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Intra-annual radial growth and water relations of trees: implications towards a growth mechanism

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Abstract

There is a missing link between tree physiological and wood-anatomical knowledge which makes it impossible mechanistically to explain and predict the radial growth of individual trees from climate data. Empirical data of microclimatic factors, intra-annual growth rates, and tree-specific ratios between actual and potential transpiration (T PET^{-1}) of trees of three species (*Quercus pubescens*, *Pinus sylvestris*, and *Picea abies*) at two dry sites in the central Wallis, Switzerland, were recorded from 2002 to 2004 at a 10 min resolution. This included the exceptionally hot and dry summer of 2003. These data were analysed in terms of direct (current conditions) and indirect impacts (predispositions of the past year) on growth. Rain was found to be the only factor which, to a large extent, consistently explained the radial increment for all three tree species at both sites and in the short term as well. Other factors had some explanatory power on the seasonal time-scale only. *Quercus pubescens* built up much of its tree ring before bud break. *Pinus sylvestris* and *Picea abies* started radial growth 1–2 weeks after *Quercus pubescens* and this was despite the fact that they had a high T PET^{-1} before budburst and radial growth started. A high T PET^{-1} was assumed to be related to open stomata, a very high net CO$_2$ assimilation rate, and thus a potential carbon (C)-income for the tree. The main period of radial growth covered about 30–70% of the productive days of a year. In terms of C-allocation, these results mean that *Quercus pubescens* depended entirely on internal C-stores in the early phase of radial growth and that for all three species there was a long time period of C-assimilation which was not used for radial growth in above-ground wood. The results further suggest a strong dependence of radial growth on the current tree water relations and only secondarily on the C-balance. A concept is discussed which links radial growth over a feedback loop to actual tree water-relations and long-term affected C-storage to microclimate.

Key words: Carbon allocation, tree rings, water relations.

Introduction

To reach a mechanistic understanding of radial growth depends essentially on linking microclimate with tree water relations and carbon (C) balance. Radial growth depends on C as a source of compounds for the cambial activity, but it also depends on tree water status as a controlling factor for the metabolism of the entire tree. Tree water deficit closes stomata and thus reduces net CO$_2$ assimilation, but it also inhibits cell division and, even more sensitively, cell enlargement (Hsiao and Acevedo, 1974). The two sides (C and water) are closely interrelated and have the potential to limit growth, both individually or in combination (Hinckley and Lassoie, 1981). A growth mechanism needs, therefore, to be able to describe the feedback loops between these two balances and it has to deal with the storage effects mainly on the C-side. One important question is, therefore, how strongly is radial growth determined by the availability of C and to what extent is it driven by water-related conditions?

In the investigation presented here, radial growth rates were continuously measured to collect dynamic information about the biggest C-sink in the stem, sap flow, and water-related stem radius changes. These changes could correlate tree water-related responses with microclimate, and microclimate could link physiology to weather conditions. Calculations of potential transpiration allowed the ratio of actual and potential transpiration (T PET^{-1}) to be

obtained and with it an approximation of the degree of stomatal aperture and thus the potential net CO_2 assimilation rate. It is not yet possible to provide a complete mechanism for radial growth, but the results at least allow some conclusions to be drawn about physiological causes and effects between climate and radial growth.

Approaching carbon allocation

Radial growth of the above-ground conducting wood was found to be one of the most important C-sinks of a tree beside the input to organs like leaves, roots, and fruits; the oxidation of C for respiration and the C-storage as a resource are further C-sinks (Cannell and Dewar, 1994). According to Hoch *et al.* (2003), the replacement of the whole canopy would need one-quarter of the total C stored in a deciduous tree, whereas the above-ground xylem increment in an average year would need about one-third of it. On the C-production side, there are well-established methods to measure the net CO_2 assimilation rate of tree canopies directly (Schulze, 1981; Häsler, 1982). It is also possible to model the carbon income of different species from microclimatic conditions (Farquhar and Sharkey, 1982; Noe and Giersch, 2004). The most difficult part is simulating stomatal regulation of gas exchange. At the individual-tree level, the newest generation of net CO_2 assimilation rate-models includes the hydraulic properties of tree water relations in stomatal regulation. This enables a reasonable simulation of the net CO_2 assimilation rate even during drought periods (Leuning *et al.*, 2003; Tuzet *et al.*, 2003).

With respect to C-sinks, important experimental steps towards a mechanistic understanding of C-allocation in trees were made through the investigation of the dynamics of C-pools (Saranpää and Höll, 1989; Fischer and Höll, 1992; Barbaroux and Breda, 2002; Ludovici *et al.*, 2002; Barbaroux *et al.*, 2003; Hoch *et al.*, 2003). Lacointe *et al.* (2004) demonstrated with potted oak and walnut trees when and under what conditions C is shared and exchanged between branches. They showed that branches are largely autonomous during the summer, but there is a strong dependence on C-reserves at budburst and during initial growth. There seems to be a balance between growth and reserves in tree species such as walnut, oak or beech: the more a tree part grows, the more carbon it stores and utilizes. The dynamics of C-storage in the stem wood of beech and oak trees was quantified by Barbaroux and Breda (2002). They showed how the non-structural carbohydrate (NSC) reserves were used in a ring-porous (oak) and a diffuse-porous species (beech) and compared them with the largely concurrent radial growth during the first part of the season. A marked decrease in NSC concentration was observed in oak trees during budburst and early wood growth, whereas seasonal fluctuations in NSC concentrations of beech trees were small despite a similar timing of radial growth. Corresponding findings were reported by Hoch *et al.* (2003), who compared ten tree species, including conifers and broadleaved species, in a forest in the midlands of Switzerland in terms of the seasonal fluctuations of their NSC-stores in above- and below-ground organs. They concluded that the NSC-stores were never a limitation for growth since the C-reserves covered more than the total C-demand of a year. Even during times of extensive fruit production (masting) of *Fagus sylvatica* the C-reserves were never substantially depleted. The C-reserves contributed about 50% of the carbon to the newly formed xylem, in conifers and broadleaved trees. The effort required to track these C-stores is considerable and produces only a rough picture of the dynamics over a season because of the limited number of samples which can be taken and analysed.

Intra-annual radial growth

By contrast with the investigation of C-reserves, the continuous detection of radial growth as one of the C-sinks is relatively easy. With an increment-punching tool, thin samples of the actual tree rings can be taken at regular time intervals on the same naturally grown trees in the field (Forster *et al.*, 2000) and the newly formed cell layers can be counted and measured. Even less labour-intensive is the application of a dendrometer for the continuous detection of radial fluctuations of a tree stem (ΔR) (Zweifel and Häsler, 2001; Zweifel *et al.*, 2001; Wullschleger *et al.*, 2004). However, ΔR consists of several components, of which radial growth and water-related swelling and shrinkage of the bark explain the fluctuation to a large extent (>90%) (Zweifel and Häsler, 2000; Daudet *et al.*, 2005; Zweifel *et al.*, 2005). Zweifel *et al.* (2005) suggested an algorithm to separate the course of ΔR into growth- and water-related fluctuations which allows intra-annual growth to be directly tracked from stem radius measurements. In addition to the growth rate, the water status of a tree is obtained as the difference between actual and fully hydrated states. This is called the tree water deficit as introduced by Hinckley and Lassoie (1981).

The application of these or similar methods (e.g. the pinning method; Schweingruber, 1996) to quantify intra-annual radial growth has been available for over 30 years (Dougherty *et al.*, 1979). Little interest, however, was paid to questions addressing the determination of radial growth of individual trees in terms of C-utilization and actual microclimatic conditions with a high temporal resolution. Many dendrochronological investigations focused on much longer timescales from decades to thousands of years for data sets with large numbers of trees (Esper *et al.*, 2002). The highest temporal resolution usually ended with the distinction between early and late wood, leading to a half-year resolution at best (Cherubini *et al.*, 1997; Rigling *et al.*, 2001, 2002). One reason for this coarse scale is that the distinction between early and late wood is morphologically preserved in the wood structure and can be analysed

at any time, whereas the information on the timing of radial growth needs to be measured in the field at the time of growth. Small variations in wood density within a seasonal structure usually cannot be back dated (Schweingruber, 1996).

Mechanism for radial growth?

Five main factors were found to be involved in a potential mechanism for radial growth: (i) carbon as a source of energy (respiration) and C-compounds to form new layers of cells (Hsiao and Acevedo, 1974; Le Roux *et al.*, 2001); (ii) nutrients and temperature as limiting factors for growth in general (Linder and Axelsson, 1982); (iii) auxin as a plant hormone determining cambial activity (Dengler, 2001; Domec and Gartner, 2002); (iv) mechanical stress as an additional activation factor for cambial activity (Osawa, 1992); and (v) tree water relations as a factor for growth-enabling water pressure conditions in the cambium (Lockhart, 1965; Hsiao and Acevedo, 1974; Lambers *et al.*, 1998; Barbaroux and Breda, 2002; Steppe *et al.*, 2006). Many C-based models of individual tree growth are based on a source and sink approach, on balanced-growth considerations or on optimality principles for shoot and root compartments. They only partially account for the known growth factors and lack a mechanism which allows the prediction of intra-annual radial growth (Cannell and Dewar, 1994; Le Roux *et al.*, 2001). Radial growth is usually proportionally attributed to leaf area which is mainly pre-set by the formation of buds in the previous season (Yang and Midmore, 2005). This follows from the pipe-model theory (Shinozaki *et al.*, 1964) but largely decouples radial growth from the current-year microclimatic conditions. There is empirical evidence that the width of a tree ring depends on the microclimatic conditions in the current year (Breda and Granier, 1996; Corcuera *et al.*, 2004) and on those in the preceding ones (Rigling *et al.*, 2002; Fonti and Garcia-Gonzalez, 2004).

Aims of this work

The investigations reported here offer an insight into the timing of radial growth, budburst, leaf expansion, and physiological processes of three tree species (*Quercus pubescens* Willd.*, Pinus sylvestris* L.*, Picea abies* L. Karst.) over 3 years at two dry south-exposed sites in the central Wallis, Switzerland (Swiss Alps). The aims of this work were (i) to show simultaneously recorded microclimate conditions, physiological dynamics (T and $T PET^{-1}$) and radial growth rates of different tree species in a high temporal resolution, (ii) to use these primary results to discover the relative importance of individual climate factors on radial growth, and (iii) to investigate how strongly radial growth determined is by the C-balance and to what extent it is driven by the tree water status. To conclude, the dependence of radial growth on current and past physiological and microclimatic factors are discussed

and a suggestion for a model is given. The fact that the data set includes the very dry summer of 2003 is a fortunate coincidence and increased the explanatory power of the results.

Materials and methods

Study sites and trees

The two study sites are located in oak and pine woodland on the south-facing slope of the main valley of the Wallis, Switzerland. The central Wallis is an inner-alpine valley characterized by a dry climate. This is mainly caused by so-called inner-valley shielding. The valley is positioned SE–NW with regard to the main storm tracks from the West. Mean annual precipitation over the past 20 years was, for both sites, approximately 600 mm per year.

The two sites Salgesch (46°19′27″ N, 7°34′40″ E, 975 m asl) and Jeizinen (46°19′21″ N, 7°43′30″ E, 1270 m asl) had similar oak and pine vegetation which primarily differed in tree height: the site at Salgesch had a shrub-like open canopy vegetation whereas at Jeizinen the same species grew as larger trees. The two sites were 11 km apart.

Salgesch (Sa)

Pubescent oak (*Quercus pubescens*) and Scots pine (*Pinus sylvestris*) were the most abundant tree species and juniper (*Juniperus communis* L.) was the most abundant woody shrub in the vegetation of this very dry site. Whereas some *Q. pubescens* were up to 110 years old, 95% of them were younger than 70 years. Most of the dominant *P. sylvestris* were between 100 and 150 years old (A Rigling, personal communication). The woody species investigated stood in one of the typical patches of trees (32 m² in area), consisting of 17 *Q. pubescens*, four *P. sylvestris*, two *Viburnum lantana* L. (⩾2 cm in stem diameter), and five *J. communis*, surrounded by grass and bare rock. Details of the sizes of the investigated trees are listed in Table 1. The soil on this steep south-facing slope (~25°) is shallow with a maximum depth of 0.1–0.3 m. It was classified as a rendzic leptosol on solid rock limestone according to the FAO classification system (Rigling *et al.*, 2002). This type of soil generally has a low water-holding capacity. Continuous measurements of the local climate and vegetation started in April 2001 (Fig. 1). For the analyses here, data from 1 January 2002 to 31 December 2004 were used.

Jeizinen (Je)

At this site, *Q. pubescens* and *P. sylvestris* were also the most abundant tree species but the deeper soil (about 0.5–1.3 m) had a better water-holding capacity and allowed the trees to grow much taller than at Salgesch (Table 1). The more moderate humidity conditions (Table 2) also allowed Norway spruce (*Picea abies*) to grow there. These three tree species built an almost closed vegetation layer. The open spots were covered by *J. communis* and *Juniperus*

Table 1. *Characteristics of the three species investigated at Salgesch and Jeizinen*

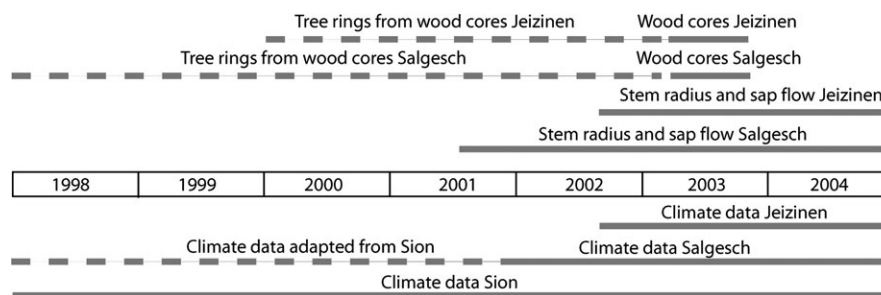| Species	Site	Number of trees	Range of tree heights (m)	Range of stem diameters (cm)
Quercus pubescens	Salgesch	6	3.5–4.0	7.2–9.5
	Jeizinen	5	5.0–12.0	12.9–25.3
Pinus sylvestris	Salgesch	2	3.5–5.0	11.9–23.2
	Jeizinen	3	8.0–15.0	27.3–53.2
Picea abies	Jeizinen	2	5.5–17.0	13.0–38.5

Fig. 1. Sampling design for the two sites at Salgesch and Jeizinen. Wood cores were sampled eight times in 2003 to estimate intra-annual growth of the current year and tree rings of the past years. Stem radius (ΔR) and sap flow measurements were recorded at 10 min intervals and led to intra-annual growth and tree water deficit (ΔW) (Zweifel *et al.*, 2005). The ratio between actual and potential transpiration (T PET^{-1}) of tree crowns was calculated for the corresponding periods from sap flow rates, canopy surface properties, and microclimate according to Zweifel *et al.* (2002). Climate data for Salgesch of the years 1998 to 2001 were linearly transformed from the data from Sion.

Table 2. *Mean daytime values (6–20 h) of microclimatic factors at Salgesch (Sa) and Jeizinen (Je), Switzerland: temperature (T_{Air}), solar radiation (R_N), vapour pressure deficit (VPD), soil water potential (Ψ_{Soil}) (seasonal minimum in brackets) and sum of rain (24 h) over the vegetation period (1 April to 30 September)*

	T_{Air} (°C)		R_N (W m^{-2})		VPD (kPa)		Ψ_{Soil} (kPa)		Rain (mm)	
	Sa	Je	Sa	Je	Sa	Je	Sa	Je	Sa	Je
2002	18.2	–	387	–	0.86	–	−82 (−283)	–	482	–
2003	21.1	18.6	407	407	1.32	1.05	−186 (−448)	−120 (−450)	258	204
2004	18.4	15.9	385	389	1.03	0.82	−118 (−324)	−105 (−327)	252	185

sabina L. and in the understorey *Amelanchier ovalis* L., *Prunus mahaleb* L., and *Cornus sanguinea* L. No systematic analysis of the age distribution of the three tree species was made, but dendrochronological measurements of selected trees showed that *Q. pubescens* and *P. sylvestris* were not only larger but also older than at Salgesch. The trees grew in a dip on a steep south-facing slope ($\sim30°$). Continuous measurements of the local climate and vegetation started in July 2002. Data from 1 January 2003 to 31 December 2004 were used (Fig. 1).

Meteorological data

Meteorological data were collected at the site with two similar solar-powered logging and steering-systems (IPS, University of Bern, Switzerland and Markasub AG, Switzerland). The heart of the system was a logger (CR10X, Campell, UK). Details about sensor types and installation are listed in Table 3. In addition to the measurements at the sites, climate data from the nearby national meteorological station at Sion (MeteoSwiss) were used to analyse the climate history of recent years (Fig. 1).

Sampling and analysing stem wood

Wood samples of two individuals of each of *Q. pubescens*, *P. sylvestris*, and *P. abies* (only at Jeizinen) were collected on eight days between April and October 2003 at both sites (Fig. 1; Table 3). The two individuals were a young and an old tree at each site. The wood samples were collected with an increment-punching tool which allowed thin cores of about 3 mm in diameter and about 1 cm in length to be extracted from the stem (Forster *et al.*, 2000). On each sampling day, two cores were taken from each stem. In total, 64 samples were taken from *Q. pubescens* and *P. sylvestris,* and 32 from *P. abies*. All 16 spots to be cored on each stem were marked with paint within a square of about 15×40 cm on the slope-parallel side of the stem before starting the sampling in spring.

For every sample the number of current-year xylem cells were counted (only conifers) and the width of the growing tree ring and the five previous ones were measured. The values of the two cores per date and species were averaged. The information of the chronological samples from the same individual trees led to the corresponding growth curves.

Stem radius changes

Stem radius changes (ΔR) were measured with point dendrometers (ZB01, University of Bern, Switzerland) on seven trees at Salgesch and six trees at Jeizinen (Table 3). The dendrometers were mounted 0.5 m above ground on the upslope (north) of each stem. The electronic part of the dendrometer was mounted on a carbon fibre frame which was fixed to the stem by three stainless steel threaded rods implanted into the heartwood. A sensing rod was slightly pressed against the tree stem by a spring. The contact point of the dendrometer head was positioned 1–6 mm into the bark surface, but still within the outermost dead layer of the bark. The sensitivity of the dendrometers to temperature was negligible because of the temperature-insensitive main parts, the carbon frame, and the electronic transformer (Weggeberpotentiometer LP-10F, Pewatron, Switzerland). Electronic resolution of the dendrometer (in combination with the logger used) was <0.4 μm.

Deducing tree ring growth and tree water deficit from dendrometer measurements

To estimate intra-annual tree ring growth from ΔR, an algorithm was applied which separated growth from water-storage-related stem radius changes (Zweifel *et al.*, 2005). The growth- and water-related components were found to be the main factors for explaining the course of ΔR (Zweifel *et al.*, 2000, 2001; Daudet *et al.*, 2005). Additional small effects of temperature and xylem-tension-related fluctuations contributed <10% to ΔR and were not separable. The water-storage-related stem radius changes were expressed as the difference between the

Table 3. *Microclimatic, morphological, and physiological factors, their assessment methods, locations and number of sensors (N) in the plot investigated at Salgesch (Sa) and Jeizinen (Je), Switzerland (tree labels in brackets)*

Factor and abbreviation		Method	Location and height above-ground (tree label)	N
Net radiation	R_n	CM3, Kipp & Zonen, NL	Sa and Je, outside vegetation: 2 m	2
			Inside vegetation: 1–2 m	3
Rain	Rain	Tipping bucket, Young, USA	Sa and Je, outside vegetation: 2 m	2
Air humidity, temperature, and vapour pressure deficit	RH T_{Air} VPD	Hygroclip S, Rotronic, CH Calculated from RH and T	Sa and Je, outside vegetation: 2 m Inside vegetation: 0.3–8 m	2 6
Soil water potential	Ψ_{Soil}	EQ2, Delta-T Devices, UK	Sa, outside vegetation: −0.15 m	1
			Sa and Je, inside vegetation: −0.15 m	5
Stem cores		Puncher, WSL, CH	Sa: *Quercus:* (2233, 2265) 0.3 m	2
			Pinus: (2205, 2208) 0.3 m	2
			Je: *Quercus:* (6236, 6267) 0.6 m	2
			Pinus: (6239, 6281) 0.7 m	2
			Picea: (6269, 6283) 0.4 m	2
Stem radius changes (stems)	ΔR	Point dendrometer ZB01, IPS University of Bern, CH	Sa: *Quercus:* (2274, 2264, 2265, 2268, 2198) 0.3 m	5
			Pinus: (2254, 2208) 0.3 m	2
			Je: *Quercus:* (6236, 6267) 0.6 m	2
			Pinus: (6281, 6282) 0.8 m	2
			Picea: (6269, 6283) 0.5 m	2
Sap flow of twigs		SGB, Dynamax, USA	Sa: *Quercus:* (2263, 2265, 2267, 2268, 2274) 0.5–3 m	5
			Pinus: (2199, 2208) 1–1.5 m	2
			Je: *Quercus:* (6235, 6237) 1.5–2.5 m	2
			Pinus: (6239) 1–4 m	2
			Picea: (6269) 0.5–8 m	2

maximum and the actual hydration status of the stem (mainly the bark). This difference was called the tree water deficit according to Hinckley and Lassoie (1981) and Zweifel *et al.* (2005). It takes into account that all living parts of a tree are hydraulically interconnected and therefore a measured water deficit in the stem takes place in the whole tree.

Calculated physiological measurements

From microclimate and crown-specific parameters, a potential twig transpiration (PET) was calculated according to Zweifel *et al.* (2002), an adaptation of the Penman–Monteith single leaf model (Penman, 1948; Monteith, 1965). The ratio of measured twig sap flow rates (T) (Dynagage, Dynamax, USA) to estimated potential twig transpiration ($T\,PET^{-1}$) was assumed to be a measure of the degree of the down-regulated transpiration and thus for the degree of stomatal aperture of the crown. Since stomatal closure is the strongest limitation for the net CO_2 assimilation of trees at dry sites (Hsiao and Acevedo, 1974; Hinckley and Lassoie, 1981), $T\,PET^{-1}$ is also a measure of the actual potential photosynthesis and therefore the potential C-income for the tree.

For the analyses, mean daytime (6–20 h) values for $T\,PET^{-1}$ were used. The 10 min values of the individual twigs were averaged per species. The sap flow gauges and the corresponding microclimate sensors used to calculate $T\,PET^{-1}$ were mounted on the trees as listed in Table 3.

Results

Weather conditions and phenological observations

Compared with weather conditions in the Wallis over the last 20 years, 2002 was wetter than the average, 2003 was extraordinarily dry and hot, and 2004 had one of the lowest amounts of rain during the vegetation period but the air temperature (T_{Air}), the mean vapour pressure deficit (VPD),

and the soil water potential (Ψ_{Soil}) were closer to 2002 than to 2003 (Table 2). In the 'wet' year 2002, there was a distinct drought period in the last three weeks of June which led to very low soil water potentials (–500 kPa). At the end of this period several rain events rehydrated the soil to moderate Ψ_{Soil}-values for the rest of the summer. The weather conditions in 2003 led to large water deficits in the soil and plants from March onwards. A considerable number of trees of all species showed morphological reactions at both sites, but this was more obvious at Salgesch. At Salgesch, leaves of *Q. pubescens* turned yellow and had already been shed by July. *Pinus sylvestris* and *P. abies* shed more needles than usual in August and September at both sites (data not shown). During the vegetation period in 2004, the soil was wet in spring and remained moderately dry until mid-summer, despite little rain. From July onwards Ψ_{Soil} dropped to low values (< −300 kPa), but these climatic conditions did not lead to early leaf senescence as in 2003.

Intra-annual radial growth in 2003

In 2003, intra-annual radial growth of the ten trees was assessed with two different methods: (i) wood coring that allowed measurement of growth increments over 1–2 week periods throughout the season, and (ii) continuous stem radius measurements (ΔR) that allowed the estimation of continuous growth rates, but with reservations about the water-related component of the fluctuations. Both methods were able to detect the course of intra-annual radial growth and led to similar results (Fig. 2). Growth deduced from ΔR
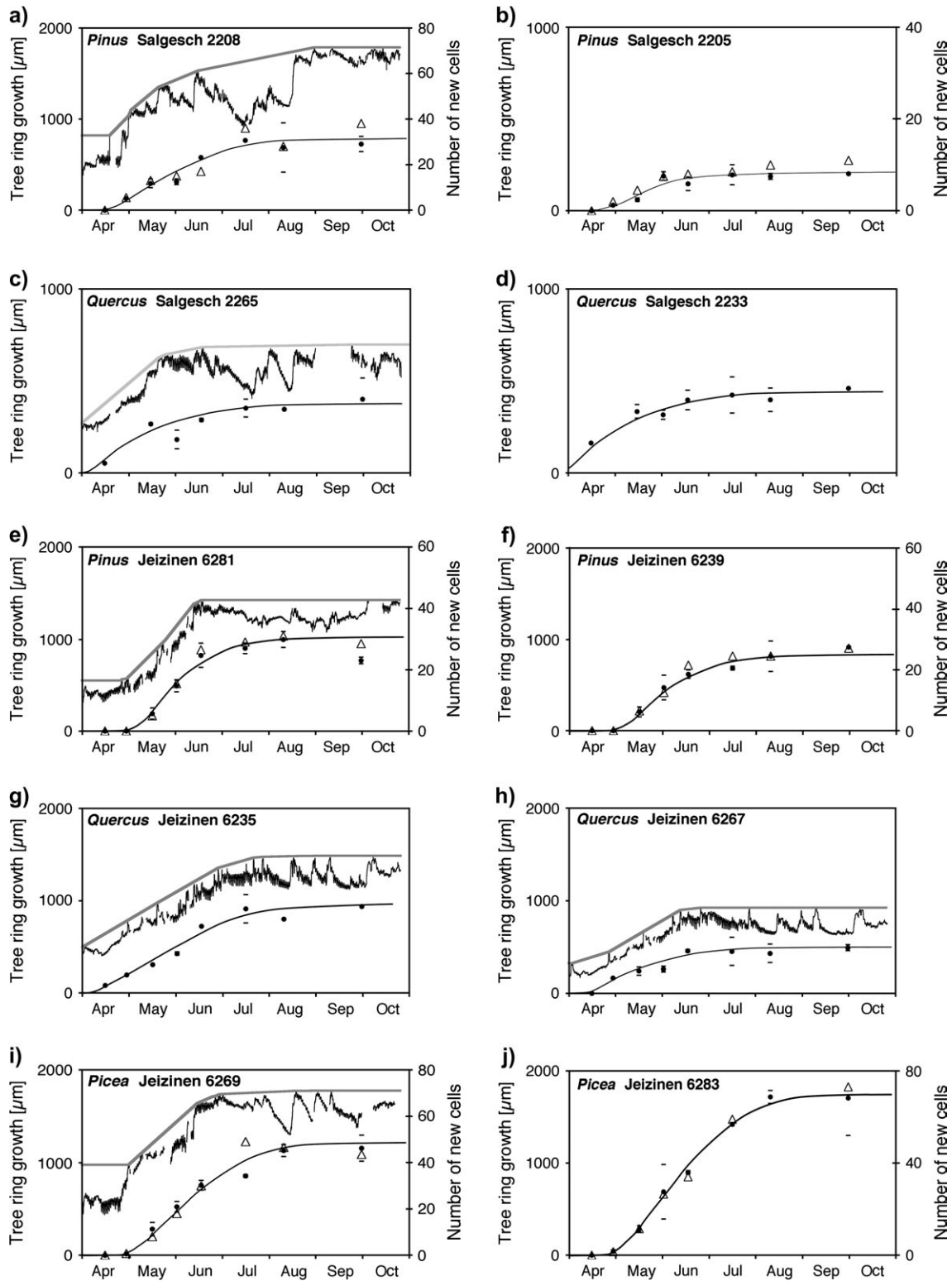
Fig. 2. Intra-annual radial growth of individual trees of *Quercus pubescens*, *Pinus sylvestris*, and *Picea abies* at the two sites Salgesch (a–d) and Jeizinen (e–j) in the year 2003. Growth was approached directly by counting new cells of the current tree ring in the wood cores (triangles) and measuring the size (black dots with range of variation), and indirectly by detrending stem radius measurements (ΔR) for water-related changes according to Zweifel *et al.* (2005) (grey lines). The difference between the grey line and the stem radius measurements represents the actual tree water deficit ΔW. Numbers in brackets indicate tree labels as listed in Table 3.

included the increment in xylem and phloem cells. This led, in general, to larger growth estimates compared with the analysis of the wood cores which included the xylem only. Slight differences occurred for the date of the initial start of the growth (Fig. 2g, h) or the shape of the growth curve (Fig. 2c, e). Nevertheless, both methods allowed the growth patterns of *Q. pubescens* and the two conifer species, *P. sylvestris* and *P. abies,* to be distinguished (Fig. 3).

Radial growth of *Q. pubescens* began earlier in the season than that of *P. sylvestris* and *P. abies* despite the fact that the conifers had a high T PET^{-1} about 1–2 months before *Q. pubescens*. At both sites, about 25–30% of the total annual radial increment of *Q. pubescens* had been achieved by the date of budburst and 40–45% of the tree ring was already formed when the leaves reached a state of full expansion and thus full physiological functionality (Table 4). The time lag between the beginning of radial growth and budburst was longer at Jeizinen than at Salgesch. By contrast, initial radial growth of *P. sylvestris* and *P. abies* only occurred shortly before budburst (Fig. 3) and radial growth had reached no more than approximately 15% of the annual radial growth at this date.

The tree rings of the year 2003, analysed from the wood cores, were, on average, wider at Jeizinen than at Salgesch for both species. The reason for the wider tree rings of *P. sylvestris* at Jeizinen was not due to a higher number of cells but to a larger cell size. *Q. pubescens* formed, on average, one row of early wood cells at Salgesch but two to three at Jeizinen. The number of late wood cells in *Q. pubescens* were not counted because of the very small cell sizes and the irregular structure of the wood.

Radial growth from 2002 to 2004

The typical growth pattern observed in 2003 also appeared in 2002 and 2004 (deduced from ΔR): *Q. pubescens* always started its growth period before the two conifer species and, at the time of full leaf expansion, a relevant part of the current tree ring was already built (Fig. 4). The extremely hot year 2003 led to smaller tree rings in all species compared with 2002 (Tables 5, 6) but the shapes of the growth curves did not differ from those of the other two years (Fig. 4).

The growth period of *Q. pubescens* was, on average, 97 d (i.e. 90% of the yearly increment, averaging over the years 2003 and 2004) and longer than that of *P. sylvestris* (60 d) and *P. abies* (64 d). Within this growth period of *Q. pubescens*, 55 d overlapped the 123 d when T PET^{-1} was >20% and thus a significant net CO_2 assimilation was likely. The 55 d is equal to 45% of the 'productive days'. *Pinus sylvestris* had the smallest ratio of 'growth days' to 'productive days' with 60 d out of 189 (32%) and the largest ratio was for *P. abies* with 64 d out of 95 (67%).

Impact of climatic conditions on radial growth

The potential impact of climatic conditions on the annual radial growth of *P. sylvestris* and *Q. pubescens* was investigated by comparing annual growth increments with the climatic conditions during the growth period over 7 years at Salgesch. The annual radial growth of both species responded significantly (Table 5) to variations in total rainfall during the growth period (Fig. 5): the more rain a growth period of a certain year had, the bigger the radial growth was. Over 90% of variance was explained with this factor (P <0.01). Moderate Ψ_{Soil} (*Q. pubescens* and *P. sylvestris*), low *VPD* (*P. sylvestris*), and low ΔW (*P. sylvestris*) also had a positive impact on growth, but were less significant than rain (Table 5). No clear trends were found for temperature and radiation (P >0.1).

The same pattern was found for intra-annual growth at Salgesch and Jeizinen, analysed by dividing the growth periods into subsets of 10 d. The corresponding microclimatic factors were related to the growth increments. Again, rain strongly determined radial growth rates for *Q. pubescens*, *P. sylvestris*, and *P. abies* at both sites (Fig. 6; Tables 5, 6). The actual water status of soil (Ψ_{Soil}) and tree (ΔW) did not seem to have a strong impact on short-term growth and factors such as radiation and *VPD* did not show a consistent pattern (Tables 5, 6). Even small rain events in dry periods accelerated radial growth, sometimes without wetting the soil (Fig. 7) or substantially rehydrating the tree.

Nevertheless, more than 90% of the growth increment was strongly limited to the growth period of April to June: before or after this period very little growth occurred, even when there were wet conditions.

Physiological processes and radial growth

The timing of growth and the corresponding growth patterns were similar for all species, compared with the big differences that occurred in the pattern of T PET^{-1} between them. Obviously, T PET^{-1} of *Q. pubescens* was strongly determined by the seasonality of its leaf development. High ratios started about 2 weeks after budburst when the leaves were fully expanded (Table 4) and ended with leaf senescence in autumn (Fig. 4). With the exception of the summer of 2003, T PET^{-1} of *Q. pubescens* was less dependent on the actual microclimatic conditions than those of the conifers. The ratio T PET^{-1} of *P. sylvestris* followed ΔW closely but hardly ever ceased completely across all four seasons, except during a couple of freezing days in wintertime and under very dry and hot conditions in the summer of 2003. Despite having evergreen needles, *P. abies* seemed to be unable to maintain a high T PET^{-1} in the winter of 2003/2004, but retained some activity in the first half of the winter 2004/2005. Both coniferous species had high T PET^{-1} in spring, several weeks before budburst (Fig. 4; Table 4).

The results of the effect of high T PET^{-1} of the tree species on their radial growth were not consistent. Intra-annual growth (10 d data) appeared to be largely independent of the actual T PET^{-1} for all three species at both sites (Tables 5, 6). In contrast to these results, the annual
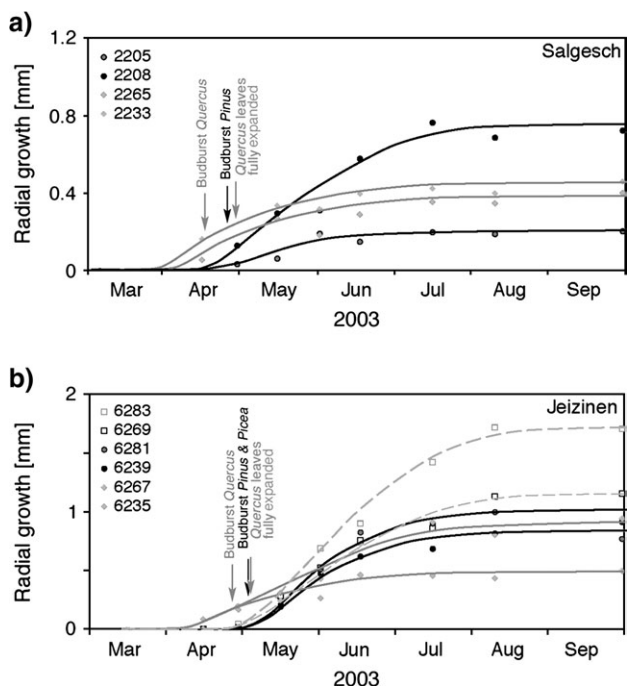
Fig. 3. Intra-annual radial growth of tree individuals of *Quercus pubescens* (grey symbols), *Pinus sylvestris* (black symbols), and *Picea abies* (open/dashed symbols) deduced from eight wood cores sampled over the vegetation period 2003 (a) at Salgesch and (b) Jeizinen. Arrows point to the time of budburst and the corresponding time of reaching full physiological activity.

growth increments corresponded with increased T PET^{-1} before (*P. sylvestris*) and during the growth period (*P. sylvestris* and *Q. pubescens*) (Fig. 5). *Q. pubescens* seemed to be less influenced by T PET^{-1} during its growth phase than *P. sylvestris*.

Discussion

Annual pattern of physiological processes and radial growth

The species-specific annual courses of T PET^{-1} were used to deduce physiological measures which were more closely related to radial growth than the transpiration rates. Since T PET^{-1} is mainly changed by the canopy conductance of a tree (Hsiao and Acevedo, 1974), this ratio can be used as a good approximation of the degree of stomatal aperture of a tree crown (as a percentage) (Zweifel *et al.*, 2002). Knowing about the stomatal aperture of a tree crown means knowing about its potential net CO_2 assimilation. This is particularly true for trees growing in dry areas because photosynthesis is mainly inhibited by a lack of CO_2 due to closed stomata (Hsiao and Acevedo, 1974; Hinckley *et al.*, 1979). A low T PET^{-1} always means closed stomata and low or no CO_2 assimilation; a high T PET^{-1} means a crown with open stomata and this was interpreted as a crown with a high net CO_2 assimilation rate. Suboptimal temperatures

(Haldimann and Feller, 2004) or disproportionally increased respiration rates can change this simple arithmetic (Hsiao and Acevedo, 1974). However, when comparing tree species in terms of periods when a net CO_2 assimilation rate was likely, T PET^{-1} was judged to be a useful measure.

The time pattern of a potential net CO_2 assimilation (C-source) and radial growth (C-sink) over a year differed widely between the broadleaved species *Q. pubescens* and the two coniferous species *P. sylvestris* and *P. abies*. Radial growth of *Q. pubescens* started 3–5 weeks before the leaves were fully expanded and new C-compounds had been assimilated. *Q. pubescens* must, therefore, have depended entirely on carbon stores at this time of the season (Hinckley and Lassoie, 1981). During the summer months, the gas exchange was, in general, much less influenced by drought than it was for the coniferous species. By contrast to *Q. pubescens*, *P. sylvestris* and *P. abies* are evergreen which allows them to remain active in winter with the exception of days with freezing temperatures. Highest T PET^{-1} ratios were measured in spring and early summer, whereas in summer, the dry conditions markedly reduced stomatal aperture and thus productivity (Fig. 4). Budburst and elongation of the new shoots as well as radial growth started 1–3 weeks after the start of radial growth in *Q. pubescens* (Table 4). There was a tendency towards shorter growth periods for the coniferous species compared with *Q. pubescens*.

In contrast to these species-specific differences, the main growth period (April to June) was very similar for all species. The main growth period (leaf expansion and wood growth) covered about 30–70% of the productive days of a year which consequently left a remarkably long time period when C was assimilated but no longer used for radial growth in the above-ground biomass (Fig. 4). During this time, carbon was probably used for below-ground growth (Teskey and Hinckley, 1981; Deans and Ford, 1986; Barbaroux *et al.*, 2003) or, alternatively, stored as C-reserves (Höll, 1985; Hoch *et al.*, 2003; Lacointe *et al.*, 2004).

The 2003 extreme year

For much of Europe including Switzerland, the year 2003 was extremely hot and dry (Beniston, 2004). As a consequence the gas exchange of *Q. pubescens* and *P. sylvestris* at Salgesch and also *P. abies* at Jeizinen ceased completely from mid July onwards and returned to a low level only in September (Fig. 4). At the cooler and wetter site Jeizinen (300 m higher in altitude), T PET^{-1} was also drastically reduced, but *Q. pubescens* and *P. sylvestris* were able to maintain a low but continuous activity throughout the summer. These climatic conditions led to narrow tree rings in all species. Radial growth in 2003 was strongly influenced by the current climatic conditions, since the previous year was, most likely, not a cause of growth limitation in 2003 because the widest tree rings and the

Table 4. *Phenological observations for* Quercus pubescens, Pinus sylvestris, *and* Picea abies *at the two sites of Salgesch and Jeizinen*

The beginning of gas exchange of *Q. pubescens* was deduced from measurements of the ratio between actual and potential transpiration (T PET^{-1}) and corresponded with about the time of completed leaf expansion. *P. sylvestris* and *P. abies* were able to be active all seasons. Radial growth was deduced from stem radius measurements.

Salgesch	*Quercus* Radial growth [Period with 90% of increment]	*Quercus* Budburst [week (date)]	*Quercus* Leaves out [week (date)]	*Pinus* Budburst [week (date)]	*Pinus* Radial growth [Period with 90% of increment]		
2002	1 April to 4 July	17 (23 April)	20 (13 May)	20	6 April to 5 July		
2003	31 March to 29 June	16 (18 April)	18 (30 April)	18	18 April to 30 June		
2004	22 March to 8 July	17 (24 April)	19 (6 May)	19	11 April to 23 June		

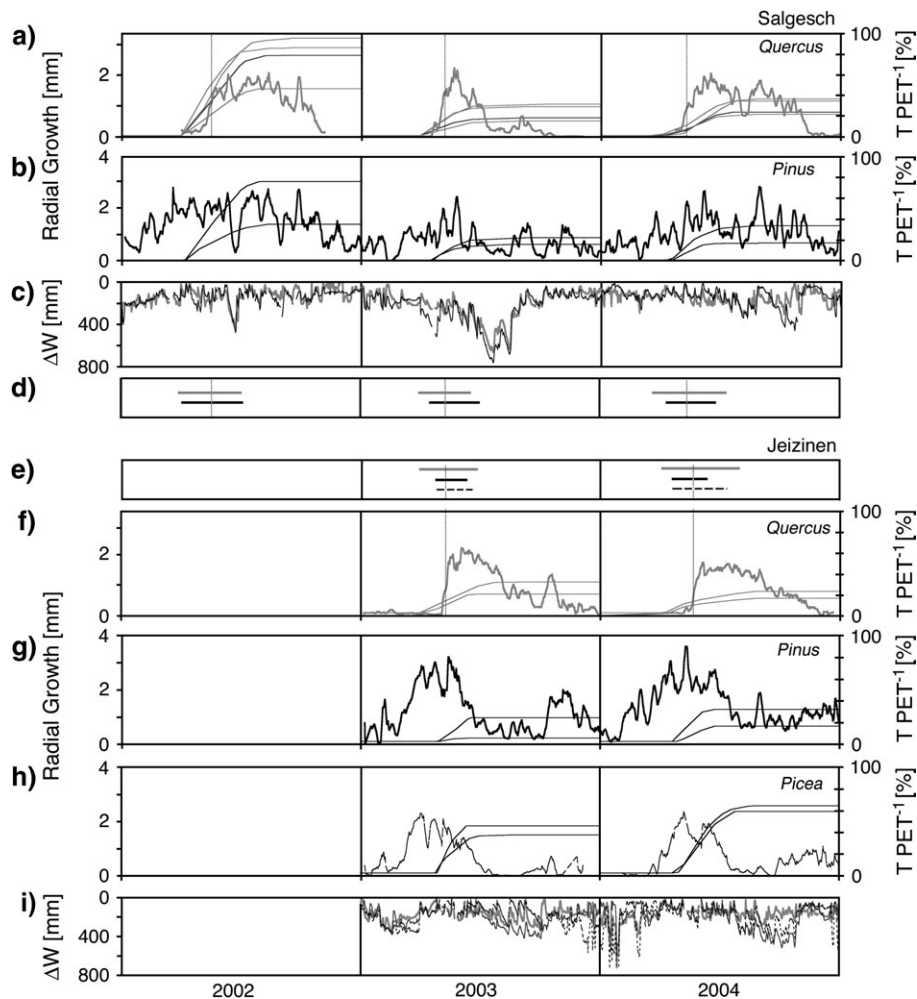| Jeizinen	*Quercus* Radial growth [Period with 90% of increment]	*Quercus* Budburst [week (date)]	*Quercus* Leaves out [week (date)]	*Pinus* Budburst [week (date)]	*Pinus* Radial growth [Period with 90% of increment]	*Picea* Budburst [week (date)]	*Picea* Radial growth [Period with 90% of increment]
2002	n.m.[a]	18	n.m.	n.m.	n.m.	n.m.	n.m.
2003	2 April to 25 June	18	19 (9 May)	19	26 April to 10 June	19–20	24 April to 8 June
2004	5 April to 29 July	19	21 (21 May)	20	20 April to 10 June	20	20 April to 10 July

[a] n.m., No measurements.

Fig. 4. Radial growth and mean daily (6–20 h) ratio between actual and potential transpiration (T PET^{-1}) of (a) *Quercus pubescens* and (b) *Pinus sylvestris* at Salgesch and of (f) *Q. pubescens*, (g) *P. sylvestris*, and (h) *Picea abies* at Jeizinen for the years 2002 to 2004. (c) and (i) The species-specific courses of tree water deficit (ΔW) for *Q. pubescens* (grey line), *P. sylvestris* (black line), and *P. abies* (broken line). (d) and (e) The growth periods (90% of the yearly increment) of the respective species. The vertical dotted lines indicate the date of full leaf expansion of *Q. pubescens*. Intra-annual radial growth of individual trees was deduced from stem radius measurements (ΔR). The species-specific course of T PET^{-1} is depicted as a running mean of the daily values.

Table 5. *Mean annual radial growth of* Quercus pubescens *and* Pinus sylvestris *in comparison to microclimatic and physiological factors during growth periods of the years 1998 to 2004 at Salgesch*

Regression analyses were done (grey-coloured cells) for annual radial growth and the respective factors and intra-annual radial growth and the corresponding factors of 10 d periods of the years 2002 to 2004. (+) and (–) indicate a positive or a negative slope of growth on the respective factor. n.a., not applicable; $T\,PET^{-1}$, ratio between actual and potential transpiration.

Salgesch	1998[c]	1999[c]	2000[c]	2001[c]	2002	2003	2004	Quercus[b] n = 7	Pinus[b] n = 7	Quercus[a] n = 26	Pinus[a] n = 26
VPD (kPa)	0.93	0.81	0.96	0.84	0.90	1.16	0.93	[grey]	** (−)	[grey]	** (−)
Ψ_{Soil}	−127	−41	−182	−59	−88	−167	−74	* (+)	** (+)	[grey]	[grey]
Net radiation (W m^{-2})	408	375	396	400	400	415	390	[grey]	[grey]	[grey]	** (−)
Temperature (°C)	16.6	16.1	17.2	16.0	16.5	19.0	15.7	[grey]	[grey]	[grey]	[grey]
Sum of rain (mm)	172	288	125	264	258	138	130	** (+)	*** (+)	*** (+)	*** (+)
ΔW *Quercus* (µm)	145	70	190	86	154	242	137	[grey]	n.a.	[grey]	n.a.
ΔW *Pinus* (µm)	169	66	234	87	146	310	172	n.a.	** (−)	n.a.	[grey]
$T\,PET^{-1}$ *Quercus* (May–July) (%)					46	38	48	n.a.	n.a	[grey]	n.a.
$T\,PET^{-1}$ *Pinus* (March–July) (%)					45	26	34	n.a.	n.a.	n.a.	n.a.
$T\,PET^{-1}$ *Pinus* (January–March) (%)					28	15	17	n.a.	n.a.	n.a.	n.a.
Radial growth *Quercus* (Core) (µm)	415	520	402	436	536	395	435	n.a.	n.a	n.a.	n.a.
Radial growth *Pinus* (Core) (µm)	945	1522	891	1414	1422	825	882	n.a.	n.a	n.a.	n.a.

[a] Regression analysis for 10 d growth phases (ΔR) between 1 April and 29 June and the respective conditions of the years 2002–2004. * P <0.1; ** P <0.05; *** P <0.01.
[b] Regression analysis for annual growth and the respective conditions between 25 March and 10 July of the years 1998–2004.
[c] Climate data adapted from Sion, ΔW calculated according to Zweifel *et al.* (2005)

Table 6. *Mean annual radial growth of* Q. pubescens, P. sylvestris, *and* Picea abies *in comparison to microclimatic and physiological factors during growth periods of the years 2003 and 2004 at Jeizinen*

Regression analyses were done (grey-coloured cells) for intra-anual radial growth and corresponding factors of 10 d periods.

Jeizinen	2003	2004	Quercus[a] n = 11	Pinus[a] n = 11	Picea[a] n = 11
VPD (kPa)	0.87	0.71	[grey]	* (−)	[grey]
Ψ_{Soil}	−67.6	−65.6	[grey]	[grey]	[grey]
Net radiation (W m^{-2})	414.7	391.1	[grey]	[grey]	[grey]
Temperature (°C)	16.2	13.0	[grey]	[grey]	[grey]
Sum of rain (mm)	106.9	90.0	*** (+)	*** (+)	***
ΔW *Quercus* (µm)	129.3	128.3	[grey]	n.a.	n.a.
ΔW *Pinus* (µm)	148.6	128.3	n.a.	[grey]	n.a.
ΔW *Picea* (µm)	118.3	123.3	n.a.	n.a.	[grey]
$T\,PET^{-1}$ *Quercus* (May–July) (%)	56	40	[grey]	n.a.	n.a.
$T\,PET^{-1}$ *Pinus* (March–July) (%)	48	56	n.a.	[grey]	n.a.
$T\,PET^{-1}$ *Picea* (March–July) (%)	21	39	n.a.	n.a.	[grey]
$T\,PET^{-1}$ *Pinus* (January–March) (%)	25	33	n.a.	n.a.	n.a.
$T\,PET^{-1}$ *Picea* (January–March) (%)	10	3	n.a.	n.a.	n.a.
Radial growth *Quercus* (Core) (µm)	618	522	n.a.	n.a.	n.a.
Radial growth *Pinus* (Core) (µm)	798	870	n.a.	n.a.	n.a.
Radial growth *Picea* (Core) (µm)	1570	2370	n.a.	n.a.	n.a.

[a] Regression analysis for 10 d growth phases (ΔR) between 21 April and 19 June and the respective conditions of the years 2003 and 2004; * P <0.1; ** P <0.0; *** P <0.01.

highest physiological activities had been measured in 2002 (Table 5). In contrast to 2003, radial growth in 2004 seemed to be influenced by the previous dry year. Radial growth was slower than expected from a comparison of the climatic conditions over 7 years: the microclimatic factors were similar between the wide-tree-ring year 2002 and the narrow-tree-ring year 2004 (Tables 3, 5). There was one important exception: the growth period in 2004 had even less rain than the growth period of the dry year 2003.

What determines radial growth?

Rainfall during the growth period explained radial growth increments for all species at both sites in the short-term (10 d), and this was in contrast to all other climatic or physiological factors which did not show a comprehensive pattern (Tables 5, 6). The importance of rain during the growth period is reported in several investigations: for example, for *P. sylvestris* (Rigling *et al.*, 2001, 2002), *Q. petraea* (Breda and Granier, 1996), and *Quercus faginea* (Corcuera *et al.*, 2004). The smallest amounts of rain were enough to accelerate growth, even for low Ψ_{Soil}-conditions or relatively high tree water deficits (Zweifel *et al.*, 2005). The wetting of the leaves alone seemed to be enough to accelerate growth. This appears to contradict the finding of other investigators who reported a strong growth dependence of mainly latewood growth on Ψ_{Soil} (Breda and
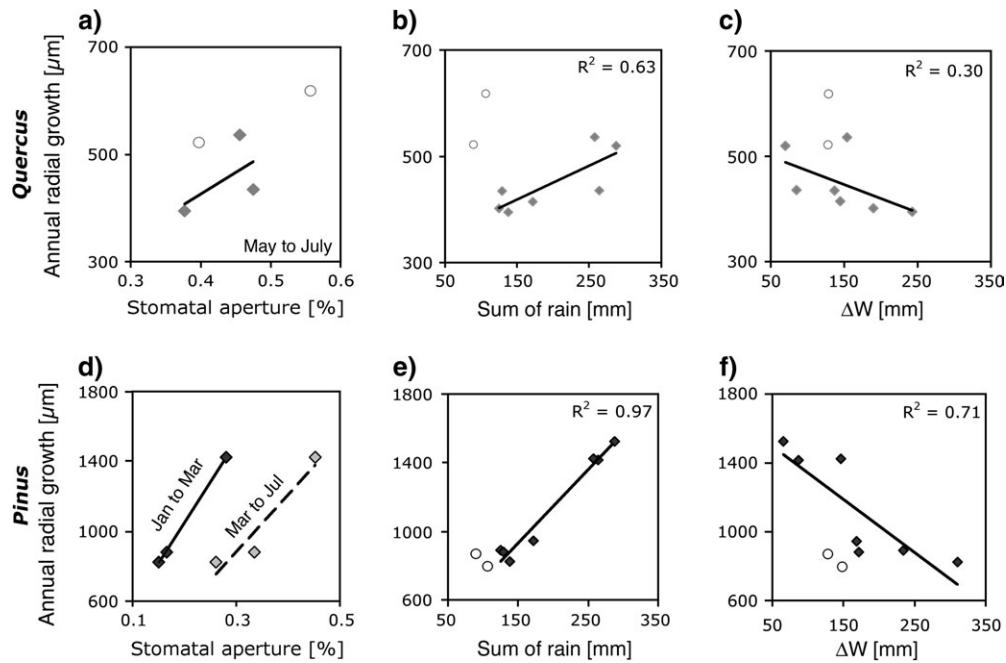
Fig. 5. Annual radial growth of *Quercus pubescens* (a–c) and *Pinus sylvestris* (d–f) compared with the mean daily (6–20 h) ratio between actual and potential transpiration (T PET^{-1}), sum of rain and mean tree water deficit (ΔW) during the growing period (25 March to 10 July when not labelled differently). Regressions for data points from Salgesch only (squares), Jeizinen (open circles).
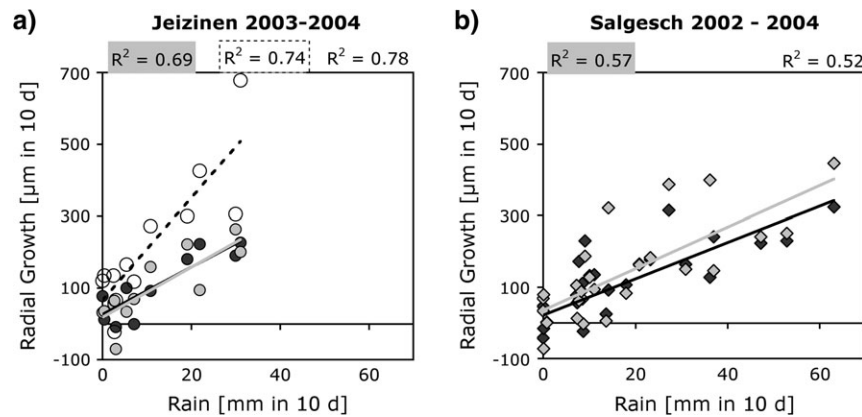

Fig. 6. Intra-annual radial growth of *Quercus pubescens* (grey symbols), *Pinus sylvestris* (black symbols), and *Picea abies* (open or dotted symbols) over 10 d periods compared with the corresponding sum of rain at (a) Jeizinen and (b) Salgesch.

Granier, 1996; Barbaroux and Breda, 2002). But this might be an artificial difference caused by the chosen temporal resolution for analysis, since Ψ_{Soil} (and other factors) in our investigation also had a higher statistical significance (Table 5) when longer periods were averaged. On an annual basis, tree ring widths were also significantly positively correlated with mean Ψ_{Soil} during the growth period (Table 5). Low Ψ_{Soil} shortened the growth period, for example, in 2003, and, consequently, this indirectly limited growth as well.

The direct effect of rain on radial growth is most likely caused by a (sudden) release of the pressure conditions in the tree, thus leading to positive pressure conditions in the

cambium (Hsiao and Acevedo, 1974; Hinckley and Lassoie, 1981; Barbaroux and Breda, 2002; Steppe and Lemeur, 2004; Steppe *et al.*, 2006). According to Lockhart (1965) and Lambers *et al.* (1998), irreversible growth occurs when a pressure threshold in the growth tissue is exceeded. This is in accordance with Hsiao and Acevedo (1974) who found that there are two different sensitivities to drought in the growth process: one is related to cell division and the other to cell expansion. Cell expansion, according to these authors, is far more sensitive to tree water deficit than cell division. These different drought sensitivities lead to the situation in which new cells are built but do not immediately expand. This means that, within a certain period of
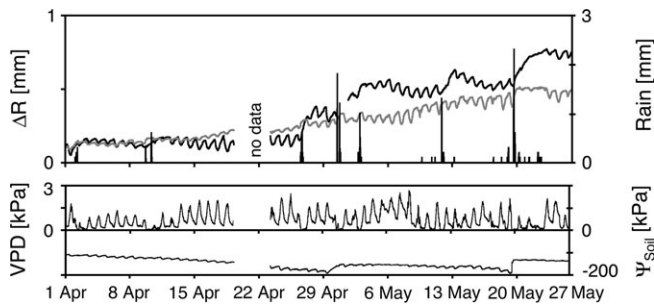
Fig. 7. Stem radius changes (ΔR) including the water-related and growth-related component (*Quercus pubescens* = grey line, *Pinus sylvestris* = black line) compared with rain, vapour pressure deficit (*VPD*) and soil water potential (Ψ_{Soil}) in 2003.

time and for a range of water deficit, growth is not inhibited but just delayed. A release of the low pressure conditions in the cambium suddenly enlarges the already existing cells to their mature sizes. Yet, when the drought conditions last too long cell division is stopped and rain occurring later may not compensate for the suppressed growth.

The trees investigated in the Wallis responded largely with this pattern. Little rain initiated growth without replenishing the soil. These rain events were wetting the dust-like soil only in the uppermost millimetres and the layers below including the equitensiometers remained completely dry (Zweifel *et al.*, 2005). It is unlikely that the tree roots were able to benefit from this superficial humidity in the soil but it cannot be ruled out. The more likely interpretation is that wetting the crown resulted in a partial release of low leaf water potential, which led to an increase in the cambial turgor and thus to an enlargement of xylem cells already produced. Such a mechanism would also explain why there was an observed decoupling between radial growth and actual Ψ_{Soil}.

Based on the idea of a pressure threshold in the cambium for initiating radial growth, Steppe *et al.* (2006) presented a water relations model which included reversible and irreversible changes of the stem radius. The positive pressure component of the cambium was deduced from the flow of water into and out of bark storage. This model was successfully applied to young *Fagus sylvatica* and *Quercus robur* growing under field conditions and only needed to be re-parameterized for data sets of 1–2 months to keep track of the changing amplitude in ΔR. On the one hand, these good simulation results indicated a high dependence of radial growth on the actual microclimatic conditions, on the other hand, the need for reparameterization suggested a dependence on non-water-related factors for growth activity, such as long-term carbon storage or a hormonally controlled seasonal regulation of growth. Besides the strong growth rates on wet days, the model predicted radial growth mainly during the night when the pressure conditions reached the threshold for growth sooner than during daytime when transpiration increased negative

pressure conditions. This agrees with our findings (Fig. 7) and those of other authors (Hsiao and Acevedo, 1974; Hinckley *et al.*, 1979; Hinckley and Lassoie, 1981; Daudet *et al.*, 2005).

Through the long-term affected component, a potential indirect effect of temperature (or other factors) on radial growth could take place. If growth at a site is temperature-limited (e.g. at the timberline), the C-assimilation rate could be increased by an increased temperature and this situation is expressed in radial growth with a certain time lag. These conclusions partially support a large number of dendroecological investigations which suggest a strong relationship between growth and temperature. These results further support experimental findings that the current tree ring seems to be determined by the current *and* the preceding climatic conditions (Breda and Granier, 1996; Rigling *et al.*, 2002; Fonti and Garcia-Gonzalez, 2004). At a dry and hot site such as the Wallis, a temperature effect is potentially negative and expected to be less pronounced since *Q. pubescens* has been shown to be drought- and heat-tolerant for a wide range of locally occurring conditions. In the cases of *P. sylvestris* and *P. abies*, a contrasting physiological response to increased temperatures is expected: on the one hand, they suffer under hot summer months but, on the other hand, they may benefit from a warmer winter season. This balance between a positive and a negative response to temperature is expected to reduce a clear temperature-related growth trend in tree rings of *P. sylvestris* at these sites. In a dendroecological investigation of *P. sylvestris* in the same area, Rigling *et al.* (2002) reported a significant negative correlation between temperature and radial growth for the month of June and a positive but non-significant relationship for the month of November of the past year. These results were based on the total annual increments and have therefore a limited power of explanation for a growth mechanism. They represent more the indirect effects on growth over a longer time-scale.

Implications towards a growth mechanism

Q. pubescens as a ring-porous species has a strongly reduced hydraulic conductivity in early spring because the large vessels in the earlywood from the past year become embolized either during the summer or during the winter (Hinckley *et al.*, 1979; Breda and Granier, 1996). The large vessels mainly determine hydraulic conductivity (Domec and Gartner, 2002). Several studies have also reported that ring-porous species formed new conducting wood before the gas exchange of new leaves started (Breda and Granier, 1996; Barbaroux and Breda, 2002; Domec and Gartner, 2002). From a hydraulic point of view this is essential, otherwise the young transpiring leaves would promote a sudden collapse of the water flow and storage system because the old sapwood could not provide the necessary water supply to the crown. As a consequence of the chronology of cambial activity before leaf expansion

and photosynthesis, the early anabolic activity for radial growth in *Q. pubescens* must be supported solely from internal C-stores, since there is no actual C-assimilation at this time. These findings correspond with the results of Barbaroux and Breda (2002), Hoch *et al.* (2003), and Lacointe *et al.* (2004) who all found that the C-stores of ring-porous species were utilized before budburst and during the time of leaf expansion. The refilling of the C-stores was reported to occur during the summer. This was in contrast to diffuse-porous species which did not have this distinct decrease of the NSC-stores around budburst. With this chronology of growth and production in mind, it is also clear, that beside the determination of the immediate climate impact, there must be a factor related to the past, since a good part of the energy and C-resources are coming from previous year(s).

Another argument for the dependence of radial growth on the past is the fact that the whole structure of the next year's leaves in a canopy are pre-built in the buds. Buds and growing shoots are reported to be an important source of the plant hormone auxin which regulates cambial activity (Larson, 1994; Aloni, 2001). High auxin concentration triggers the production of earlywood, whereas low auxin concentration leads to latewood cells. Drought stress decreases auxin concentration and affects the formation of new sapwood (Domec and Gartner, 2002).

In terms of a functional growth mechanism, the results were less clear for *P. sylvestris* and *P. abies*, since these species were already highly photosynthetically active before and during radial growth and leaf expansion. These investigations did not allow it to be determined whether C was coming from the actual assimilation process or from C-stores in the coniferous species. According to Hoch *et al.* (2003), coniferous species receive about 50% of their C for radial growth from actual assimilation and the other part from internal C-stores, which is no different from broadleaved species. Also, similar to *Q. pubescens*, was the response of radial growth to rain. Despite the different timing of radial growth, budburst, leaf expansion, and C-production, there was no evidence for a completely different radial growth mechanism for the three species investigated.

To conclude, a potential mechanism for radial growth should account for (i) the strong impact of the actual tree water status on cell division and cell enlargement, (ii) the water-relations-dependent C-assimilation, and (iii) the long-term effect due to the use of C-reserves stored in earlier years and the predisposition through the buds built in the preceding year.

The relationships between the different factors are suggested as follows: Radial growth builds a feedback loop with the current leaf area which itself was predisposed by the bud formation of the previous year. In other words, the maximum leaf area and thus the maximum conducting area in the wood are preset through conditions of the past year(s). Yet, the current radial growth rate is mainly altered by the current weather conditions through tree water relations. A limited C-reserve or a non-sufficient actual C-assimilation rate could reduce growth as well, but this seems to have less weight than the actual tree water relations (at least for the species investigated). Further, tree water status strongly alters the actual C-assimilation under drought conditions when stomata are closing and the assimilation rate ceases. The hydraulic conductivity of the wood plays an important role in stomatal regulation and therefore builds another feedback loop to radial growth. The less the current tree rings has grown, the smaller is the conductivity and the less is the water supply to the crown, which in turn causes a high tree water deficit, stomatal closure, reduced C-assimilation, and, consequently, poorer growth conditions. Finally, a potential growth model needs to link the actual climate conditions to bud formation and thus the predisposition for the following year. It is suggested that the C-assimilation of the entire vegetation period or alternatively, only the period after radial growth, determines the accumulation of carbon in C-stores and the formation of buds. This relationship builds the third feedback loop between climate and growth and includes the long-term aspect.

A water-relations model like the one of Steppe *et al.* (2006), combined with a stomatal regulation approach (Tuzet *et al.*, 2003) and an additional model which describes the feedback between cambial activity and leaf area (e.g. plant hormone regulation as suggested by Larson, 1994; and Aloni, 2001) would largely cover the mechanistic background. In such a carbon–water relations model, the buds (as a result of the productivity of the past year) trigger a nominal growth rate by producing a growth-accelerating plant hormone and the current microclimatic conditions alter the growth rate through tree water relations.

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