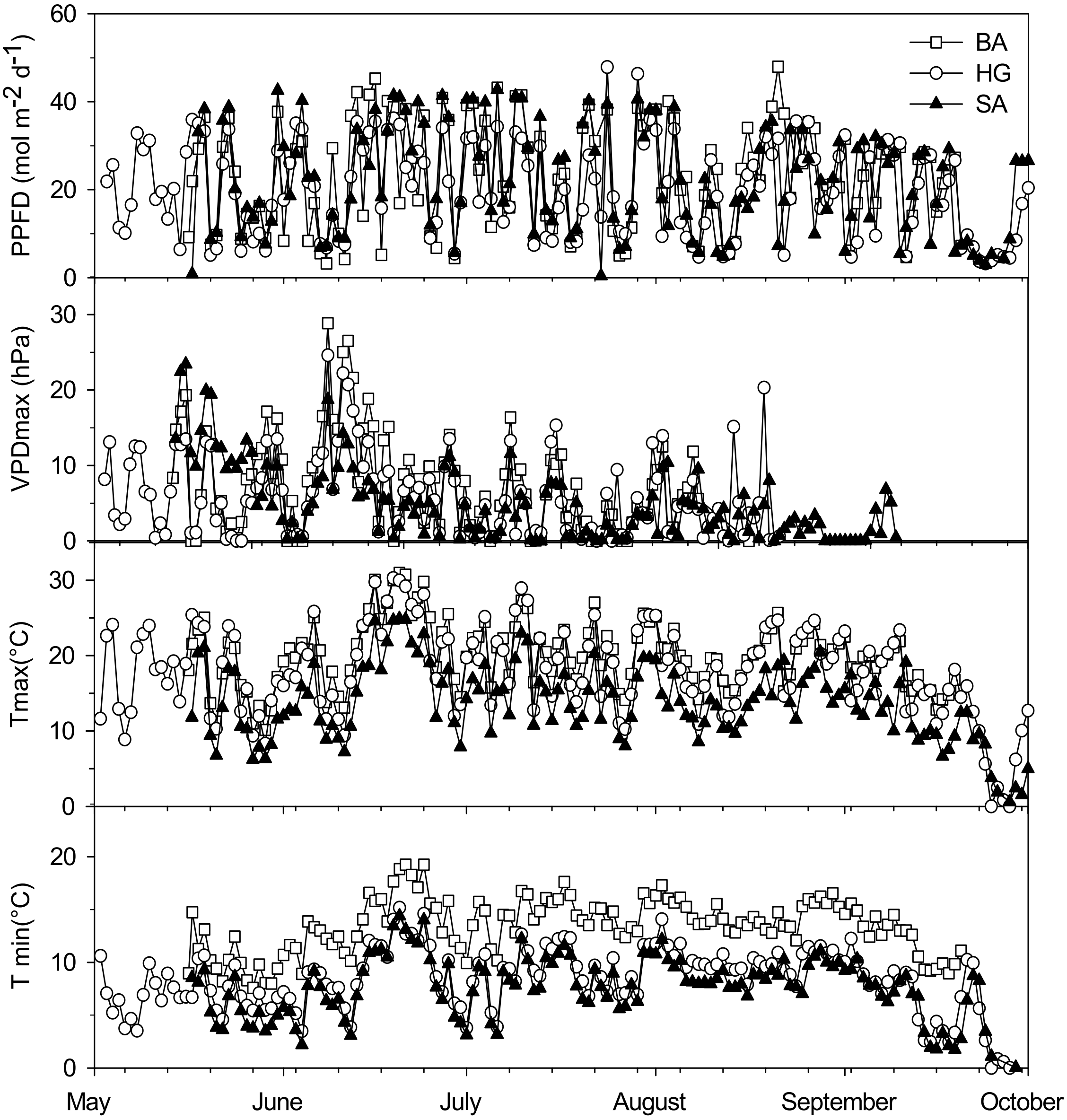


Fig. 4.10: Monthly climate data for Berchtesgaden National Park during summer 2002. BA= Bartholomä, HG=, Hirschengarten, SA= Seeangerl. PPFD radiation input was evaluated according to Wang et al. (2004).

Tab. 4.10: Monthly microclimate data for three investigated stands in Berchtesgaden National Park during summer 2002, BA = Bartholomä, HG =, Hirschengarten, SA = Seeangerl, KB = Kederbichl. PPFD values were evaluated according to Wang et. al (2004).

	T_{max} (°C)			T_{mean} (°C)			T_{min} (°C)		
	BA	HG	SA	BA	HG	SA	BA	HG	SA
May	24.7	21.7	21.1	12.9	11.3	8.5	6.1	3.7	3.5
June	29.5	27.9	24.9	16.3	14.5	12.2	7.2	5.0	2.2
July	25.8	25.6	23.0	15.6	13.7	11.8	8.3	5.4	3.2
August	23.6	21.7	20.5	15.2	13.3	11.5	10.4	8.6	6.8
September	20.3	19.2	19.1	11.1	8.1	6.9	2.9	-0.4	-2.2

	PPFD $_{integr.max}$ (mol m^{-2} d^{-1})			PPFD $_{integr.mean}$ (mol m^{-2} d^{-1})		
	BA	HG	SA	BA	HG	SA
May	37.7	35.9	42.6	18.3	19.5	20.9
June	45.3	36.2	41.4	23.4	23.0	25.7
July	43.2	47.9	42.7	24.4	22.1	25.8
August	47.9	35.5	38.8	24.8	19.8	19.2
September	30.4	31.3	32.0	19.2	15.7	17.5

	VPD_{max} (hPa)			Precipitation		
	BA	HG	SA	BA	HG	SA
May	19.3	13.4	-	65	*	128
June	28.9	24.6	18.7	81	150	165
July	16.3	15.3	11.5	193	195	*
August	12.5	13.9	14.6	352	262*	262*
September	-	20.3	8	61	*	*

The highest values of air temperature and vapor pressure deficit (VPD) were observed at the site Bartholomä, lower in Hirschengarten and the lowest in Seeangerl. Vapor pressure deficit at the three investigated spruce stands reached the highest values in June – the average daily VPD_{max} was for Bartholomä ca 12.0, Hirschengarten 9.1 and Seeangerl 6.1 hPa. The highest mean daily radiation by month was measured in Bartholomä in August (24.8), in Hirschengarten in June (23.0) and in Seeangerl in July (25.8 mol m^{-2} d^{-1}). Differences in radiation input along the elevation gradient were not large.

Precipitation increased with altitude above sea level. During the measurement period, the highest precipitation was observed in August and July (**Tab. 4.10**). At the beginning of August, strong rain events occurred and measurement of precipitation was not possible due to small volumes of the rain-gauges.

Seasonal changes in soil temperatures at 2 cm depth are shown in **Fig. 4.11** for the three experimental spruce stands. The temperature time courses exhibited similar seasonal patterns with higher temperatures at Bartholomä, namely an increase in maximum soil temperatures from May to July and a decrease after the beginning of September (**Tab. 4.11**). The highest mean soil temperatures at different depths were measured at Bartholomä and Seeangerl in August, and in the Hirschengarten stand in July and August. For the spruce site Bartholomä, the soil temperatures for June and July were taken from the beech stand at the same elevation because of data gaps.

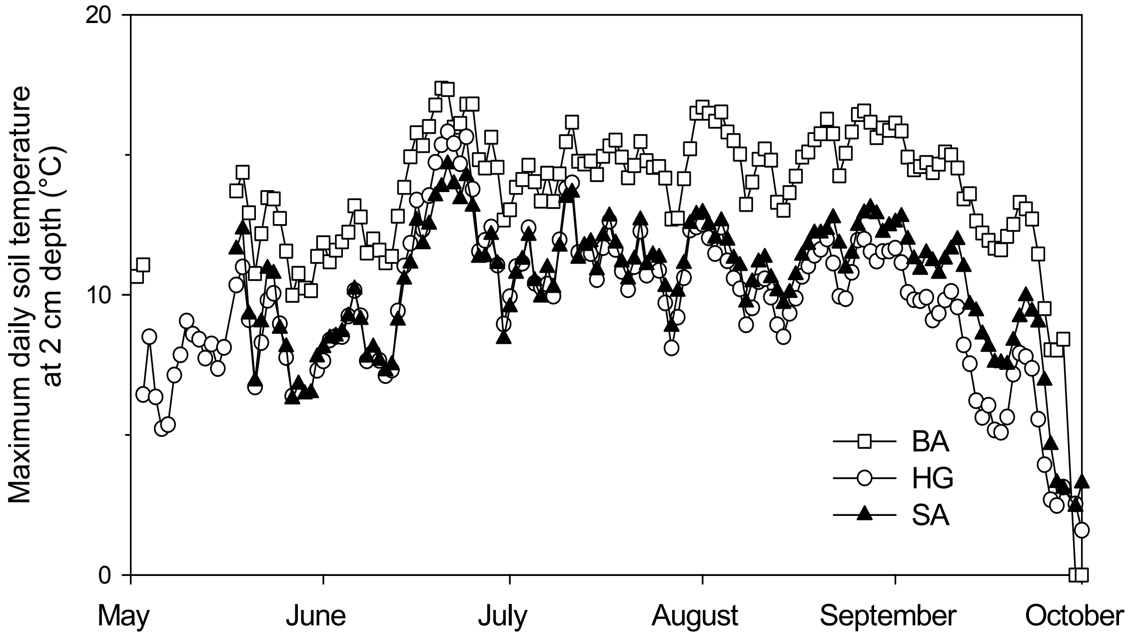


Fig. 4.11: Seasonal changes in maximum daily soil temperature at 2 cm depth in three investigated spruce stands during the measurement period in 2002. BA= Bartholomä, HG=, Hirschengarten, SA= Seeangerl.

Tab. 4.11: Seasonal changes in soil temperatures in three experimental *Picea abies* stands in National Park Berchtesgaden in 2002. Measurements were conducted for a single vertical profile. BA= Bartholomä, HG=, Hirschengarten, SA= Seeangerl.

BA	T_{max}				T_{mean}				T_{min}			
	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)
May	14.4	14.7	11.5	10.1	10.9	10.7	9.8	8.6	6.7	6.8	6.8	5.8
June*	17.4	17.0	15.9	17.0	13.3	13.0	12.2	11.8	9.5	9.7	9.9	9.5
July*	16.2	15.3	16.0	15.9	14.0	13.8	13.5	13.8	10.8	11.9	12.1	11.2
August	16.6	16.2	15.9	13.8	14.7	14.3	14.4	12.9	12.3	11.8	12.4	11.8
September	15.9	15.8	15.5	13.6	12.1	12.0	12.3	11.6	7.6	7.5	8.2	8.7

HG	T_{max}				T_{mean}				T_{min}			
	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)
May	11.0	13.5	10.9	10.0	7.0	9.5	8.9	8.2	3.6	6.2	6.2	5.5
June	15.8	18.2	15.1	13.9	10.1	12.6	11.8	10.9	5.4	8.0	8.7	8.5
July	14.0	16.4	14.5	13.2	10.3	12.9	12.5	11.9	7.2	10.0	11.0	10.7
August	12.4	14.7	13.6	12.8	10.1	12.8	12.5	11.9	7.8	10.5	11.1	11.1
September	10.1	13.2	12.8	12.0	6.0	9.3	9.7	8.9	0.5	3.9	5.2	4.8

SA	T_{max}				T_{mean}				T_{min}			
	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)	-2 (cm)	-5 (cm)	-10 (cm)	-20 (cm)
May	12.4	8.4	8.3	7.9	7.3	6.6	6.6	6.3	4.9	5.2	5.1	4.7
June	14.7	12.6	11.9	12.2	9.8	9.0	8.9	8.6	4.9	5.9	5.9	5.7
July	13.7	11.6	11.4	10.9	10.6	10.1	10.0	9.8	7.1	8.2	8.3	8.3
August	13.1	11.8	11.7	11.6	11.0	10.6	10.5	10.4	8.9	9.3	9.4	9.4
September	12.1	11.5	11.4	11.2	8.0	8.4	8.5	8.5	2.0	3.5	3.7	3.9

Soil moisture measurements, were carried out at 5, 20 and 50 cm below the ground surface. At the site Bartholomä, water content was measured only at 5 cm depth because of the occurrence of large stones in the soil profile. The seasonal patterns of soil moisture were similar at three experimental spruce sites. A strongly decline in soil moisture in the 630, 1040 and 1360 m stands was observed in the middle of June and beginning of July. At Bartholomä, the longest dry period occurred between 10 and 23 June, when the soil water content at 5 cm depth decreased from 0.47 to 0.08 m^3 m^{-3}. Also at Hirschengarten (1040 m) the longest dry period occurred between 9 and 24 June. The soil water content declined from 0.53 to 0.33, from 0.43 to 0.34, and from 0.58 to 0.46 m^3 m^{-3} at –5, -20, and –50 cm depth, respectively.

The highest mean monthly radiation was measured in Bartholomä in August (24.8 mol m^{-2} d^{-1}), and the lowest in May and September (**Tab. 4.10**). Less than 10% of the solar radiation penetrated to the forest floor in the beech stand (**Fig.

4.12). The seasonal changes in air moisture, radiation and precipitation were described above with respect to the *Picea abies* sites.

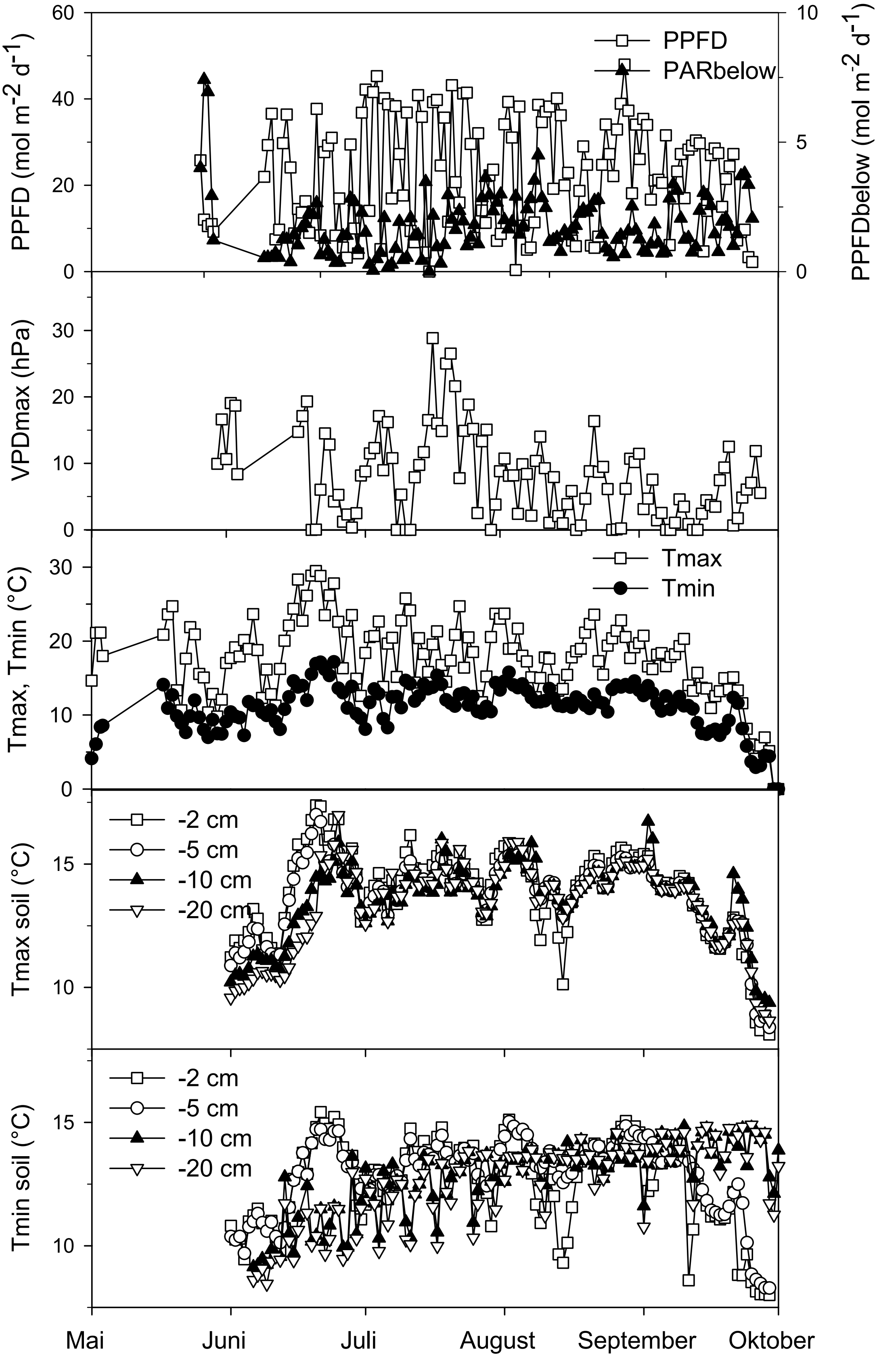


Fig. 4.12: Monthly climate data for the investigated stand of *Fagus sylvatica* at Bartholomä in Berchtesgaden National Park during summer 2002.

At the European beech site in Bartholomä, the highest mean air temperature (16. 4 °C) was observed in June and the lowest mean temperature (11 °C) was measured in September. In spring before the leaves developed, the minimum air temperatures in the beech stand were higher than in spruce stand at the same elevation (**Tab. 4.12**).

Tab. 4.12: Monthly microclimate data for investigated *Fagus sylvatica* stand in Berchtesgaden National Park during summer 2002, PPFD values were evaluated according to Wang et. al (2004).

	T_{max} (°C)	T_{mean} (°C)	T_{min} (°C)	PPFD $integ_{max}$ (mol m^{-2} d^{-1})	PPFD $integ_{mean}$ (mol m^{-2} d^{-1})
May	17.2	14.1	10.1	37.7	18.3
June	28.6	16.4	7.5	45.3	23.4
July	25.1	15.6	8.4	43.2	24.4
August	22.9	15.0	9.6	47.9	24.8
September	19.2	11.0	3.2	30.4	19.2

	VPD_{max} (hPa)	Precipitation (mm)
May	19.3	65
June	28.9	81
July	16.3	193
August	12.5	352
September	-	61

In **Fig. 4.12** seasonal changes of minimum and maximum soil temperatures at 2, 5, 10 and 20 cm depth are shown. The temperature courses at different soil depths had similar patterns. A slow increase in soil temperatures from May to July and a decrease from the beginning of September were observed. In June the highest maximum soil temperatures occurred at 2 and 5 cm depth. From July to September the maximum soil temperature at different depths reached similar values. The lowest soil temperature was measured at 10 and 20 cm depth in June and at 2 and 5 cm in September.

In comparison with the spruce site Bartholomä, the soil temperatures at the beech site at -2, -5 and -10 cm depth were generally higher from July to September (**Tab. 4.13**). During the measurement period, the monthly mean soil temperature at the 20 cm depth at the beech site was 0.6 to 2.4 °C higher than at spruce site at the same elevation a.s.l.

Tab. 4.13: Monthly mean soil temperature in the *Fagus sylvatica* stand at Bartholomä.

	T-2 (°C)	T-5 (°C)	T-10 (°C)	T-20 (°C)
May	10.9	10.6	10.0	9.5
June	13.3	13.0	12.2	11.8
July	14.0	13.8	13.5	13.8
August	13.8	14.1	14.1	14.1
Saptember	11.9	12.1	12.5	12.3

Seasonal trends in meteorological conditions in the investigated *Larix decidua* and *Pinus mugo* stands (1720 m a.s.l.) are shown in **Fig. 4.13**. A large data gap occurred in July due to equipment failure. Nevertheless, the highest mean daily radiation by month at elevation 1720 m a.s.l. was measured in July and September and the lowest in August. The maximum daily integrated radiation was observed in July and reached 43.7 mol m^{-2} d^{-1}. The highest mean air temperatures recorded were in July (17.2 °C) and the lowest (12.1 °C) in September (**Tab. 4.14**). The highest maximum temperature (26.0 °C) was measured in June. The vapor pressure deficit (VPD) at Kederbichl also reached the highest values in June – the average daily VPD_{max} in this month was ca. 8.4 hPa.

During the measurement period, the highest precipitation (362 mm) was observed in June (however, between 9 and 23 July no data are available due to power failure) and the lowest (214 mm) in August. The seasonal courses of daily precipitation are shown in **Fig. 4.13**. Precipitation was frequent each month, and at the beginning of August strong rain events occurred. During the season, precipitation at the highest situated site was much higher (ca. 150 – 447%) than measured at Bartholomä.

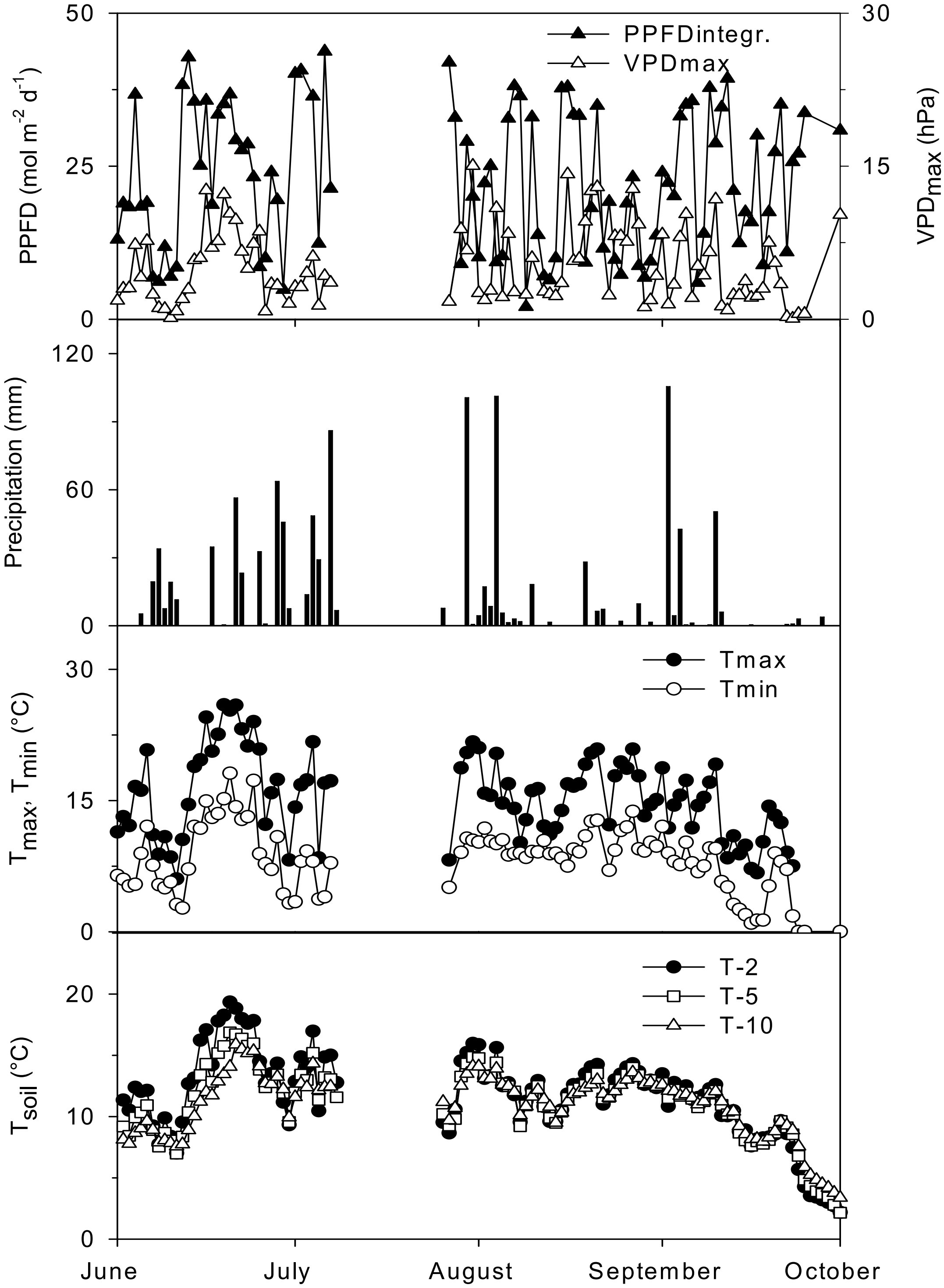


Fig. 4.13: Monthly climate data for *Larix decidua* and *Pinus mugo* stands in Berchtesgaden National Park during summer 2002.

Tab. 4.14: Monthly climate data for the investigated *Larix decidua* and *Pinus mugo* stands in Berchtesgaden National Park during summer 2002.

Month	T_{max} (C°)	T_{mean} (C°)	T_{min} (C°)
June	26.0	16.9	6.0
July	21.7	17.2	8.2
August	20.9	16.0	10.2
September	19.2	12.1	6.8

Month	VPD $_{max}$ (hpa)	VPD $_{mean}$ (hpa)
June	21.1	8.4
July	15.0	6.7
August	14.2	6.2
September	11.7	3.6

Month	PPFD integ.$_{max}$ (mol m^{-2} d^{-1})	PPFD integ.$_{mean}$ (mol m^{-2} d^{-1})
June	42.8	22.2
July	43.7	26.9
August	38.1	19.3
September	39.3	25.0

Month	Precipitation (mm)
June	362
July	297
August	214
September	220

A decline in maximum soil temperature at different depths (-2, -5 and -10 cm) was observed from June to August (**Tab. 4.15**). The differences between maximum temperatures at different soil depths were highest in June and declined over the measurement period. As at the spruce sites, a strong decrease in soil moisture occurred in the middle of June. A second long dry period occurred from 7 to 17 August.

Tab. 4.15: Maximum soil temperature in *Larix decidua* and *Pinus mugo* stands during summer 2002.

Month	T-2 (C°)	T-5 (C°)	T-10 (C°)
June	19.3	17	15.9
July	17	15.2	14.3
August	15.6	14.4	13.9
September	12.8	12.2	12.1

4.5. Sapflow – diurnal changes and seasonal changes

The daily sapflow courses are affected by radiation (PPFD) and vapor pressure deficit in the air (VPD). The sapflow starts in early morning after sunrise, reaches its maximum near midday, approximately at the time when the radiation intensity and VPD reach their maximum, then decreases to a minimum towards sunset (**Fig. 4.14**). In **Fig. 4.14 to 4.17**, a similar response to the time courses of change in PPFD and VPD within outer and inner sapwood layers in individual trees at different forest sites is illustrated. Usually sapflow occurred only during the day, but during some periods, with low humidity and high air temperatures, significant fluxes were measured also at night.

Daily courses of PPFD, VPD and sap flow rates at two xylem depths (0 to 2 and 2 to 4 cm) for one spruce tree (F1) and one beech tree (Bu1) are shown in **Fig. 4.14**. In general, the diurnal sapflow time courses for different xylem layers were similar in form, but the magnitude for sapflow decreased with increasing depth within the sapwood (see below). The maximum value for flow is attained at approximately the time when PPFD and VPD have their maximum, but these controlling factors, though strongly correlated, are not always in phase. Furthermore, depending on storage capacity of the trunks, shifts in the timing for onset and maximum sapflow can be recognized. Finally, the mentioned differences in microclimate between the measurement stations and observed stands make a complete analysis difficult.

At Bartholomä (630 m), the radiation sensor was shaded earlier in the afternoon than the tree canopy by trees bordering the Eisbach (**Fig. 4.14**). After midday there was a slow and continual decrease in radiation since the stand receives diffuse sky radiation. At Bartholomä the maximum sap flux density was reached with maximum PPFD, before VPD reached its maximum. This suggests that radiation plays a stronger role in determining water use, at least during the afternoon period. The same response to the PPFD and VPD courses can be observed for beech trees.

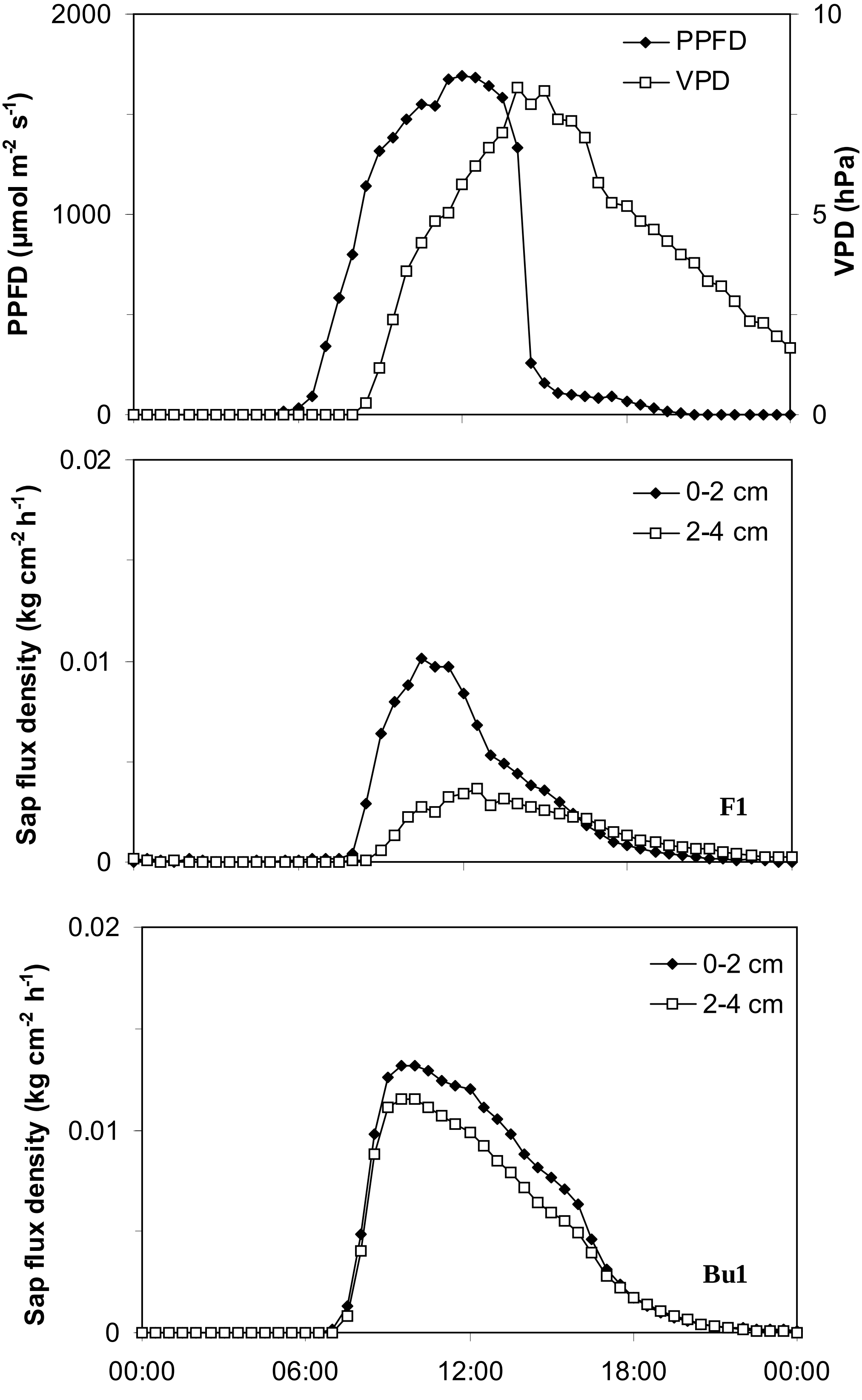


Fig. 4.14: Diurnal changes in measured radiation (PPFD) and vapor pressure deficit (VPD) in relation to sapflow rates in 0 – 2 and 2 – 4 cm sapwood depths in one experimental spruce tree (F1) and one beech tree (B1) at the Bartholomä site on 30.05.2002.

At the site Hirschengarten, the sapflow was measured in some trees at three xylem depths (2, 4, and 6 cm). A strong decrease in sap flux densites with increasing sapwood depth was observed in all investigated trees. The maximum sap flux densities in different sapwood layers were reached at the same time (**Fig 4.15**). At Hirschengarten the radiation sensor has a better exposure and the recorded data represent well the radiation input to the stand (**Fig 4.15**). The maximum sap flux density at the 1040 m site was reached at noon when maximum radiation and vapor pressure deficit were measured. Nevertheless, the short-term peak in VPD was not reflected in the sapflow data, suggesting either a stronger influence of radiation or a compensating control response by stomata in the observed trees.

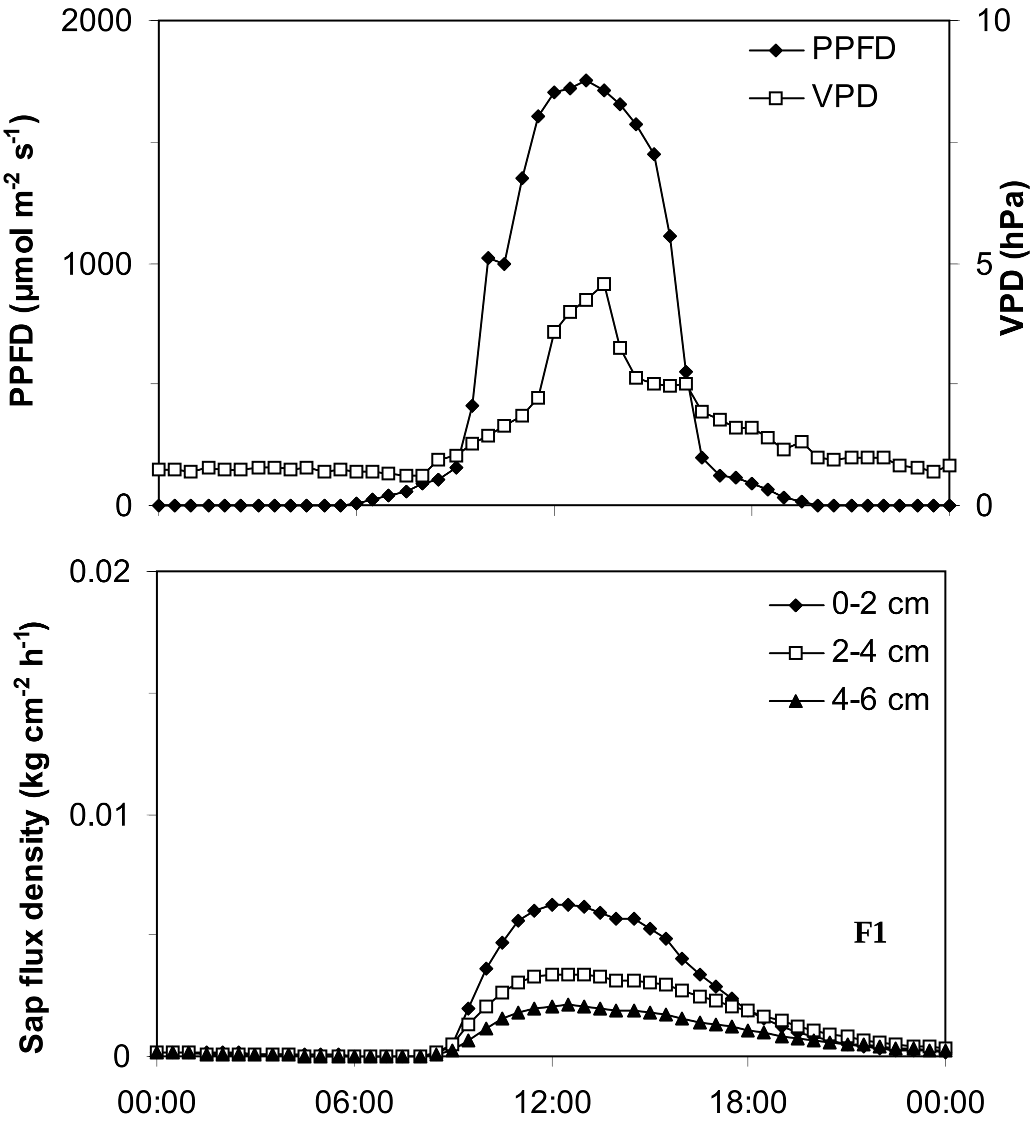


Fig. 4.15: Diurnal changes in measured radiation (PPFD) and vapor pressure deficit (VPD) in relation to sapflow rates in 0 – 2 and 2 – 4 cm and 4 – 6 cm sapwood depths in one experimental spruce tree (F1) at the Hirschengarten site on 23.08.2002.

At the 1360 m Seeangerl site, the radiation sensor was shaded longer in the morning and earlier in the afternoon than the investigated trees, but the radiation measurements were a good indicator during the high radiation period (**Fig. 4.16**). At Seeangerl the maximum sapflow rates do not decrease as quickly as in other stands, but remain constant reaching a plateau at midday.

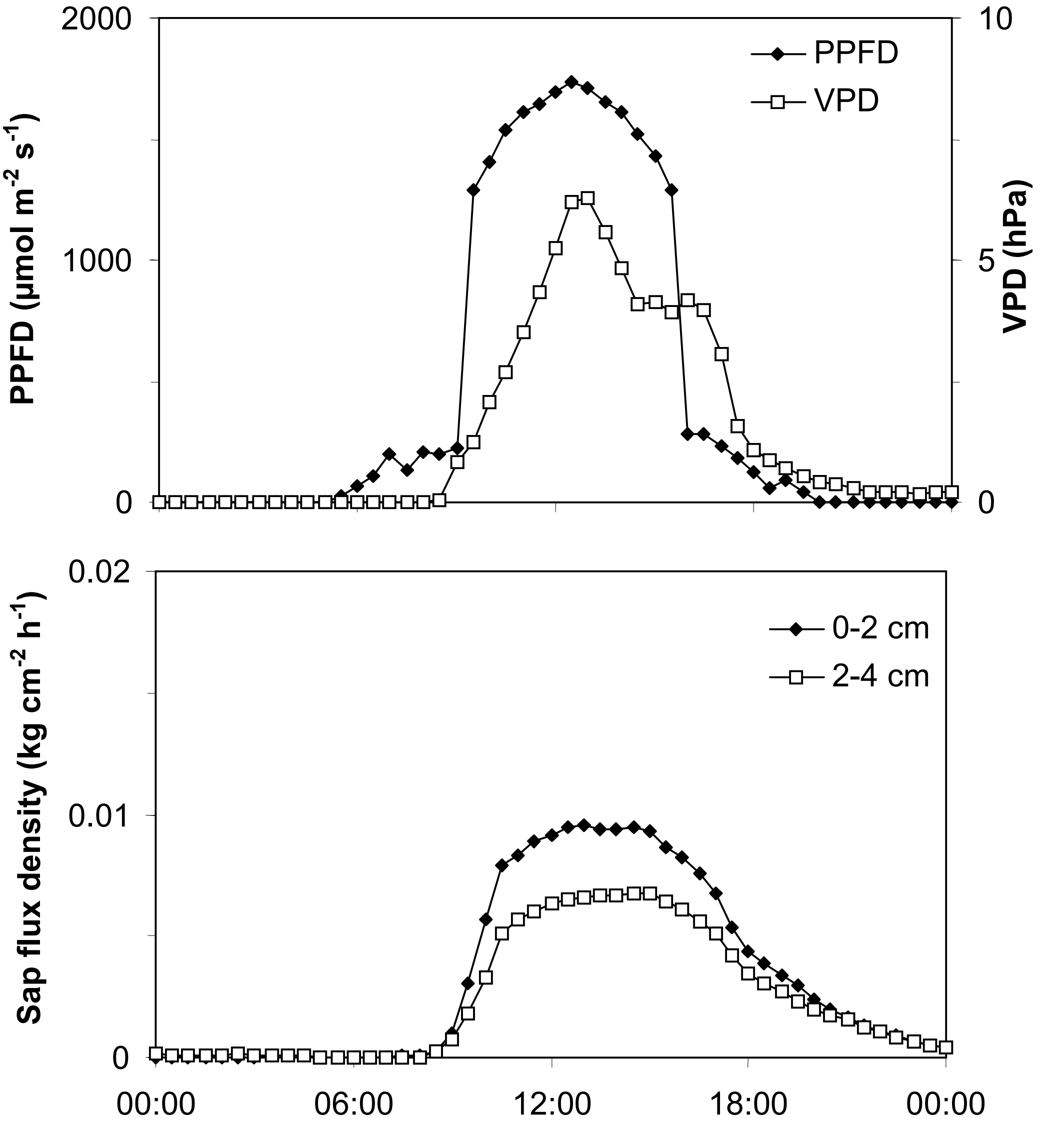


Fig. 4.16: Diurnal changes in measured radiation (PPFD) and vapor pressure deficit (VPD) in relation to sapflow rates in 0 – 2 and 2 – 4 cm sapwood depths in one experimental spruce tree (F7) at the Seeangerl site on 28.07.2002.

At the site Kederbichl, the measured radiation agreed with radiation input to the stand, but VPD seems to influence more the sap flux response early and late on the selected day. European larch and dwarf-pine quickly open the stomata at low light and the daily sapflow courses seem dominated by VPD influences (**Fig. 4.17**). On the other hand, a decline in sapflow occurs after midday, suggesting the simultaneous influence of additional control factors.

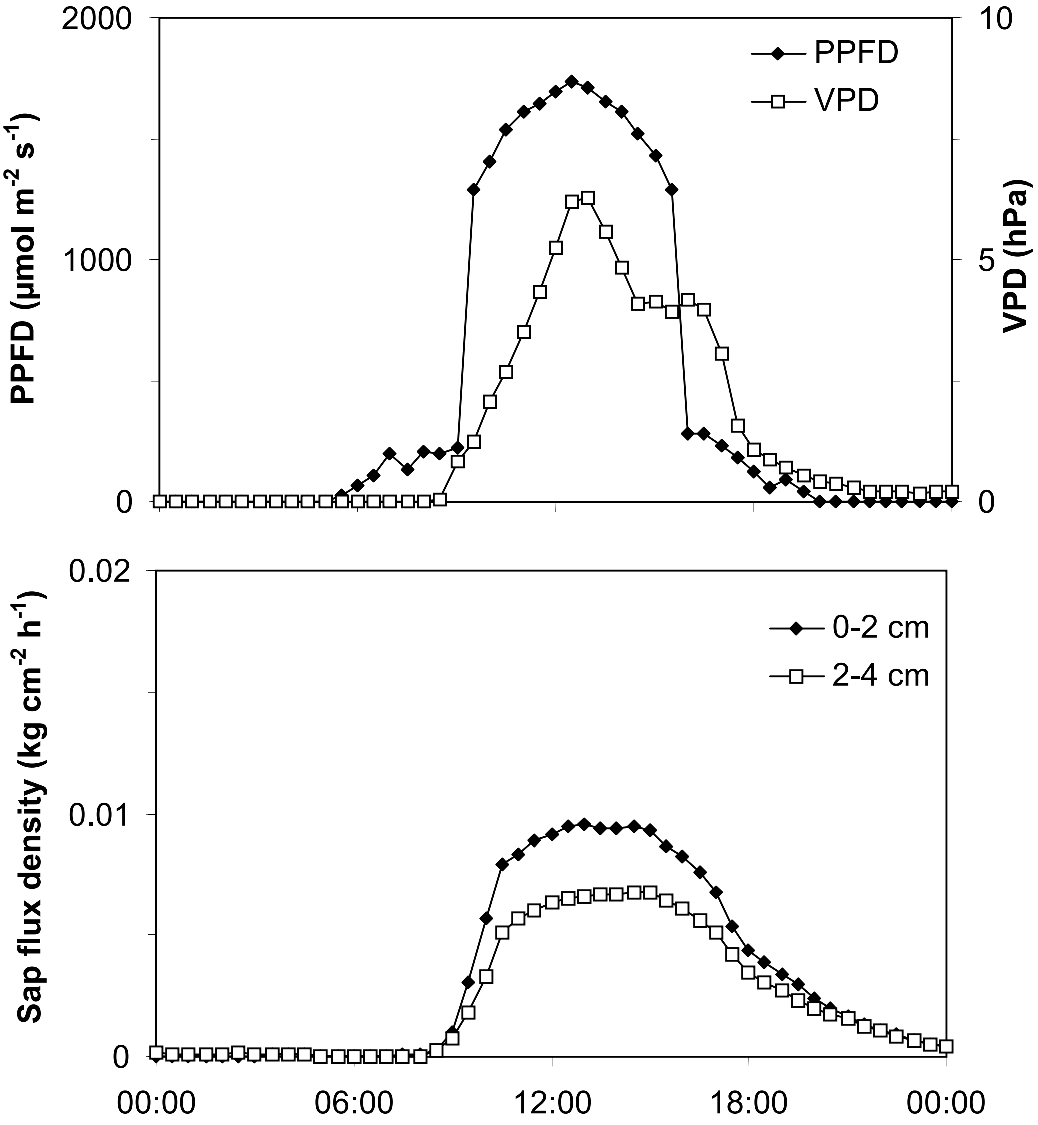


Fig. 4.17: Diurnal changes in measured radiation (PPFD) and vapor pressure deficit (VPD) in relation to sapflow rates in 0 – 2 cm sapwood depths in one experimental larch tree (L1) and one dwarf-pine (P1) at the Kederbichl site on 03.07.2002.

In spruce trees, the sap flux measurements are affected by transpiration and storage capacity. There is often a shift between the time courses of crown transpiration rate and xylem water flow in the trunk (Wieser et al. 2003). The xylem flow starts 0.5 to 3 hours later than the measured transpiration. In general, it is difficult to recognize such time lags in the current data set, because the meteorological measurements do not provide exact information to relate to canopy response. However, changes in storage may provide the basis for changing correlations of sapflow with radiation or VPD as described above. In other studies, investigators have made corrections in their observed sapflow data to compensate for storage (by shifting the rates with respect to time) before estimating transpiration of the stand (an imprecise correction in any case). Uncorrected data for sapflow have been used for estimating canopy transpiration in this study. On a daily basis, the time lags are unimportant with respect to total water use.

At the location Kederbichl, the sapflow in *Larix decidua* and *Pinus mugo* was measured only at 2 cm depth because of the thin xylem layer in *Larix* and relatively small stems of *Pinus*. The daily sapflow courses in both species were similar with respect to changes in meteorological parameters as described for the other tree species above (**Fig 4.17**).

At the site Bartholomä; similar seasonal patterns in the sap flux densities can be recognized in all experimental trees. The sap flux densities increased from the beginning of the measurement period, reached their maximum in the middle of July, and then declined. Maximum sap flux denisties measured at the 630 m site approximated 0.03 kg cm^{-2} h^{-1}. In the stand Hirschengarten, two trends were observed. In most trees, a slight decrease occurred in daily sap flux densities during the season, while in two experimental trees the sap flux densities increased from May to the end of July and then remained constant until the end of September. The maximum densities reached 0.03 kg cm^{-2} h^{-1}. At the site Seeangerl, an increase in sap flux densities occurred in most trees from the end of May to the end of July. After this, a rapid decline in sapflow rates occurred, that probably was linked to the strong rain events in the first two weeks of August. At the end of August, the sap flux densities increased again. Maximum rates measured in June and in July reached ca. 0.03 kg cm^{-2} h^{-1} as at Hirschengarten. At the *Fagus sylvatica* site the sap flux densities increased from the beginning of the measurement period to the middle of June and stayed relatively constant to the beginning of September. The maximum sap flux densities approximated 0.04 kg cm^{-2} h^{-1}. At the *Larix decidua* site, sap flux densities increased from the beginning of June to the end of July; maximum flow densities were high and reached ca. 0.03 kg cm^{-2} h^{-1}. In the case of *Pinus mugo*, a continuous decrease in sap flux density occurred from the beginning of the measurement period until the end of September. The maximum rates were measured in the middle of June and approximated 0.015 kg cm^{-2} h^{-1}.

For the estimation of forest stand transpiration based on total-tree water use, information about sap flux density at different xylem depths is required (Lambs and Muller 2002). The diffuse porous trees like beech (Kubota et al. 2003), willow and poplar (Lambs and Muller 2002), or coniferous trees like spruce (Alsheimer 1997) use several tree rings for xylem sap transfer (Lambs and Muller 2002). Maximum sap flux densities have in general been recorded near to the cambium layer and they decrease with xylem depth (Ford et al. 2004; Nadezhdina et al. 2002).

The measurements at three spruce sites (a total of 30 spruce trees) showed large variation in sap flux density with xylem depth and among trees and stands. The comparison between flux densities at 2 - 4 and 4 - 6 cm xylem depth with 0 to 2 cm depth in spruce trees from different sites is shown in **Fig. 4.18**. At sites Bartholomä and Hirschengarten, the sap flux densities in deeper sapwood layers (2 - 4 and 4 - 6 cm) in most investigated trees were lower than in the outer sapwood ring (0 – 2 cm) (see **Fig. 4.18 a, b, c, d**). Difficulties were encountered during the season at the Seeangerl site with recording of the temperature differences of sapflow sensors. As a result, only an estimation of mean flows over the course of the day was possible. All observations for which comparison in different layers was possible show higher sap flux density rates in the outer xylem ring (**Fig. 4.18 e**).

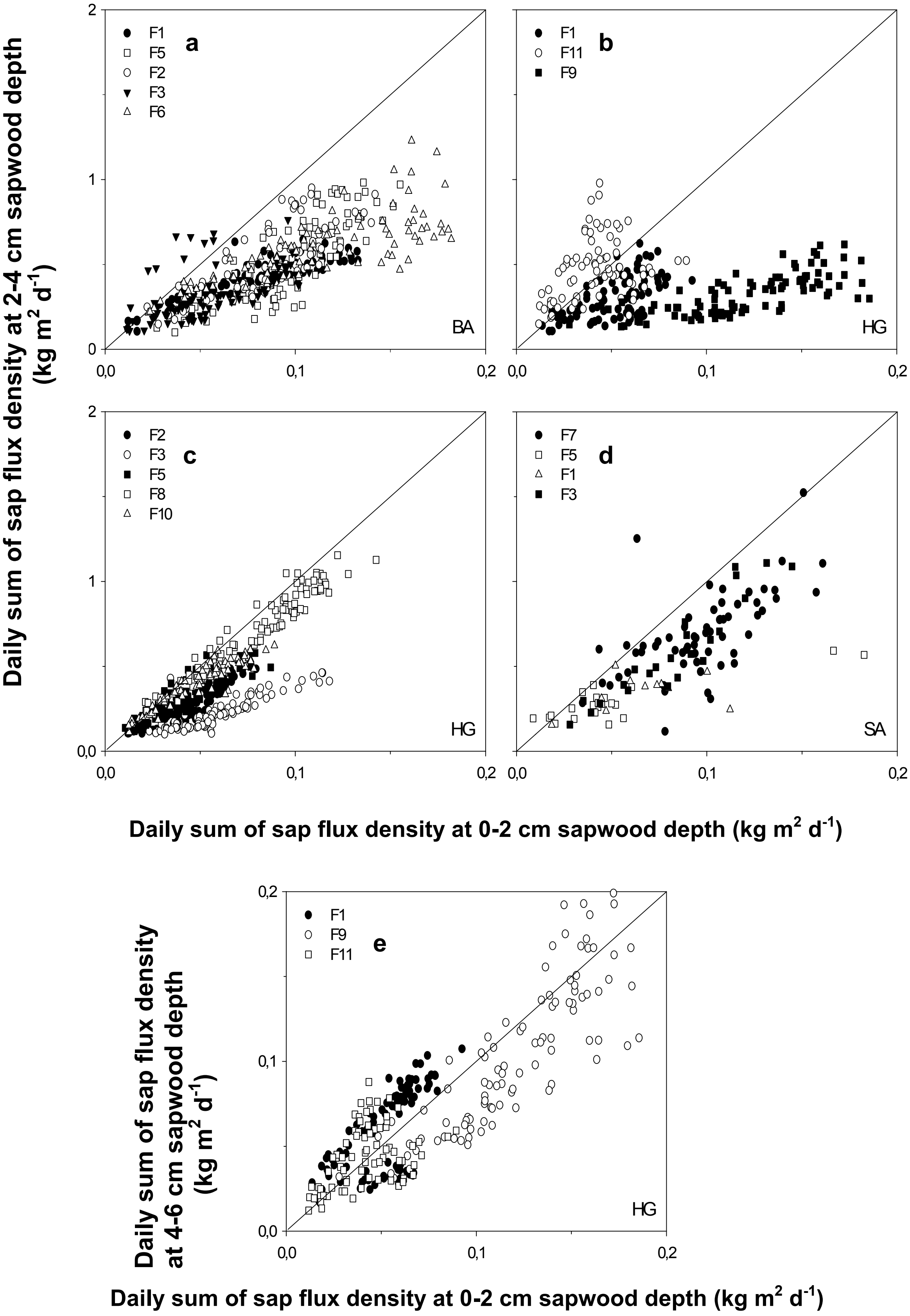


Fig. 4.18: Relationship between sap flux densities at 2 – 4 cm and 4 – 6cm sapwood depth in *Picea abies* trees at three experimental sites with sap flux density measured at 0 – 2 cm. BA = Bartholomä, HG= Hirschengarten, SA = Seeangerl.

The relationship between sap flux densities at 0 – 2 cm and 2 – 4 cm sapwood depth differed among trees and over the course of the season. Seasonal changes in the daily ratios between inner and outer sap flux densities in *Picea abies* trees at the site Bartholomä in 2002 are shown in **Fig. 4.19**. At the 630 m site, the highest mean monthly fluxes at 2 – 4 cm sapwood depth in comparison to 0 – 2 cm depth occurred in May, and then they continuously decreased (F2, F5). However, in some experimental trees (F1, F6) the sap flux densities at 2 – 4 cm depth decreased from May to July and increased again from August to September. The highest transport rates in the deeper sapwood layer were measured in tree F3. Actually, for five experimental trees at this site, a similar seasonal pattern in sap flux densities was observed. During the entire season, significantly higher sapflow rates in inner as compared to outer sapwood were measured in only one spruce tree (F4, data not shown). In this case, the result may have been obtained due to problems with the sensor.

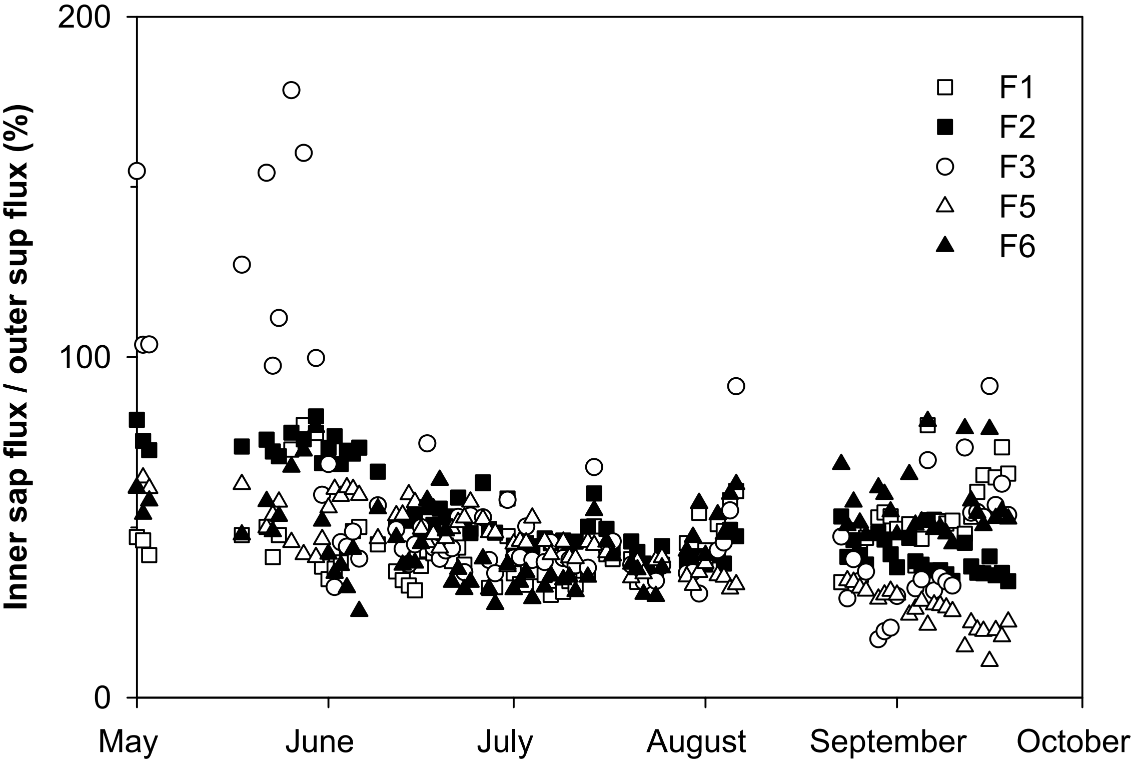


Fig. 4.19: Seasonal changes in the ratio of sap flux densities at 2 - 4 cm depth in comparison to 0 - 2 cm depth of *Picea abies* trees at the site Bartholomä in 2002.

The mean monthly percentage of sap flux density at 2 – 4 cm depth in comparison to sap flux densities in the 0 – 2 cm ring decreased significantly in all investigated trees in spruce stand Hirschengarten (**Fig. 4.20**). The same pattern was observed for mean monthly flux densities at 4 – 6 cm xylem depth in comparison to the 0 - 2 cm ring. The response at the 1040 m site was more variable than at Bartholomä. In some trees the ratio of sap flux density in inner to outer xylem was only realized late in the season. In trees F2, F3, F5, F10, only a slightly decrease in sap flux densities in deeper sapwood rings in comparison to the outer sapwood layer can be observed. During some periods in a few trees (F3, F5), the flows in the 2 - 4 cm layer were higher, perhaps due to faulty sensor installation in the bark to xylem transition, but the seasonal trend toward 50% of the 0 – 2 cm flux density in deeper layers is still observed. A strong decline in the proportion between fluxes at different depths was
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measured in trees with the deepest active sapwood layer (F1, F9 and F11), in which the sapflow was measured at 2, 4 and 6 cm depths.

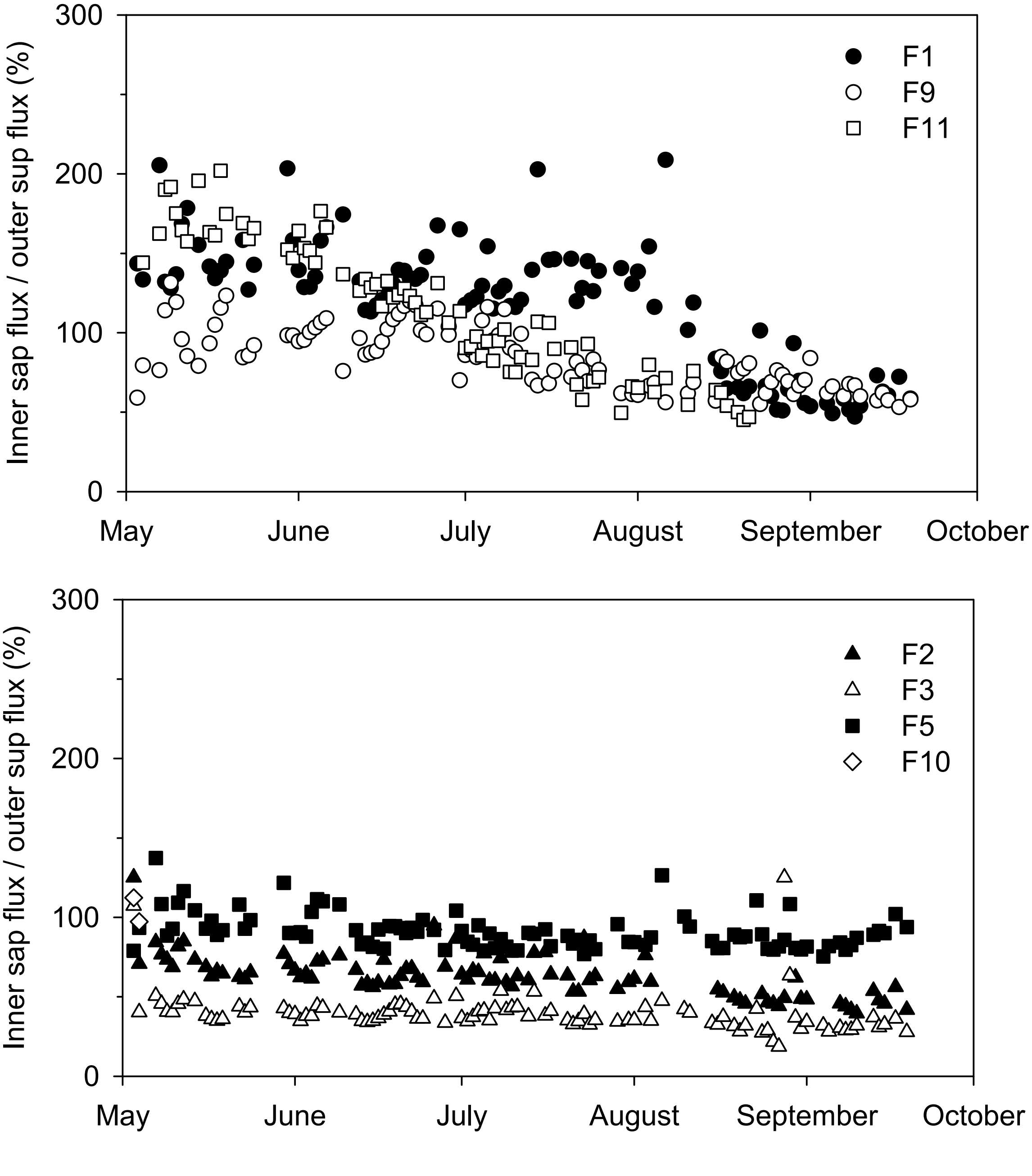

Fig. 4.20: Seasonal changes in the ratio of sap flux densities at 2 - 4 cm depth in comparison to 0 - 2 cm depth sap flux densities for *Picea abies* trees at the site Hirschengarten, in 2002.

At the highest situated site at Seeangerl, the sap flux rates in three sapwood depths 0 - 2, 2 - 4 and 4 - 6 cm were measured. However, an hourly estimation of fluxes was possible only in outer sapwood.

The **Fig. 4.21** is included to provide better overview of differences among individual trees at two experimental spruce sites.

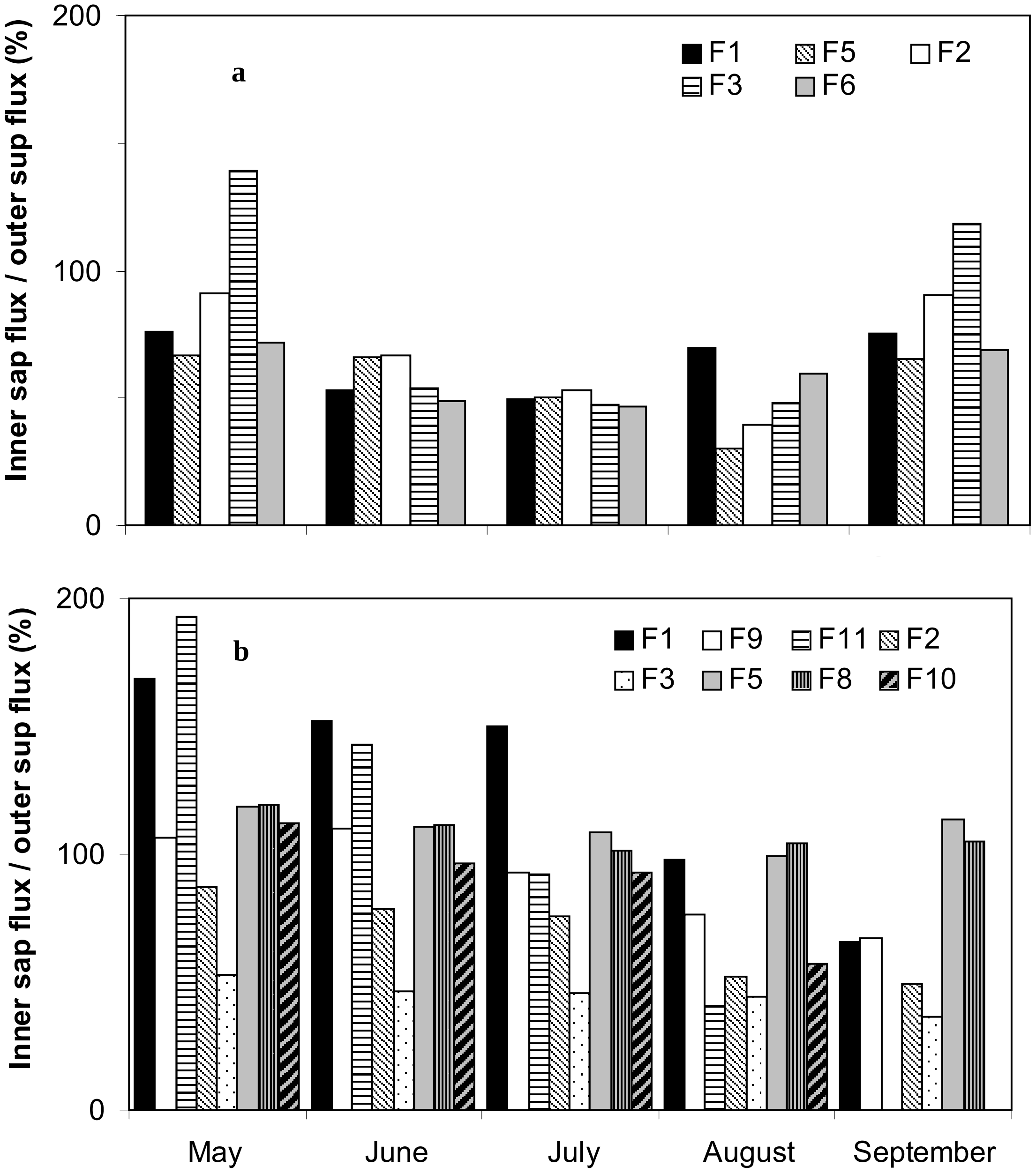

Fig. 4.21: Seasonal changes in the monthly mean ratio of sap flux densities at 2 - 4 cm depth in comparison to 0 - 2 cm depth sap flux densities at two Picea abies sites a) Bartholomä and b) Hirschengarten. The sapflow rates were standardized on a cm^2 sapwood basis.

During the measurement period in the spruce stand at Bartholomä, the total daily sapflow ranged from 1.6 to 41 kg day^{-1} per tree. In Hirschengarten, the sapflow rates varied from 0.4 to 112 kg day^{-1}, and in the highest situated stand Seeangerl from 0.5 to 51.5 kg day^{-1} per tree. Daily maximum transpiration over the season were in the range of 21 – 41, 3 – 112, and 9 – 51.5 kg day^{-1} per tree in the 630 m, 1040 m and 1360 m stands, respectively.

In European beech stand Bartholomä, a variation in flux densities at different sapwood depths was also observed. In all investigated beech trees at the 630 m site, the daily sapflow rates at 0 – 2 cm depth were significantly higher than at 2 – 4 cm (**Fig. 4.22**). The relationship between sap flux rates at 0 – 2 cm and 2 - 4 cm sapwood depth changed very little during the season (**Fig. 4.23**). The reductions in fluxes with increasing sapwood depth were different for different individual trees. The highest sap flux densities in the 2 – 4 cm xylem layer appeared in trees Bu1 and Bu5, the lowest in Bu4.

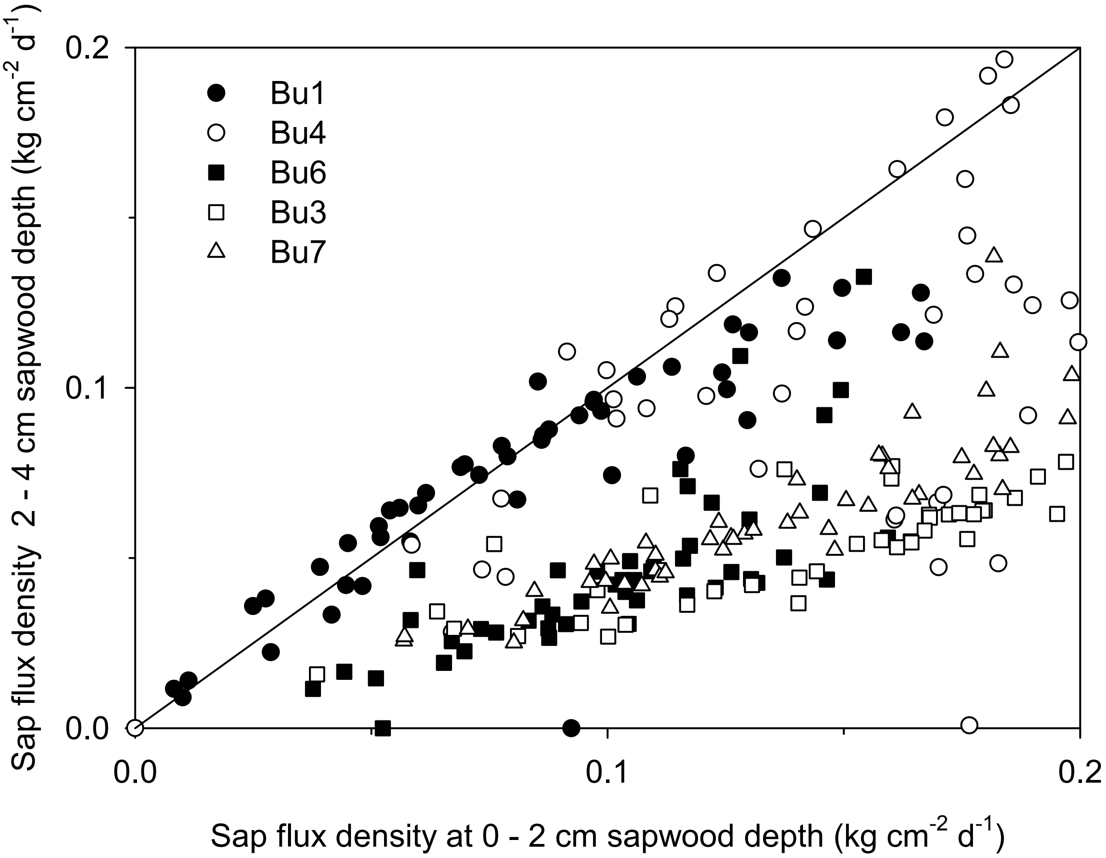

Fig. 4.22: Relationship between sap flux densities at 0 – 2 and 2 – 4 cm sapwood depth in experimental *Fagus sylvatica* trees in June and July 2002 in Berchtesgaden National Park.

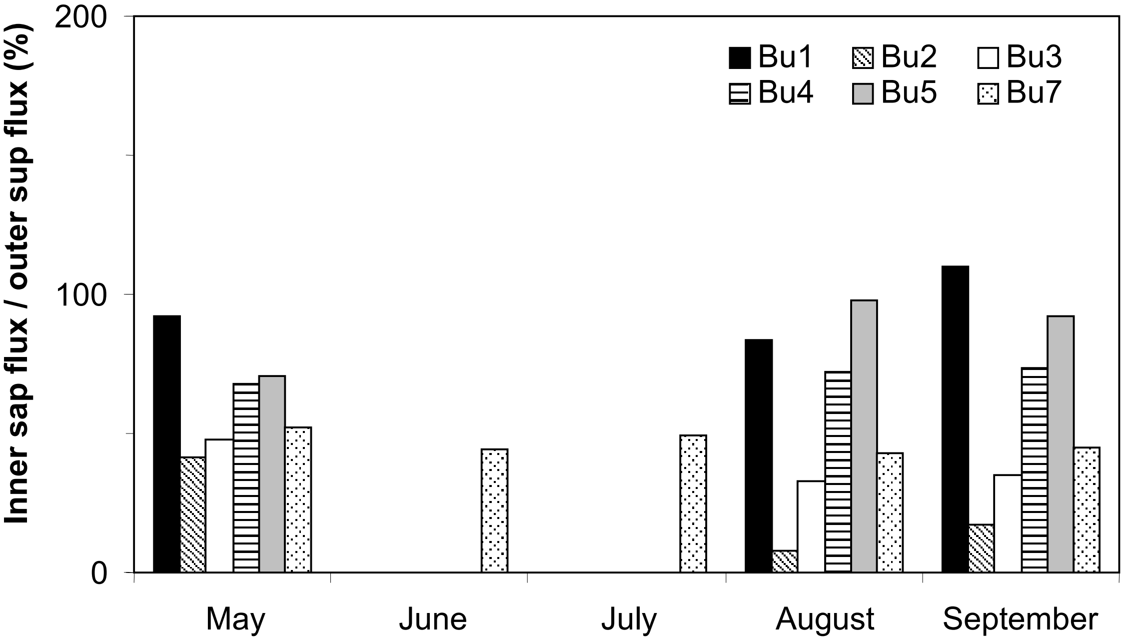

Fig. 4.23: Seasonal changes in the monthly mean ratio of sap flux densities at 2 - 4 cm depth in comparison to 0 - 2 cm depth sap flux densities in *Fagus sylvatica* trees at site Bartholomä. The sapflow rates were standardized on a cm^2 sapwood basis.

The sapwood ring in stems of *Larix decidua* is very thin. For estimation of sap flux density the signals for 0 - 2 cm long sensors were related to the actual hydroactive sapwood. When the flowmeters were not entirely installed in the conductive tissue, a correction was carried out relating flow to the actual depth of sapwood. The analysis of seasonal sapflow courses showed a strong reduction in sapflow rates after the data gap at the end of July. In some investigated trees, the difference between fluxes before and after the data gap was more than 50%. It can be explained by resin production around the sensors. Shortly after sensors installation an increase in resin exudation along the electrodes was observed which changes the thermal properties of the tissue. The same problems with resin production after sensor installation were observed for *Larix gmelinii* trees (Arneth 1994; 1996). The data from late in the season have, therefore, been eliminated from further consideration in the analysis.

The mean sap flux densities measured in *Larix decidua* trees in June were in the range of 0.06 kg m^{-2} d^{-1} to 0.22 kg m^{-2} d^{-1}, whereas the maximum fluxes reached ca. 0.3 kg m^{-2} d^{-1}. During June and July 2002 in experimental European larch trees, the mean water use per tree ranged between 0.3 and 74 kg d^{-1}. Maximum tree water use reached ca. 195 kg d^{-1}. Higher sap flux rates were measured at the end of June and beginning of July than in early June. The mean sap flux densities measured in dwarf-pine during the season ranged from ca. 0.01 to 0.02 kg m^{-2} d^{-1} and the maximum sap flux density reached ca. 0.05 kg m^{-2} d^{-1}. The maximum sapflow rates in 6 experimental *Pinus mugo* branches during the season ranged between 2.8 – 4.6 kg d^{-1}. The average water use varied from 0.7 to 1.7 kg d^{-1}. The branches are, of course, not immediately comparable to the tree level values given for the other species.

4.6. Stand transpiration – diurnal and seasonal changes

Norway spruce: It was apparent from first survey of the results that regulation of water use at landscape level is complex. Because of differences in elevation a.s.l. and in turn in climate conditions, significant differences in rates and in diurnal courses of transpiration were observed (**Fig. 4.24**). Thus, between 17 May and 21 September 2002, the patterns in diurnal transpiration at three experimental *Picea abies* sites were compared and categorized as summarized below:

- Usually – on 31 days – the transpiration was initiated earlier at Seeangerl (1360 m a.s.l.) than at two other spruce sites. Within these: on 11 days water use started earlier at Seeangerl than in Bartholomä (630 m a.s.l.) and latest at Hirschengarten (1040 m a.s.l.) (see **Fig. 4.24 a**), on 20 days the spruce trees at Bartholomä and Hirschengarten started to transpire approximately at the same time (**Fig. 4.24 b**).
- On 17 days at 630 m (Bartholomä) and 1360 m (Seeangerl) sites the spruce trees started to transpire at the same time, while at the 1040 m site the transpiration process started later (**Fig. 4.24 c**).

- On 10 days the transpiration at three experimental sites was initiated at the same time (**Fig. 4.24 d**).
- On 10 days the transpiration was observed only at Bartholomä and Hirschengarten (**Fig. 4.24 e**). On 3 days the transpiration was measured only at the 630 m site, while the water use in Hirschengarten and Seeangerl was very low (**Fig. 4.24 f**).
- On 14 days the transpiration was initiated in Bartholomä earlier than at Hirschengarten and Seeangerl (**Fig. 4.24 g**). Within these on 7 days at 1040 m and 1360 m sites water use started at a similar time; on 4 days the transpiration started latest at Seeangerl and on 3 days at Hirschengarten.

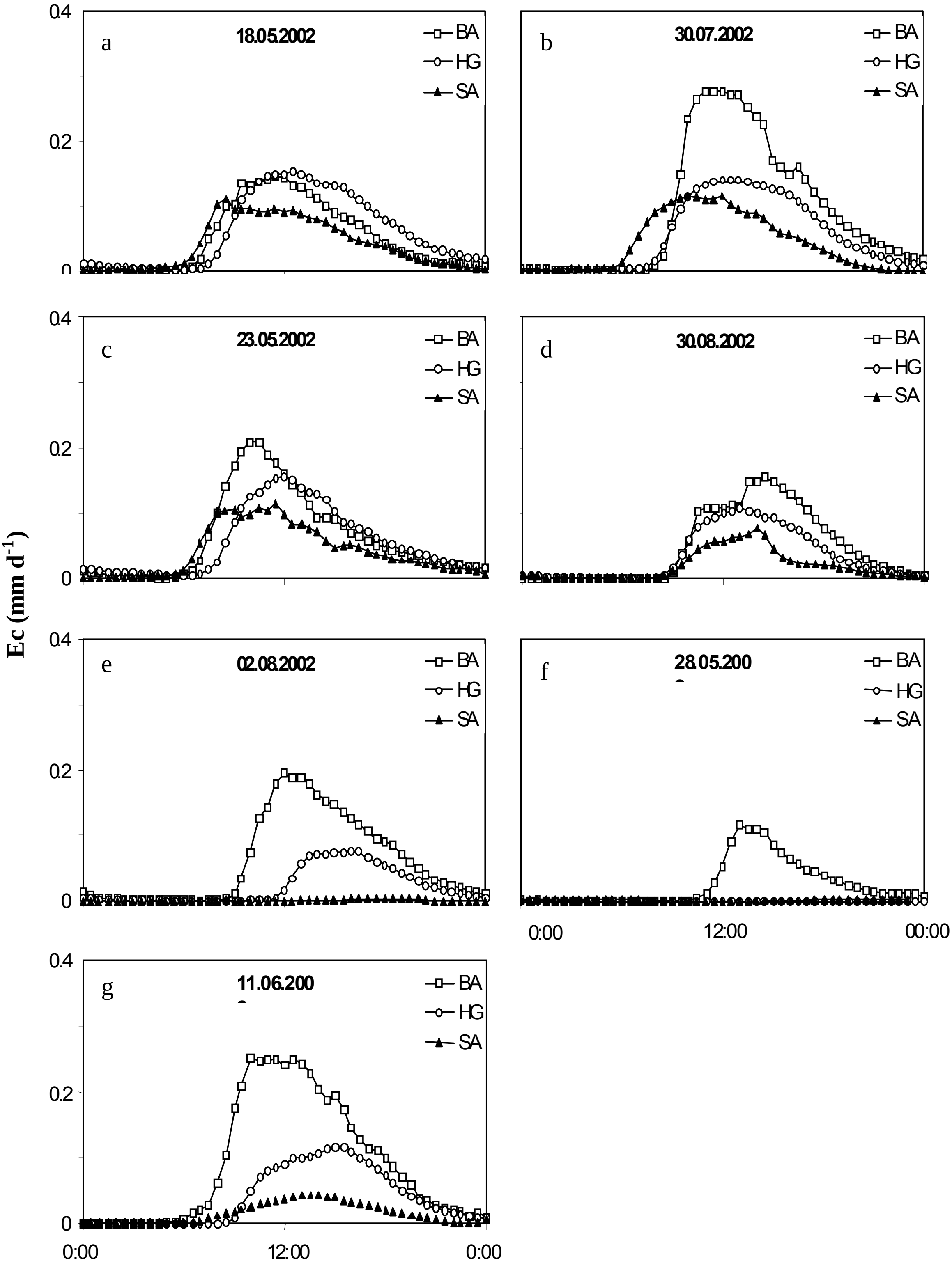

Fig. 4.24: Different types of patterns in transpiration on days during summer 2002 at three experimental *Picea abies* sites in National Park Berchtesgaden, BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl.

Usually (40 days) the maximum transpiration was reached at Seeangerl earlier than at two other investigated sites. On 24 days the maximum water use was measured in three experimental spruce stands at the same time. On 10 days the maximum water use was measured earlier at the 630 m site than at the 1040 m and 1360 m sites, while the maximum transpiration at Hirschengarten and Seeangerl occurred at a similar time.

The seasonal changes in daily canopy transpiration in three Norway spruce stands in National Park Berchtesgaden are shown on a monthly average basis in **Fig. 4.25** and on a daily basis in **Fig. 4.26.** Maximum hourly transpiration rates reached at site Bartholomä 0.3 mm h^{-1}, at Hirschengarten and at Seeangerl 0.2 mm h^{-1}. Maximum daily water loss at the three sites was measured in July and June. The highest daily transpiration rates were measured in June at Bartholomä (2.5 mm) and Hirschengarten (1.6 mm) and in July at Seeangerl (1.8 mm) (**Tab. 4.16**).

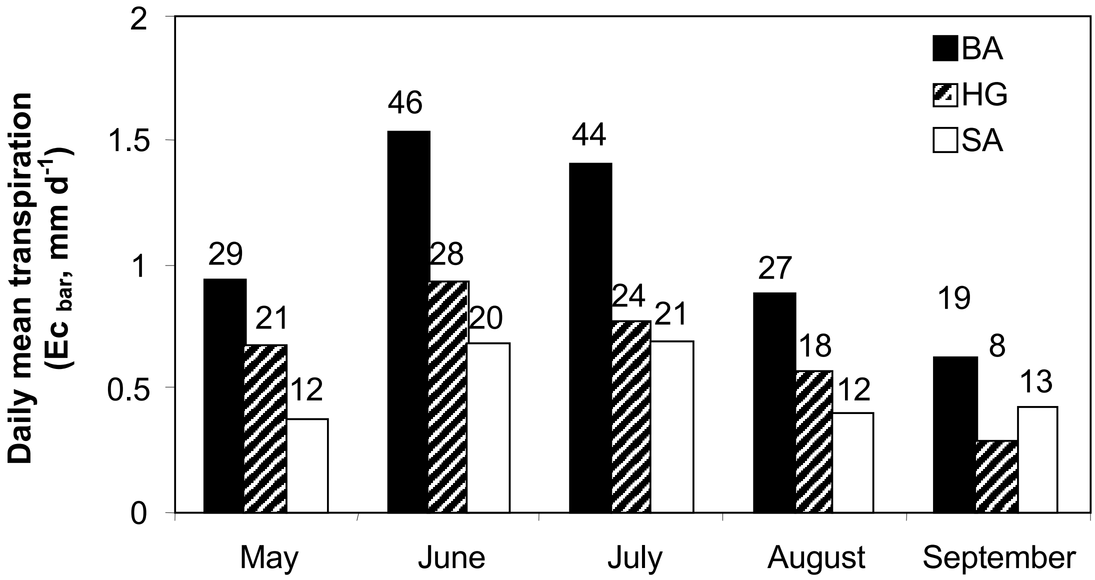

Fig. 4.25: Daily mean transpiration for each month at three experimental *Picea abies* sites in Berchtesgaden National Park during 2002. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl. Numbers on top of columns are estimates of the total monthly water use.

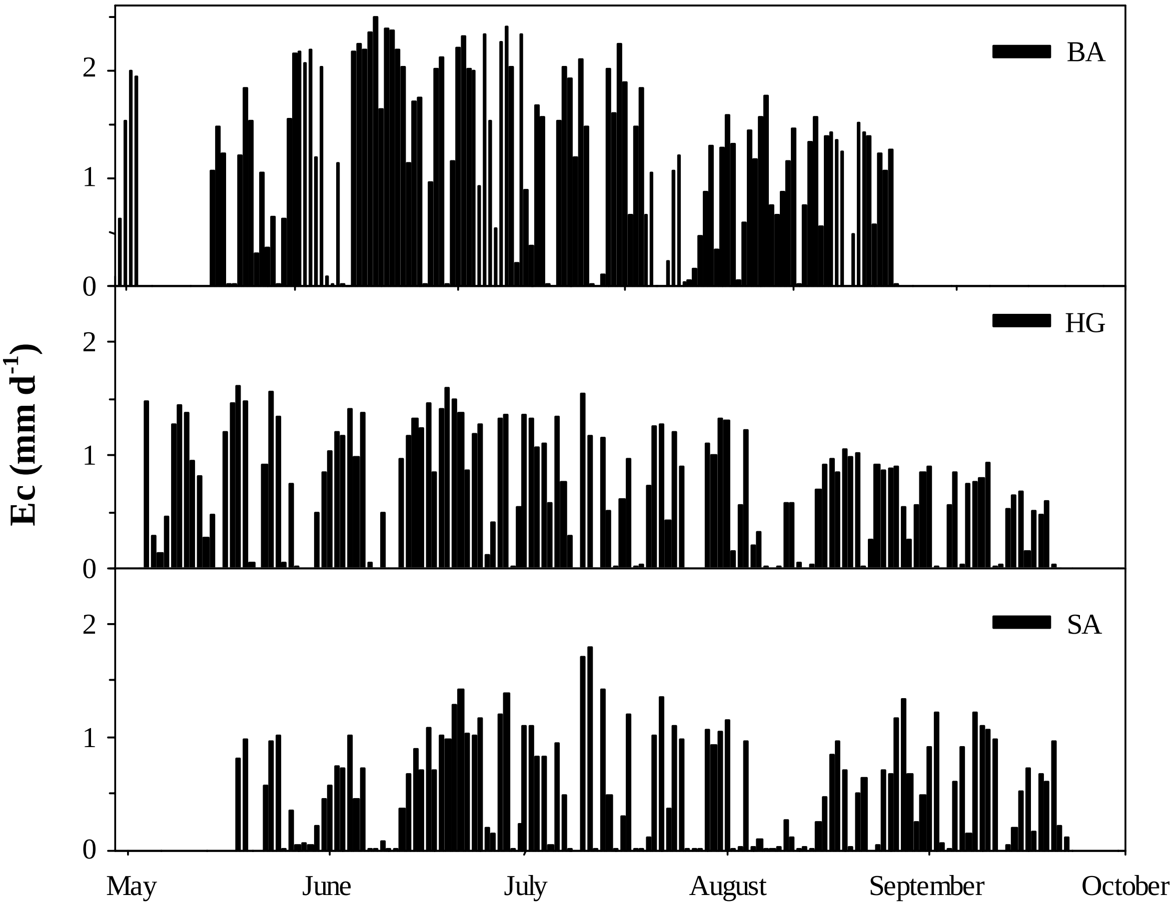

Fig. 4.26: Seasonal variation during summer 2002 in the daily sum of tree canopy transpiration measured at three spruce sites in Berchtesgaden National Park.

The estimated daily mean transpiration increased from May to July and decreased from August to September (**Fig. 4.26**). The largest differences between months in mean transpiration rates were observed in Bartholomä, the lowest in Seeangerl. The transpiration rates varied from 0.6 to 1.5 mm d^{-1} at Bartholomä, 0.3 to 0.9 mm d^{-1} at Hirschengarten and 0.4 to 0.7 mm d^{-1} at Seeangerl.

Tab. 4.16: Monthly sums of canopy transpiration, absolute daily maximum canopy transpiration rates and daily mean of canopy transpiration for each month ($E_{c\ bar}$) at three experimental *Picea abies* sites in Berchtesgaden National Park during 2002. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl.

	Monthly sum (mm month^{-1})			Daily$_{max}$ (mm d^{-1})			$E_{c\ bar}$ (mm d^{-1})		
	BA 630 m	HG 1040 m	SA 1360 m	BA 630 m	HG 1040 m	SA 1360 m	BA 630 m	HG 1040 m	SA 1360 m
May	29	21	12	2.2	1.6	1.0	0.9	0.7	0.4
June	46	28	20	2.5	1.6	1.4	1.5	0.9	0.7
July	44	24	21	2.4	1.5	1.8	1.4	0.8	0.7
August	27	18	12	1.8	1.2	1.3	0.9	0.6	0.4
September	19	8	13	1.6	0.9	1.2	0.6	0.3	0.4
May-September	165	99	78						

Because of data gaps, the monthly sums for each site were calculated by multiplying the daily mean on successful observation days by the number of days in the month. During the measurement period in the experimental spruce stands, the monthly transpiration varied from 19 to 46 mm month^{-1} at Bartholomä, 8 to 28 mm month^{-1} at Hirschengarten and 12 to 21 mm month^{-1} at Seeangerl (**Fig. 4.25**). In the three investigated stands, the highest water use was measured in June and July. The lowest water loss was observed in September for the 630 m and 1040 m stands and in May for the 1360 m stand. The variation in transpiration rates along the elevation gradient must be examined together with variation in the climate conditions.

European beech: Maximum hourly transpiration rates at the beech site in Bartholomä was measured in August and estimated as ca. 0.2 mm h^{-1}; in other months the maximum rates were similar (0.1 mm h^{-1}). During the measurement period, various daily transpiration courses were observed. The daily maximum transpiration rates were in the range of 0.6 – 1.3 mm d^{-1}. They increased from May to July and decreased from August to September (**Fig. 4.27**).

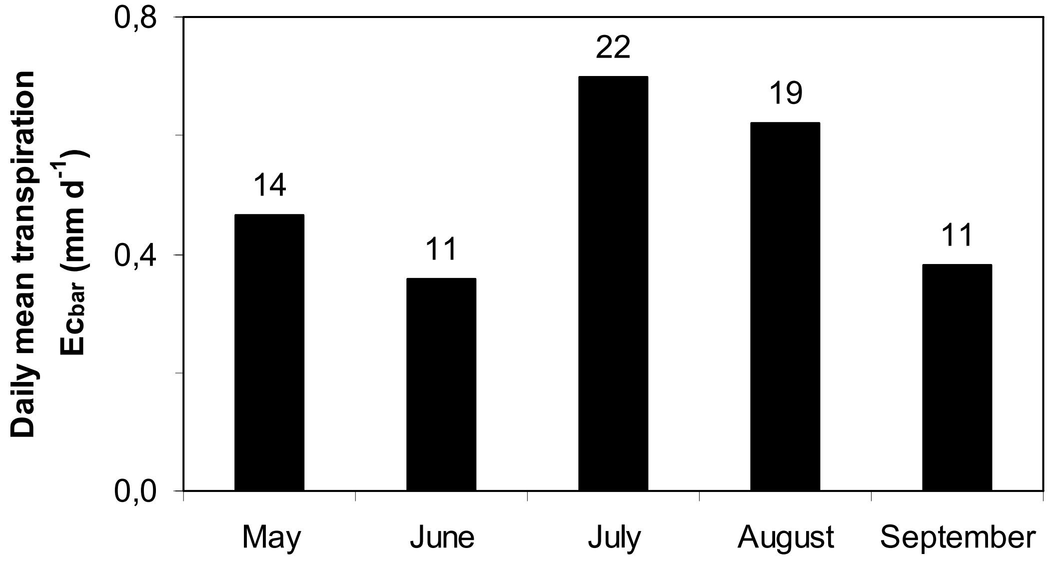

Fig. 4.27: Daily mean transpiration for each month at experimental *Fagus sylvatica* site in Berchtesgaden National Park during 2002. Numbers on top of columns are estimates of the total monthly water use.

Because of problems with the power supply in June, the measured signals were very noisy and the estimation of water use for only two trees was possible. More representative data were recorded in July, but the sapflow data were not available for all experimental beech trees. The highest mean values of daily transpiration rates were measured in the middle of season (**Tab. 4.17**). The highest maximum daily transpiration rate (1.3 mm) occurred in August. Monthly water use was estimated by multiplying the daily mean on successful observation days by the number of days in the month. During the measurement period, the monthly water use of the beech stand varied from 11 to 22 mm month $^{-1}$. The monthly transpiration rates were 8 – 35 mm lower than in the spruce stand at the same elevation. The highest differences in water loss between spruce and beech stands occurred in June (35 mm) and the lowest in August and September (8 mm). However, the technical problems in sampling response of the beech trees may have a strong influence on this comparison. The seasonal water use of beech stand reached 78 mm.

Tab. 4.17: Daily and monthly transpiration rates in *Fagus sylvatica* stand in Berchtesgaden National Park during summer 2002.

	Monthly sum ($mm\ month^{-1}$)	$Daily_{max}$ ($mm\ d^{-1}$)	$E_{c\ bar}$ ($mm\ d^{-1}$)
May	15	1.0	0.5
June	11	0.6	0.4
July	22	1.2	0.7
August	19	1.3	0.6
September	11	0.9	0.4
May-September	78		

European larch and dwarf-pine: Transpiration of *Larix decidua* was only measured successfully during June and during a few days in July. A significant decrease in measured transpiration rates in larch trees between July and August was observed. It was explained by intensive exudation of resin (Arneth 1994; 1996) that disturbed the measurements. These data were discarded from consideration. During the early summer period, maximum hourly transpiration (0.2 mm h^{-1}) in the larch stand was measured in July. Similar maximum daily transpiration rates were observed in June and July. At the *Pinus mugo* site, the maximum hourly (0.15 mm h^{-1}) and daily (1.1 mm d^{-1}) transpiration rates were measured in June. Daily mean transpiration rates per month ($E_{c\ bar}$) reached highest values in June and July (**Tab. 4.18**).

Tab. 4.18: Monthly sums of canopy transpiration, absolute daily maximum canopy transpiration rates and daily mean canopy transpiration for each month ($E_{c\ bar}$) in *Larix decidua* and *Pinus mugo* stand in Berchtesgaden National Park measured during 2002. * the daily mean was calculated for 2 weeks of successful observations and the monthly sum was calculated by multiplying the daily mean on observation days by the number of days in the month.

	Monthly sum (mm)		Daily maximum ($mm\ d^{-1}$)		Daily mean for each month (E_{cbar}) ($mm\ d^{-1}$)	
	Larix decidua	*Pinus mugo*	*Larix decidua*	*Pinus mugo*	*Larix decidua*	*Pinus mugo*
June	11	16	0.6	1.1	0.4	0.5
July	-	13*	-	1.0*	-	0.4*
August	-	9	-	0.9	-	0.3
September	-	6	-	0.2	-	0.2
June-September	-	44	-	-	-	-

For months with data gaps the monthly sum was calculated by the daily mean on successful observation days by the number of days in the month. During the measurement period, the transpiration was 11 mm in the larch stand in June, and varied from 6 to 16 mm month $^{-1}$ in the case of the dwarf pine (**Fig. 4.28**). The changes in climatic conditions – decrease in air and soil temperatures, vapor pressure deficits, and radiation inputs – could also partially explain the reduction in transpiration rates (ca. 40%) in August at the *Pinus mugo* site.

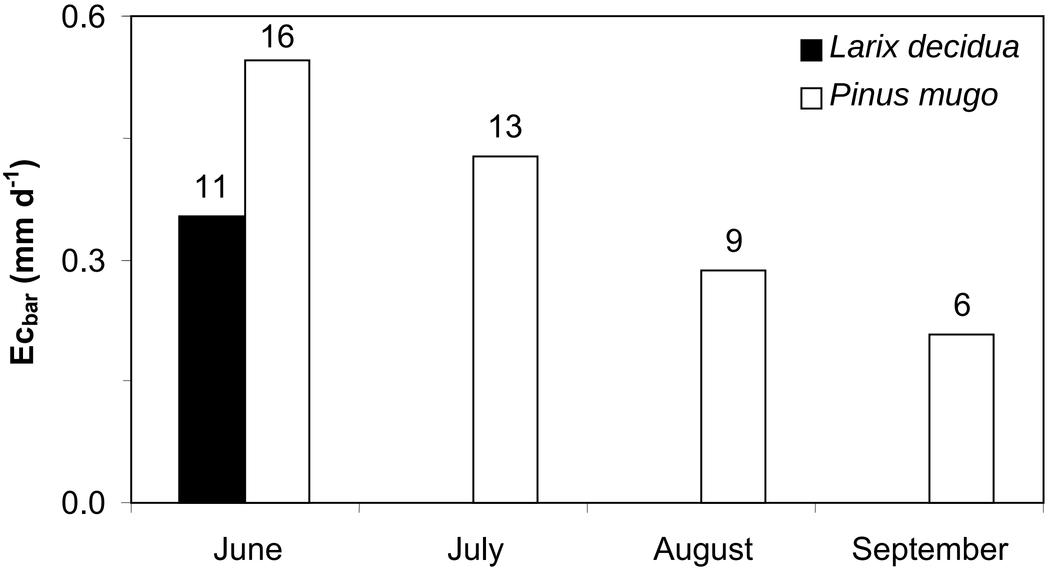

Fig. 4.28: Daily mean for each month in Larix decidua and Pinus mugo stand in Berchtesgaden National Park measured during 2002. Numbers on top of columns are estimates of the total monthly water use.

Significant higher monthly transpiration rates in June and July (ca. 5 and 3 mm) were measured for dwarf-pine shrub stands in comparison to larch trees (**Fig. 4.29**). The differences declined during the season.

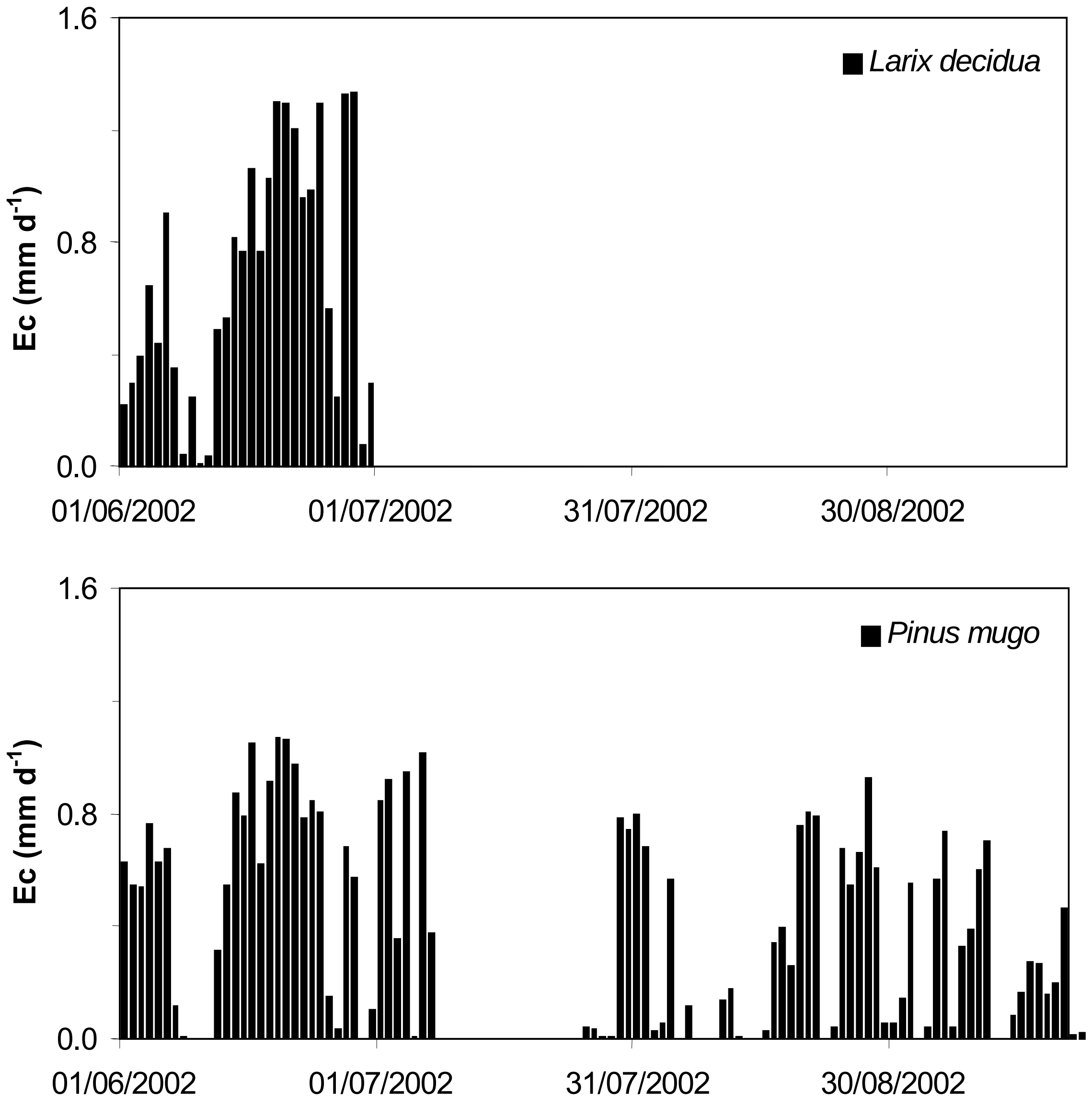

Fig. 4.29: Seasonal variation during summer 2002 in the daily sum of tree canopy transpiration measured at *Larix decidua* and *Pinus mugo* sites in Berchtesgaden National Park.

4.7. Lysimeter measurements

To estimate stand transpiration at the Kederbichl site, sapflow measurements in trees and *Pinus mugo* shrubs (to estimate water use of the "canopy") and lysimeter measurements (to estimate water loss from understory), were carried out. The average daily evapotranspiration from soil monoliths in *Larix decidua* stand measured on three summer days, 24, 29 and 31 of July 2002, reached

0.1 – 0.3 mm per day (**Fig. 4.30**). For a calculation of total stand water use on a clear day, 31 July was chosen, when the lysimeter and sapflow data for dwarf-pine shrubs are available. Because of faulty transpiration data for larch in July (see **3.5**), for an estimation of total stand water loss, the transpiration data from 3 June 2002 were used, when similar meteorological conditions occurred. The $PPFD_{max}$ and $PPFD_{integr.}$ measured on 3 June reached 1352 µmol m^{-2} s^{-1} and 37 mol m^{-2} d^{-1} and on 31 July reached 1437 µmol m^{-2} s^{-1} and 31 mol m^{-2} d^{-1}. The transpiration of *Larix decidua* trees (on 3 June) reached nearly 0.6 mm and from *Pinus mugo* (on 31 July) 0.7 mm; the evapotranspiration from the understory measured with the small weighing lysimeters approximated (on 31 July) 0.2 mm. In comparison, the modelled evapotranspiration of unshaded grass stands in Stubai valley (Tenhunen et al. unpublished) on the same day 31 July 2002 ($PPFD_{max}$ 1713 µmol m^{-2} s^{-1}) was much higher and reached 1.5 mm.

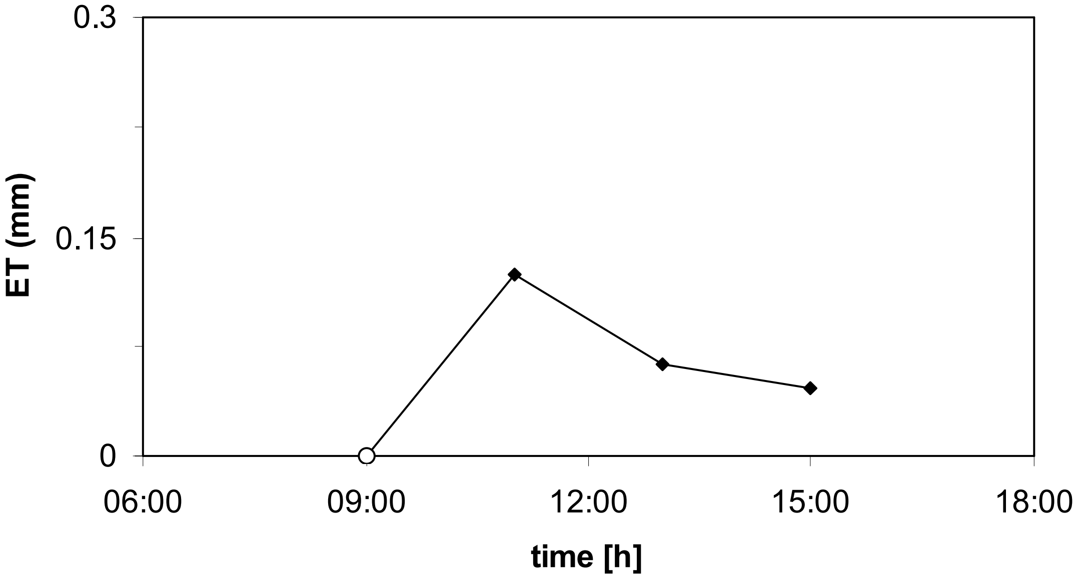

Fig. 4.30: Daily mean evapotranspirations course from understory in *Larix decidua* stand, measured with small lysimeters on 31.07. 2002. The start of measurements is marked with the circle.

4.8. Daily controls on canopy transpiration

Vapor pressure deficit of the air and PPFD can be used individually to predict the daily canopy transpiration in the spruce stands. The stomatal behaviour and in turn stand transpiration is regulated by air humidity (Alsheimer 1997; Köstner et al. 1996; Köstner et al. 1992). With an increase in maximum vapor pressure deficit in the air (VPD_{max}), a non-linear increase in daily water use (**Fig. 4.31**) occurred. Similar responses were described for all three experimental spruce sites. For mathematical description of the E_c - VPD relation a logarithmic function was chosen, i.e., an equation in which transpiration saturates with increasing vapor pressure deficit. The determined regression equations are as follows:

Bartholomä: $E_c = 0.614 \text{ Ln } (VPD_{max}) + 0.40$; $r^2 = 0.73$, **Eq. 4.4**,

Hirschengarten: $E_c = 0.360 \text{ Ln } (VPD_{max}) + 0.37$; $r^2 = 0.78$, **Eq. 4.5**,

Seeangerl: $E_c = 0.313 \text{ Ln } (VPD_{max}) + 0.33$; $r^2 = 0.60$, **Eq. 4.6**,

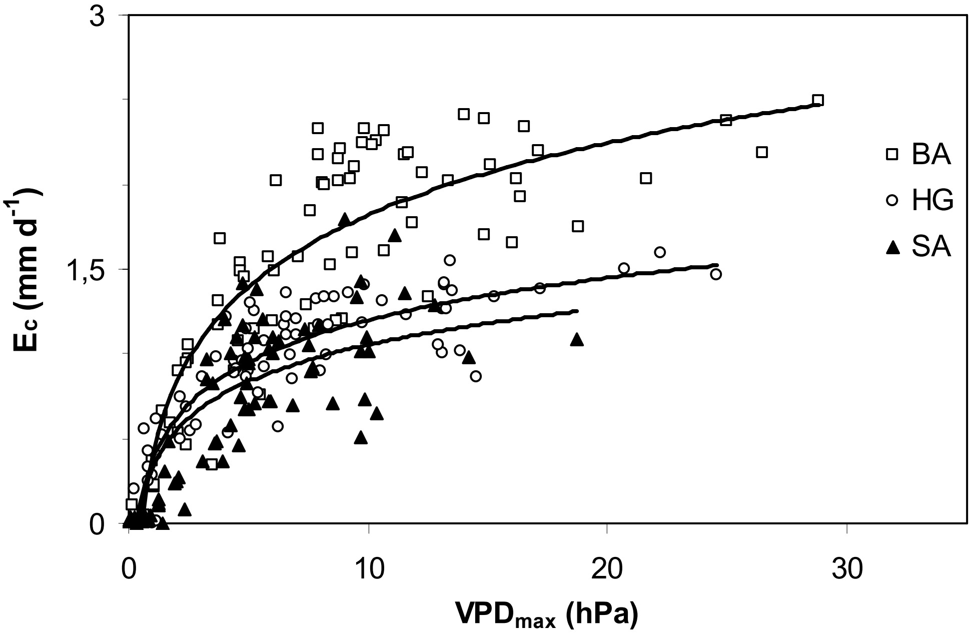

Fig. 4.31: Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily maximum half-hourly value of vapor pressure deficit (VPD_{max}) during the measurement period in 2002 in the three investigated spruce stands.

In the 630 m stand, the water use was much higher in comparison to the other two spruce sites.

A linear increase in daily stand transpiration with radiation integrated over the day at site Bartholomä is demonstrated in **Fig. 4.32**. On some days directly after rain periods, the measured stand water use was very low, despite high incoming radiation. Similarly, with low radiation input, transpiration was low on days with low humidity.

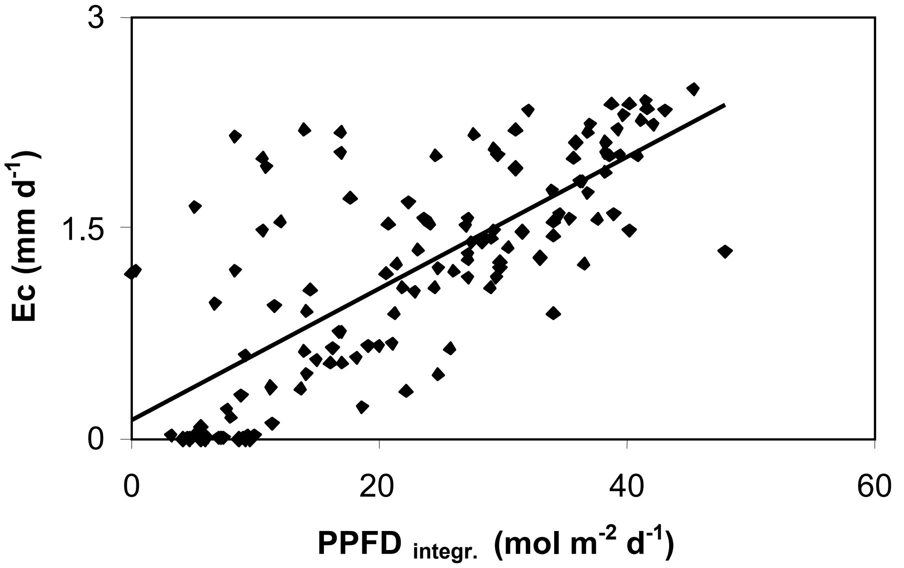

Fig. 4.32: **Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily sums of photosynthetic photon flux density (PPFD) during the measurement period in 2002 in the investigated spruce stand Bartholomä.**

The correlation between the daily spruce stand transpiration and PPFD integrated over the day can be described as:

$E_c = 0.047\ \mathrm{PPFD}_{\mathrm{integr.}} + 0.1293$, $r^2 = 0.56$ **Eq. 4.7**,

In the experimental beech stand, an increase in daily water use also occurred with an increase of maximum vapor pressure deficit in the air ($\mathrm{VPD}_{\mathrm{max}}$) (**Fig. 4.33**), but for each month the transpiration capacities were associated with different $\mathrm{VPD}_{\mathrm{max}}$ values. The lowest increase in daily water use with the $\mathrm{VPD}_{\mathrm{max}}$ was observed in June. The saturation curve for June incline gently, while in July and August a rapidly rise in transpiration rates with increasing maximum vapor pressure deficit can be observed.

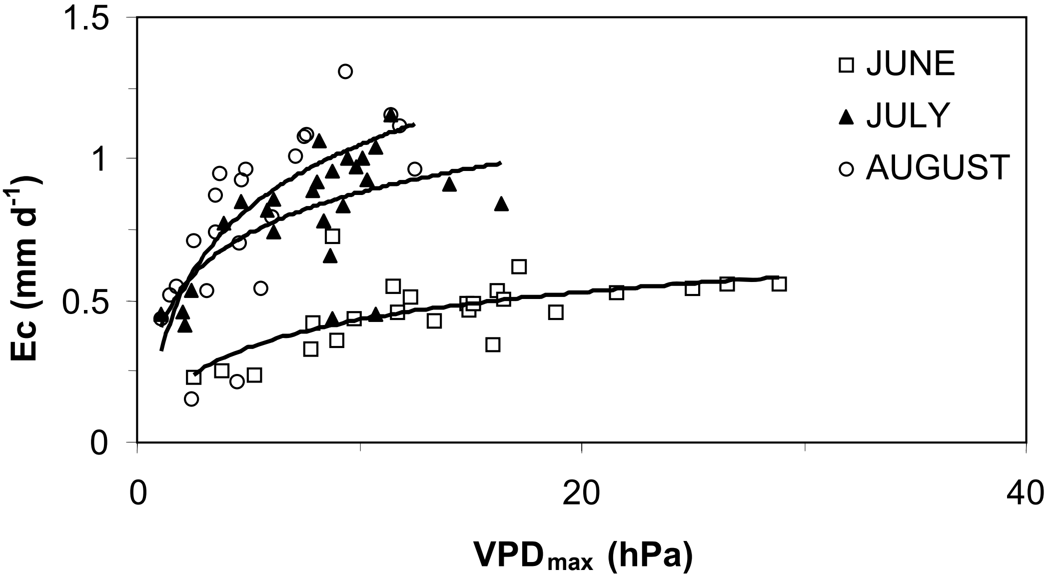

Fig. 4.33: Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily maximum half-hourly value of vapor pressure deficit (VPD_{max}) during the measurement period in 2002 in the investigated beech stand.

The determined regression equations are as follows:

June: $E_c = 0.141 \ln(VPD_{max}) + 0.1083$; $r^2 = 0.47$, **Eq. 4.8**,

July: $E_c = 0.211 \ln(VPD_{max}) + 0.3941$; $r^2 = 0.41$, **Eq. 4.9,**

August: $E_c = 0.325 \ln(VPD_{max}) + 0.3009$; $r^2 = 0.52$, **Eq. 4.10**,

As reported in other studies (Stickan and Zhang 1992), photosynthetic photon flux density (PPFD) has been used as a useful predictor of daily canopy transpiration in the beech stands (**Fig. 4.34**). In some periods after rain events or on the days with high relative humidity the transpiration rates were low despite high radiation input. Low transpiration rates were recorded in the middle of August after two weeks of strong rain events.

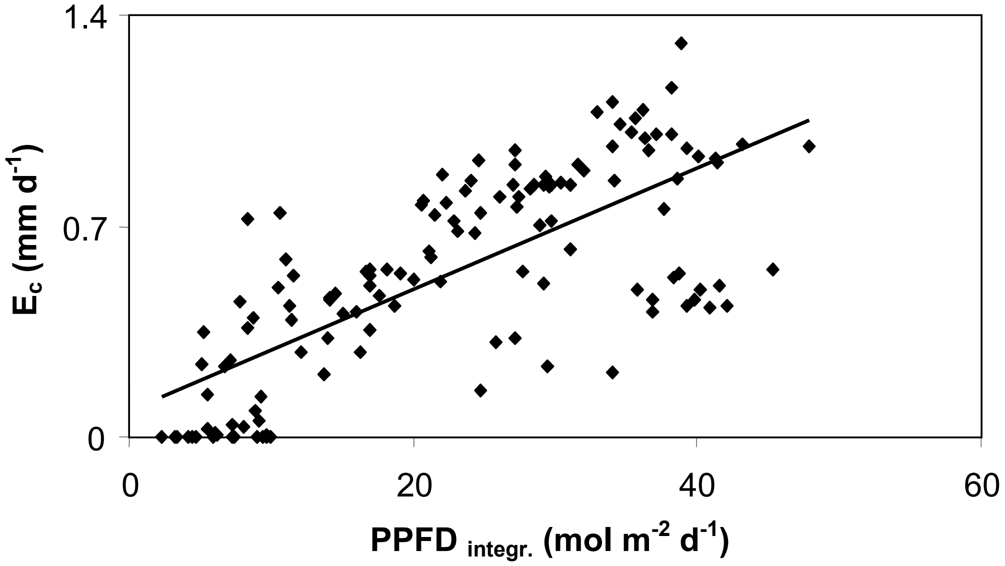

Fig. 4.34: Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily sums of photosynthetic photon flux density (PPFD) during the measurement period in 2002 in the investigated beech stand.

The following regression equation was found:

$E_c = 0.020 \text{ PPFD}_{\text{integr.}} + 0.09$ $r^2 = 0.53$, **Eq. 4.11**

An increase in the daily transpiration rates with increase in maximum vapor pressure deficit in the air (VPD_{max}) was observed also for larch and dwarf-pine sites (**Fig. 4.35**). The response of transpiration to maximum vapor pressure deficit for dwarf-pine shrubs differed from that of European larch trees growing at the same site.

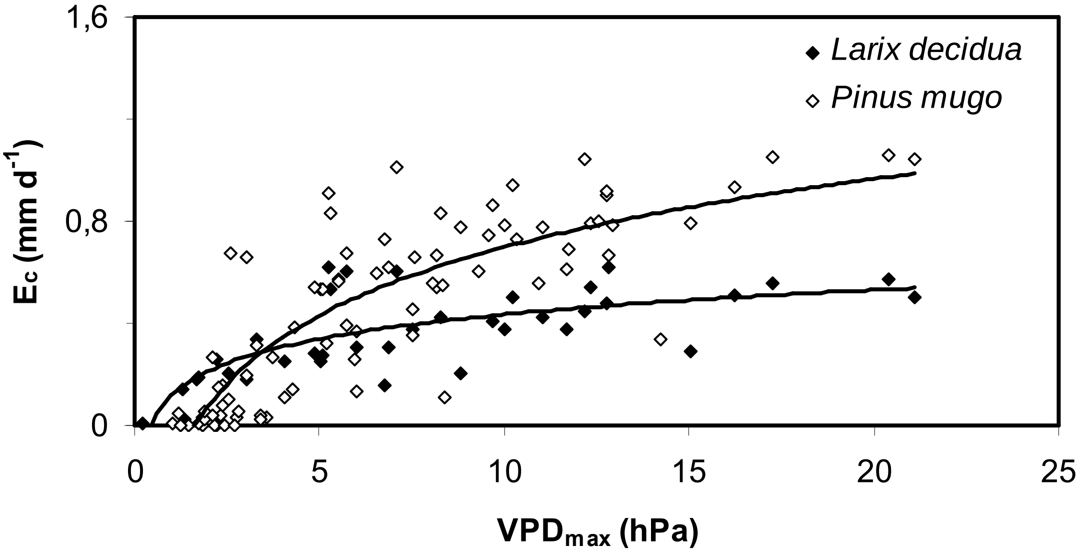

Fig. 4.35: Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily maximum half-hourly value of vapor pressure deficit (VPD_{max}) during the measurement period in 2002 in investigated larch and dwarf-pine stands. For larch trees only data from June and July were considered.

Regression equations are as follows:

Larix decidua: $E_c = 0.138 \ln (VPD_{max}) + 0.12$; $r^2 = 0.53$ **Eq. 4.12**,

Pinus mugo: $E_c = 0.386 \ln (VPD_{max}) - 0.19$; $r^2 = 0.069$ **Eq. 4.13**,

The linear response of transpiration of the larch and pine stands to increasing radiation is demonstrated in **Fig. 4.36**. A better correlation between transpiration and PPFD was found for larch trees than for the dwarf-pine shrubs. Because of frequently occurring short rain events and fog, the transpiration rates, especially for dwarf-pine, were low despite relatively high integrated PPFD values.

The following regression equations were found:

Larix decidua: $E_c = 0.027\ PPFD_{integr.} + 0.063$ $r^2 = 0.49$, **Eq. 4.14**,

Pinus mugo: $E_c = 0.016\ PPFD_{integr.} + 0.098$ $r^2 = 0.27$, **Eq. 4.15**,

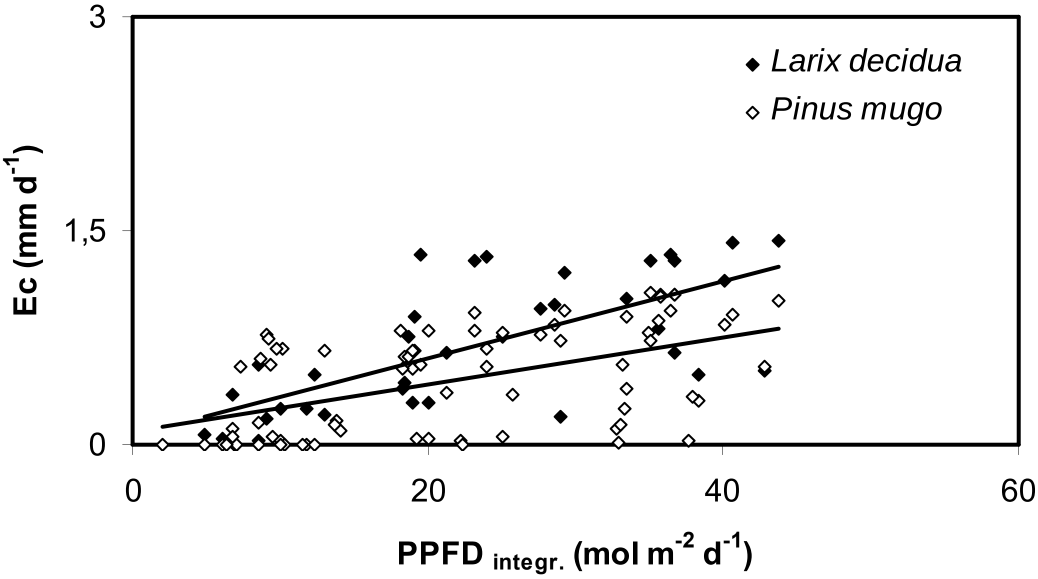

Fig. 4.36: Relationship of diurnal integrated tree canopy transpiration (E_c) to the daily sums of photosynthetic photon flux density (PPFD) during the measurement period in 2002 in investigated larch and dwarf-pine stands. For larch trees only data from June and July were considered.

4.9. Daily controls on canopy conductance

Canopy conductance (g_t) was derived from canopy transpiration, vapor pressure deficit in the air (VPD) and air temperature. In this study, g_t was analyzed only for data from clear days between 7 a.m. and 2 p.m. Canopy conductance increased in the morning, reached its maximum toward noon and decreased during the afternoon. In **Fig. 4.37**, the relationships between g_t and VPD at three experimental spruce sites are shown. In three spruce stands, canopy conductance declined with increasing vapor pressure deficit. In contrast to transpiration, the maximum canopy water vapor transfer conductance (g_{tmax}) decreased linearly with maximum vapor pressure deficit (VPD_{max}). During the measurement period, in three investigated spruce stands, the maximum canopy conductance – estimated for clear days between 7 a.m. and 2 p.m. – reached similar values, at Bartholomä approximately 20 mm s^{-1}, at Hirschengarten and Seeangerl 15 mm s^{-1}.

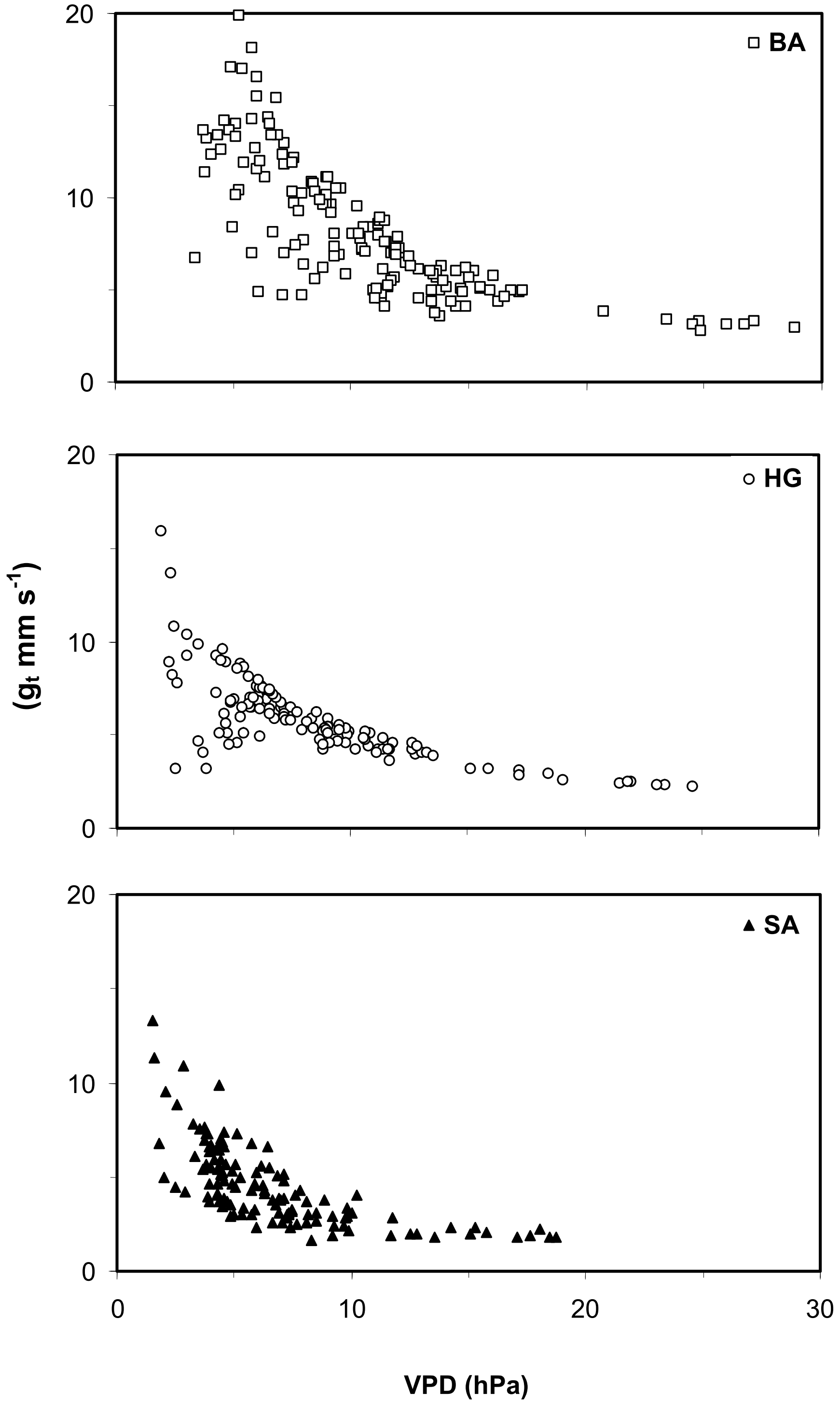

Fig. 4.37: Relationship between half hourly data of vapor pressure deficit in the air (VPD) and canopy conductance (g_t) in three investigated spruce stands.

A strong decrease in the canopy conductance with increasing maximum vapor pressure deficit was also observed for the beech stand (**Fig. 4.38**). The maximum value of g_t measured on clear days between 7 and 14 hour reached ca. 30 mm s^{-1}.

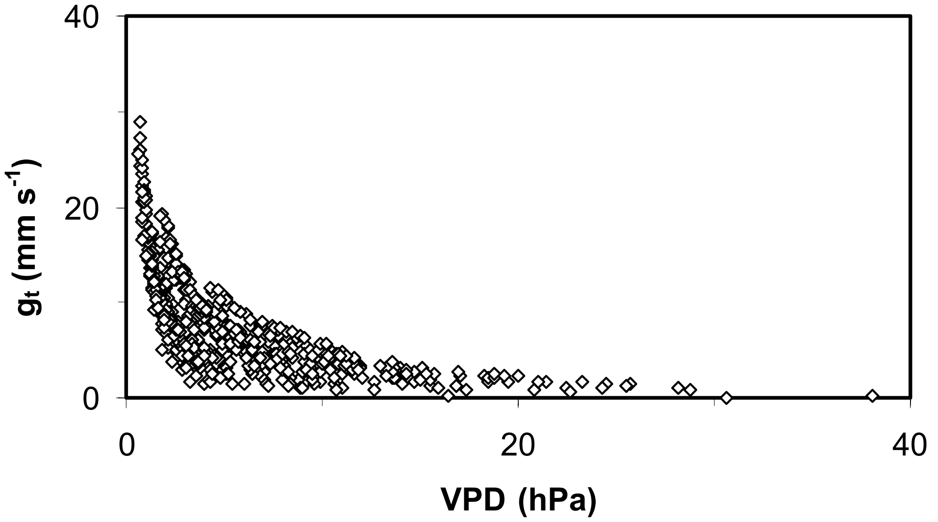

Fig. 4.38: Relationship between half hourly data of vapor pressure deficit in the air (VPD) and canopy conductance (g_t) in the *Fagus sylvatica* stand.

The daily courses of canopy conductance (gt) for *Larix gmelinii* (Rupr.) stand was similar to the courses for spruce trees (Bauer 1993; Fischer 1993) and *Nothofagus fusca* in New Zealand (Köstner et al. 1992). These species seem to show a high sensitivity to light, quickly opening the stomata, and the daily course of sapflow is parallel to the VPD course. In the morning occurred a strong increase in the gt, and the maximum was reached before the sapflow reached its maximum value. After reaching its maximum the canopy conductance continuously declined, whereas the transpiration rates increased.

Because the larch trees do not build a closed canopy, the precise estimation of canopy conductance is not possible at this location. For analysis of canopy conductance at *Pinus mugo* site, only periods between 8 a.m. and 2 p.m. on clear days were considered. The maximum canopy conductance observed for dwarf-pine reached ca. 10 mm s^{-1}. The response of g_t to the VPD is similar to other investigated species; with increasing vapor pressure deficit, a strong decrease in the conductance is demonstrated in **Fig. 4.39**.

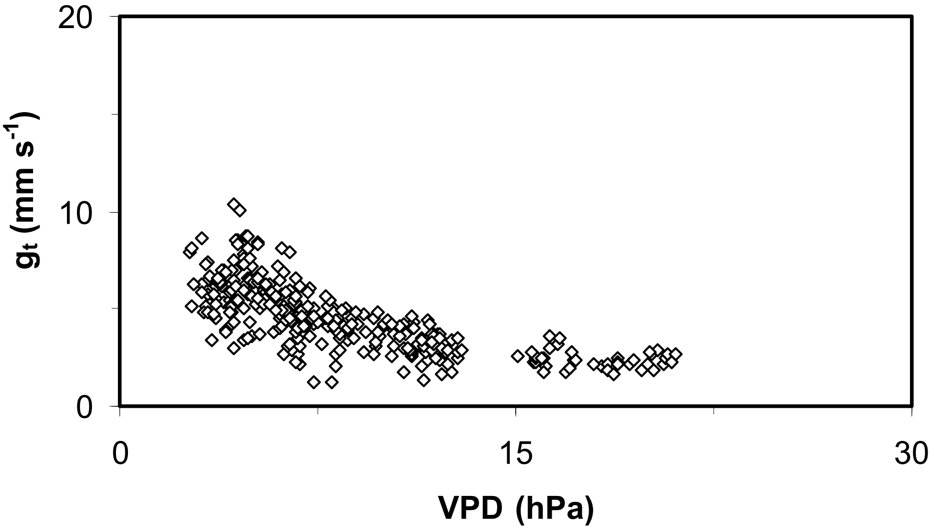

Fig. 4.39: Relationship between half hourly data of vapor pressure deficit in the air (VPD) and canopy conductance (g_t) in the *Pinus mugo* stand.

4.10. Model

In this work for estimation of water fluxes in Norway spruce stands along an elevation gradient, the GAS-FLUX model was used as an analysis tool. The changes in transpiration rates between stands were estimated according to two hypotheses: 1) differences in carboxylation capacity (Vc_{max}) depending on N concentration in the leaves occur along the elevation gradient, and 2) changes in the portion of leaves that are active occur, i.e., the degree of expression of patchy stomatal closure changes along the elevation gradient.

The leaf nitrogen content should influence photosynthetic capacity, which in turn in the model has an impact on stomatal conductance and transpiration. The highest mean nitrogen concentration in current-year needles was measured at the site Bartholomä. At the other, higher situated spruce sites, the N-contents were ca. 15 – 25% lower (see chapter **4.3**). In 1-year-old needles nitrogen concentrations varied between stands, but changes along an elevation gradient were not observed. However the measurements of nutrient concentration were done only once – in the middle of July – and they might change during the season. In GAS-FLUX, the parametrization is only implicitly affected by nitrogen concentration, for instance by changing the value of Vc_{max} according to the nitrogen content of the leaves. Due to the lack of the seasonal information on leaf N content, we avoided parametrization changes with N, but estimated Vc_{max} to match the observed transpiration rates. Values of fvc (Vc_{max}) obtained for three investigated stands are given in **Tab. 4.19**.

Tab. 4.19: Parameters of the GAS-FLUX model which were used in this study. I. Physiology - changed fvc, II. Patchiness - changed proportion of leaves that are active. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl. c = 0.75*fvc.

	Stand	I. Physiology	II. Patchiness	Unit
fvc	BA	7.0	7.0	µmol m^{-2} s^{-1}
	HG	3.7	7.0	µmol m^{-2} s^{-1}
	SA	3.45	7.0	µmol m^{-2} s^{-1}
Portion of leaves	BA	1	1	-
that is alive	HG	1	0.66	-
	SA	1	0.33	-

The relationships between measured ($E_{c\ meas}$ mm d^{-1}) and modelled ($E_{c\ mod}$ mm d^{-1}) canopy transpiration for three Norway spruce stands are shown in **Fig. 4.40**.

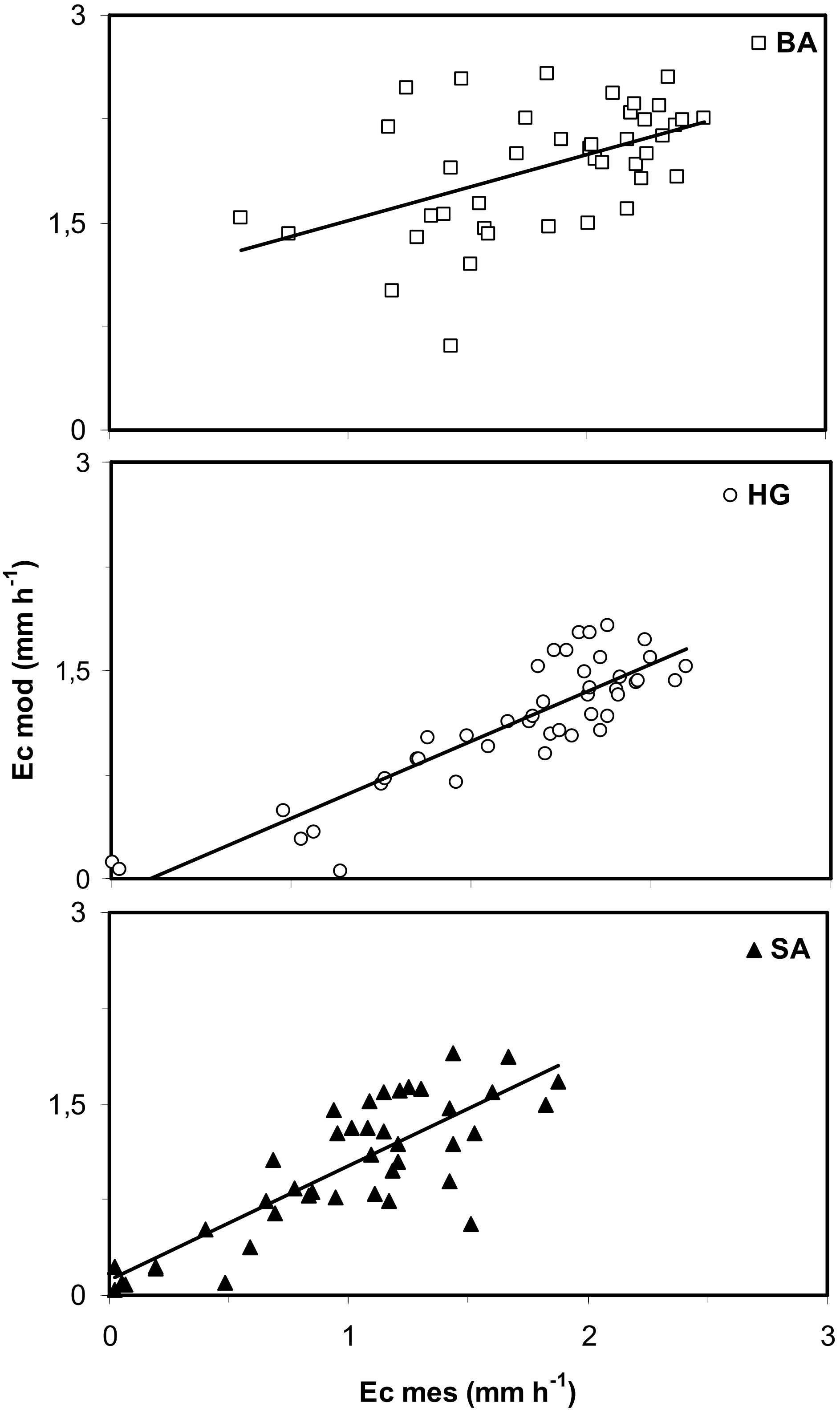

Fig. 4.40: Relationship between measured and modelled daily transpiration on the clear days for three investigated spruce stands. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl. Portion of leaves that is alive was kept constant, the fvc was changed.

The following relationships between modelled and observed data were found:

Bartholomä: $E_{c\,mod} = 0.478\, E_{c\,meas} + 1.032$, $r^2 = 0.25$ **Eq. 4.16**

Hirschengarten: $E_{c\,mod} = 1.105\, E_{c\,meas} - 0.117$, $r^2 = 0.78$ **Eq. 4.17**

Seeangerl: $E_{c\,mod} = 0.894\, E_{c\,meas} + 0.119$, $r^2 = 0.68$ **Eq. 4.18**

According to the second hypothesis for estimation of differences in transpiration rates, the patchiness factor for three measuring sites was adjusted. Stomata in adjacent areas or patches on a leaf may respond differently to environmental stimuli (Buckley et al. 1999; Mott and Buckley 1998). The stomatal behaviour on the same leaf can therefore be heterogeneous and the conductance of each patch may change independently from other areoles. The relationships between measured ($E_{c\ measured}$) and modelled ($E_{c\ mod}$) canopy transpiration are shown in **Fig. 4.41** and the required parameter changes in **Tab 4.19.** The following relationships between modelled and observed daily transpiration data were found:

Bartholomä: $E_{c\,mod} = 0.478\, E_{c\,meas} + 1.032$, $r^2 = 0.25$ **Eq. 4.19**,

Hirschengarten: $E_{c\,mod} = 1.072\, E_{c\,meas} - 0.10$, $r^2 = 0.78$ **Eq. 4.20**,

Seeangerl: $E_{c\,mod} = 0.890\, E_{c\,meas} + 0.13$, $r^2 = 0.7$ **Eq. 4.21**,

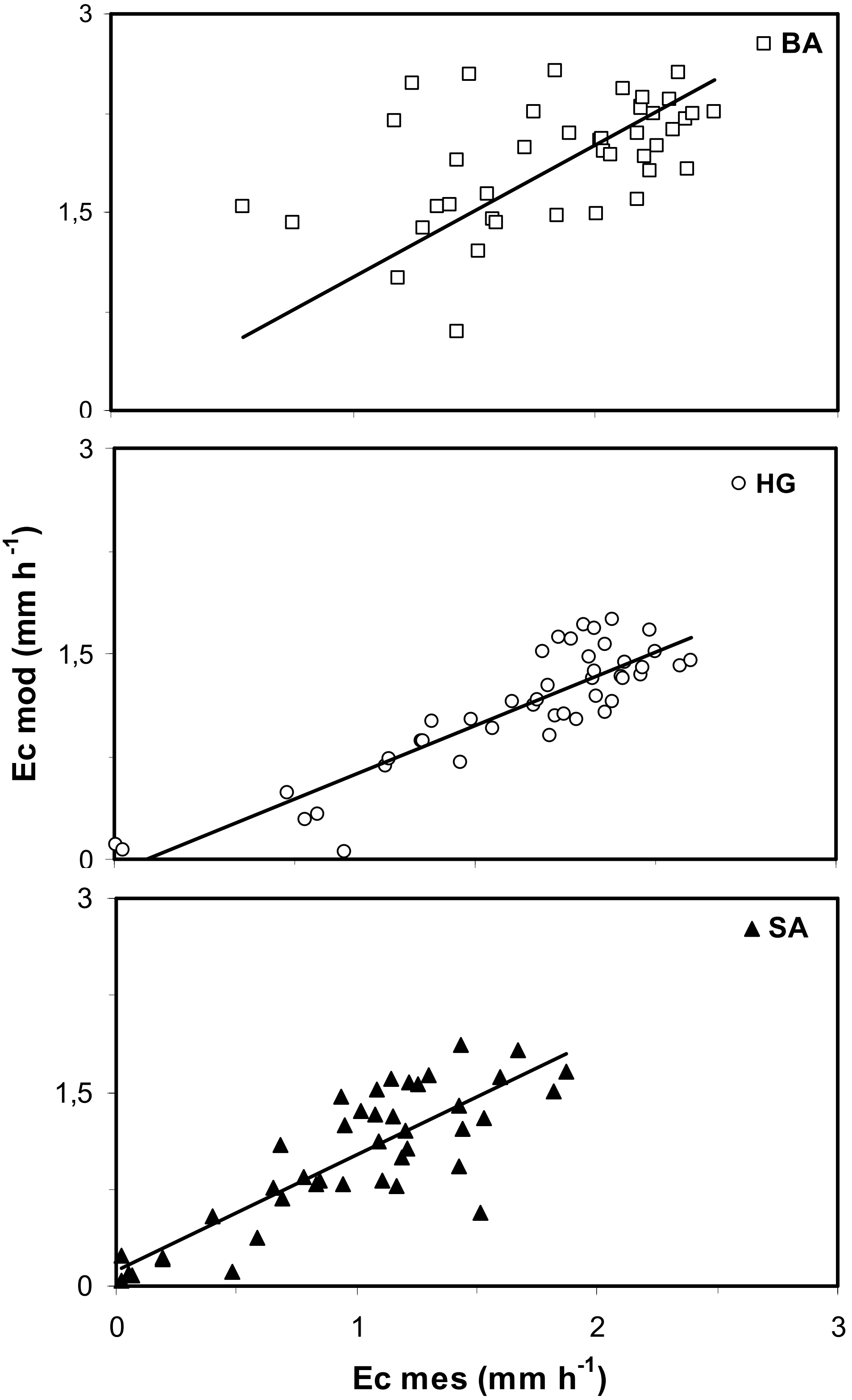

Fig. 4.41: Relationship between measured and modelled daily transpiration on the clear days for three investigated spruce stands. BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl. The fvc was kept constant; the portion of leaves that is alive was changed.

The mean daily transpiration rates for each month estimated with the GAS-FLUX model are shown in the **Tab. 4.20**. The daily transpiration was predicted for days, on which the sapflow measurements were successful. Because of gaps in radiation data, the monthly transpiration rates cannot be calculated. The transpiration rates estimated with changing of Vc_{max} and portion of leaves that is active in gas exchange give similar results.

Tab. 4.20: Daily means of transpiration rates estimated with changing fvc (Physiology) and with changing proportion of leaves that are active (Patchiness) BA = Bartholomä, HG = Hirschengarten, SA = Seeangerl.

	I. Physiology			II: Patchiness		
	BA (630 m)	HG (1040 m)	SA (1360 m)	BA (630 m)	HG (1040 m)	SA (1360 m)
	$E_{c\ mean}$ (mm d^{-1})					
May	1.1	0.7	0.4	1.1	0.7	0.4
June	1.5	0.9	0.8	1.5	0.9	0.8
July	1.4	0.8	0.8	1.4	0.8	0.8
August	0.9	0.6	0.4	0.9	0.6	0.4
September	0.6	0.3	0.5	0.6	0.3	0.5

For simplification of the calculation and due to the lack of “in situ” data, identical temperature constants from Davos (see **3.8.1**) were chosen for the three experimental sites, which have an influence of the modelled results. The results from the GAS-FLUX model for Hirschengarten and Seeangerl show better agreement with the measured data than for Bartholomä, whereas the correlation between the empirical PPFD and VPD models (see **4.7**) and observed data are more strongly correlated for 630 m site. Also the index of agreement (IA) for the higher situated stands is better than for the lowest situated spruce stand (see section **5.9**).

For the investigated stands, small trends in residual plots (modelled minus measured daily transpiration) in the “Physiology” and “Patchiness” model can be recognized whereas in the empirical models (VPD, PPFD) a trend with the not used factor was observed. In residual plots of the VPD model no trends with maximum VPD **(Fig. 4.42**) and an obvious trend with PPFD integrated over the day (**Fig. 4.43**) for Bartholomä and Seeangerl were observed, while for Hirschengarten a slight trend with VPD_{max} can be recognized.

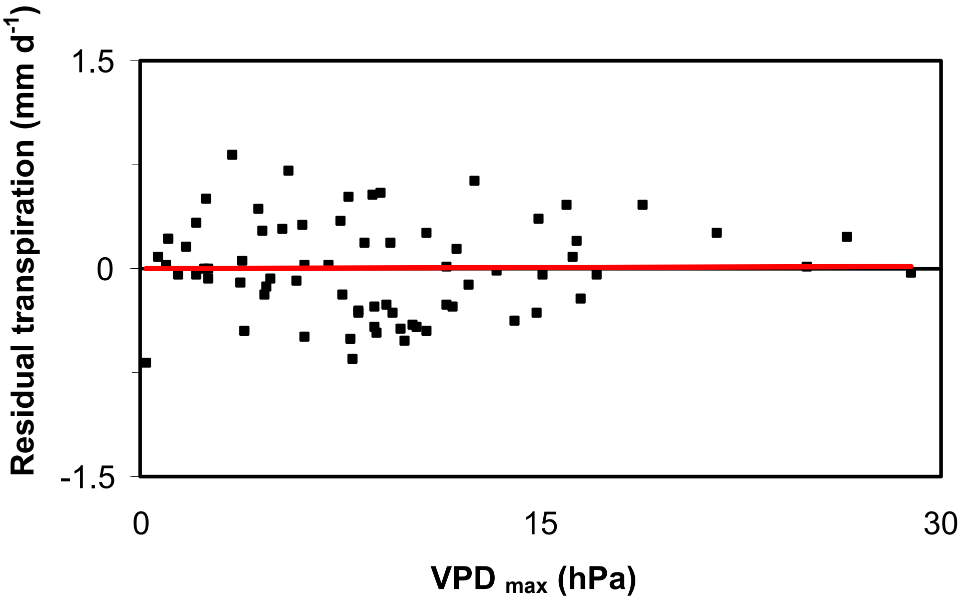

Fig. 4.42: Residual plots (observed minus modelled) for daily forest stand transpiration against VPD max for Bartholomä (VPD model).

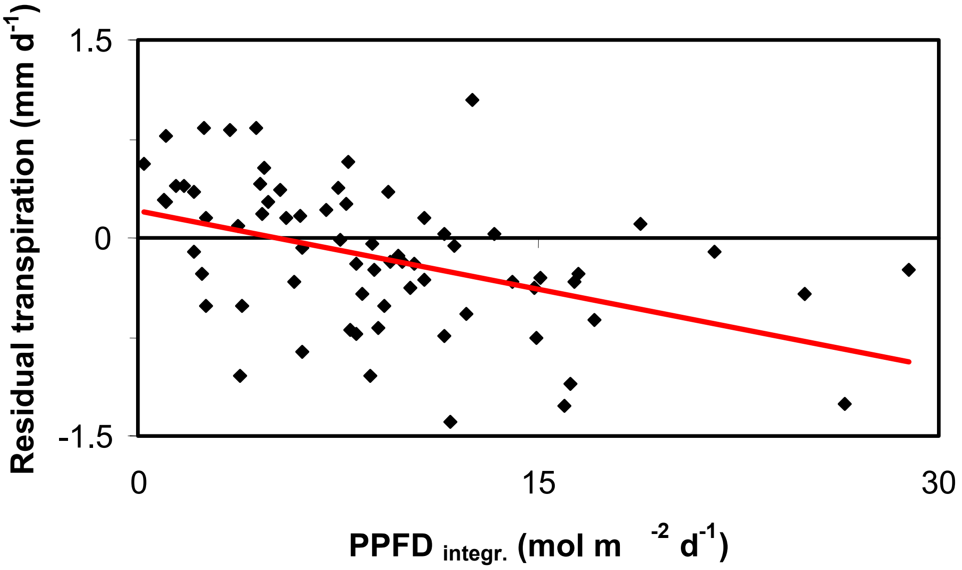

Fig. 4.43: Residual plots (observed minus modelled) for daily forest stand transpiration against PPFD integr. for Bartholomä (VPD model).

In residual plots of the PPFD model for the three experimental sites no trends with radiation but a trend with maximum vapor pressure deficit can be observed (data not shown).

Residual plots of “Physiology” and “Patchiness” model for Bartholomä show slight trends both with PPFD $_{integr.}$ and VPD_{max} (**Fig. 4.44**), whereas for Hirschengarten (in “Patchiness” model shows only a slight trend with VPD_{max}) and Seeangerl no trends with daily integrated radiation and maximum vapor pressure deficit can be found. The differences between predicted and measured stand water use were lower for Hirschengarten and Seeangerl than for Bartholomä - the daily residual transpiration were lower than 0.5 mm for the 1040 m and the 1360 m site, whereas for the 630 m site it reached ca. 1 mm.

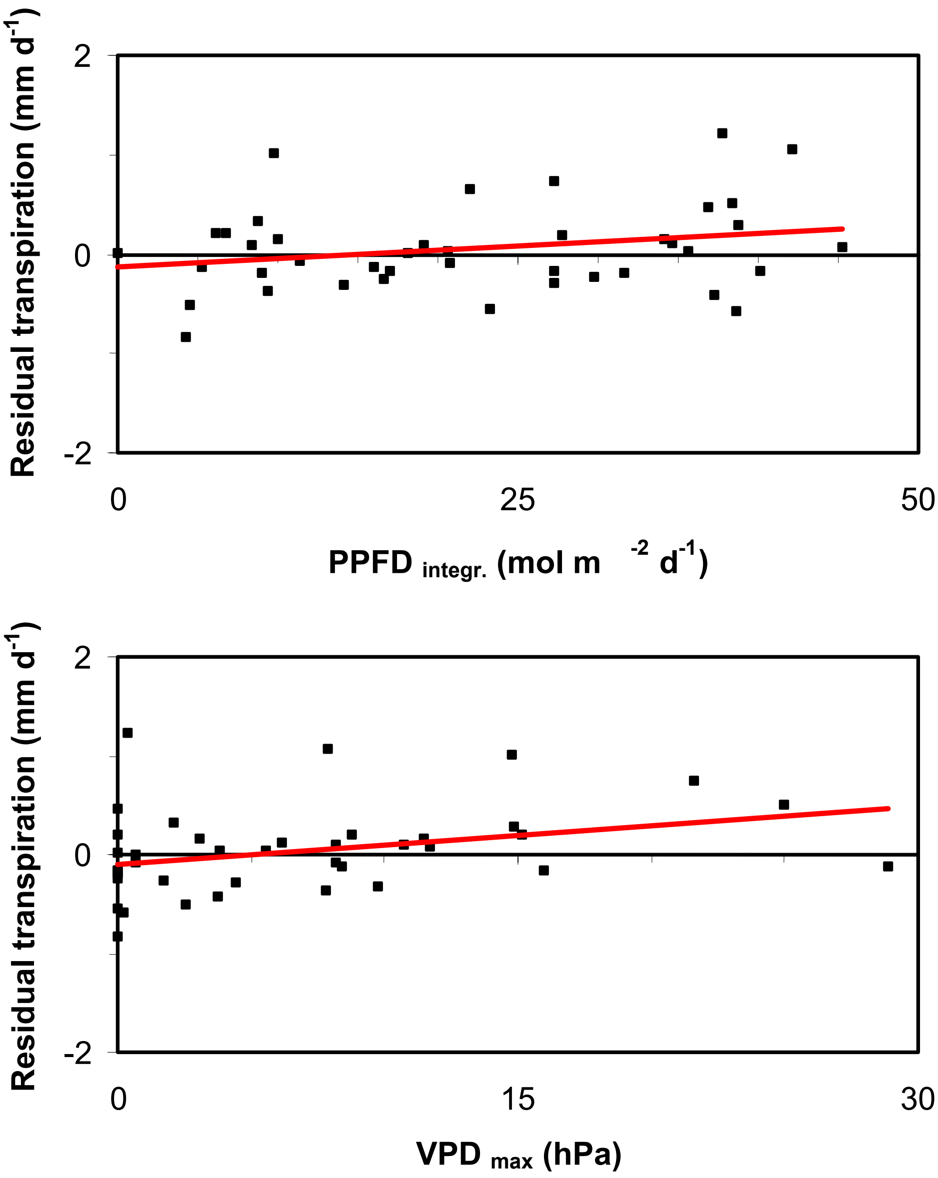

Fig. 4.44: Residual plots (observed minus modelled) for daily stand transpiration at the site Bartholomä ("Patchiness" model).

Data used for the half-hourly residual plots were collected on clear days between 10 and 14 hour. At Bartholomä, small trends with relative humidity, radiation and temperature were observed (**Fig. 3.45**). The model tends to overestimate the transpiration with air temperatures above 25°C and underestimates at lower temperatures. The half-hourly residual plots for Seeangerl show no trends with radiation and relative humidity (data not shown), while for both the Hirschengarten and Seeangerl sites a trend with temperature can be recognized. The trend in residual transpiration with air temperature at the Seeangerl site is shown in **Fig. 3.46**. At the beginning of season until 24 June, a model overestimation of transpiration and afterwards an underestimation can be observed. Half-hourly residual transpiration in “Physiology” and “Patchiness” models show a similar pattern (data not shown).

The significance and usefulness of the analysis is discussed in detail below (see section **5.9**).

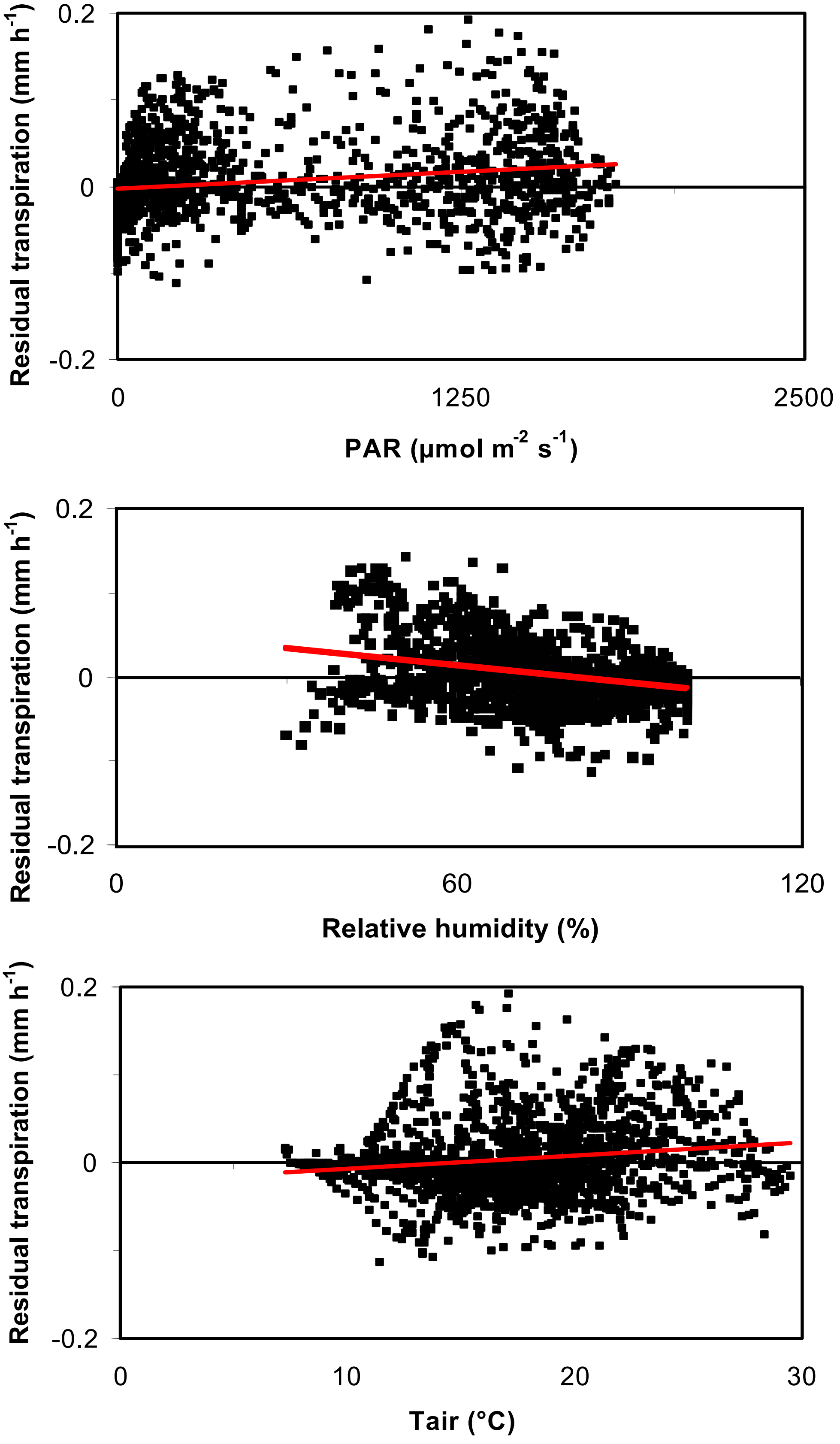

Fig. 4.45: Residual plots (observed minus modelled) for stand transpiration at site Bartholomä a) photosynthetically active radiation, b) air temperature, c) relative humidity ("Physiology" model).

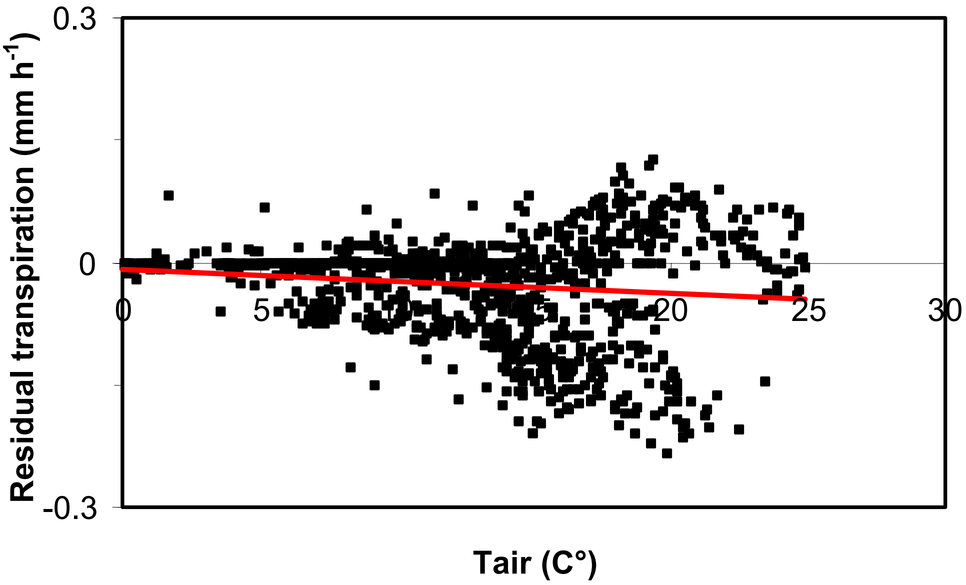

Fig. 4.46: Residual plots (observed minus modelled) for forest stand transpiration against air temperature for Seeangerl (“Patchiness” model).

5. DISCUSSION

5.1. Sapwood depth, sapwood area and annual growth

The growth and water use of forests depend on stand structure, stand age, climate and soil conditions (Alsheimer 1997; Granier 1985; Köstner et al. 1998b; Köstner 1996) and pollutants (Likens et al. 1996). With an increase of altitude the importance of air temperature for plant growth increases and the limiting effect of precipitation decreases. Air temperature is a crucial factor which modifies, the beginning, intensity and the end of annual growth of trees (Körner 1999; Tranquillini 1979), and seems to be limiting for tree growth at high elevations (Bassman et al. 2003) whereas at low altitudes water availability has often been reported as the main growth limiting factor (Alavi 1996; Burczyk and Giertych 1991; Cienciala et al. 1994; FAIR3-CT96-1310 2002). The decrease in diameter growth with increasing altitude is predominantly caused by the decline in air temperatures, because at lower temperatures the photosynthates are transformed to sugars and starch rather than cellulose, which can limit diameter increment (Tranquillini 1979). In this study, sapwood depth, current growth and stand age were estimated with fresh cores. The measurements of sapwood area with fresh cores, stem disks and computer tomography provide similar results (Alsheimer 1997; 1998; Granier et al. 1996a).

Norway spruce: Among three experimental *Picea abies* sites in National Park Berchtesgaden different incremental growth was observed. A correlation between air temperature and growth of Norway spruce has previously been found (FAIR3-CT96-1310 2002) at high altitude. The measurements of annual growth rings show a decline along the elevation gradient in Berchtesgaden, which can be related to the observed decreases in air and soil temperature with increasing altitude.

The mean stem diameter increment based on sapwood rings reached 0.31 cm year^{-1} at 630 m, 0.26 cm year^{-1} at 1040 m and 0.25 cm year^{-1} at the 1360 m site. However, the data based on forest inventory (Konnert 2001) suggest that the best climate conditions (soil and air temperature, humidity) for tree growth occurred at an elevation of 1040 m a.s.l., where the highest growth 7 – 8 m^3 year^{-1} ha^{-1} was measured. According to the forest growth map, 4 – 5 and 5 – 6 m^3 year^{-1} ha^{-1} were measured at the 630 m and 1360 m sites, respectively. But it should be noted that for the inventory, not only spruce trees but all species occurring in the experimental forest stands were taken into account, which may have an influence on the results.

Similarly to this study, the annual radial growth at breast height in spruce trees in the Seetal Alps, Austria, decreased from 0.6 cm at low altitude (700 m) to ca. 0.2 cm at the forest limit (1700 m) (Tranquillini 1979). The reduction in radial increment with elevation a.s.l. is related also to the shortening of the season length. According to Tranquillini (1979), the annual timber volume increment in 75-year-old stands of *Picea abies* at elevation between 1000 and 1300 m in the Central Massif, France, were 11-12 m^3 ha^{-1} year^{-1}, while at the timberline (1650 m) it was reduced to 1.3 m^3 ha^{-1} year^{-1} (Oswald 1969). Along elevation gradients, an increase in bark thickness was measured, which could be caused by the decrease in air temperatures or be stimulated by increased physical stress, e.g. snow abrasion, at high altitude. Bark builds a barrier which protects trees against biological, chemical, mechanical (abrasion, strain) as well as thermal factors (Legrand et al. 1996). The variation in bark structure is related to the age of the trees and tree species. Bark depth also changes depending on the location on the tree; it decreases from the base up to the top of the tree. A mean value of ca. 0.6 cm was reported by Legrand et al. (1996), which agrees well with the values found in this study.

The correlation between sapwood area and circumference at breast height for three investigated spruce sites in National Park Berchtesgaden may be expressed as S_A= 8.66 CBH – 304; r^2 = 0.94 (see **4.1**). In comparison, the correlation between sapwood area and circumference at breast height for 40-years old spruce stands in the Lehstenbach catchment derived from fresh cores (Alsheimer 1997) equals: $S_A = 0.047\ CBH^{2.02}$, $r^2 = 0.93$ and the correlation derived from different methods – coring, stem disks, computer tomography – equals: $S_A = 0.122\ CBH^{1.797}$, $r^2 = 0.89$. Correlations between stem circumference at breast height and cross–sectional sapwood area at the same height in three *Picea abies* stands in National Park Berchtesgaden and in the Fichtelgebirge are shown in **Fig. 5.1**.

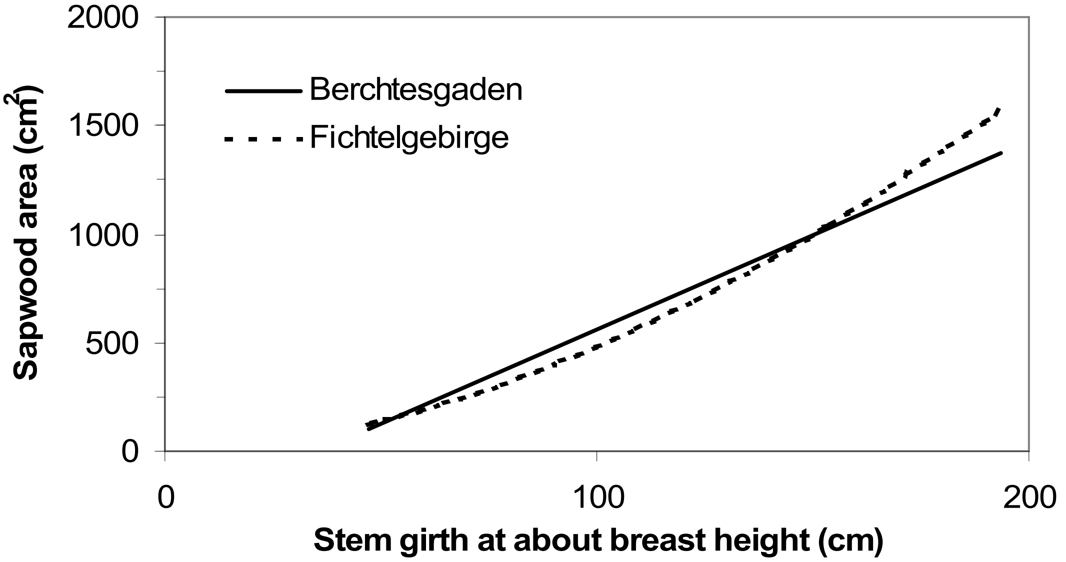

Fig. 5.1: Correlation between stem circumference at breast height and cross–sectional sapwood area at the same height in three *Picea abies* stands in National Park Berchtesgaden derived via coring in this study and in the Fichtelgebirge derived from different methods –coring, stem disks and computer tomography (Alsheimer 1997).

For the spruce stands in Berchtesgaden National Park a linear regression was chosen, whereas for the stands in Fichtelgebirge a power function was found (Alsheimer 1997). The estimation of sapwood area with both regressions gives similar results for the trees with circumference smaller than ca. 150 cm. For trees with circumference larger than 150 cm the sapwood areas estimated with the power function are larger in comparison to the areas calculated with the linear regression.

The up-scaling from tree to stand level for water fluxes is based on different tree-size classes. For the estimation of stand water use, tree classes have also been used in other studies (Cermak et al. 1995; Granier et al. 2000; Köstner et al. 1998a; Köstner et al. 1998b). The cumulative cross-sectional area for sapwood in the three experimental spruce stands was estimated from correlations between stem circumference at breast height and sapwood area of individuals trees. With an increase in circumference, an increase both in sapwood depth and sapwood area was observed. The relationship between sapwood area and tree size was very similar in all three experimental spruce stands. Because of this, and because the highest stand basal area was measured in the 1360 m stand and the lowest in the 630 m stand, it must be concluded that the differences in transpiration rates along the elevation gradient are caused by other than structural factors, i.e., meteorological parameters or physiological regulation.

Köstner et al. (1996) observed a decrease in canopy transpiration with stand age. However, in this study, the variations in water use among three investigated *Picea abies* stands could not be explained by differences in the age of trees. The three experimental Norway spruce sites, Bartholomä, Hirschengarten and Seeangerl, are of similar age: 40-, 60-, 50-year-old, respectively. Furthermore, the highest water use was observed in the 40-year-old stand Bartholomä and the lowest in 50-year-old stand Seeangerl.

European beech: Unfortunately, in beech trees, the visual distinction between sapwood and heartwood is very difficult (Granier et al. 2000; Kubota et al. 2005). To improve estimation of the active sapwood ring, a bromocresol green dye was used (Fischer et al. 2002). The cumulative cross-sectional sapwood area for the investigated European beech stand in the National Park Berchtesgaden, was estimated from the correlation between stem circumference at breast height and sapwood area of individuals trees. With an increase in circumference an increase in sapwood depth and in sapwood area occurs. For the investigated beech site Bartholomä, the following correlation between sapwood area and stem circumference at breast height $S_A = 0.049$ CBH $^{2.078}$; $r^2 = 0.98$ was found (see **4.1**). In comparison, the relationship between stem diameter (DBH) and sapwood area for Bartholomä can be described as $S_A = 0.6025$ DBH$^{2.0546}$ and for beech trees with diameters from 18 to 34 cm in a similar stand Farrenleite, Fichtelgebirge as $S_A = 0.793$ DBH$^{1.935}$. (Schmidt, M. personal communication). Correlations between stem diameter at breast height and cross–sectional sapwood area in the *Fagus sylvatica* stand in National Park Berchtesgaden and in the Farrenleite are shown in **Fig**. **5.2.**

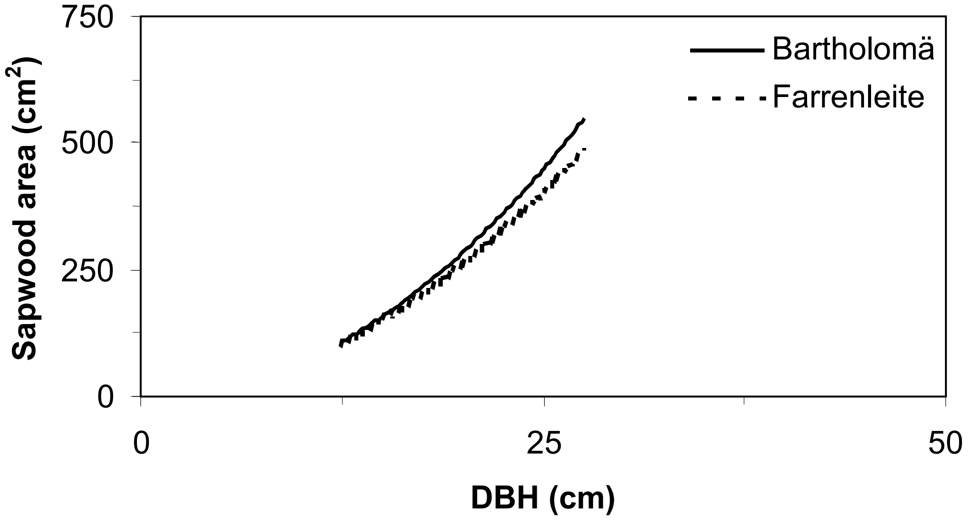

Fig. 5.2 Correlation between stem diameter at breast height and cross–sectional sapwood area at the same height in *Fagus sylvatica* stand in National Park Berchtesgaden and in the Farrenleite (Schmidt, M. personal communication).

For these two 40-year-old *Fagus sylvatica* sites similar relationships between sapwood area and stem diameter were found.

The average xylem thickness, measured in the beech stand Bartholomä, was 7.1 cm resulting in a total cross-sectional sapwood area for the stand of 14.1 m^2 ha^{-1}. In comparison, the sapwood thickness measured in three *Fagus sylvatica* trees in mountainous Mediterranean region ranged between 0.9 – 2.2 cm (Marc and Robinson 2004). The investigated European beech trees were ca. 40 years old, but several old trees were scattered within the stand. The beech trees are of similar age to the Norway spruce trees occurring at the same elevation. In comparison the mean tree age of the Sapine experimental site (Marc and Robinson 2004) was estimated as 38 years, the circumference of sampled trees was in the range of 16 – 47 cm, whereas the beech trees at Bartholomä had a circumference from 45 to 225 cm. Although of similar age the Mediterranean beech trees at elevation 1300 m a.s.l. are characterized by a significantly lower growth and a lower sapwood depth as the investigated comparison trees occurring in Berchtesgaden at 630 m a.s.l.

The mean bark thickness reached 0.56 cm in beech trees, and was similar to bark measured in spruce trees at the same elevation.

European larch and dwarf-pine: European larch trees are characterized by a thin active sapwood layer. In experimental *Larix decidua* trees in the National Park Berchtesgaden, the sapwood thickness ranged from 1.0 to 3.2 cm and the sapwood area ranged from 143 to 611 cm^2. Mean age determined for three larch trees in which the annual ring was best defined was 190 years. A thin sapwood layer was also observed in *Larix gmelinii* in Siberia (Arneth 1994; 1996). The mean sapwood depth at their measurement site, with the average age of 127 years, reached 0.94 ± 0.13 cm and the sapwood area of individual trees with circumference of 36.5 – 80.0 cm, ranged from 27.2 to 76.3 cm^2. The sapwood depth measurements suggest that only a slight increase in the xylem increment occurs with larch trees' age. The annual growth in larch trees decline along an elevation gradient. According to Tranquillini (1979) the annual radial increment measured in larch seedlings along an altitudinal transect decline from 1.43 mm at 700 m to 0.97 mm at 1300 m and 0.34 mm at 1950 m.

The estimation of tree age and annual growth in larch trees at the site Kederbichl was very difficult because the annual increment was very low. In *Larix decidua* trees, sapwood area increases slightly with increasing circumference at breast height (**Fig. 4.3**), but the correlation is poor. In mixed stands of *Picea abies*, *Larix decidua* and *Pinus cembra* trees, occurring at elevations between 1600 – 2020 m, the annual volume increments were in the range of 2 – 2.5 m^3 ha^{-1}, whereas in open-crowned stands, the annual growth was much lower and ranged from 0.6 to 1.0 m^3 ha^{-1} (Tranquillini 1979). The mean bark depth measured at the site Kederbichl reached 1.1 cm. In comparison the bark thickness of two larch trees occurring at elevation 630 m a.s.l. reached 1.1 and 1.8 cm.

In *Pinus mugo* branches no heartwood was present. The sapwood depth was equal to the mean diameter of branches (under bark) and reached 4.6 – 8 cm. The xylem area was in the range of 15 – 45 cm^2. The sapwood depth and sapwood area in dwarf-pine were much lower than values measured in other *Pinus* species occurring in northern Arizona. Mean sapwood depth measured in *Pinus ponderosa* varied between 3.1 and 26 cm, and in *Pinus flexilis* between 3.8 and 13.6 cm (Fischer et al. 2002). The xylem area varied from 123 to 3134 cm^2 and from 132 to 1375 cm^2 in *P. ponderosa* and *P. flexilis* trees, respectively. The mean bark thickness measured in dwarf-pine in this study reached ca. 0.3 cm.

5.2. Leaf area index

For the estimation of LAI in three spruce stands and one beech stand allometric functions were used. This method is nondestructive and inexpensive, but is more suitable for LAI estimations for conifer forests. With an allometric function, only one LAI value may be calculated, while the seasonal dynamics in leaf area in deciduous forests are not taken into account. On the other hand, the expansion time period of leaves is usually short (ca. two weeks after bud break). More gradual change occurs during leaf shedding in fall; however, the physiological activity of leaves over this period is reduced. Thus, the LAI maximum is an important value determining fluxes for most of the period when high rates of transpiration occur.

Norway spruce: The LAI was calculated with an allometric function (section 3.2.4.1). Along the elevation gradient in the National Park Berchtesgaden, no significant changes in leaf area index among experimental spruce sites were observed. The estimated LAI for the 630 m site reached 6, and for the other two spruce stands 7 m^2 m^{-2}. The values are typical for spruce stands. The leaf area index in a 142-year-old *Picea abies* stand Waldstein, Germany, with tree density of 363 tree ha^{-1}, at an elevation 700 m, reached 6.8 m^2 m^{-2} (Bauer et al. 1997). The projected leaf areas for six Norway spruce stands measured by Alsheimer (1997) were in the range of 5.3 - 7.9 m^2 m^{-2}.

European beech: LAI was derived from an allometric relationship (section 3.2.4.2). The leaf area index of the European beech stand Bartholomä, where the tree density reached 1205 trees ha^{-1}, was 6 m^2 m^{-2}. Schäfer et al. (2000) used a harvesting method for estimating of LAI in a *Fagus sylvatica* stand in the Steigerwald and obtained a function: logLA=1.6180 log*d* – 0.2266, where *d* is diameter at 1.35 m height. The LAI was calculated as the sum of LA for all individual trees growing in the investigated plot and divided by plot area. The estimated leaf area index for the beech stand has a value of 6 m^2 m^{-2}. The estimated LAI in Berchtesgaden National Park was similar to values for other closed canopy stands of beech at this elevation (Bauer et al. 1997; Granier et al. 2000). The LAI measured in a 120-year-old *Fagus sylvatica* stand (Schacht) in the Fichtelgebirge, Germany, with tree density of 304 tree ha^{-1} at an elevation 850 m, was less, reaching only 4.12 m^2 m^{-2} (Bauer et al. 1997).

European larch and dwarf-pine: The LAI of the European larch stand in National Park Berchtesgaden at an elevation 1720 m was very low and reached 1.5 m^2 m^{-2}, because trees occurring at the treeline do not build a closed canopy. The tree density of the investigated stand was only 197 trees ha^{-1}. Similar values of LAI were measured in a Siberian *Larix gmelinii* forest with a stand density of 230 tree ha^{-1} (Arneth 1994).

Leaf area index of dwarf-pine estimated with destructive biomass harvesting was much higher in comparison to the larch stand and reached 5.0 m^2 m^{-2}. The LAI of the grass understory between and under the larch trees at the

Kederbichel site in 2002, reached 5 m^2 m^{-2}. In comparison the maximum LAI of the understory measured in Stubai Valley in the same year, reached ca. 4 m^2 m^{-2} (Bahn, M. Univ. Innsbruck, personal communication).

5.3. Needle nutrient concentrations

Needle nutrient concentrations depend on the element concentrations in the soil, pH-values and soil water content, physical properties of the soil, weather conditions and plant species. Elevated element concentrations in the needles may also be caused by pollution. The nutrient contents of needles change between years, and they are lower during drought seasons (Dittrich and Hermsdorf 1990).

Nitrogen is an important protoplasm and enzyme component and a critical component of vegetative growth. An increase of nitrogen inputs can have an influence on long-term CO_2 and H_2O exchanges and in parallel on plant growth. The concentration of nitrogen in needles is related to the CO_2 demand and gives information about photosynthetic capacity, which in turn has an impact on stomatal conductance and water use.

In this work it was difficult to recognize a trend in the nitrogen concentration in spruce needles sampled in 2002 at four sites in the National Park Berchtesgaden. The highest N concentrations were found in 0-year-old needles at the 630 m site; in the 1-year-old needles no significant differences along the elevation gradient were found. The highest average concentration of 1.46 % was observed in 0-year-old needles at Bartholomä (630 m a.s.l.), 1.21% at the forest limit and the lowest values of 1.10% at Hirschengarten (1040 m a.s.l.). In 1-year-old needles the highest average N concentration of 1.33% were measured at Seeangerl, the lowest of 1.14 % at Hirschengarten. In the stand Bartholomä the foliar N concentration (%) was higher in younger needles than in older (**Tab. 4.7**). Körner (1999) found that the concentrations of nitrogen and phosphate in tissues from alpine plants increase with increasing altitude. This tendency is more obvious, when N per unit leaf area is considered, because leaf thickness increases with elevation. Hultine and Marshall (2000) described a decrease in stomatal density and an increase in leaf mass per area along an elevation gradient while the nitrogen content did not change. The mean nitrogen concentration in the 0-year-old needles varied among stands from 11 to 14.6 mg g^{-1} dw, and in 1-year-old needles from 11.4 to 13.3 mg g^{-1} dw. The nitrogen concentrations were in the same range as concentrations measured in Berchtesgaden National Park by other authors (Dittrich and Hermsdorf 1990), but lower than in the Fichtelgebirge (Alsheimer 1997). Dittrich and Hermsdorf (1990) measured in 1986 in spruce needles from the Berchtesgaden National Park nitrogen concentrations in the range of 7.1 – 18.5 mg g^{-1} dw. The values for spruce stands in National Park Berchtesgaden do not differ from concentrations measured along a transect extending from northern Sweden to central Italy (1.0 ± 0.1 mmol N g^{-1} dw). In two forest stands in Germany at elevations of 750 and 800 m the foliar N concentration in spruce needles reached 1.1 ± 0.1 mmol N g^{-1} dw and in beech leaves 1.9 ± 0.2 mmol N g^{-1} dw (Bauer et al. 1997). Mean nitrogen concentration in needles of *Picea abies* trees, found for Bavaria (Germany) reached 0.98 ± 0.10 mmol g dw^{-1} (Bauer et al. 1997). The mean N-concentration in spruce needles from different stands in the Fichtelgebirge were in the range from 11.7 to 15.5 mg g^{-1} dw (Alsheimer 1997), whereas the nitrogen concentration in the needles of 40-year-old spruce stands measured by Köstner (1996) reached 15 –16 mg g^{-1} dw. Values of 13.7 and 14.2 mg g^{-1} dw for sun and shaded Norway spruce needles were found by Matyssek (1985). Bauer et al. (1997) measured nitrogen concentration in European beech leaves of ca. 2.0 mmol N g^{-1} dw. Average nitrogen concentration measured in *Larix gmelinii* needles reported in Arneth (1994) reached 15.6 mg g^{-1} and in larch trees near to Bayreuth 26 mg g^{-1} (Matyssek 1985). Differences in N concentration were observed between sun leaves of *Larix decidua* (27 mg g^{-1}) and larch hybrids *Larix decidua* x *leptolepsis* (28.5 mg g^{-1}) (Matyssek 1985). In general, higher nitrogen concentrations occurred in the shaded leaves. Significant lower values were found in a Siberian larch forest. Nitrogen concentration in the *Larix gmelinii* needles was ca. 9 mg g^{-1} (Kelliher et al. 1997). Ingestad (1959) described nitrogen content in spruce needles between 15 and 23 mg g^{-1} dw as optimal and according to Baier (2004) the value of 13 mg g^{-1} dw is limiting for spruce growth. The mean values of N concentration in our sites are very close to the limit for spruce growth.

Isotope ratios of plant material provide information on environmental conditions. Carbon isotope discrimination could be used for the long-term estimation of water use efficiency (Farquhar 1989), which depends on CO_2 exchange. $\delta^{13}C$ express the balance between mesophyll CO_2-demand against its supply through the stomata (Hultine and Marshall 2000). Shifts in $\delta^{13}C$ at the intraspecific level are consistently observed over altitude gradients (Hultine and Marshall 2000; Körner et al. 1988). Carbon isotope concentration in the leaves depends on morphological and physiological traits – stomatal density and conductance, nitrogen content (which generally changes along elevation transects). This difference in carbon isotope content could be explained by climatic and soil conditions like air temperature, CO_2 concentration in the air, barometric pressure and soil moisture (Beerling et al. 1996; Sun et al. 1996). For *Pinus contorta*, *Abies lasiocarpa* and *Pseudotsuga menziesii* more positive carbon isotopes ratios along altitudinal gradients were observed (Hultine and Marshall 2000). In the needles of *Picea abies* they found an increase in isotope ratios from ca. -28 ‰ at 800 m a.s.l. to ca. -27 ‰ at 2300 m a.s.l. and *Pinus contorta* from ca. -29 ‰ at 1000 m to ca. -24‰ at 2500 m a.s.l. At 1500 m a.s.l. $\delta^{13}C$ reached -26.13 ‰ for *Picea engelmannii*, -25.70 ‰ for *Pseudotsuga menziesii*, -27.30 ‰ for *Abies lasiocarpa* and -27.44 ‰ for *Pinus contorta*. The carbon isotope ratio for *Picea abies* measured at the forest limit (1500 m a.s.l.) in the Berchtesgaden National Park reached -26.23 ‰. In this study no significant differences in carbon concentrations in current-year and 1-year-old needles along the elevation gradient were found. The lowest $\delta^{13}C$ (-27.00 ‰) ratio was measured in the 0-year-old needles sampled at Bartholomä. In the one-year-old needles the $\delta^{13}C$ increased with altitude from -27.92 ‰ at Bartholomä to -26.39 ‰ at the forest limit, with the exception of Seeangerl where $\delta^{13}C$ of -28.06 ‰ was measured. In general, higher isotope ratios and total carbon concentrations per gram dry weight were measured in 1-year-old needles.

Magnesium is the central element of chlorophyll, therefore essential for photosynthesis; Mg plays also a role in phosphate transfer. In the investigated needles no correlation between Mg^{2+} content and altitude was found although the highest magnesium concentration was measured in current and 1-year-old needles for the 630 m site (see **Tab. 4.8**). At Bartholomä and the spruce forest limit the mean magnesium concentrations in 1-year-old needles were slightly higher than in current-year needles. Mean magnesium concentrations in spruce needles measured in Berchtesgaden National Park in 2003 (ca. 0.86 and 1.07 mg g^{-1} dw for 0- and 1-year-old needles, respectively) were lower than the concentrations reported in Dittrich and Hermsdorf (1990) but higher than concentrations found in the Fichtelgebirge (Alsheimer 1997). The mean Mg^{2+} content at the four spruce stands in Berchtesgaden National Park in years 1985 – 1987 ranged from 1.61 to 1.73 mg g^{-1} dw. In the current study and in the work of Dittrich and Hermsdorf (1990) an increase in magnesium concentration with needle age was observed. Alsheimer (1997) measured in spruce needles from different stands mean Mg^{2+} concentrations from 0.25 to 0.82 mg g^{-1} dw, whereas higher concentrations occurred in 0-year-old needles. The mean magnesium concentrations in spruce needles from this study were similar to that reported in Zech et al. (1985), and Altherr and Evers (1975). The mean concentration of magnesium found in *Picea abies* needles reached 0.94 mg g^{-1} dw and in *Larix decidua* and *Pinus sylvestris* 1.98 and 1.27 mg g^{-1}, respectively (Matyssek 1985). Limiting values of magnesium concentration described by Baier (2004) reach 0.75 mg g^{-1}. Smidt and Stefan (1980) recognized Mg^{2+} concentration under 1.1 mg g^{-1} dw as not sufficient. Thus, we conclude that the magnesium supply in Berchtesgaden National Park is too low for optimal growth.

Calcium is essential for the formation and structure of cells, takes part in enzyme activation (amylase, ATPase) and regulates the strengthening of stems and shoot system. The mean calcium concentrations in current year needles in the Berchtesgaden National Park in 2002 were in the range of 4.2 – 4.6 mg g^{-1} dw, in 1-year-old needles from 5.8 to 7.6 mg g^{-1} dw. In comparison in the years 1985 – 1987, the Ca^{2+} concentrations in spruce needles in the Berchtesgaden National Park ranged from 6.7 to 10.8 mg g^{-1} dw (Dittrich and Hermsdorf 1990). Alsheimer (1997) observed in 1-year-old needles mean concentrations of 1.4 – 7.4 mg g^{-1} dw, while concentrations increased with the needle age. In all above mentioned studies an increase in calcium concentrations with needle age was observed. The calcium concentrations in *Picea abies* needles measured by other authors varied from 2 mg g^{-1} (Ferraz and Zöttl 1979) to 3 mg g^{-1} dw (Bosch et al. 1983). According to Matyssek (1985) the mean Ca^{2+} concentration measured for *Picea abies* reached 9.85 mg g^{-1} dw and was higher than for *Larix decidua* (7.81 mg g^{-1} dw), and *Pinus sylvestris* (5.24 mg g^{-1} dw). Baier (2004) described a value of 1 mg g^{-1} calcium as limiting. The mean calcium concentrations found in the Berchtesgaden National Park exceed significantly the value of 3.6 mg g^{-1} dw, which Smidt and Stefan (1980) reported as not sufficient.

Potassium plays a critical role in enzyme activation (photosynthese, nitrate reductase), osmoregulation and stomata behaviour. The K^+ concentration also has an influence on membrane potential. High potassium levels are necessary for protein synthesis and fruit production. For our three experimental sites (630 m, 1040 m and 1360 m), in 1-year-old needles a slight increase in the mean potassium content with altitude was observed, while in the highest situated stand (spruce forest limit) the mean K^+ concentration was visibly lower (3.99±1.33 mg g^{-1} dw). The mean potassium concentrations in 0-year-old needles were in the range of 6.43 – 8.34 mg g^{-1} dw, whereas in 1-year-old needles they ranged from 3.99 to 5.72 mg g^{-1} dw. The low K^+ content in needles sampled in the Berchtesgaden National Park is related to high Ca^{2+} concentrations in the soils (the potassium and calcium cations are in antagonism). The mean potassium concentrations in current year needles sampled in the Berchtesgaden National Park during 1985 – 1987 reached 3.6 – 4.8 mg g^{-1} dw (Dittrich and Hermsdorf 1990). Because of high mobility in the plant, higher K^+ concentrations occurred in younger needles. Similar potassium concentrations from 3.5 to 6.6 mg g^{-1} dw were measured in spruce needles in the Fichtelgebirge (Alsheimer 1997). There, the concentrations were also higher in younger needles. The mean values of potassium concentration in the three species measured by Matyssek (1985) reached 2.8, 2.65, and 2.89 mg g^{-1}dw for *Picea abies*, *Larix decidua*, and *Pinus sylvestris*, respectively. Baier (2004) described the potassium concentration of 3.5 mg g^{-1} dw as limiting and according to Smidt and Stefan (1980) a concentration of 4.2 mg g^{-1} dw as not sufficient. Overall, K^+ concentrations at our sites were sufficient.

Phosphorus is an important macroelement in metabolism and synthese reactions; it stimulates early growth and root formation. A strong increase in the mean phosphorus content with increasing elevation as well in 0-year-old as compared to 1-year-old needles was observed. Significantly higher mean P concentrations were measured in current year (0.78 – 1.37 mg g^{-1} dw) than in 1-year-old needles (0.53 – 0.93 mg g^{1} dw). These values for 1-year-old needles are similar to the range of 0.83 – 1.46 mg g^{-1} dw reported in Alsheimer (1997). She also reports higher phosphorus content occurred in 0-year-old needles. Matyssek (1985) found the highest phosphorus concentrations in *Picea abies* needles (1.06 mg g^{-1} dw), lower in *Larix decidua* (1.04 mg g^{-1} dw) and the lowest in *Pinus sylvestris* (0.84 mg g^{-1} dw) needles. Baier (2004) described the P concentrations in spruce needles lower than 1.2 mg g^{-1} dw as not sufficient. Data from our sites are close to this limiting value.

No significant differences in sulfur content (which is an important protoplasm and enzyme component, and is present in some amino acids and vitamins) with needle age or with altitude was found. The mean sulfur concentrations measured in 2002 in 0- and 1-year-old needles (0.75 – 1 mg g^{-1} dw) were in the same range of measurements at four stands in the National Park Berchtesgaden in years 1984 – 1987 (Dittrich and Hermsdorf 1990). The needle sulfur content varied among stands, the maximum concentrations were observed at 860 m and 1400 m sites and the lowest at a 1000 m site. Typical needle sulfur concentrations reported by other authors were in a range from 0.6 to 2.0 mg g^{-1} dw (Alsheimer 1997; Braun 1986; Rehfuess 1983; Zech et al. 1985; Zöttl and Mies 1983). Alsheimer (1997) observed an increase in sulfur concentration with increasing needle age. In all investigated stands in the Berchtesgaden National Park sulfur concentrations were sufficient.

Manganese plays an important role in metabolism of photosynthesis and phosphate transfer, stabilisation of chloroplast structure, and synthesis of nucleic acids. It activates enzymes used in chlorophyll synthesis. The mean manganese concentration increased strongly with increasing elevation a.s.l. The Mn^{2+} content in current year needles ranged from 0.05 to 0.14 mg g^{-1} dw, and in 1-year needles from 0.07 to 0.3 mg g^{-1} dw. In the investigated stands, the mean Mn^{2+} concentrations in 1-year-old needles were 1.3 – 1.8 times higher than in needles from the current year. The mean Mn^{2+} concentration measured in 1-year-old spruce needles in the Berchtesgaden National Park (in 1985) was 0.162 mg g^{-1} dw (Dittrich and Hermsdorf 1990). Higher concentrations occurred in older needles because of the low mobility of this element. The same tendency was described by Alsheimer (1997): mean Mn^{2+} concentrations in current year needles were in the range of 0.19 to 0.54 mg g^{-1} dw and in 1-year-old needles 0.25 – 1.1 mg g^{-1} dw. A value of 0.05 mg g^{-1} dw was found as not sufficient (Baier 2004). In the investigated sites no Mn^{2+} limitation was observed.

Fe^{2+} takes part in metabolism in the oxidoreductions, N-exchange, and chlorophyll synthesis reactions. It is important for photosynthesis as a chlorophyll activator. The mean iron concentrations in the needles change with the needle age. In 1-year-old needles, the Fe^{2+} content was 1.1 – 1.6 times higher than in 0-year-old needles. The mean concentration in 1-year-old needles varied among stands from 0.03 to 0.05 mg g^{-1} dw. Higher iron concentrations (0.04 – 0.09 mg g^{-1} dw) were measured in 1-year-old spruce needles in the Fichtelgebirge (Alsheimer 1997). No correlation between Fe^{2+} content and elevation was found. After Baier (2004) iron concentration in the spruce needles lower than 0.02 mg g^{-1} dw are not sufficient. Data from our investigated sites indicate no Fe^{2+} limitation.

Zinc as part of certain enzymes and growth regulators take part in chlorophyll synthesis activation, metabolism, and protein decomposition. In the Berchtesgaden National Park the mean zinc concentrations do not differ among stands. In current-year and 1-year-old needles the highest concentrations were observed at the site Bartholomä. The Zn^{2+} concentrations in 0-year-old needles (0.05 mg g^{-1} dw) were higher than in the older needles (0.04 – 0.05 mg g^{-1} dw). A decrease in zinc concentration with the age of spruce needles was measured by Alsheimer (1997). In 0-year-old needles the concentration varied from 0.02 to 0.05 mg g^{-1} dw, while in 1-year-old needles from 0.01 to 0.04 mg g^{-1} dw. The zinc concentration of 0.015 mg g^{-1} dw is not sufficient (Baier 2004). Data from our sites are above this limiting threshold.

Aluminium toxicity is an important factor that limits plant metabolism, growth and development in many acid soils, particularly in pH of 5.0 or below (Mossor-Pietraszewska 2001; Rout et al. 2001) and can be often recognized through morphological and physiological symptoms. In this respect, Mossor-Pietraszewska (2001) reported:
"The plasma membrane of root cells, particularly at the root apex, seems to be a major target of aluminium toxicity. However, strong interaction of Al^{3+}, the main Al toxic form, with oxygen donor ligands (proteins, nucleic acids, polysaccharides) results in the inhibition of cell division, cell extension, and transport" (Mossor-Pietraszewska 2001). In general, larger aluminium concentrations (typically by a factor of 1.5) were observed in needles than in stem tissue, whereas the concentrations in the roots were found to be about 4-5-fold larger than in needles (van Hees et al. 2004). The authors measured concentrations of Al in *Picea abies* needles within the range of 0.007-0.015 mg g^{-1}, which can be usually observed in mature trees growing on acid soils under field conditions. In the Berchtesgaden National Park in 0-year-old needles the mean aluminium concentration decreased with increasing elevation. The

highest mean Al^{3+} content was measured at Bartholomä (0.03 mg g^{-1} dw), the lowest at the forest line (0.02 mg g^{-1} dw). Higher aluminium content was observed in 1-year-old needles in comparison to current-year needles. Very high mean Al^{3+} concentration occurred in the spruce needles at the site Seeangerl (0.06 mg g^{-1} dw). An increase in aluminium concentrations with the needles age was reported in Alsheimer (1997). The author measured mean concentrations in the range of 0.08 – 0.96 mg g^{-1} dw in 1-year-old needles from different stands. According to Mossor-Pietraszewska (2001), in most plants aluminium concentrations do not exceed a value of 0.2 mg g^{-1} dw. At our sites relatively high Al concentrations were measured, but at the three investigated sites they were close to the typical values observed in conifers.

Both the nutrient concentrations and the relations between nutrients are important for growth and development of plants. The K/Ca relations in the spruce needles (from 1.52 to 2.50 and 0.78 to 1.12 for 0- and 1-year-old needles, respectively) were low because of the low potassium concentrations in the soils (see **Tab 4.9**). The soils in the Berchtesgaden National Park are rich in Ca^{2+} cations, which react antagonistically with cations K^{+}, which are not stored in the soil. Low K/Ca ratios in spruce needles were also measured in other experiments in the Berchtesgaden National Park. In the years 1985 – 1987 the mean potassium/calcium ratios in 1-year-old needles ranged from 0.47 to 0.57 (Dittrich and Hermsdorf 1990). Hüttl (1992) measured K/Ca ratios from 0.8 to 2.4 in spruce needles. Different authors reported different optimal K/Ca ratios for spruce needles: Hunger (1964) 1.7, Zech (1970) 3.1, and Altherr and Evers (1975) 2.15. At all experimental sites the K/Ca ratios were significantly higher in current year needles than in 1-year-old needles. Because of magnesium deficiency at our sites in spruce needles the K/Mg and Ca/Mg relations were relatively high. The values of mean K/Mg ratios in 1-year-old needles described in Dittrich and Hermsdorf (1990) were in the range of 2.35 – 3.04, while Hunger (1964) reported a value of 4.5. K/Mg ratios measured by Hüttl (1992) ranged from 2.2 to 6.4. The potassium/magnesium ratios were higher in 0-year-old needles. In all our experimental sites the calcium/magnesium ratios were higher in older needles. They ranged from 4.0 to 4.9 in current year needles and from 5.8 to 7.8 in 1-year-old needles. Similar mean Ca/Mg ratios, from 4.4 to 6.7, were measured in 1-year-old spruce needles sampled in the Berchtesgaden National Park in the years 1985 – 1987 (Dittrich and Hermsdorf 1990). Hunger (1964) found Ca/Mg ratios of 2.7 with higher ratios in older needles.

The mean N/K ratios in the investigated spruce needles were low (1.62 – 3.39) because of relatively low nitrogen concentrations. Higher nitrogen/potassium ratios were found in 1-year-old needles. Alsheimer (1997) measured nitrogen/potassium ratios from 2.3 to 4 in 1-year-old spruce needles in the Fichtelgebirge, whereas Hüttl (1992) described N/K ratios from 1 to 3.

The mean N/P ratios varied strongly among stands from 9.3 to 30.1. The values of nitrogen/phosphorus ratios reported in Alsheimer (1997) were in the range of 8.6 – 18.9. Hüttl (1992) found N/P ratios in spruce needles ranged from 6 to 12. According to Matyssek (1985) a N/P ratio of 15 - 18 indicates an adequate P supply.

The N/S ranged from 13.4 to 14.8 in the 0-year-old and from 13.0 to 14.9 in the 1-year-old needles. The N/S ratios measured in different spruce stands in the National Park Berchtesgaden in other studies varied from 7.3 to 19.8 with a mean of 12.6 (Dittrich and Hermsdorf 1990). The nitrogen/sulfur ratios did not change significantly with the needle age. Normal values are in the range of 8 – 12 (Evers 1986).

Mean N/Mg values ranged from 11.9 to 14.4. N/Mg ratios measured in spruce stands in the Fichtelgebirge varied strongly between 12.6 to 61.2 (Alsheimer 1997). The value of 61.2 indicate a heavy Mg limitation.

Along the elevation gradient in spruce needles a sufficient supply of Mg, K, Ca, Zn, Mn and S were observed, while the concentrations of N and P were almost in all experimental stands too low for optimal growth. The relations between nutrients were not optimal. The mean K/Ca ratios in 1-year-old needles in all experimental sites were to low. The mean N/P ratios at Bartholomä in 0- and 1-year-old needles and at the Hirschengarten in 0-year-old needles were too high, whereas at forest limit the nitrogen/potassium ratios were to low. In general the mean N/S ratios had too high values. Baier (2004) investigated the nutrition status of Norway spruce on dolomite sites in the Bavarian Limestone Alps. The author examined how spruce is naturally adapted to this nutrient poor environment, where the phosphorus and nitrogen supplies in the soils are insufficient. Because spruce is not able to scoop out nutrients in great quantities, the deficit concentration of N and P has a consequence of inadequate growth. Higher fine root density and slow growth are adaptations on these nutrient poor conditions. Similar adaptations could have taken place at our sites.

The element concentrations in the needles are not only correlated with the concentrations in the soils. The needle element contents depend also on other factors – plant species, soils, pH-value, water supply, climate conditions, imissions (Dittrich and Hermsdorf 1990). The nutrient concentrations in the plant tissues change over the year– they decline in dry periods and seed years, but the deficit concentration may be determined via one analysis (Evers 1972). In spring the reallocation of nitrogen from older to new needles occurs. Seasonal remobilization of N from old foliage decreases with increasing needle age. Because the nutrient concentrations change during the season, the needle harvesting is usually carried out at the end of growing season when the fluctuations in nutrient contents are low (Stefan 1971). Dry weight and N content of mature Norway spruce needles increased to reach the maximum in autumn, while N concentration remained constant (Bauer et al. 1997). In this study the sampling of needles were carried out in the middle of summer.

5.4. Microclimate Conditions

Different climate conditions in forest stands may be a reason for different stand's water use (Alsheimer 1997; Kelliher et al. 1993). In this study for investigation of forest transpiration along an elevation gradient, three Norway spruce stands in the area on the Watzmann Mountain in Berchtesgaden National Park were chosen because of the large gradients in climate conditions and elevation that occur there in a comparatively small area. The investigated sites (Bartholomä, Hirschengarten, Seeangerl) occur with similar exposition, inclination and soil characteristics, but situated at different elevations above sea level (630, 1040, and 1360 m) which are under the influence of different meteorological conditions. Additionally, transpiration of one beech site (Bartholomä at elevation 630 m), and one European larch together with a dwarf-pine site (Kederbichl at elevation 1720 m a.s.l.) were studied.

Very important for the analysis of meteorological influences on the stand transpiration is the installation of monitoring instruments. However, in the mountain regions on steep slopes, an ideal placement of instrumentation, which will allow measurements of the same conditions which affect tree canopy, is very difficult. For this reason, the meteorological stations (for PPFD and relative humidity measurements) were located not above but in open areas near to the experimental stands, while the air and soil temperatures, and soil water contents were measured within the stands (see **4.4**).

The water fluxes in trees depend on aboveground and belowground factors. The most important aboveground factors that have an effect on the transpiration process are vapor pressure deficit (VPD), that creates water potential gradient between shoots and the atmosphere (Kaufmann 1975), radiation and air temperature, which also have pronounced effects on gas exchange regulation (Körner 1999; Tranquillini 1979). The values of air temperature, and in turn vapor pressure deficit, decreased with increasing elevation above sea level (temperature declines by about 0.6 °C per 100 m). However, on some days with valley fog, lower air humidity occurred at the higher situated stands. In general, the highest air temperature and vapor pressure deficit (VPD) were observed at the site Bartholomä (630 m), the lowest at Kederbichl (1720 m), though during clear, sunny periods, because of high radiation intensity, the maximum air temperatures and VPD at the 1720 m site were comparable to the lower situated stands.

At the three investigated spruce sites, the highest radiation input (PPFD integrated over the day) was measured from June to August. In the highest situated stand at 1720 m a high mean radiation was observed also in September. Differences in radiation intensity along the elevation gradient were not large. The mean daily radiation at timberline measured in Gurglertal, Austria, at 2000 m elevation was only 10 – 20% higher than at 200 m (Turner 1961). The tree canopy is an active sphere of radiation and thermal balance (Bac et al. 1993). Within the beech stand, only a small part of the solar radiation reaches the forest bottom floor (**Fig. 4.12**). During the measurement period, the radiation measured at the soil surface ($PPFD_{below}$) varied from 0.1 to 92% of the PPFD measured at the open area. As in this study, Bac et al. (1993) described that in dense beech stands only a few percent of energy coming to the top of canopy reaches the forest floor. Also the highest temperatures occur in the highest part of the canopy. The relationship between PPFD reaching tree crowns and the stand bottom changes during the season according to the development of leaves in spring and the senescence in autumn.

The highest mean daily air temperatures of 16.3, 14.5, and 12.2 °C were observed in June at Bartholomä, Hirschengarten and Seeangerl, respectively. In Kederbichl the highest mean daily temperature 17.2 °C occurred in July, and the highest maximum temperature (26.0 °C) was measured in June. The lowest air temperatures occurred at Bartholomä in May and at the two other spruce stands in September. In the beech stand in spring before the leaves develop, the minimum air temperatures were higher than in the spruce stand at the same elevation.

Because of the moist air rising in mountains regions, precipitation generally increases with increasing elevation above sea level (Tranquillini 1979). During the growing season 2002, precipitation was frequent each month and the highest precipitation rates were measured at 1720 m and the lowest at 630 m. The monthly precipitation measured at the highest situated stand was 104.6 to 281.2 mm higher than at the lowest site, with the exception in August, when strong rain events occurred. At the 630 m, 1040 m and 1360 m sites the highest precipitation was observed in August and July (**Tab. 4.10**), while at the 1720 m site the highest rain events were measured in June and they decreased during the season.

An important belowground factor that has an influence on transpiration is soil water content. Water absorption by the roots is often limited by soil drought and by low soil temperatures, which reduce soil and plant hydraulic conductance and induce water stress (Kramer and Boyer 1995; Mellander et al. 2004). Leaf water potential is influenced by hydraulic resistance which in turn affects stomatal behaviour (Comstock and Mencuccini 1998; Fuchs and Livingston 1996; Givnish 1986).

The seasonal patterns of soil moisture were similar at three investigated spruce sites. A strong decline in soil moisture in the 630, 1040 and 1360 m stands was observed in the middle of June and at the beginning of July. At the Bartholomä, Hirschengarten and Seeangerl sites, the longest dry period began around June 9. Generally, at 1040 m the highest water content occurred at the –50, lower at –5 cm and the lowest at –20 cm depth, while at the 1360 m site, the highest moisture content was measured at 20 cm depth, and the lowest at –50 cm.

In the experimental larch stand the water content increased with soil depth. In the middle of June, similar to the spruce sites, a strong decrease occurred in soil moisture. The second long dry period occurred from 7 to 17 August. No changes in soil moisture in the upper soil profile could be recognized, while a strong increase in soil moisture at 20 cm and 50 cm soil depth was observed.

In the spruce and beech stands, an increase in maximum soil temperatures from May to July and a decrease from the beginning of September were observed (**Tab. 4.11** and **Tab. 4.13**). The highest mean soil temperatures at different depths were measured at the Bartholomä and Seeangerl sites in August and in the Hirschengarten stand in July and August. In comparison with the spruce site Bartholomä, the soil temperatures at the beech site at -2, -5 and -10 cm depth were generally higher from July to September (**Tab. 4.13**). At Kederbichl a decline in maximum soil temperature in the soil profile (at the -2, -5 and -10 cm depths) was observed from June to August (**Tab**. **4.15**). The differences between maximum temperatures at different soil depths were highest in June and declined over the measurement period.

The mean soil temperature decreased with increasing elevation. At Seeangerl the mean monthly temperatures in May, June, and September were in the range of 6.3 to 8.6 °C, which may partially explain lower transpiration rates in comparison to the two other spruce stands. Mellander et al. (2004) found that soil temperature below +8 °C in Scots pine stands leads to a reduction in transpiration rates by a decline in root permeability and lower stomatal conductance. Low soil temperatures have a strong influence on plant water use after the growing season has started (Mellander et al. 2004). With a decrease in soil temperatures, the resistance for water flows through the soil-plant-atmosphere-continuum increases. 20% lower transpiration rates for *Larix decidua* and *Picea abies* were observed with a decrease in soil temperature from 25 °C to 15 °C (Havranek 1972a), and the temperature of 5 °C caused stomatal closure. Low soil temperatures have inhibiting effects on water relations and gas exchange for seedlings and saplings (Day et al. 1991; Grossnickle 1988; Pavel and Fereres 1998; Wang and Zwiazek 1999).

5.5. Xylem sapflow measurements

The sap flux density in the stand depends on stand structure, social position of trees within the stand, thinning, soil moisture (Granier et al. 1996a; Lu et al. 1995), pollution (Granier et al. 1996a), and possibly infection (Alsheimer 1997). Sap flux measurements have become a key instrument in forest ecosystem research (Wullschleger et al. 1998). They can be used for up-scaling of water loss from the individual tree to the stand level (Alsheimer 1997; Granier et al. 1996a; Köstner et al. 1998a). In this study, transpiration rates in three Norway spruce stands, one beech stand, one larch and one dwarf pine stand were determined by xylem sapflow measurements according to Granier (1985; 1987). This technique is suitable for simultaneous sap flux measurements in many trees and allowed continuous observations of water use over the season. The heat dissipation system is easy to use, can be powered by 12 V batteries and is relatively inexpensive. In comparison to the Cermak method (Cermak et al. 1992), the Granier-type needs less energy for heating and is less destructive. Sap flux densities derived simultaneously with these two systems varied in the same range and daily courses of sapflow had similar patterns (Alsheimer 1997; Köstner et al. 1998b). The difference in cumulative sapflow rates between Granier and Cermak techniques reported by Köstner (1998b) was 9%. Transpiration rates derived with sap flow measurements scaled to the stand level with evapotranspiration rates from understory agreed with results obtained by eddy-covariance methods (Kelliher et al. 1992).

With the Granier-method the sap flux density in the stem can be measured only along the sensor needle, so for trees with a deep active sapwood ring the sensors have to be installed at different depths (Alsheimer et al. 1998; Köstner et al. 1998b). To estimate water use of a single tree the sum of fluxes in different xylem rings should be summed. In this study, xylem sapflow measurements, the estimation of sapwood area and cumulative cross-sectional sapwood area for forest stands were used for up-scaling of canopy transpiration and obtaining canopy conductance. The sap flux density changes with the depth of sapwood, between trees, forest stands and also during the season. To achieve reasonable precision of transpiration estimates at the stand level and to minimize the error to 7 – 22% on average, 8 to 12 trees of every species in the stand should be measured (Alsheimer 1997; Cermak et al. 1995). Sapflow measurements started at all investigated sites shortly after snowmelt when soil water content was high. In this respect Cermak at al. (1995) strongly recommend:

“Measurement of the sapflow rate should start in spring as early as possible after snow melt, when sufficient soil water after winter may be expected. This would allow better assessment of potential transpiration and the level of drought stress (if any) over the growing season”.

Norway spruce: In this study, for spruce trees no correlation between tree size and sap flux density was found. The same results are described in Köstner (2001). Generally, in the three Norway spruce stands in National Park Berchtesgaden higher sap flux densities were measured in the outermost (0 - 2 cm) sapwood ring than at 2 - 4 cm or 4 - 6 cm sapwood depths. The decrease in sap flux densities along the radial axis of the xylem for *Picea abies* was described by Alsheimer (1997). The reduction of flux densities from outer to inner sapwood was also observed in oak (Köstner et al. 1998b) and beech (Kubota et al. 2005).

In most experimental trees, the sapflow rates decreased with sapwood depth, but those radial differences (in xylem flux densities) varied during the measurement period. Between May and September, changes in the flux rates at 0 - 2 and 2 - 4 cm sapwood depth were observed. At Bartholomä, in most trees, the highest mean monthly fluxes occurred in May at 2 - 4 cm sapwood depth (and not as one would expect at the 2 cm depth) and then decreased. However, in some experimental trees an increase in sap flux rates at 2 - 4 cm sapwood depth occurred again from August to September. During the measurement period, in all investigated trees at the site Hirschengarten, the mean monthly percentage of sap flux densities in deeper xylem layers with respect to sap flux densities in outer xylem ring decrease significantly. The same patterns were observed for trees with deeper active sapwood. However, in some experimental trees the xylem densities in the 2 - 4 cm layer were permanently higher, perhaps due to faulty sensor installation in the bark to xylem transition, although the seasonal trend to decline toward 50% of the 0 - 2 cm fluxes in deeper layers can be recognized. During the season, the mean monthly flux densities at 4 - 6 cm xylem depth decreased in comparison to sap flux densities in the outer sapwood ring. In general, a high variability in sap flux density as well as between trees and between sapwood layers in individual trees was found. At Seeangerl, the disturbances in power supply caused some difficulties in sapflow measurements at 2 - 4 and 4 - 6 cm depths, allowing only an estimation of mean flows.

In this work large differences in hourly and daily sap flux densities between trees and stands were found, however the maximum hourly densities reached at the three spruce sites 0.03 kg cm^{-2} h^{-1}. Maximum daily sap flux densities measured in *Picea abies* trees reached at Bartholomä 0.29 kg cm^2 d^{-1}, at Hirschengarten 0.1 kg cm^2 d^{-1} and at Seeangerl 0.35 kg cm^2 d^{-1}. During the measurement period, the total daily sapflow ranged in the stand Bartholomä between 1.6 and 41 kg d^{-1} per tree, in Hirschengarten between 0.4 and 112 kg d^{-1} per tree, and in the highest situated stand Seeangerl between 0.5 and 51.5 kg d^{-1} per tree. Daily water use of *Picea abies* trees measured with thermal dissipation method according to Granier reported in different studies ranged from 10 to 175 kg d^{-1} (Wullschleger et al. 1998). Daily transpiration rates measured in *Abies amabilis* reached more than 100 kg d^{-1} (Martin et al. 2001).

European beech: In *Fagus sylvatica* trees, higher sap flux densities were observed in the most external measurement layer (0 – 2 cm), as compared to the deeper (2 – 4 cm) layers. This decline in sap flux densities with sapwood depth in beech trunks was also described in Kubota (2005). In most experimental trees, the sapflow rates decreased with xylem depth and the proportion between fluxes at different sapwood depths changed during the season. The highest mean monthly denisties at 2 – 4 cm sapwood depth occurred in August. At the *Fagus sylvatica* site the sap flux densities increased from the beginning of the measurement period to the middle of June and stayed relatively constant to the beginning of September. The maximum sap flux densities approximated 0.04 kg cm^{-2} h^{-1} and 0.45 kg cm^{-2} d^{-1}. The maximum fluxes measured in beech trees in this study ranged from 61 to 141 kg d^{-1}.

The differences among trees in the sap flux reduction with the xylem depth may be caused by different sapwood density. Trees with the highest sapwood density have the lowest sapwood capacitance and in turn the lowest xylem vulnerability to cavitation (Meinzer et al. 2003). In beech trees the cavitation can be affected seasonally by drought in summer and freeze-thaw cycles in winter, while in spring, with bud burst, a maximum in xylem conductivity occurs. The variation among trees might be also explained by different exposition to the light and different water demand. The strong variation in sapflow rates might also be influenced by sensor installation because of differing activity of the xylem, radial as well as longitudinal.

European larch and dwarf-pine: The sap flow measurements in European larch trees were carried out in 0 – 2 cm below the cambium. Between June and September 2002 the mean sapflow rates in the experimental European larch trees ranged between 0.3 and 74 kg d^{-1}. The maximum observed sapflow rate reached ca. 195 kg d^{-1}. Maximum daily sapflow rates measured for *Larix gmelinii* trees in Siberia ranged from 6.8 to 75.9 l d^{-1} (Arneth 1994). Matyssek (1985) measured maximum values for transpiration per crown needle dry weight in *Larix decidua* trees as 0.8 kg kg^{-1} dw h^{-1} and for *Larix decidua* x *leptolepis* as 10 kg kg^{-1} dw h^{-1}. Our mean sap flux densities in larch trees in June were in the range of 0.06 kg cm^{-2} d^{-1} to 0.22 kg cm^{-2} d^{-1}, whereas the maximum denisties reached ca. 0.3 kg cm^{-2} d^{-1}. At the end of June and beginning of July sap flux rates were measured higher than in early June. The mean sap flux densities measured in dwarf-pine during the season ranged from ca. 0.01 to 0.02 kg cm^{-2}

d^{-1} and the maximum sap flux density reached ca. 0.05 kg cm^{-2} d^{-1}. The maximum sapflow rates in 6 experimental *Pinus mugo* branches during the season ranged between 2.8 – 4.6 kg d^{-1}. The average fluxes varied from 0.7 to 1.7 kg d^{-1}. The branches are, of course, not immediately comparable to the tree level values given for the other species. At the *Larix decidua* site, sap flux densities increased from the beginning of June to the end of July; maximum flow densities were high and reached ca. 0.03 kg cm^{-2} h^{-1}. In the case of *Pinus mugo*, a continuous decrease in sap flux density occurred from the beginning of the measurement period until the end of September. The maximum densities were measured in the middle of June and approximated 0.015 kg cm^{-2} h^{-1}.

During the measurement period, the maximum daily sapflow rates at the *Pinus mugo* site were in the range of 2.8 – 4.6 kg d^{-1}. Significantly higher sapflow was measured in other *Pinus* species. Ford (2004) reported rates in the range of 36 – 218 kg d^{-1} for *Pinus palustris*, 188, 99 and 138 kg d^{-1} in *P. echinata*, *P. elliottii* and *P. taeda*, respectively.

The sap flux measurements are affected by transpiration and storage capacity. There is often a shift in spruce trees between the time courses of crown transpiration rate and xylem water flow in the trunk (Alsheimer 1997; Köstner et al. 1998a; Wieser et al. 2003). The xylem flow starts 0.5 – 3 hours later than the measured transpiration. This time lag between sap flux and transpiration was not considered in this study, because the meteorological measurements did not provide the exact information that would be needed for evaluation. In this work for estimating of canopy transpiration only measured, not corrected data were used, because the sensors for climate measurements were not put above the canopy, which allowed only a partial evaluation of dependencies on PPFD and VPD. The sap flow rates in beech trees depend more on the crown status than on trees size (Granier et al. 1996a; Köstner et al. 1998b) and the higher rates in dominant trees are caused by higher light interception by crowns. The time lag that occurs in coniferous trees was not observed in beech, in which the sap flow is initiated simultaneously with canopy transpiration (Granier et al. 2000). The influences of water storage were also not observed in larch trees, which have very thin sapwood (Arneth 1994). Differences between conifers and deciduous trees could also be partially explained by different xylem structure. In spruce trees only tracheids occur with small diameter, whereas in diffuse porous trees like beech occur larger trachees.

In general, for trees in which the sapflow was measured at different xylem depths, in spruce as well as in beech, higher rates were observed in the outermost xylem ring. The proportion of flow densities in different sapwood layers change during the season. In most experimental trees they decrease from May to September, however in some trees opposed trends can be recognized. The measurements at three Norway spruce sites, one European beech, one European larch and one dwarf-pine site showed large variability in sap flux densities between tree species. Experimental trees and species differ in daily maximum sapflux densities, however for spruce trees the hourly maximum densities were very similar. The highest flow densities were measured for beech and the lowest for dwarf-pine. The differences in sap flux densities occurred also among trees within stands and between stands. The large variability in spruce trees with xylem depth as well as among trees and stands were described also by other authors. This phenomenon was reported i.e. by Alsheimer (1997), Köstner et al. (1998a), who tried to explain it by the alteration in xylem density and distribution. This high variation in sapflow rates may also be affected by sensor placement, because sapwood has different activity depending on azimuth and height. The differences in sap flux densities at different xylem depths can also depend on different storage capacities of the trunks.

5.6. Diurnal and seasonal transpiration rates

Water balance is determined by water uptake and water loss. Water may be stored in the soil or evaporated due to the vapor pressure deficit in the air. The relations between water storage and water loss change vary with altitude (Tranquillini 1979).

Norway spruce: Maximum hourly water use for Norway spruce trees reached at site Bartholomä 0.3 mm h^{-1}, at Hirschengarten and at Seeangerl 0.2 mm h^{-1}. In comparison, maximum hourly values of transpiration observed in the Lehstenbach catchment (700-800 m a.s.l.) reached 0.25 mm h^{-1} in a 40-year-old spruce stand, 0.11 mm h^{-1} in a 140-year-old and 0.15 mm h^{-1} in a 120-year-old stands (Alsheimer 1997).

The typical trend of seasonal transpiration in temperate forests shows an increase in spring, exhibits a maximum in July and decreases thereafter in August (Alsheimer 1997; Granier 1987). This pattern was observed also in this study (**Fig. 4.25**, **4.26**). Transpiration varied from 0.6 to 1.5 mm d^{-1} at Bartholomä, 0.3 to 0.9 mm d^{-1} at Hirschengarten and 0.4 to 0.7 mm d^{-1} at Seeangerl. The highest daily water loss was observed in June at Bartholomä (2.5 mm) and Hirschengarten (1.6 mm) and in July at Seeangerl (1.8 mm). The maximum values of transpiration at the Bartholomä site were similar to the daily water use observed at 40-year-old spruce sites in the Fichtelgebirge (Alsheimer 1997). According to that study in 1994 and 1995 the daily maximum transpiration rates occurred in July and reached 2.8 mm d^{-1}. The maximum daily water loss measured in the Berchtesgaden National Park was much lower than the 5 mm rates observed in a 24-year-old Norway spruce stand in Sweden (Cienciala et al. 1994) and a 30-year-old stand in France (Lu et al. 1995). The maximum daily transpiration measured for Douglas fir growing in France at an elevation of 250 m reached 3.1 mm (Granier 1987).

The highest differences between months in mean transpiration rates occurred at the 630 m site and the lowest at the 1360 m site. Between May and September the water use of spruce stands varied from 19 to 46 (Bartholomä), 8 to 28 (Hirschengarten) and 12 to 21 (Seeangerl) mm month $^{-1}$ (**Tab. 4.16**). Between May and September 2002, the monthly sums of transpiration at the Bartholomä site (630 m) were 8 – 20 mm higher than at Hirschengarten (1040 m) and 6 – 26 mm higher than at Seeangerl (1360 m).

During the measurement period, a decline in transpiration rates along the elevation gradient was observed. The highest monthly water use was observed at Bartholomä (165 mm), lower at Hirschengarten (99 mm), and the lowest in the highest situated stand, Seeangerl (79 mm). A similar relationship between water use of spruce forests and their elevation a.s.l. was reported by Köstner (2001). The sums of water use from May to October in six investigated spruce stands within Lehstenbach catchment reached 112 – 217 mm in 1994 and 110 – 209 mm in 1995 (Alsheimer 1997; Köstner 1996). Highest daily transpiration rates of spruce occurred in 40 – 60-year-old stand at 380 m a.s.l. (Hohe Warte, Bayreuth), whereas the lowest occurred in a 140-year-old stand at 790 m a.s.l. (Coulissenhieb, Fichtelgebirge). Peck and Mayer (1996) analysed the water use in 20 spruce stands. They measured transpiration rates of 199 – 516 mm year^{-1}. The heterogeneity of canopy transpiration along an elevation gradient was associated with climate conditions, which change strongly with altitude a.s.l. At higher altitudes, because of lower air temperatures, the evaporative demand to the atmosphere decreases. Plants in the subalpine and alpine zones usually use less water (Körner 1999; Tranquillini 1979).

The situation among the three experimental *Picea abies* stands in the National Park Berchtesgaden, nevertheless, is very complex. During the measurement period various types of “transpiration days” were found. Depending on rain events, vapor pressure deficit in the air and temperature along the elevation gradient, shifts in water use initiation and differences in transpiration rates were observed – the water use was initiated and often reached its maximum in the three investigated stands at different times.

European beech: In 2002, the maximum hourly water use in the beech stand Bartholomä reached 0.2 mm h^{-1}. Sap flow rates of 0.2 mm h^{-1} were also observed, but only on cloudy days in a beech stand in Hesse, France (Granier et al. 2000). During the season at the site Bartholomä, mean daily sapflow ranged between trees from 7 to 79 kg d^{-1} and the maximum daily transpiration rates were in the range of 12 – 141 kg d^{-1} per tree. In comparison, the whole tree water use observed for deciduous trees reported in Wullschleger (2001) varied from 46 to 153 kg d^{-1}. Mean sapflow rates measured with deuterium tracing method in *Fagus sylvatica* trees at an elevation of 1270 m in Southern France reached 2.5 – 16.6 kg d^{-1} (Marc and Robinson 2004). During the measurement period, the daily maximum canopy transpiration at the site Bartholomä ranged between 0.6 and 1.3 mm. These rates are very similar to the daily water use in beech stands reported by other authors. Ladefoged (1963) measured transpiration of 0.6 – 1.5 mm d^{-1} for *Fagus sylvatica* trees. The maximum water loss of a 35-year-old beech stand growing at 1230 m elevation in the Northern Apennines in Italy and reported in Kowalik et al. (1997) was 1.3 mm d^{-1}. Higher maximum transpiration rates, ca. 4 – 5 mm d^{-1}, were estimated in large homogenous beech forests in eastern France (Granier et al. 2000) and in eastern Germany (Herbst et al. 1999). Mean daily transpiration rates of 5 mm in a 160-year-old beech stand in Germany were derived with the Tissue-Heat-Balance-Method and compared with eddy covariance method (Heimann and Constantin 1999). According to Marc and Robinson (2004) the daily water use in a beech stand in Southern France reached 5.45 ± 0.8 mm.

Köstner (2001) observed more than 100% variation between forest patches of different structure, i.e. daily maximum rates of canopy transpiration (E_{cmax}) ranged in spruce stands from 1.5 to 3 mm d^{-1} and in the beech stands from 2.6 to 6.4 mm d^{-1}. The author found higher variability in sapflow rates in spruce trees in comparison with beech trees, which may be connected with changes in sapwood depth within tree cross-sections. In comparison, during the early growing season, the stand transpiration in an upland oak forest in Walker Branch Watershed, US, reached a value of 2.2 mm d^{-1}. Daily transpiration rates for the multi-species stand were predicted to average 1.1 mm d^{-1}. In the period from April to November the transpiration from the overstory was in the range of 221 – 267 mm (Wullschleger et al. 2001). The monthly transpiration of beech trees measured in 1999 in Steigerwald, Germany ranged between 32 – 66 mm a month. The highest monthly water loss in beech stands in Berchtesgaden and

Steigerwald was measured in July and August, and the lowest was in September. This variation in observed transpiration is probably linked to large variation in meteorological conditions and in senescence (Granier et al. 2003). The fluxes in the outer and inner xylem are influenced by habitat conditions as well as by physiological changes (Kubota et al. 2005).

European larch and dwarf-pine: The maximum hourly water loss measured in 2002 in the European larch stand Kederbichl at 1720 m elevation reached 0.03 mm h^{-1}. The hourly xylem fluxes in *Larix* trees described by other authors reached from 4.5 l h^{-1} (Cienciala et al. 1992) to 8 (Arneth 1994) and 10 l h^{-1} (Matyssek 1985). During the season, in National Park Berchtesgaden, the mean daily sapflow ranged between trees from 0.3 to 74 kg d^{-1}. Daily xylem flux measured in a *Larix gmelinii* stand in Siberia reached 7 – 67 l d^{-1} (Arneth et al. 1996). The daily mean canopy transpiration rate for June at the larch site in National Park Berchtesgaden reached 0.6 mm d^{-1}.

During the measurement period, a significant decrease was observed in transpiration rates in *Larix decidua* trees between July and August. This can be explained by intensive resin exudation (Arneth 1994; 1996) that disturbed the measurements. Therefore, these data were discarded from consideration. Tree canopy transpiration rates measured in the *Larix gmelinii* stand in Siberia were in the range of 1 – 2 mm d^{-1} (Arneth 1994; 1996). The daily transpiration rates estimated for the *Larix gmelinii* stand, including tree canopy and understory, varied from 1.6 to 2.2 mm (Kelliher et al. 1997).

The stand level maximum hourly water flow observed in this study in dwarf-pine was 0.15 mm h^{-1}. Higher hourly rates of 0.33 mm h^{-1} were measured for *Pinus sylvestris* stands in Germany (Granier et al. 1996b). The mean daily water use of *Pinus mugo* in the Berchtesgaden National Park reached 0.2 – 0.5 mm d^{-1} in different months. The water use of a 64-year-old *Pinus pinaster* stand in Portugal ranged from 0.8 to 3 mm d^{-1} depending on water content in the soil (Loustau et al. 1996). According to Cermak (1995) the transpiration rates in an old Scots pine and Norway spruce stand in central Sweden measured in July reached ca. 0.7 mm d^{-1}.

5.7. Daily controls on canopy transpiration

Norway spruce: The transpiration rates at the 630 m site, where generally the highest air and soil temperatures and highest vapor pressure deficit in the air occurred, were significantly higher than at 1040 and 1360 m a.s.l. The highest water loss was observed in June and July, when the highest temperatures and vapor pressure deficit in the air were measured. The daily maximum VPD or daily mean VPD was the best single atmospheric predictor of daily E_c (Köstner 2001). The transpiration rates increased with increasing $VPD_{max.}$ In the three investigated spruce stands, similar correlations with respect to the vapor pressure deficit could be described (**Fig. 4.31**). However, the transpiration rates at the three investigated sites reached ca. 90% of maximum at different VPD_{max} values: 25 – 30, 20 – 25, 15 – 20 hPa at Bartholomä, Hirschengarten and Seeangerl respectively. A similar correlation between canopy transpiration and vapor pressure deficit was reported in Köstner (2001). In principle, similar patterns between vapor pressure deficit (VPD) and canopy conductance (E_c) were observed at various forest sites differing in species, forest structure and site conditions (Alsheimer 1997; Köstner 2001; Köstner et al. 1996). The observed differences in transpiration rates could be due to the differential optimal photosynthesis temperature and meteorological conditions at different elevations (Falge 1997).

The daily transpiration increases approximately linearly with increasing radiation. The relationship between daily stand water use and PPFD integrated over the day at the site Bartholomä is demonstrated in **Fig. 4.32**. However, directly after rain periods, the measured stand water use was very low, despite high incoming radiation. Similar responses of the transpiration rates (Fischer et al. 2002; Köstner 2001) and sap flux densities (Kubota et al. 2005) to the radiation intensity in forest stands were found in other studies.

European beech: According to Stickan and Zhang (1992), the transpiration in beech stands is influenced more by PPFD than by vapor pressure deficit. The authors reported that in beech trees, the stomatal opening primarily depends on irradiance and there is no strong relationship between transpiration rate and vapor pressure saturation deficit. In contrast, in this work strong relationships between maximum vapor pressure deficit and daily canopy transpiration in different months were found (**Fig. 4.33**). The variation of the relationships over the season may be associated with leaf development in spring and their maturation and senescence in autumn. In the experimental beech stand, an increase in maximum vapor pressure deficit in the air (VPD_{max}) again was correlated with an increase in daily water use, but the maximum transpiration rates for each month were associated with different VPD_{max} values. The maximum transpiration rates were reached at ca. 25 – 30 hPa, 17 hPa, and 15 hPa, in June, July and August, respectively. The lowest increase in daily water use with VPD_{max} was observed in June. An increase in sapflow densities with increasing daily VPD values in beech stands was also described by Kubota et al. (2005).

Similar to the spruce site, a linear increase in canopy transpiration rates with increasing radiation intensity was measured for the beech trees (**Fig. 4.34**). During periods after rain events and on days with high relative humidity, the stand water loss was low despite high radiation input. An increase in transpiration rates was recorded in the middle of August after two weeks of strong rain events. The relationships between sapflux density and PPFD, and transpiration at different CO_2 enrichments in response to PPFD for beech trees was described with saturation curves in studies by Kubota et al. (2005) and Overdieck and Forstreuter (1994).

European larch and dwarf-pine: Daily transpiration rates increased with increasing maximum vapor pressure deficit in the air (VPD_{max}). This correlation was observed at larch as well as at dwarf pine sites. Maximum transpiration capacity for *Pinus mugo* occurred with VPD_{max} of ca. 20 hPa (**Fig. 4.35**). The transpiration relationship to maximum vapor pressure deficit was more obvious for dwarf-pine shrubs than for European larch trees. It was in part difficult to determine characteristic changes in transpiration capacity for larch trees, because they do not build a closed canopy at our site, but the results of this study were comparable to observations in other sparse *Larix* stands. Arneth (1994) observed maximum xylem flux at a vapor pressure deficit of 20 hPa, Matyssek (1985) measured 10 l h^{-1} rates in *Larix* hybrids at a VPD of 15 hPa.

The linear response of transpiration of the larch stand to the increase in radiation is demonstrated in **Fig. 4.36**. A better correlation between transpiration and PPFD was found for larch trees than for the dwarf-pine shrubs. Because of frequently occurring short rain events, fog, and dew formation, the transpiration rates for dwarf-pine may remain often low despite relatively high integrated PPFD values. A linear response of sapflow rates to increasing radiation in a *Larix gmelinii* stand was demonstrated by Arneth (1994) and for *Larix decidua x leptolepis* by Matyssek (1985).

5.8. Canopy conductance

The water balance of plants is controlled by water absorption by roots or by stomatal closure. The stomatal water loss is regulated by light, vapor pressure deficit in the air, temperature, water potential of leaves and by nutrients. The canopy conductance depends also on tree species, canopy structure and nitrogen distribution within the canopy (Köstner 2001). In this study the total water vapor transfer conductance (g_t) was estimated from canopy transpiration (E_c) and vapor pressure deficit in the air (VPD) (see **Eq. 3.8 – 3.9**). In contrast to the transpiration rates, the canopy conductance declines with increasing vapor pressure deficit, because an increase in VPD stimulates stomatal closure. In the three experimental spruce stands, the maximum canopy conductance (g_{tmax}) decreased strongly with increasing VPD_{max}. The same correlation between canopy conductance and vapor pressure deficit was demonstrated in Alsheimer (1997), Falge (1997), Köstner et al.(1996), Köstner (1999c), Loibl (2004).

Norway spruce: The maximum canopy conductance in the three investigated spruce stands reached different values. During the measurement period, the maximum g_t (on clear days, between 7 a.m. and 2 p.m.) reached at Bartholomä 20 mm s^{-1}, and at Hirschengarten and at Seeangerl 15 mm s^{-1}. The average canopy conductance estimated for a 220-year-old *Abies amabilis* forest reached 12.2 mm s^{-1}, the maximum g_t was 37.5 mm s^{-1} (Martin et al. 2001).

The differences between the three spruce stands in canopy conductance and canopy transpiration could possibly be explained by stomatal patchiness. Stomata may build groups that respond differently from stomata in adjacent areas to environmental stimuli (Buckley et al. 1999; Mott and Buckley 1998). The stomata behaviour on the same leaf can be heterogeneous and the conductance of each patch may change independently from other areoles. The optimal stomata behaviour is to maximize photosynthesis and minimize transpiration; the patchiness could help conserve water but allow for high rates of photosynthesis at optimum temperatures. At the highest elevation, the stomata may close earlier than in other stands, as soon as the optimum for photosynthetic enzyme activity has been achieved.

The stomata patchiness could be also caused by different ozone concentrations in the air along an elevation gradient, which in turn may have an impact on transpiration rates. During the last decades, ozone became an important air pollutant influencing the vegetation in Europe (Ashmore et al. 2004; Loibl 2004). Study of *Picea abies*, *Pinus cembra*, and *Larix decidua* showed that in evergreen trees, the O_3 uptake is higher than by deciduous trees (Wieser et al. 2003). With exposure to ozone, a decline in stomatal conductance by Aleppo pine was observed (Anttonen et al. 1998). The diffusive resistance in needles increased with the time and dose of ozone exposure. Also by poplar clones (*Populus deltoides x maximowiczii* clone Eriadno), during fumigation with ozone, a strong decrease in maximum photosynthesis, stomatal conductance and transpiration were observed (Guidi et al. 1997). The mechanism of stomatal closure affected by ozone is not clear. The increasing ozone concentration in the air can also have a negative impact on plant growth. Karlsson (2004) found a significant correlation between the reduction of total biomass for *Picea abies* saplings and the estimated cumulative ozone uptake. The same relationship between relative biomass of the Norway spruce and ozone exposure expressed as AOT40 (µl $l^{-1}h^{-1}$) was demonstrated in Skärby et al. (2004). In that study a significant negative correlation between biomass acumulation and AOT40 for the European data set was shown. The model predicted a 6% reduction in growth for the most sensitive Norway spruce trees at the present ozone critical level. However, at our study sites ozone deposition was not determined, and effects for conductance in our study remain speculative.

European beech: For calculation of the canopy conductance (g_t), only data from clear days were used. The maximum value of canopy conductance (g_t) in the beech stand Bartholomä measured on clear days between 7 a.m. and 2 p.m. reached 30 mm s^{-1}. The maximum canopy conductance measured in a beech stand in France reached ca. 20 mm s^{-1} (Granier et al. 2000). The authors observed a strong limitation of canopy conductance for ambient temperatures below 15 – 17 °C. Stomatal conductance measured at the top of an ash and beech canopy during dry summer days reached maximum values of 0.3 mol m^{-2} s^{-1} (Roberts and Rosier 1994). At the canopy base, g_s was ca. half of this value. The g_s at canopy level was more closely associated with specific humidity deficit than with any other meteorological variable.

European larch and dwarf-pine: Because the larch trees do not build a closed canopy, the estimation of canopy conductance was not possible. The maximum canopy conductance for a *Larix gmelinii* stand in Siberia was in the range of 1.8 – 9.1 mm s^{-1} (Arneth 1994). The maximum bulk surface conductance for *Larix gmelinii* trees reached 10 mm s^{-1} (Kelliher et al. 1997).

For analysis of canopy conductance at the *Pinus mugo* site, only periods between 7 a.m. and 2 p.m. on clear days and were considered. The maximum canopy conductance observed for dwarf-pine reached ca. 10 mm s^{-1}. The correlation between g_t and VPD is similar to other investigated species in this study. A rapid decrease in canopy conductance with decreasing air humidity is associated with stomatal closure. A strong decline in total conductance with increasing VPD was observed also for *Pinus sylvestris* (Köstner et al. 1996).

5.9. Model

On the basis of measured transpiration rates and meteorological conditions at the investigated forest sites, empirical models based on correlation between transpiration and VPD_{max}, and transpiration and daily integrated PPFD (see **4.8**) were developed. These models might be used for the estimation of transpiration rates in similar forest stands. To explain the differences in water loss between forest stands along the elevation gradient the GAS-FLUX model was used. The changes in transpiration rates between stands were estimated according to two hypotheses: 1) differences in carboxylation capacity (Vcmax) and 2) changes in stomatal patchiness (the portion of leaves that are active) (see **4.10**). The optimal stomata behaviour is to maximize photosynthesis and minimize transpiration, and patchiness could help conserve water and prevent photoinhibition at our sites. Stomata patchiness could also be caused by different ozone concentrations in the air along the elevation gradient. Values of fvc (Vc_{max}) at 25 °C and portion of leaves that are active obtained for three investigated stands are given in **Tab. 4.19.** In GAS-FLUX, the parametrization is only implicitly affected by nitrogen concentration, for instance by changing the value of Vc_{max} according to the nitrogen content of the leaves. In this work the Vc_{max} values and the patchiness factor were estimated separately to match the observed transpiration rates.

For the three experimental sites the same temperature constants from Davos (see **3.8.1** and **4.10**) were chosen. The results from the GAS-FLUX model for Hirschengarten and Seeangerl show a better agreement with the measured data than for Bartholomä **(Fig. 4.40 – 4.41)**. For the 630 m site (Bartholomä) empirical PPFD and VPD models give better results than GAS-FLUX. To obtain better results for the 630 m site other temperature sensitivities should probably be used reflecting the lower elevation of the site.

For the empirical models (VPD and PPFD) and GAS-FLUX with changing of Vc_{max} (fvc) or portion of leaves that is active (live) used in this work, the following indices of agreement (IA) were found:

Tab. 5.1: Index of agreement for empirical (PPFD and VPD), and GAS-FLUX models for investigated spruce stands in the Berchtesgaden National Park.

Model type		Bartholomä (630 m)	Hirschengarten (1040 m)	Seeangerl (1360 m)
Empirical	PPFD	0.84	0.87	0.87
	VPD	0.92	0.87	0.85
GAS-FLUX	fvc	0.71	0.93	0.91
	Live	0.71	0.93	0.91

The index of agreement in all the models, except the VPD model, are higher for the 1040 m and 1360 m than for the 630 m site (**Tab. 5.1**). The best agreement between modelled and observed data was found for Hirschengarten, however, the differences in the IA between Hirschengarten and Seeangerl are not obvious.

In general, in residual plots for the GAS-FLUX model (with changing fvc and portion of leaves that is alive) no trends could be recognized (only for Bartholomä for the “Physiology” and “Patchiness” model slight trends both with $PPFD_{integr.}$ and VPD_{max} were found), whereas in the empirical models (VPD, PPFD) a trend with the not used factor was observed. The residuals for the 630 m site have a wider range than those for the two other experimental sites. The maximum differences between modelled and observed transpiration reached ca. 1 mm for Bartholomä, and 0.5 mm for Hirschengarten and Seeangerl.

Model parameter values were modified to study potential reasons for differences in flux control at different elevations. The model results can be extrapolated in the future studies for other similar mountain locations, but the extrapolation to other sites can involve difficulties because of several parameters that are needed to run the model. To obtain a good agreement with observed data, detailed measurements of meteorological parameters (radiation, temperature) should be carried out as close as possible to (or above) the experimental sites. This study shows also, that i.e. the temperature sensitivities (extrapolated from other sites) used for estimations in similar locations should be carefully chosen. The GAS-FLUX model seems to be useful for examination of the mechanisms and processes that occur in the ecosystems and to predict the changes in the ecosystems with changing environment. This is a very good tool for investigation of connections between vegetation and atmosphere and also for analyzing of ecosystem sensitivities e.g. to the change in meteorological (air temperature), physiological (nitrogen content), or structural (LAI) changes. In addition, the model may be used for gap filling, which permitted estimates of water use over longer growth periods.

6. CONCLUSIONS

In this work, the hypothesis that transpiration rates of Norway spruce forests decreased with increasing elevation a.s.l. was supported. Differences in water fluxes among trees species occurring at the same altitude were also found. Variations in tree water use and canopy conductance along elevation gradients with of similar exposition, inclination, LAI and soils characteristics might be partially explained by the influences of climate conditions.

With an increase of tree circumference an increase in sapwood area for spruce, beech, and larch trees was determined. Along the elevation gradient, a decrease in growth and an increase in bark thickness were observed. The differences in transpiration rates between spruce stands cannot be explained by differences in leaf area index. The LAI for the three experimental spruce stands was very similar and typical for Norway spruce, ranging from 6.1 to 7.0 m^2 m^{-2}. The leaf area index estimated for the beech stand, 6.4 m^2 m^{-2}, was similar to the LAI of spruce at the same elevation. The measured leaf area index of European larch at the treeline site Kederbichl was low (1.5 m^2 m^{-2}).

The analyses of nutrient concentrations in spruce needles suggest differences in nutrient supply between stands. The differences in transpiration rates between stands, however, cannot be definitely explained by the differences in needle nutrients concentrations.

The daily sapflow courses are affected by radiation (PPFD) and vapor pressure deficit in the air (VPD). In general, the diurnal sapflow time courses for different xylem layers were similar in form, but the magnitude for sapflow decreased with increasing depth within the sapwood. The measurements at three spruce stands showed large variation in sap flux density with xylem depth and among trees and stands. The relationship between sap flux densities at outer and inner sapwood layers differed among trees and over the course of the season.

It was apparent from the first survey of the results that regulation of water use at the landscape level is complex. Because of differences in elevation a.s.l. and in turn in climate conditions, significant differences in rates and in diurnal courses of transpiration at three experimental spruce sites were observed. Similar patterns of seasonal water losses, influenced by meteorological factors at three experimental spruce sites were observed, however, large differences (78-165 mm) between stands can be described. During the measurement period, the monthly transpiration rates of the beech stand were from 8 to 35 mm lower than in the spruce stand at the same elevation. The seasonal water use of the beech stand reached 78 mm. The transpiration in the European larch stand was successfully measured only in June, and the monthly rate was 5 mm lower than that of the dwarf-pine shrub stand. The seasonal water loss at the *Pinus mugo* site reached 44 mm.

Vapor pressure deficit of the air and PPFD can be used individually to predict the daily canopy transpiration in the spruce stands. With an increase in maximum vapor pressure deficit in the air (VPD_{max}), a non-linear increase in daily water use for all experimental stands and species occurred. A linear increase in daily stand transpiration with radiation was also found. In all investigated stands, canopy conductance declined with increasing vapor pressure deficit. In contrast to transpiration, the maximum canopy water vapor transfer conductance (g_{tmax}) decreased linearly with maximum vapor pressure deficit (VPD_{max}).

Field data were used to estimate water fluxes in mountain regions with a stand level model in order to develop an extrapolation potential for other similar mountain locations. Model calculations showed that the differences in transpiration rates between stands may be estimated according to differences in carboxylation capacity (Vc_{max}), or changes in the portion of leaves that are active (stomatal patchiness). The transpiration rates estimated with changing of Vc_{max} and portion of leaves that is alive give similar results. The results from the GAS-FLUX model for the 1040 and the 1360 m sites show better agreement with the measured data than for the 630 m site, whereas the correlations between the empirical PPFD and VPD models and observed data are stronger for the 630 m site.

7. SUMMARY

Forests are major sources of water vapor to the atmosphere and have an important influence on both regional and global climate. Understanding of the water exchange between the vegetation and the atmosphere, and recognition of factors to predict the water fluxes is necessary to estimate the changes in water use according to possible climate change. In this study the processes affecting the transpiration of Norway spruce (*Picea abies*) in the Berchtesgaden National Park along an elevation gradient were investigated. Sapflow and meteorological measurements were carried out during the summer of 2002. For each stand, structural differences (tree height, circumference, diameter (DBH), tree density, basal area) were also analyzed. For the experiment, three Norway spruce stands – with similar inclination, exposition, LAI and soil conditions, but situated at different elevations a.s.l in the Berchtesgaden National Park were selected. The transpiration rates of spruce were compared with those of other species: *Fagus sylvatica*, *Larix decidua* and *Pinus mugo*. In each stand, six to fifteen trees were selected for sapflow measurements. Xylem sap flux was observed with constant-heating-method according to Granier. Sapflow rates of individual trees were scaled up to the stand level according to the cross-sectional sapwood area of the DBH class (for spruce and beech) or total cross-sectional sapwood area (for larch). Within the sparse *Larix decidua* stand, both the sapflow in trees and water loss from understory vegetation were measured. Strong correlations between transpiration rates and maximum VPD and daily integrated PPFD were found for the experimental species. For the Norway spruce stands, needle nutrient concentrations were also determined.

During the 2002 growing season (May- September), the seasonal patterns of tree canopy transpiration were similar for the different experimental stands. The highest water use was observed in June and July for spruce and dwarf-pine, and in July and August for beech. The seasonal changes in canopy transpiration and conductance, and the variation between spruce stands, may be in part explained by differences in meteorological conditions. Canopy conductance was calculated from canopy transpiration (Ec) and vapor pressure deficit (VPD).

Absolute rates of seasonal canopy transpiration within experimental *Picea abies* sites differed greatly from 78 to 165 mm. The highest transpiration rates occurred in the lowest situated stand and they decreased with increasing elevation. The seasonal water loss from the *Fagus sylvatica* site (78 mm) was similar to the water loss at the highest situated spruce site. The seasonal transpiration of *Pinus mugo* site reached 44 mm. Transpiration of *Larix decidua* was only measured successfully during June and during a few days in July.

A strong decrease of canopy conductance (g_t) with increasing VPD was observed for all stands. The highest maximum canopy conductance for spruce, 20 mm s^{-1}, was calculated for the 630 m site, while for the 1040 m and the 1360 m sites the maximum g_{tmax} reached 15 mm s^{-1}. In comparison the maximum canopy conductance for the beech site was higher than for the spruce site at the same elevation a.s.l. (630 m) and reached 30 mm s^{-1}. The lowest maximum g_t, 10 m s^{-1}, was estimated for dwarf-pine shrub.

For the examination of controls on spruce forest water use that were found along the elevation gradient, the GAS-FLUX model was used. Model simulations support two alternative hypotheses, namely that stomatal patchiness as well as carboxylation capacity (Vc_{max}) may have had an influence on stand water use. The modelled transpiration with changes in Vc_{max} was similar to estimated transpiration rates obtained by changing the “portion of leaves that are active” (stomatal patchiness). The developed model can be used for estimation of water use for other similar mountainous locations or for examination of ecosystem sensitivities to environmental changes (nitrogen supply, air temperature).

The current work should stimulate further research on the detailed study of e.g. stomatal patchiness and its influence on transpiration rates, or to test the results at other sites.

8. ZUSAMMENFASSUNG

Wälder, die eine wichtige Quelle des Wasserdampfes in der Atmosphäre sind, haben einen grossen Einfluß sowohl auf das regionale als auch das globale Klima. Die Kenntnis des Wasseraustausches zwischen der Vegetation und der Atmosphäre und Erkennung der Faktoren um die Veränderungen in der Wasseraufnahme mit der eventuellen Klimaänderung abzuschätzen, ist notwendig. In dieser Arbeit wurden die Prozesse untersucht, die die Transpiration der Fichtenwälder (*Picea abies*) beeinflussen. Saftfluß- und meteorologische Messungen wurden während des Sommers 2002 durchgeführt. Für jeden Bestand wurden auch die strukturellen Unterschiede (Baumhöhe, Umfang, Durchmesser (DBH), Baumdichte, Bestandesgrundfläche) analysiert. Zur Untersuchung wurden drei Fichtenbestände – mit ähnlicher Hangneigung, Exposition, LAI und Bodenbedingungen – ausgewählt, die sich auf verschiedener Höhe über den Meeresspiegel im Nationalpark Berchtesgaden befinden. Die Transpirationsraten der Fichte wurden verglichen mit den Raten anderer Baumarten: *Fagus sylvatica*, *Larix decidua* und *Pinus mugo*. In jedem Bestand wurden sechs bis fünfzehn Bäume für Saftflußmessungen ausgewählt. Xylemsaftfluß wurde gemessen anhand der Konstant-Temperaturdifferenz-Methode nach Granier. Saftflußraten der einzelnen Bäume wurden hochskaliert für die Bestandesebene anhand der Splintholzfläche der einzelnen DBH-Klassen (für Fichte und Buche) oder der Splintholzfläche des ganzen Bestandes (für Lärche). In dem Lärchenbestand wurden sowohl der Saftfluß in den Bäumen als auch der Wasserverlust von der Vegetation des Unterwuchses gemessen. Die Kronendachleitfähigkeit wurde aus der Kronendachtranspiration (Ec) und dem Wasserdampfsättigungsdefizit (VPD) berechnet. In den Fichtenbeständen wurden die Nährstoffkonzentrationen der Nadeln bestimmt.

Während der Vegetationsperiode 2002 (Mai – September), waren die saisonalen Verläufe der Kronendachtranspiration in verschiedenen Beständen sehr ähnlich. Der höchste Wasserverbrauch wurde beobachtet für die Fichte und Bergkiefer im Juni und Juli und für die Buche im Juli und August. Die saisonalen Änderungen in Kronendachtranspiration und Leitfähigkeit und zwischen den Beständen können teilweise erklärt durch die Unterschiede in den meteorologischen Bedingungen werden. Eine starke Korrelation wurde zwischen den Transpirationsraten und dem maximalem VPD und dem über den Tag integrierten PPFD festgestellt.

Die absolute Raten der saisonalen Kronendachtranspiration in den *Picea abies* Beständen unterschieden sich stark und betrugen 78 bis 165 mm. Die höchsten Transpirationsraten wurden gemessen in dem am tiefsten gelegenen Bestand. Transpirationsraten wurden niedriger mit steigender Höhe über dem Meeresspiegel. Der saisonale Wasserverlust des *Fagus sylvatica* Bestandes (78 mm) war vergleichbar zu der Summe des am höchsten gelegenen Fichtenbestandes. Die saisonale Transpiration des *Pinus mugo* Bestandes betrug 44 mm. Die Transpiration des *Larix decidua* Bestandes wurde nur im Juni und ein paar Tagen im Juli erfolgreich gemessen.

Eine starke Abnahme der Leitfähigkeit (g_t) mit dem ansteigenden VPD wurde beobachtet. Die höchste maximale Kronendachleifähigkeit 20 mm s^{-1} in den Fichtenbeständen wurde für den 630 m Bestand berechnet, während für die 1040 und 1360 m Bestände g_{tmax} 15 mm s^{-1} betrug. Im Vergleich war die maximale Kronendachleitfähigkeit des Buchenbestandes höher als für den auf derselben Höhe (630 m) gelegenen Fichtenbestand und betrug 30 mm s^{-1}. Die niedrigste g_{tmax} (10 m s^{-1}) wurde für den Bergkieferbestand bestimmt.

Für die Überprüfung der Kontrollfaktoren der Wassernutzung, die entlang des Höhengradientes festgestellt wurde, wurde das GAS-FLUX Model angewendet. Modellsimulationen bestätigen zwei alternativen Hypothesen, dass sowohl Unterschiede in stomatärer „patchiness“ als auch der Karboxylierungskapazität (Vc_{max}) die Wassernutzung des Bestandes beeinflusst haben könnten. Das entwickelte Model kann benutzt werden für die Abschätzung der Wasserabgabe in anderen ähnlichen Gebirgsstandorten oder für die Untersuchung der Ökosystemsensitivität auf die Änderungen der Umweltfaktoren (Stickstoffverfügbarkeit, Lufttemperatur).

Diese Arbeit sollte weitere Forschung zu detaillierten Untersuchungen stimulieren, wie z.B. zu „stomatal patchiness“ und deren Einfluss auf die Transpirationsraten, oder zur Überprüfung der Resultate auf anderen Versuchsflächen.

9. REFERENCES

ACE Information Programme. 17. Climate Change, Hydrology & Water Resources.

Alavi, G. 1996. Radial stem growth of Picea abies in relation to spatial variation in soil moisture conditions. Scandinavian Journal of Forest Research. 11:209-219.

Alsheimer, M. 1997. Xylemflußmessungen zur Charakterisierung raum-zeitlicher Heterogenitäten in der Transpiration montaner Fichtenbestände (*Picea abie*s (L.) KARST.) Ed. Bfö. Universität Bayreuth.

Alsheimer, M., B. Kostner, E. Falge and J.D. Tenhunen 1998. Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany. Annales Des Sciences Forestieres. 55:103-123.

Altherr, E. and F.H. Evers 1975. Magnesium-Düngungseffekt in einem Fichtenbestand des Buntsandstein-Odenwaldes. Allgemeine Forst Und Jagdzeitung. 146:217-225.

Amiro, B.D. and E.E. Wuschke 1987. Evapotranspiration from a Boreal Forest Drainage-Basin Using an Energy-Balance Eddy-Correlation Technique. Boundary-Layer Meteorology. 38:125-139.

Anttonen, S., M. Kittila and L. Karenlampi 1998. Impacts of ozone on Aleppo pine needles: Visible symptoms, starch concentrations and stomatal responses. Chemosphere. 36:663-668.

Arneth, A. 1994. Transpiration und Kronendachleitfähigkeit eines sibirischen Lärchenbestandes (*Larix gmelinii* (Rupr.) RUPR.). University Bayreuth, Bayreuth, p. 93.

Arneth, A., F.M. Kelliher, G. Bauer, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, W. Ziegler, N.N. Vygodskaya, I. Milukova, A. Sogatchev, A. Varlargin and E.D. Schulze 1996. Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia

Ashmore, M., L. Emberson, P.E. Karlsson and H. Pleijel 2004. New directions: A new generation of ozone critical levels for the protection of vegetation in Europe. Atmospheric Environment. 38:2213-2214.

Bac, S., C. Kozminski and M. Rojek 1993. Agrometeorologia. Wydawnictwo Naukowe PWN, Warszawa. 249 p.

BAHC 1993. The Operational Plan. Biological Aspects of the Hydrological Cycle.

Baier, R. 2004. Ernährungszustand und mögliche Anpassungsmechanismen der Fichte (Picea abies (L.) Karst.) auf Dolomitstandorten der bayerischen Kalkalpen. Schweiz. Z. Forstwes. 9:378-391.

Ball, J.T., Woodrow I.E. and J.A. Berry 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *In* Binggins, I.: Progress in photosynthesis research, Vol. IV.5. Proc of the VII Photosynthesis Congress, pp. 211-224.

Bartelnik, H. 1997. Allometric relationships for biomass and leaf area for beech (*Fagus sylvatica* L.). Annales Des Sciences Forestieres. 54:39-50.

Bassman, J.H., J.D. Johnson, L. Fins and J.P. Dobrowolski 2003. Rocky Mountain ecosystems: diversity, complexity and interactions. Tree Physiology. 23:1081-1089.

Bauer, G. 1993. Die Transpiration eines Fichtenbestandes (*Piecea abies* (L.) Karst.) und ihre Abhängigkeit von bestimmenden Größen. *In* Pflanzenökologie. Universität Bayreuth.

Bauer, G., E.D. Schulze and M. Mund 1997. Nutrient contents and concentrations in relation to growth of Picea abies and Fagus sylvatica along a European transect. Tree Physiology. 17:777-786.

Beerling, D.J., J. Heath, F.I. Woodward and T.A. Mansfield 1996. Drought-CO2 interactions in trees: Observations and mechanisms. New Phytologist. 134:235-242.

Benecke, U. 1972. Wachstum, CO_2-Gaswechsel und Pigmentgehalt einiger Baumarten nach Ausbringung in verschiedene Höhenlagen. Angewa.Bot. 46

Berger-Landefeldt, U. 1936. Der Wasserhaushalt der Alpenpflanzen. Bibl. Bot. 115:38-49.

Black, T.A. and F.M. Kelliher 1989. Processes Controlling Understorey Evapotranspiration. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences. 324:207-231.

Bobeva, A. 2003. Quantifying the distribution of forest functional types and forest Leaf Area Index in the Alps. *In* Biologie, Chemie und Geowissenschaften. Bayreuth, Bayreuth.

Bonan, G.B. 1993. Importance of Leaf-Area Index and Forest Type When Estimating Photosynthesis in Boreal Forests. Remote Sensing of Environment. 43:303-314.

Bosch, C., E. Pfannkuch, U. Baum and K.E. Reuhfuess 1983. Über die Erkrankung der Fichte in den Hochlagen des Bayerischen Waldes. Forstwissenschaftliches Centralblatt. 102:167-181.

Braun, G. 1986. Zu den Ursachen der Waldschäden im Bergwald. Allgemeine Forstzeitschrift. 41:936-937.

Buckley, T.N., G.D. Farquhar and K.A. Mott 1999. Carbon-water balance and patchy stomatal conductance. Oecologia. 118:132-143.

Burczyk, J. and M. Giertych 1991. Response of Norway Spruce (Picea-Abies [L] Karst) Annual Increments to Drought for Various Provenances and Locations. Silvae Genetica. 40:146-152.

Burger, H. 1939. Kronenaufbau gleichartriger Nadelholzbestände. Mitt.Schweiz.Anst.f.d. forstl. Versuchswesen. 21:5-56.

Burger, H. 1942. Holz, Blattmenge und Zuwachs. V. Mitteilung: Fichten und Föhren verschiedener Herkunft auf verschiedenen Kulturorten. Mitt. Schweiz.Anst.f.d.forstl. Versuchswesen. 22:10-62.

Burger, H. 1945. Holz, Blattmenge und Zuwachs - Die Buche. Mitt. Schweiz. Anst. f.d.forstl.Versuchswesen. 26:419-468.

Burger, H. 1953. Holz, Blattmenge und Zuwachs. XIII. Mitteilung: Fichten im gleichaltigen Hochwald. Mitt.Schweiz. Anst. f.d.forstl.Versuchswesen. 29:38-130.

Caldwell, M.M., H.P. Meister, J.D. Tenhunen, O.L. Lange and . 1986. Canopy structure, light microclimate and leaf gas exchange of Quercus coccifera L. in a Portugese macchia: Measurements in different canopy layers and simulations with a canopy model. Trees. 1:25-41.

Cermak, J., E. Cienciala, J. Kucera and J.E. Hallgren 1992. Radial-Velocity Profiles of Water-Flow in Trunks of Norway Spruce and Oak and the Response of Spruce to Severing. Tree Physiology. 10:367-380.

Cermak, J., E. Cienciala, J. Kucera, A. Lindroth and E. Bednarova 1995. Individual Variation of Sap-Flow Rate in Large Pine and Spruce Trees and Stand Transpiration - a Pilot-Study at the Central Nopex Site. Journal of Hydrology. 168:17-27.

Cermak, J., Jenik.J, Kucera, J. Zidek, V. 1984. Xylem water flow in a crack willow tree (Salix fragilis [L.]) in realtion to diurnal changes of envinronment. Oecologia. 64:145-151.

Change, U.N.F.C.o.C. Climate Change Information Sheet 12, Biological diversity and ecosystems. http://unfccc.int/resource/iuckit/fact12.html.

Chen, J.M. and J. Cihlar 1995. Quantifying the Effect of Canopy Architecture on Optical Measurements of Leaf-Area Index Using 2 Gap Size Analysis-Methods. Ieee Transactions on Geoscience and Remote Sensing. 33:777-787.

Christensen, K.I. 1987. Taxonomic Revision of the Pinus-Mugo Complex and Pxrhaetica (Pxrhaetica-Mugoxsylvestris) (Pinaceae). Nordic Journal of Botany. 7:383-408.

Cienciala, E., A. Lindroth, J. Cermak, J.E. Hallgren and J. Kucera 1992. Assessment of Transpiration Estimates for Picea-Abies Trees During a Growing-Season. Trees-Structure and Function. 6:121-127.

Cienciala, E., A. Lindroth, J. Cermak, J.E. Hallgren and J. Kucera 1994. The Effects of Water Availability on Transpiration, Water Potential and Growth of Picea-Abies During a Growing-Season. Journal of Hydrology. 155:57-71.

Commission of the European Communities 2002. Growth Changes of Norway Spruce Under Varying Climatic Conditions on Sites in Northern and Central Europe-SPRUCE GROWTH -. Commission of the European Communities under FAIR3-CT96-1310.

Comstock, J. and M. Mencuccini 1998. Control of stomatal conductance by leaf water potential in Hymenoclea salsola (T & G), a desert subshrub. Plant Cell and Environment. 21:1029-1038.

Day, T.A., S.A. Heckathorn and E.H. Delucia 1991. Limitations of Photosynthesis in Pinus-Taeda L (Loblolly-Pine) at Low Soil Temperatures. Plant Physiology. 96:1246-1254.

Department of Communications, M.a.N.R. http://www.marine.gov.ie/display.asp/pg=316

Dittrich, B. and U. Hermsdorf 1990. Biomonitoring in Waldökosystemen. National Park Berchtesgaden, pp. 5-63.

Evers, F.H. 1972. Die Jahrweisen Fluktuationen der Nährelementkonzentrationen in Fichtennadeln und ihre Bedeutung für die Interpretation nadelanalytischer Befunde. Allgemeine Forst Und Jagdzeitung. 143:68-74.

Evers, F.H. 1986. Die Blatt- und Nadelanalyse als Instrument der Bioindikation. Allgemeine Forstzeitschrift

FAIR3-CT96-1310 2002. Growth changes of norway spruce under varying climatic conditions on sites in Northern and Central Europe. Spruce growth.

Falge, E., D. Baldocchi, J. Tenhunen, M. Aubinet, P. Bakwin, P. Berbigier, C. Bernhofer, G. Burba, R. Clement, K.J. Davis, J.A. Elbers, A.H. Goldstein, A. Grelle, A. Granier, J. Guomundsson, D. Hollinger, A.S. Kowalski, G. Katul, B.E.

Law, Y. Malhi, T. Meyers, R.K. Monson, J.W. Munger, W. Oechel, K.T. Paw, K. Pilegaard, U. Rannik, C. Rebmann, A. Suyker, R. Valentini, K. Wilson and S. Wofsy 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agricultural and Forest Meteorology. 113:53-74.

Falge, E., W. Graber, R. Siegwolf and J.D. Tenhunen 1996. A model of the gas exchange response of Picea abies to habitat conditions. Trees-Structure and Function. 10:277-287.

Falge, E., R.J. Ryel, M. Alsheimer and J.D. Tenhunen 1997. Effects of stand structure and physiology on forest gas exchange: a simulation study for Norway spruce. Trees-Structure and Function. 11:436-448.

Falge, E., J.D. Tenhunen, M. Aubient, C. Bernhofer, R. Ceulemans, R. Clement, H. Dolman, A. Granier, P. Gross, T. Grünwald, N.-O. Jensen, A. Kowalski, J. Moncrieff, E. Moors, K. Pilegaard, Ü. Rannik, C. Rebmann, T. Vesala and R. Valentini 2003. A model-based study of carbon fluxes at ten European forests sites. *In* Fluxes of Carbon, Waterand Energy of European Forests. Ecological Studies, Springer Verlag, Heidelberg.

Falge, E.M. 1997. Die Modellierung der Kronendachtranspiration von Fichtenbeständen (*Picea abies* (L.) K$_{\text{ARST}}$.). *In* Bayreuther Forum Ökologie Ed. BITÖK.

Farquhar, G.D. 1989. Models of Integrated Photosynthesis of Cells and Leaves. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences. 323:357-367.

Farquhar, G.D., S.V. Caemmerer and J.A. Berry 1980. A Biochemical-Model of Photosynthetic Co2 Assimilation in Leaves of C-3 Species. Planta. 149:78-90.

Farquhar, G.D., J.R. Ehleringer and K.T. Hubick 1989. Carbon Isotope Discrimination and Photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology. 40:503-537.

Farquhar, G.D. and S. von Caemmerer 1982. Modelling of photosynthetic response to environment. *In* Encyclopedia of plant physiology 12B, Physiological plant ecology II, Water relations and carbon assymilation Ed. O.L. lange, Nobel, P.S., Osmond, C.B., Ziegler, H. Springer, Berlin Heidelberg New York, pp. 549-587.

Ferraz, J. and H.W. Zöttl 1979. Nährelementspiegel und Spurenelementeverteilung in Fichtenbeständen des Grungdebirgs-Schwarzwaldes. Mitteilungen Deutsche Bodenkundliche Gesellschaft. 29:587-594.

Fischer, D. 1993. Bestimmung der Bestandestranspiration und der Kronendachleitfähigkeit durch Xylemsaftflußmessungen in einem

Hochlagenwald [Picea abies (L.) Karst.]des Fichtelgebirges. *In* Ökosystemare Botanik des BITÖK, Bayreuth.

Fischer, D.G., T.E. Kolb and L.E. DeWald 2002. Changes in whole-tree water relations during ontogeny of Pinus flexilis and Pinus ponderosa in a high-elevation meadow. Tree Physiology. 22:675-685.

Ford, C.R., M.A. McGuire, R.J. Mitchell and R.O. Teskey 2004. Assessing variation in the radial profile of sap flux density in Pinus species and its effect on daily water use. Tree Physiology. 24:241-249.

Friedel, H. 1967. Verlauf der alpinen Waldgrenze im Rahmen anliegender Gebirgsgelände. Mitt. Forstl. Bundesversuchsanst. Wien. 75:81-172.

Fryer, J.H. and F.T. Ledig 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. Canadian Journal of Botany. 50:1231-1235.

Fuchs, E.E. and N.J. Livingston 1996. Hydraulic control of stomatal conductance in Douglas fir [Pseudotsuga menziesii (Mirb) Franco] and alder [Alnus rubra (Bong)] seedlings. Plant Cell and Environment. 19:1091-1098.

Gansert, D., K. Backes, T. Ozaki and Y. Kakubari 2002. Seasonal variation of branch respiration of a treeline forming (Betula ermanii Cham.) and a montane (Fagus crenata Blume) deciduous broad-leaved tree species on Mt. Fuji, Japan. Flora. 197:186-202.

Gates, D.M. 1980. Biophysical ecology. Springer New York. pp 661 p.

Gieger, T. and C. Leuschner 2004. Altitudinal change in needle water relations of Pinus canariensis and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife. Flora. 199:100-109.

Givnish, T.J. 1986. Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. *In* On the Economy of Plant Form and Function Ed. T.J. Givnish. Canbridge University Press, London.

Grace, J., J. Lloyd, J. Mcintyre, A. Miranda, P. Meir, H. Miranda, J. Moncrieff, J. Massheder, I. Wright and J. Gash 1995. Fluxes of Carbon-Dioxide and Water-Vapor over an Undisturbed Tropical Forest in South-West Amazonia. Global Change Biology. 1:1-12.

Granier, A. 1985. A New Method of Sap Flow Measurement in Tree Stems. Annales Des Sciences Forestieres. 42:193-200.

Granier, A. 1987. Evaluation of Transpiration in a Douglas-Fir Stand by Means of Sap Flow Measurements. Tree Physiology. 3:309-319.

Granier, A., M. Aubinet, D. Epron, E. Falge, J. Gudmundsson, N.O. Jensen, B. Köstner, G. Matteucci, K. Pilegaard, M. Schmidt and J. Tenhunen 2003. Deciduous forests: carbon and water fluxes, balances and ecophysiological determinants. *In* Fluxes of carbon, water and energy of European forests Ed. R. Valentini, pp. 55-70.

Granier, A., P. Biron, N. Breda, J.Y. Pontailler and B. Saugier 1996a. Transpiration of trees and forest stands: short and longterm monitoring using sapflow methods. Global Change Biology. 2:265-274.

Granier, A., P. Biron, B. Kostner, L.W. Gay and G. Najjar 1996b. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. Theoretical and Applied Climatology. 53:115-122.

Granier, A., P. Biron and D. Lemoine 2000. Water balance, transpiration and canopy conductance in two beech stands. Agricultural and Forest Meteorology. 100:291-308.

Grossnickle, S.C. 1988. Planting Stress in Newly Planted Jack Pine and White Spruce .2. Changes in Tissue Water Potential Components. Tree Physiology. 4:85-97.

Gu, S., Y.H. Tang, M.Y. Du, T. Kato, Y.N. Li, X.Y. Cui and X.A. Zhao 2003. Short-term variation of CO2 flux in relation to environmental controls in an alpine meadow on the Qinghai-Tibetan Plateau. Journal of Geophysical Research-Atmospheres. 108:-.

Guidi, L., C. Nali, S. Ciompi, G. Lorenzini and G. Franco 1997. The use of chlorophyll fluorescence and leaf gas exchange as methods for studying the different responses to ozone of two bean cultivars. Journal of Experimental Botany. 48:173-179.

Häsler, R. 1991. Vergleich der Gaswechselmessungen der drei Jahre (Juli 1986-Juni 1989). *In* Luftschadstoffe und Wald, Lufthaushalt, Luftverschmutzung und Waldschäden in der Schwiez, Ergebnisse aus dem nationalen Forschungsprogramm 14 Ed. M. Stark. Eidgenossische Technische Hochschule, Zurich, pp. 177-184.

Havranek, W.M. 1972a. Über die Bedeutung der Bodentamperatur für die Photosynthese und Transpiration junger Forstpflanzen und die Stoffproduktion an der Waldgrenze. Angew. Bot. 46:101-116.

Havranek, W.M. 1972b. Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die stoffproduktion an der Waldgrenze. Angew. Bot. 46:101-116.

Heimann, J. and J. Constantin 1999. Wasserflüsse in einem Buchenwaldökosystem (*Fagus sylvatica* L.) - Vergleich von Saftfluss und atmosphärischem

Wasserfluss am Beispiel der Buchenfläche B1 im Solling. *In* Jahrestagung der Gesellschaft für Ökologie, Bayreuth, p. Poster.

Herbst, M., C. Eschenbach and L. Kappen 1999. Water use in neighbouring stands of beech (Fagus sylvatica L.) and black alder (Alnus glutinosa (L.) Gaertn.). Annals of Forest Science. 56:107-120.

Hultine, K.R. and J.D. Marshall 2000. Altitude trends in conifer leaf morphology and stable carbon isotope composition. Oecologia. 123:32-40.

Hunger, W. 1964. Untersuchungen über den Einfluß der Kalkdüngung auf die Ernährungsverhältnisse eines älteren Fichtenbestandes. Tagungsberichte Nr. 66 Düngung und Meliorationin der Forstwirtschaft:47-58.

Hüttl, R.F. 1992. Die Blattanalyse als Diagnose- und Moimtoringinstrument in waldökosystemen. Freibg. bodenkd. 30:31-59.

Ingestad, T. 1959. Studies on the nutrition of foresttree seedlings. II. Mineral nutrition of spruce. Physiologia Plantarum. 12:568-593.

James, J.C., J. Grace and S.P. Hoad 1994. Growth and Photosynthesis of Pinus-Sylvestris at Its Altitudinal Limit in Scotland. Journal of Ecology. 82:297-306.

Johnson, D.M., M.J. Germino and W.K. Smith 2004. Abiotic factors limiting photosynthesis in Abies lasiocarpa and Picea engelmannii seedlings below and above the alpine timberline. Tree Physiology. 24:377-386.

Karlsson, P.E., E.L. Medin, S. Ottosson, G. Sellden, G. Wallin, H. Pleijel and L. Skarby 2004. A cumulative ozone uptake-response relationship for the growth of Norway spruce saplings. Environmental Pollution. 128:405-417.

Kaufmann, M.R. 1975. Leaf water stress in Englemann spruce: influence of the root and shoot environments. Plant Physiology. 58:841-844.

Kelliher, F.M., D.Y. Hollinger, E.D. Schulze, N.N. Vygodskaya, J.N. Byers, J.E. Hunt, T.M. McSeveny, I. Milukova, A. Sogatchev, A. Varlargin, W. Ziegler, A. Arneth and G. Bauer 1997. Evaporation from an eastern Siberian larch forest. Agricultural and Forest Meteorology. 85:135-147.

Kelliher, F.M., B.M.M. Kostner, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. Mcseveny, R. Meserth, P.L. Weir and E.D. Schulze 1992. Evaporation, Xylem Sap Flow, and Tree Transpiration in a New-Zealand Broad-Leaved Forest. Agricultural and Forest Meteorology. 62:53-73.

Kelliher, F.M., R. Leuning and E.D. Schulze 1993. Evaporation and Canopy Characteristics of Coniferous Forests and Grasslands. Oecologia. 95:153-163.

Kindermann, G., S. Slovik, W. Urbach and U. Heber 1992. Long-Term Resistance of Spruce to So2 Requires Mobilization of Cations. Phyton-Annales Rei Botanicae. 32:63-68.

Kirby, C., M.D. Newson and K. Gilman 1991. Plynlimon research: the first teo decades. Inst. Hydrol. Wallingford Rep. 109:188.

Konnert, V. 2001. Mapping site characteristics in the National Park Berchtesgaden - Project with cooperation with Technical University of Munich, Dept. of Ecology, the faculty of Forest Science and Resource Management, Dept. of Geobotany (Prof. Dr. Anton Fischer), and the Administration of National park Berchtesgaden

Körner, C. 1999. Alpine Plant Life Functional. Plant Ecology of High Mountain Ecosystems. Springer Verlag.

Körner, C., G.D. Farquhar and Z. Roksandic 1988. A Global Survey of Carbon Isotope Discrimination in Plants from High-Altitude. Oecologia. 74:623-632.

Köstner, B. 1999a. Die Transpiration von Wäldern - Quantifizierung als Xylemfluß und Faktorenabhängigkeit von Teilflüssen. *In* Lehrstuh für Pflanzenökologie Bayreuther Institut für Terrestrische Ökosystemforschung. Universität Bayreuth.

Köstner, B. 1999b. Die Transpiration von Wäldern - Quantifizierung als Xylemsaftfluß und Faktorenabhängigkeit von Teilflüssen. *In* Lehstuhl für Pflanzenökologie Gayreuther Institut für Terrestrische Ökosystemforschung. Bayreuth, pp. 1-63.

Köstner, B. 2001. Evaporation and transpiration from forests in Central Europe relevance of patch-level studies for spatial scaling. Meteorology and Atmospheric Physics. 76:69-82.

Köstner, B., M. Alsheimer and J. Tenhunen 1996. Tree transpiration at different sites of a spruce forest ecosystem. Verhandlungen der Gesellschaft für Ökologie. 26:61-68.

Kostner, B., P. Biron, R. Siegwolf and A. Granier 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. Theoretical and Applied Climatology. 53:105-113.

Köstner, B., E.M. Falge, M. Alsheimer, R. Geyer and J.D. Tenhunen 1998a. Estimating tree canopy water use via xylem sapflow in an old Norway spruce forest and a comparison with simulation-based canopy transpiration estimates. Annales Des Sciences Forestieres. 55:125-139.

Köstner, B., A. Granier and J. Cermak 1998b. Sapflow Measurements in Forest Stands: Methods and Uncertainties. Annales Des Sciences Forestieres. 55:13-27.

Köstner, B., J.D. Tenhunen, M. Alsheimer, M. Wedler, H.-J. Scharfenberg, R. Zimmermenn, E.Falge, U.Joss 1999c. Controls on Evapotranspiration in Spruce Forest Stands. Ecological Studies

Köstner, B., M. Alsheimer, J.D. Tenhunen 1996. Tree Canopy Transpiration at Different Sites of Spruce Forest Ecosystem. Verhandlungen der Gesellschaft für Ökologie. 26

Köstner, B., Schmidt M, F.S. Falge E and T. JD 2004. Atmospheric and structural controls on carbon and water relations in mixed-forest stands of beech and oak. *In* Ecol Stud Ed. Springer-Verlag, Berlin. 69-98 pp.

Köstner, B.M.M., E.D. Schulze, F.M. Kelliher, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. Mcseveny, R. Meserth and P.L. Weir 1992. Transpiration and Canopy Conductance in a Pristine Broad-Leaved Forest of Nothofagus - an Analysis of Xylem Sap Flow and Eddy-Correlation Measurements. Oecologia. 91:350-359.

Kowalik, P., M. Borghetti, L. Borselli, F. Magnani, G. Sanesi and R. Tognetti 1997. Diurnal water relations of beech (Fagus sylvatica L) trees in the mountains of Italy. Agricultural and Forest Meteorology. 84:11-23.

Kramer, P.J. and J.S. Boyer 1995. Water Relations of Plants and Soil. Academic Press, San Diego

Kremer, B. 1996. Drzewa. *In* Leksykon przerodniczy. GeoCenter, Warszawa. 26,30,120 pp.

Kubota, M., J. Tenhunen, R. Zimmermann, M. Schmidt, S. Adiku and Y. Kakubari 2005. Influences of environmental factors on the radial profile of sap flux density in Fagus crenata growing at different elevations in the Naeba Mountains, Japan. Tree Physiology:545-556.

Kubota, M., J.D. Tenhunen, Z. R., S. M., A. S. and K. Y. 2003. Influences of radiation input, vapor pressure deficit and soil moisture on the radial profile of sap flux density in *Fagus crenata* at different elevations in the Naeba Mountains, Japan

Kurpius, M.R., J.A. Panek, N.T. Nikolov, M. McKay and A.H. Goldstein 2003. Partitioning of water flux in a Sierra Nevada ponderosa pine plantation. Agricultural and Forest Meteorology. 117:173-192.

Ladefoged, K. 1963. Transpiration of Forest Trees in Closed Stands. Physiologia Plantarum. 16:378-&.

Lajtha, K. and J. Getz 1993. Photosynthesis and Water-Use Efficiency in Pinyon-Juniper Communities Along an Elevation Gradient in Northern New-Mexico. Oecologia. 94:95-101.

Lambs, L. and É. Muller 2002. Sap flow and water transfer in the Garonne River riparian woodland, France:first results on poplar and willow. Ann. For. Sci. 59:301–315.

Legrand, I., J. Asta and Y. Goudard 1996. Variations in bark acidity and conductivity over the trunk length of silver fir and Norway spruce. Trees-Structure and Function. 11:54-58.

Liebscher, H. 1972. Results of research on some experimental basis in the Upper Harz Mountains. IAHS Publ. 97:150-162.

Liebscher, J.H. and K. Wilke 1981. Simulation of runoff by means of statistical processes in the experimental basins in the upper Harz mountains. Proceedings of the IUFRO workshop on water and nutrient simulation models. Swiss Federal Institute for Forestry Research, Birmensdorf:87-110.

Likens, G.E., C.T. Driscoll and D.C. Buso 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. Science. 272:244-246.

Loibl, W., Harald, R. Bolhàr-Nordenkampf, Friedl Herman, Stefan Smidt 2004. Modelling Critical Levels of Ozone for the Forested Area of Austria. Modifications of the AOT40 Concept. Environmental Science and Pollution Research:1-10.

Loustau, D., P. Berbigier, P. Roumagnac, C. ArrudaPacheco, J.S. David, M.I. Ferreira, J.S. Pereira and R. Tavares 1996. Transpiration of a 64-year-old maritime pine stand in Portugal .1. Seasonal course of water flux through maritime pine. Oecologia. 107:33-42.

Lu, P., P. Biron, N. Breda and A. Granier 1995. Water Relations of Adult Norway Spruce (Picea-Abies (L) Karst) under Soil Drought in the Vosges Mountains - Water Potential, Stomatal Conductance and Transpiration. Annales Des Sciences Forestieres. 52:117-129.

Marc, V. and M. Robinson 2004. Application of the deuterium tracing method for the estimation of tree sap flow and stand transpiration of a beech forest (Fagus silvatica L.) in a mountainous Mediterranean region. Journal of Hydrology. 285:248-259.

Martin, T.A., K.J. Brown, J. Kucera, F.C. Meinzer, D.G. Sprugel and T.M. Hinckley 2001. Control of transpiration in a 220-year-old Abies amabilis forest. Forest Ecology and Management. 152:211-224.

Maruyama, K. 1971. Effect of altitude on dry matter productionof primeval japanese beech fores communitiesin Naeba mountains. Mem. Fac. Agric. Niigata Univ. 9:87-171.

Maruyama, K. and M. Yamada 1968. Ecological studies on beech forest. 16. Seasonal course on apparent photosynthesis and respiration rate in detached leaves of japanese beech at different altitudes. Bull. Niigata Univ. For. 3:17-26.

Matyssek, R. 1985. Der Kohlenstoff-, Wasser-, und Nährstoffhaushalt der wechselgrünen und immergrünnen koniferen Lärche, Fichte, Kiefer. *In* Lehrstuhl Pflanzenökologie der Universität bayreuth.

Mcculloch, J.S.G. and M. Robinson 1993. History of Forest Hydrology. Journal of Hydrology. 150:189-216.

Mclaughlin, S.B., M.G. Tjoelker and W.K. Roy 1993. Acid Deposition Alters Red Spruce Physiology - Laboratory Studies Support Field Observations. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere. 23:380-386.

Meinzer, F.C., G. Goldstein and J.L. Andrade 2001. Regulation of water flux through tropical forest canopy trees: Do universal rules apply? Tree Physiology. 21:19-26.

Meinzer, F.C., S.A. James, G. Goldstein and D. Woodruff 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant Cell and Environment. 26:1147-1155.

Mellander, P.E., K. Bishop and T. Lundmark 2004. The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. Forest Ecology and Management. 195:15-28.

Mooney, H.A., R. Brayton and M. West 1968. Transpiration Intensity as Related to Vegetation Zonation in White Mountains of California. American Midland Naturalist. 80:407-&.

Mossor-Pietraszewska, T. 2001. Effect of aluminium on plant growth and metabolism. Acta Biochimica Polonica. 48:673-686.

Mott, K.A. and T.N. Buckley 1998. Stomatal heterogeneity. Journal of Experimental Botany. 49:407-417.

Nadezhdina, N., J. Cermak and R. Ceulemans 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. Tree Physiology. 22:907-918.

Neilson, R.E., M.M. Ludlow and P.G. Jarvis 1972. Photosynthesis in Sitka spruce (*Picea sitchensis* (BONG.) CARR.). II Response to temperature. Journal of Applied Ecology. 9:721-745.

Neuwirth, G., D. Garelkov, W. Klemm, M. Klemm, S. Naumov and D. Welkov 1966. Ökologisch-physiologische Untersuchungen in Walsbeständen Westbulgariens. Arch. Forstweswes. 15:379-428.

Oberdorfer, E.A., . 1990. Pflanzensoziologische Exkursionsflora, Stuttgart.

Oren, R., E.D. Schulze, R. Matyssek and R. Zimmermann 1986. estimating photosynthesis rate and annual carbon gain in conifers from specific leaf weight and leaf biomass. Oecologia. 70:187-193.

Oswald, H. 1969. Conditions forestières et potentielé de l'epice'ea en haute ardèche. Ann. Sci. For. 26

Overdieck, D. and M. Forstreuter 1994. Evapotranspiration of Beech Stands and Transpiration of Beech Leaves Subject to Atmospheric Co2 Enrichment. Tree Physiology. 14:997-1003.

Pahl-Wostl 2002. Nachhaltige Nutzung von Wasserressourcen - regionale Probleme mit globalen Dimensionen. 6. Nationale Tagung zur Alpenforschung. das Wasser der Alpen. Nutzungskonflikte und Lösungsansätze.:15.

Pavel, E.W. and E. Fereres 1998. Low soil temperatures induce water deficits in olive (Olea europaea) trees. Physiologia Plantarum. 104:525-532.

Peck, A. and H. Mayer 1996. Influence of stand parameters on evaporation in forests. Forstwissenschaftliches Centralblatt. 115:1-9.

Pellinen, P. 1986. Biomassenuntersuchungen im Kalkbuchenwald. Universität Göttingen, Göttingen.

Pharis, R.P., H. Hellmers and E. Schuurmans 1967. Kinetics of the daily rate of photosynthesis at low temperatures for two conifers. Plant Physiology. 42:525-531.

Phillips, N., A. Nagchaudhuri, R. Oren and G. Katul 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. Trees-Structure and Function. 11:412-419.

Pisek, A. and E. Cartellieri 1939. Zur Kenntnis des Wasserhaushaltes der Pflanzen. IV. Bäume und Sträucher. Jahrb. Wiss. Bot. 88:22-68.

Pisek, A. and E. Winkler 1958. Assimilationsvermögen und Respirtaion der Fichte (*Picea excelsa* LINK) in verschiedener HÖhenlage under Zirbe (*Pinus cembra*) an der alpinen Waldgrenze. Planta. 51:518-543.

Price, M., Bjonness, I-M., Becker, A., Collins, D., Corominas, J. 2003. Global chnage in the mountaines. U.S. Department of the Interior, U.S. Geological Survey
Northern Rocky Mountain Science Center, BOX 173492, Montana State University, Bozeman, Montana, 59717-3492
first gov Maintainer: mrblair@usgs.gov.

Rada, F., F.A. Squeo, A. Azocar and H.M. Cabrera 1999. Water and carbon relations in the genus Adesmia (Papilionaceace) at different altitudes in the high north-central Chilean Andes. Revista Chilena De Historia Natural. 72:201-211.

Reasoner, M.G., L., Messerli B., Bugmann, H. 2002. Global change and mountains. The need an integrated approach to address human security in the 21st century. UPDATE Newsletter of the International Human Dimensions Programme on Global Environmental Change. 1

Rehfuess, K.E. 1983. Eine Arbeitshypothese über Fichtenerkrankung in Hochlagen des bayerischen Waldes. GSF-Bericht A3/83, pp. 9-13.

Reichstein, M. 2001. Drought efects on carbon and water exchange in three mediterranean ecosystems. *In* Lehrstuhl für Pflanzenökologie. Universität Bayreuth, Bayreuth.

Reichstein, M., J. Tenhunen, O. Roupsard, J.M. Ourcival, S. Rambal, F. Miglietta, A. Peressotti, M. Pecchiari, G. Tirone and R. Valentini 2003. Inverse modeling of seasonal drought effects on canopy CO2/H2O exchange in three Mediterranean ecosystems. Journal of Geophysical Research-Atmospheres. 108:-.

Reichstein, M., J.D. Tenhunen, O. Roupsard, J.M. Ourcival, S. Rambal, F. Miglietta, A. Peressotti, M. Pecchiari, G. Tirone and R. Valentini 2002. Severe drought effects on ecosystem CO2 and H2O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? Global Change Biology. 8:999-1017.

Reynolds, J.F., J.D. Tenhunen, P.W. Leadley, H. Li, D.L. Moorhead, B. Ostendorf and F.S. Chapin 1996. Patch and landscape models of Arctic Tundra: Potentials and Limitations. *In* Landscape Function and disturbance in Arctic Tundra. Springer-Verlag Berlin Heidelberg, pp. 293-324.

Roberts, J. and P.T.W. Rosier 1994. Comparative Estimates of Transpiration of Ash and Beech Forest at a Chalk Site in Southern Britain. Journal of Hydrology. 162:229-245.

Rook, D.A. 1969. The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. N.Z.J. Bot. 7:43-55.

Rout, G.R., S. Samantaray and P. Das 2001. Aluminium toxicity in plants: a review. Agronomie. 21:3-21.

Running, S.W. 1992. A bottom-up evolution of terrestrial ecosystem modeling theory; and ideas toward global vegetation modeling. *In* Modeling the Earth system. Ed. O.f.I.E.S. D. Ojima (ed.) Univ. Corp for Atmospheric research, Global Change Institute. Boulder, CO., pp. 163-280.

Sala, A. and J.D. Tenhunen 1996. Simulations of canopy net photosynthesis and transpiration in Quercus ilex L under the influence of seasonal drought. Agricultural and Forest Meteorology. 78:203-222.

Schafer, K.V.R., R. Oren and J.D. Tenhunen 2000. The effect of tree height on crown level stomatal conductance. Plant Cell and Environment. 23:365-375.

Schreuder, M.D.J. and C.A. Brewer 2001. Effects of short-term, high exposure to chlorine gas on morphology and physiology of Pinus ponderosa and Pseudotsuga menziesii. Annals of Botany. 88:187-195.

Skärby, L., S. Ottosson, P.E. Karlsson, G. Wallin, G. Sellden, E.L. Medin and H. Pleijel 2004. Growth of Norway spruce (Picea abies) in relation to different ozone exposure indices: a synthesis. Atmospheric Environment. 38:2225-2236.

Slatyer, R.O. and P.A. Morrow 1977. Altitudinal variation in the photosynthesis characteristics of Snow Gum, *Eucalyptus pauciflora* Sieb. ex Spreng. I. Seasonal changes under field conditions in the Snowy Mountains Area of South-eastern Australia. Aust. J. Bot. 25:1-20.

Smidt, S. and K. Stefan 1980. Nadelanalytische Ergebnisse aus dem Raum Breitenau. Mitteilungen der Forstlichen Bundes-Versuchsanstalt. 131:64-102.

Smith, W.K., M.J. Germino, T.E. Hancock and D.M. Johnson 2003. Another perspective on altitudinal limits of alpine timberlines. Tree Physiology. 23:1101-1112.

Stefan, K. 1971. Chemische Nadelanalyse Schadffbestimmung. Mittlungen der Forstlichen Bundes-Versuchsanstalt, Wien. 92:84-102.

Stickan, W. and X.M. Zhang 1992. Seasonal-Changes in Co2 and H2o Gas-Exchange of Young European Beech (Fagus-Sylvatica L). Trees-Structure and Function. 6:96-102.

Sun, Z.J., N.J. Livingston, R.D. Guy and G.J. Ethier 1996. Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce (Picea glauca (Moench) Voss) seedlings. Plant Cell and Environment. 19:887-894.

Tenhunen, J. 2000. Altitudinal Gradients, Treelines and Forest Ecosystem Properties

Tenhunen, J.D., R. Hanano, M. Abril, E.W. Weiler and W. Hartung 1994a. Aboveground and Belowground Environmental-Influences on Leaf Conductance of Ceanothus-Thyrsiflorus Growing in a Chaparral Environment - Drought Response and the Role of Abscisic-Acid. Oecologia. 99:306-314.

Tenhunen, J.D., R. Siegwolf and S.F. Oberbauer 1994b. Effects of phenology, physiology, and gradients in community composition, structure, and microclimate on tundra ecosystem CO2 exchange. *In* Ecophysiology of Photosynthesis Ed. E.-D.S.a.M.M. Caldwell. Springer Verlag, Heidelberg, pp. 431-460.

Thalmann, E., R. Burkard, T. Wrzesinsky, W. Eugster and O. Klemm 2002. Ion fluxes from fog and rain to an agricultural and a forest ecosystem in Europe. Atmospheric Research. 64:147-158.

Tranquillini, W. 1979. Physiological Ecology of the Alpine Timberline. Tree Existance at High Altitudes with Special Reference to the European Alps. *In* Ecological Studies. Vol. 31. Springer-Verlag.

Tranquillini, W. and W. Schütz 1970. Über die Rindeatmung einiger Bäume an der Waldgrenze. Zentralbl. Geasmte Forstwes. 87:42-60.

Turner, H. 1961. Jahresgang und biologische Wirkungen der Sonnen- und Himmelsstrahlung an der Waldgrenze der Ötztaler ALpen. Wetter und Leben. 13:93-113.

UNFCCC, U.N.F.C.o.C.C. Climate Change Information Kit, Biological diversity and ecosystems. http://unfccc.int/resource/iuckit/fact30.html.

UNFCCC, U.N.F.C.o.C.C. Climate Change Information Sheet 12, Biological diversity and ecosystems. http://unfccc.int/resource/iuckit/fact12.html.

United Nations Framework Convention on Climate Change. Climate Change Information Sheet 12, Biological diversity and ecosystems. http://unfccc.int/resource/iuckit/fact12.html.

van Hees, P.A.W., D.L. Jones, G. Jentschke and D.L. Godbold 2004. Mobilization of aluminium, iron and silicon by Picea abies and ectomycorrhizas in a forest soil. European Journal of Soil Science. 55:101-111.

Wang, Q., J. Tenhunen, E. Falge, C. Bernhofer, A. Granier and T. Vesala 2004. Simulation and scaling of temporal variation in gross primary production for coniferous and deciduous temperate forests. Global Change Biology. 10:37-51.

Wang, Y.F. and J.J. Zwiazek 1999. Spring changes in water relations, gas exchange, and carbohydrates of white spruce (Picea glauca) seedlings. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere. 29:332-338.

Wedler, K.M. 1991. Photosynthese, Transpiration und Chlorophyllfluoreszenz von Fichten an einem Waldschadensstandort im Fichtelgebirge und unter experimenteller SO_2-Ozonbelastung im Freiland. Universität Würzburg, p. 171.

Wedler, M., R. Geyer, B. Heindl, S. Hahn and J.D. Tenhunen 1996a. Leaf-level gas exchange and scaling-up of forest understory carbon fixation rates with a '"patch-scale" canopy model. Theoretical and Applied Climatology. 53:145-156.

Wedler, M., B. Heindl, S. Hahn, B. Kostner, C. Bernhofer and J.D. Tenhunen 1996b. Model-based estimates of water loss from "patches" of the understory mosaic of the Hartheim Scots pine plantation. Theoretical and Applied Climatology. 53:135-144.

Whitehead, D. and T.M. Hinckley 1991. Models of Water Flux through Forest Stands - Critical Leaf and Stand Parameters. Tree Physiology. 9:35-57.

Whitehead, P.G. and I.R. Calder 1993. Special Issue - the Balquhidder Catchment and Process Studies - Foreword. Journal of Hydrology. 145:215-216.

Wieser, G., R. Matyssek, B. Kostner and W. Oberhuber 2003. Quantifying ozone uptake at the canopy level of spruce, pine and larch trees at the alpine timberline: an approach based on sap flow measurement. Environmental Pollution. 126:5-8.

Willmott, C.J. 1981. On the validation of models. Phys. Geogr. 2:184-194.

Willmott, C.J., S.G. Ackleson, R.E. Davis, J.J. Feddema, K.M. Klink, D.R. Legates, J. O'Donnell and C.M. Rowe 1985. Statistics for the evaluation and comparison of models. Journal of Geophysical Research-Atmospheres. 90:8995-9005.

Willstätter, R. and A. Stoll 1918. Untersuchungen über die Assimilation der Kohlensäure. Berlin: Springer

Winkler, E. 1957. Klimaelemente für Innsbruck (582m) und Patscherkofel (1909m) im Zusammenhang mit Assimilation von Fichten in verschiedenen Höhenlagen. Veröff. Museum Ferdinandeum Innsbruck. 37:19-48.

Wullschleger, S.D., P.J. Hanson and D.E. Todd 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. Forest Ecology and Management. 143:205-213.

Wullschleger, S.D., F.C. Meinzer and R.A. Vertessy 1998. A review of whole-plant water use studies in trees. Tree Physiology. 18:499-512.

Zech, W. 1970. Besonderheiten im Ernährungszustand chlorotischer Fichten auf kalkreichen Böden. Forstwissenschaftliches Centralblatt. 102:50-55.

Zech, W., T. Suttner and E. Popp 1985. Element analyses and physiological responses of forest trees in SO_2-polluted areas of NE-Bavaria. Water, Air and Soil Pollution. 25:175-183.

Zimmermann, L., C. Fruhauf and C. Bernhofer 1999. The role of interception in the water budget of spruce stands in the Eastern Ore Mountains/Germany. Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere. 24:809-812.

Zöttl, H.W. and E. Mies 1983. Die Fichtenerkrankung in Hochlagen des Südschwarzwaldes. Allgemeine Forst Und Jagdzeitung. 154

10. APPENDIX 1

List of understory species occurring at the *Larix decidua* stand Kederbichel at the tree line (1720 m a.s.l.) site. Nomenclature after Oberdorfer (1990): Pflanzensoziologische Exkursionsflora (B. Tenhunen personal communication)

Grasses and rushes
Agrostis agrostiflora
Agrostis capillaris
Anthoxanthum odoratum
Calamagrostis villosa
Carex ferruginea
Deschampsia cespitosa
Luzula sylvatica
Phleum rhaeticum
Poa nemoralis
Sesleria albicans
Herbs
Aconitum vulparia
Achillea atrata
Adenostyles alliariae
Alchemilla hoppeana
Alchemilla monticola
Aquilegia atrata
Campanula scheuchzeri
Carduus defloratus
Centaurea montana
Chaerophyllum hirsutum
Cicerbita alpina
Cirsium spinosissimum
Crepis aurea
Crepis pyrenaica
Dentaria enneaphyllos
Epipactis spec.
Erigeron uniflorus
Euphrasia picta
Galium anisophyllum
Gentiana asclepiadea
Gentiana pannonica
Geranium sylvaticum
Geum rivale
Globularia cordifolia
cf. Gymnadenia conopsea
Gypsophila repens
Heracleum austriacum
Hieracium cf. x caesium
Hieracium murorum
Hieracium villosum
Homogyne alpina
Hypericum maculatum
Knautia dipsacifolia
Leontodon hispidus
Ligusticum mutellina
Lilium martagon
Listera ovata
Melandrium rubrum
Melampyrum sylvaticum
Mercurialis perennis
Oxalis acetosella
Paris quadrifolia
Parnassia palustris
Peucedanum ostruthium
Phyteuma orbiculare
Phyteuma spicatum
Pinguicula alpina
Polygonatum verticillatum
Polygonum viviparum
Potentilla erecta
Prenanthes purpurea
cf. Pulsatilla alpina
Ranunculus nemorosus
Rhinanthus glacialis
Rumex acetosa
Saxifraga rotundifolia
Scabiosa lucida
Senecio abrotanifolius
Senecio fuchsii
Silene vulgaris
Soldanella spec.
Solidago virgaurea
Stachys alopecuros
Thalictrum aquilegifolium
Thesium alpinum
Trifolium pratense
Trollius europaeus
Valeriana montana
Valeriana tripteris
Veratrum album
Woody plants
Alnus viridis iuv.
Daphne mezereum
Larix decidua
Pinus mugo
Polygala chamaebuxus
Rhododendron hirsutum
Rhodothamnus chamaecistus
Rosa cf. pendulina
Salix appendiculata
Salix waldsteiniana
Sorbus chamaemespilus
Vaccinium myrtillus
Vaccinium vitis-idaea
Ferns and lower plants
Asplenium trichomanes
Dryopteris dilatata
Dryopteris expansa
Lycopodium annotinum
Polystichum lonchitis
Selaginella selaginoides

11. APPENDIX 2

LIST OF IMPORTANT ABBREVIATIONS

Super- and subscripts

Symbol	Meaning
max	maximum
min	minimum
meas	measured
mod	modelled

Greek symbols

Symbol	Meaning	Unit
α	Leaf-level light-use efficiency	μmol CO_2 mol quantum^{-1}
ΔH_a (Pml)	activation enthalpy for enzymatic reactions	J mol^{-1}
ΔH_d (Pml)	deactivation enthalpy for enzymatic reactions	J mol^{-1}
ΔS (Pml)	entropy terms for deactivation of enzymes	J mol^{-1} K^{-1}
$\Delta E_a(Vc_{max})$	activation energy for calculation of Vc_{max}	J mol^{-1}
$\Delta H_d(Vc_{max})$	deactivation energy for calculation of Vc_{max}	J mol^{-1}
$\Delta S(Vc_{max})$	entropy terms for calculation of Vc_{max}	J mol^{-1} K^{-1}
ΔT	temperature of reference sensor	K
ΔT_{max}	temperature of heated xylem	K
ρ_w	density of water	kg m^{-3}
τ	factor of substrate specificity	-

Latin symbols

Symbol	Meaning	Unit
CBH	tree circumference at the breast height	cm
c (Pml)	constant for calculation of Pml	μmol m^{-2}s^{-1}
c_s	CO_2 concentration on the leaf surface	ppm
D	dark respiration	μmol m^{-2}s^{-1}
DBH	tree diameter at the breast height	cm
E	activation energy for calculation of Kc, K_O, τ	J mol^{-1}
$E_a(K_C)$	activation energy for calculation of Kc	J mol^{-1}

Symbol	Meaning	Unit
$E_a(K_O)$	activation energy for calculation of K_O,	J mol^{-1}
$Ea(\tau)$	activation energy for calculation of τ	J mol^{-1}
E_c	canopy transpiration	mm s^{-1}
E_{cbar}	daily mean transpiration rates per month	mm d^{-1}
E_{tree}	total sapflow per tree	m^3 s^{-1}
$f(K_C)$	scaling factor for calculation of K_C	µmol l^{-1}
$f(K_O)$	scaling factor for calculation of K_O	ml l^{-1}
$fvc(Vc_{max})$	maximum rate of carboxylation	µmol m^{-2}s^{-1}
$f(\tau)$	scaling factor for calculation of τ	-
g_b	boundary layer conductance	mmol m^2 s^{-1}
g_{fac}	Ball-Berry proportionality	-
g_l	leaf conductance	mmol m^2 s^{-1}
g_{min}	conductance of the leaf with closed stomata	mmol m^2 s^{-1}
g_s	stomatal conductance	mmol m^2 s^{-1}
g_t	canopy conductance	mm s^{-1}
G_v	gas constant of water vapor	m^3 kPa/ g*K
H	ground heat flux	W m^{-2}
IA	index of agreement	-
J_{mean}	mean sapflow density of CBH-class	kg m^2 s^{-1}
K	flow index	
K_C	Michaelis-Menten constant for carboxylation	µl l^{-1}
K_O	Michaelis-Menten constant for oxygenation	ml l^{-1}
LA	total surface leaf area of individual trees	m^2
LAI_{stand}	leaf area index of the stand	m^2 m^{-2}
LA_{tree}	total leaf area of individual trees	m^2 m^{-2}
N	number of half-hourly or daily values	-
O_i	observed values	-
P	photosynthetic assimilation	µmol m^2 s^{-1}
P	air pressure	hPa
PA	plot area	m^2
PAR	photosynthetically-active radiation	mmol m-2 s-1
PAR_{below}	photosynthetically-active radiation measured under canopy	mmol m-2 s-1
P_i,	model results	

Symbol	**Meaning**	**Unit**
P_{ml}	maximum RuBP regenerations rate of a leaf at radiation and CO2	µmol m^{-2} s^{-1}
PPFD	photosynthetic photon flux density	mmol m^{-2} s^{-1}
PPFD $_{integr.}$	photosynthetic photon flux density integrated over the day	ml m^{-2} d^{-1}
R_n	net radiation	W m^{-2}
RDFAC	Dark respiration	-
rh_s	relative humidity on the leaf surface	fraction
S_A	cross-sectional sapwood area at the heated thermocouple	m^2
$S_{A\text{-class}}$	cumulative sapwood area per ground area for CBH-class	m^2 m^{-2}
SAI	Stem area index	m^2 m^{-2}
Tair	air temperature	°C
T_k	air temperature	K
$T_{\Delta a}$	current temperature difference in xylem	K
$T_{\Delta M}$	temperature difference for no flow in xylem	K
tr	transpiration rate	mmol m^{-2} s^{-1}
u	sap flux density	m s^{-1}
VPD	vapor pressure deficit	hPa, kPa
WUE	water-use efficiency	µmol CO_2/mmol H_2O

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ERKLÄRUNG

Hiermit erkläre ich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

Ferner erkläre ich, dass ich anderweitig mit oder ohne Erfolg nicht versucht habe, diese Dissertation einzurichten. Ich habe keine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden.

Bayreuth, den 27. Juni 2005

(Olimpia Kolcun)