

Helmut Schume · Michael Grabner · Otto Eckmüller

## The influence of an altered groundwater regime on vessel properties of hybrid poplar

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**Abstract** The development of vascular features in stems of *Populus x euramericana* was studied in two adjacent floodplain forest stands near the Danube in Austria. The construction of a hydropower plant caused one of the stands to loose contact with the groundwater at the age of 12 years, whereas the other stand remained uninfluenced. The investigation estimated the extent of vascular acclimation to altered site hydrology. Vessel lumen areas were separately measured for 26 tree-rings from six trees. Vessel densities (VD) and the percentages of the total vessel-lumen area per tree-ring area (PLA) were determined. Our results suggest that vessel size and density are correlated with circumferential stem growth, which is in turn governed by site water supply. In relation to the control trees, basal area increment (BAI) of the hydrologically altered trees was 66% lower. BAI was positively correlated to vessel size and negatively to VD and PLA. Vessel diameters of the mature control trees were large (with a mean of 95  $\mu\text{m}$  and maxima around 160  $\mu\text{m}$ ), while average VD (42 no.  $\text{mm}^{-2}$ ) and PLA (31%) were within the normal ranges. In comparison to controls, the hydrologically altered trees reduced their vessel-lumen area by 15% (i.e. 8% in terms of diameter); average VD increased by 43%, and average PLA increased relatively by 19%. Vessel density proved to be the most sensitive

indicator of hydrological alterations. Intra-annual development of vessel size indicated a rapid response to the hydrological conditions of the current growing season.

**Keywords** Danube · Floodplain forest · Site hydrology · Vascular acclimation · Xylem anatomy

### Introduction

The water balance of floodplain forest sites is primarily governed by flood- and groundwater, while precipitation is of secondary importance (Busch et al. 1992; Willms et al. 1998). This abundant water supply guarantees high productivity even when riparian sites are embedded in a dry environment, as is the case in eastern Austria.

In the floodplains along the Austrian stretch of the Danube, Euroamerican hybrid poplar [*Populus x euramericana* (Dode) Guinier] is an economically important tree species, covering about 25% of the total floodplain forest area. River regulation and the construction of hydropower plants on the river have locally impacted the hydrology of the forest sites by lowering the water table and reducing the annual amplitude (Nachtnebel 1989). Depending on the severity of the alteration, hybrid poplar stands have been replaced by other species (e.g. mixed oak and ash stands) or have exhibited reduced productivity. Similar observations are reported from the United States, where hydrologic engineering has contributed to the decline of floodplain forests [reviewed in Rood and Mahoney (1990) and Braatne et al. (1996)].

Like their parental species, *P. deltoides* and *P. nigra*, all cultivars belong to the black poplars (section *Aigeiros*), which are adapted to dynamic riparian zones in semi-arid floodplains. Despite some morphological and physiological adaptations to warmer and drier climate, e.g., a leaf orientation to avoid heat loads and early stomatal closure in response to water deficits, black poplars are very vulnerable to prolonged drought (Braatne et al. 1992; Hinckley et al. 1992; Tyree et al. 1994b).

H. Schume (✉)

Institute of Forest Ecology,  
BOKU—University of Natural Resources and Life Sciences,  
Peter Jordan Strasse 82, 1190 Vienna, Austria  
e-mail: helmut.schume@boku.ac.at  
Tel.: +43-1-476544104  
Fax: +43-1-4797896

M. Grabner

Institute of Botany—Group of Wood Biology  
and Tree-Ring Research,  
BOKU—University of Natural Resources and Life Sciences,  
Gregor Mendel Strasse 33, 1180 Vienna, Austria

O. Eckmüller

Institute of Forest Growth and Yield Research,  
BOKU—University of Natural Resources and Life Sciences,  
Peter Jordan Strasse 82, 1190 Vienna, Austria

Cultivar I-214, for instance, responded to limited drought with an elevated concentration of abscisic acid in the xylem and pronounced leaf shedding (Chen et al. 1997). In fact, the abscission of leaves is an effective and quick reaction to temporary drought (Taize and Zeiger 1998), when stomatal closure is insufficient to maintain a favorable water balance. Kozłowski and Pallardy (1997) describe the shedding of whole twigs as characteristic of poplars. The sacrifice of branches is an even more extreme form of lowering transpirational water losses by crown reduction, typical for poplars growing in riparian zones (Rood et al. 2000). A high rate of crown die-back in a given year considerably reduces the probability of surviving the following season (Scott et al. 1999).

The adjustment of the sapwood area, on the other hand, is thought to be a gradual response to lasting water limitation, resulting from reduced stem growth, and lagging behind leaf area adjustment. The relation between sapwood area and leaf area has been described repeatedly. Huber (1928) was the first to express transverse-sectional xylem areas of stems and branches per fresh weight of leaves supplied by that part of the axis. Shinozaki et al. (1964) who formulated the "pipe model theory of tree form", found a similar ratio between the sapwood area of a stem or branch and the amount of supported leaves at any height within a tree crown. Eckmüller and Sterba (2000) report that early sapwood area alone (i.e. sapwood without non-conductive latewood) proved to be a better estimator for the needle mass of Norway spruce than total sapwood area, independent of soil properties, tree age, social position and crown condition. The sum of the conduit lumen areas within the sapwood is probably the closest approximation to a tree's pipe in the sense of Shinozaki et al. (1964), its hydraulic efficiency still depending on the diameters of the single conduits.

The concept of leaf-specific conductivity, which relates the conductivity of sapwood to the potential evaporative surface (Zimmermann 1978; Gartner 1995), integrates the fact that the hydraulic efficiency of a vessel increases proportionally to the 4th power of its radius (Hagen-Poiseuille law). Therefore the variation of vessel size and density can contribute to adjusting the equilibrium between the water supply system and transpiring surface and be part of a strategy for acclimation to drier site conditions.

In our study area, the leaf area index and the productivity of hybrid poplar stands ( $n=33$ ) were positively correlated with parameters directly related to water supply, such as duration of groundwater contact, soil depth and water storage capacity of the soil (Hager et al. 1999). Given these significant dependencies and considering findings from Switzerland (Sass and Eckstein 1995) and Spain (Villar-Salvador et al. 1997), where precipitation influenced the vessel size in stems of European beech and branches of evergreen oaks, respectively, we hypothesize that a significant change in site hydrology, such as the loss of groundwater contact, should be reflected in xylem anatomy variations of poplar.

We tested this assumption by a comparative investigation of two hybrid poplar stands. One stand had lost

groundwater contact at the age of 12 years after the construction of a hydropower plant, whereas the other stand remained largely unaffected. This natural experiment is an extreme example of acclimation to drier site conditions in several respects: (1) a drought sensitive cultivar of a highly water consuming species was investigated, (2) the sudden loss of groundwater contact means a severe reduction of water supply and (3) the drought-affected experimental trees were the last poplars that survived this change in water supply along a steep gradient in site hydrology.

## Materials and methods

### Study area

The study area is situated in the Tullner Feld (Lower Austria), an alluvial basin of about 560 km<sup>2</sup> (approximately 13 km north-south and 45 km east-west), drained by the river Danube from west to east. The region is dominated by agriculture. Floodplain forests occur as a belt of up to 4-km width along the river banks.

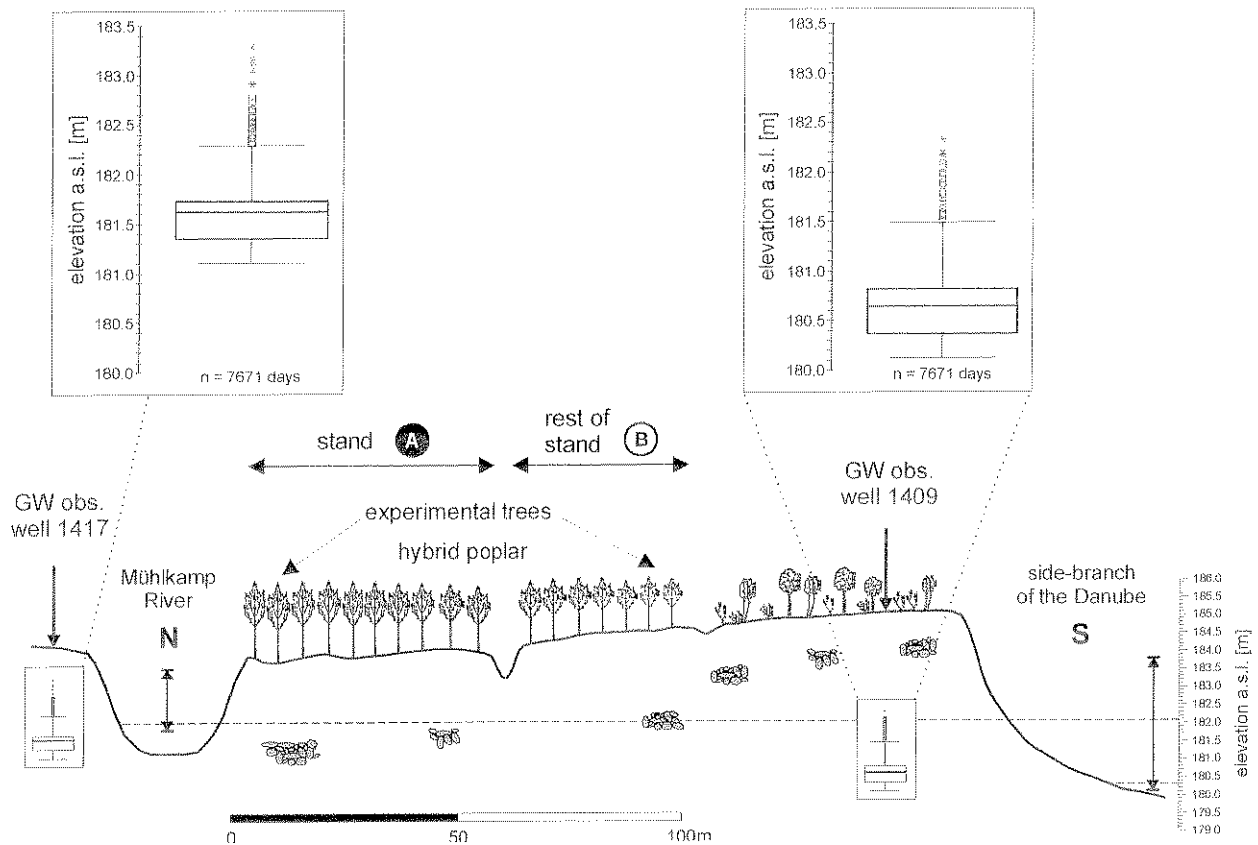
Tertiary fine-textured marine marls and claystones form a water-impermeable barrier, over which a layer of coarse quaternary sediments, 8–12 m thick, has been deposited by the river. This body of gravel functions as an aquifer with high hydraulic conductivity, so that under undisturbed conditions the river's water-level fluctuations of up to 7 m are passed with little delay to the alluvial groundwater (Nachtnebel 1989). The morphology of this gravel layer is distinct, affecting the thickness of the upper fine-sediment layer, which varies between a few decimeters and several meters. The fine sediment represents the rooting zone for the vegetation, and its depth and water holding capacity are important determinants of the water balance, particularly at sites lacking groundwater contact (Hager et al. 1999).

Mean annual precipitation (520 mm) has declined by 20% since the early seventies relative to the two preceding decades. This decrease resulted from reduced rainfall during the growing season. The mean annual temperature is 9.5°C (the January mean being -0.9°C and the July mean 19.6°C). Precipitation was recorded at a weather station 5 km from the research sites; temperature data were measured at a distance of 17 km (Hydrographischer Dienst in Österreich 1994).

### Study sites and stands

The hydrology of the floodplain forests around Altenwörth (48° 23'17" N, 15° 50'48" E and 184 m altitude) was strongly affected by the construction of a hydropower plant on the Danube River in the middle of the 1970s. Diking caused a lowering of the groundwater table and reduced its annual amplitude by 2–3 m. Flooding, which occurred annually before 1976, was completely stopped (Nachtnebel 1989). Continuous records of 19 groundwater wells were available for the period 1976 until 1996. They show that at many forest sites the groundwater has remained in the gravel layer since that time, and has therefore been inaccessible to hybrid poplars, which do not root in this coarse substrate (Mader 1989).

The two research sites were located on a peninsula-like headland of approximately 1-km length and 200-m width between a side-branch of the Danube River and the small tributary, the Mühlkamp River (Fig. 1). Between the two watercourses, the mean groundwater table was tilted by about 1‰ from the horizontal as a result of the power plant's construction. During 1996 the water levels of the Mühlkamp River and the Danube side-branch were monitored weekly using a geodetic survey instrument (Wild TC 1010). Fine-sediment thickness and the elevation of the underlying gravel deposits were determined along a grid (2.5 m by 2.5 m) with



**Fig. 1** Position of the experimental trees on the headland between the Mühlkamp River and the side-branch of the Danube (schematic cross section). Length-to-height of the site is presented in a ratio of 8:1. The depth of the gravel layer was determined at the locations symbolized by stones. Dashed lines represent the mean river water

levels in 1996, vertical arrows indicate the range between minimum and maximum. Box plots (SPSS graphics) show summary statistics for the distribution of the groundwater levels observed at wells 1417 and 1409 between 1976 and 1996

a soil coring tool on an area of 20 m by 20 m around the experimental trees, and less intensively across the headland.

The experimental trees near Mühlkamp River (stand A) had—except for a few years (see Table 1)—groundwater access, whereas all trees of stand B had lost groundwater contact by 1976. The southern part of site B, which is characterized by a lower fine-sediment depth, was affected by a severe decline of hybrid poplars starting in 1978. Eventually, this part of the plantation was replaced by black locust and shrub vegetation. The experimental trees of stand B belonged to the last surviving rows of the original plantation. For comparability, the two study locations had to fulfill the following criteria:

- Same site unit before 1976 (moist poplar site)
- Similar average soil depth (1.9 m for site A and 2.1 m for site B)
- Same poplar clone (cultivar Jacometti 75A)
- Similar age and stand structure (evenly aged and two-layered)

Belonging to two different management units, the stands were slightly different in age. After clear-cutting, both sites were reforested with 2-year-old hybrid poplar saplings. At site A, 10 rows of hybrid poplar were planted in 1969, at site B 16 rows in 1966.

The first canopy layers, consisting of pure hybrid poplar, had reached dominant heights of 35 m (A) and 29 m (B) in 1996. In both stands, the second canopy layer (10–22 m high) was composed of *Sambucus nigra*, *Prunus padus*, *Robinia pseudacacia*, *Juglans nigra*, *Fraxinus excelsior* and *Quercus robur*.

The cultivar of *Populus x euramericana* (Dode) Guinier that was investigated, is an outcome of the Italian selection program by Jacometti and Piccarolo, with the designation “75A”. The genetic relationship with the better known cultivars I-214 and 78B, which

is expressed in anatomical similarities, such as stomata geometry and frequency (Pallardy and Kozłowski 1979) or vascular properties (Peszlen 1994; Mátyás and Peszlen 1997), results in a comparable hydrological behavior at a given site, i.e. high productivity on sites well supplied with water, but enhanced susceptibility to drought (Günzel 1954).

#### Sample collection and preparation

At each of the two sites, three increment cores per tree were taken from three dominant poplar trees at 0°, 120° and 240° from north at 1.3-m height. The tree-ring widths were measured to the nearest 0.01 mm and averaged per tree. For each tree, the core showing the least deviation from the mean tree radius was chosen for further analysis.

The remaining six cores were divided into approximately 3-cm long segments exactly at the tree-ring borders and fixed to wooden sample supporters with polyurethane glue. To prepare the segments for sectioning, they were soaked in a solution of glycerol, methanol and water at temperatures of 40–50°C. Using a slide microtome, 25- $\mu$ m thin sections were transversally cut from these samples. The sections were dehydrated, stained with methylene blue and mounted in Malinol on slides (Gerlach 1984).

#### Measurements and data processing

Vessel-lumen area, circumference and the major (radial) as well as the minor (tangential) axis of the best adjustable ellipse were

**Table 1** Occurrence of groundwater contact by site and annual precipitation in relation to significant differences between the stands regarding vessel properties (Student's *t*-test)

	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	
Ground water contact at site A	Yes	Yes	Yes	Yes	No	Yes	No	No	Yes	Yes	Yes	No	No	No	No	Yes	Yes	No	No	Yes	Yes	Yes	No	No	Yes	
Ground water contact at site B	Yes	Yes	Yes	Yes	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No	Yes
Precipitation (mm)	541	475	470	571	504	569	410	469	560	428	612	493	445	580	559	528	502	600	593	495	486	423	483	380	669	
Vessel diameter	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	**	**	*	*	ns	ns	"	*	ns	ns	ns	ns	ns	ns	
Lumen area (L.A)	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	**	**	*	*	ns	ns	"	*	ns	ns	ns	ns	ns	ns	
Vessel density	ns	ns	ns	ns	ns	ns	*	**	***	**	***	***	***	**	**	***	ns	ns	ns	*	ns	ns	***	*	**	ns
Percentage of L.A	ns	*	ns	ns	ns	ns	ns	*	*	*	ns	ns	ns	ns	**	**	*	ns	**	*	ns	ns	ns	ns	ns	

\* 0.01 < *P* < 0.05, \*\* 0.001 < *P* < 0.01, \*\*\* *P* < 0.001, ns not significant

measured using a light microscope with a CCD camera connected to a Macintosh computer. Vessel diameter was calculated as the corresponding circular diameter from the lumen area. Analysis was performed with NIH-Image analysis software (Rasband 1996). Vessel dimensions were measured within an area of 1 mm in tangential direction by ring width. The measurements progressed systematically from the beginning to the end of a tree-ring, in order to reconstruct the seasonal development of vessel size. For each tree the 26 annual rings from 1971 to 1996 were examined.

Working with conifers, Vaganov (1990) termed plots of the variation of vessel size against the growth period "tracheidograms". Adjusting his terminology to the vessels of poplar, these plots will be called "tracheograms" in the subsequent text. For reasons of comparability, growing season length was standardized. This standard period, lasting from the middle of April until the middle of September, was deduced from local phenological observations and from dendrometer-band measurements of hybrid poplar over several years. Considering climatic year-to-year variability there might be a deviation of a few weeks in spring or autumn for an individual year.

Since the number of vessels per tree-ring was different for every ring depending on its width, it was necessary to standardize the sample size per year, in order to compare the tracheograms between trees and years. Therefore a procedure described by Vaganov (1990) was applied. The number of 35 values for the standard tracheogram was obtained by dividing the average annual vessel number over all analysed tree-rings (=350) by 10, the approximate number of vessels across the examined area of 1 mm width.

In order to estimate the influence of a change in vessel diameter distribution on the hydraulic efficiency of the conductive xylem, the theoretical hydraulic conductivity  $k_h$  (mm<sup>3</sup>) was calculated as the sum of the 4th power diameters of all vessels within the measured sections per year.

#### Statistical analyses

Stand-wise annual means of the vessel properties were tested for equality using Student's *t*-test. A two-way analysis of variance (ANOVA) was applied to the vessel and the stem increment data to separate the influence of the stands from that of the periods (before versus after the onset of poplar decline at site B) and to identify possible interactions. Linear regression models with stepwise variable selection were developed to explain (1) the variance inherent in each of the vessel parameters by stem growth and water supply and (2) the variance of stem growth characteristics by water supply.

The models used were as follows:

$$\text{vessel property} = A + B \times \text{stem growth} + C \times \text{water supply} \quad (1)$$

and

$$\text{stem growth} = A + C \times \text{watersupply} \quad (2)$$

with

$$A = a_0 + a_1 \times S_A P_{\text{after}} + a_2 \times S_A P_{\text{before}} + a_3 \times S_B P_{\text{after}} \quad (3)$$

$$\begin{aligned} B \times \text{stem growth} = & b_1 \times \text{BAI} + b_2 \times S_A P_{\text{after}} \times \text{BAI} \\ & + b_3 \times S_A P_{\text{before}} \times \text{BAI} + b_4 \times S_B P_{\text{after}} \times \text{BAI} \\ & + b_5 \times \text{RI} + b_6 \times S_A P_{\text{after}} \times \text{RI} \\ & + b_7 \times S_A P_{\text{before}} \times \text{RI} + b_8 \times S_B P_{\text{after}} \times \text{RI} \end{aligned} \quad (4)$$

$$\begin{aligned} C \times \text{water supply} = & c_1 \times \text{PREC} + c_2 \times S_A P_{\text{after}} \times \text{PREC} \\ & + c_3 \times S_A P_{\text{before}} \times \text{PREC} \\ & + c_4 \times S_B P_{\text{after}} \times \text{PREC} + c_5 \times \text{GW} \\ & + c_6 \times S_A P_{\text{after}} \times \text{GW} + c_7 \times S_A P_{\text{before}} \times \text{GW} \\ & + c_8 \times S_B P_{\text{after}} \times \text{GW} + c_9 \times \text{GW} \times \text{PREC} \end{aligned} \quad (5)$$

where vessel property is one of diameter, lumen area, density or percentage of lumen area per tree-ring area (PLA). Stem growth is represented either by BAI (basal area increment) or RI (radial increment). Water supply variables are PREC (annual precipitation) and GW (groundwater), the latter encoded as dummy variable: GW is equal to 1 if there is **no** groundwater contact and 0 otherwise. PREC was calculated for a modified hydrological year [1 July<sub>(preceding)</sub> until 30 June<sub>(current)</sub>], considering that the increment and the vessel formation within a year can be influenced by the climatic conditions prevailing in the second half of the preceding year (e.g. Fritts 1976; Sass and Eckstein 1995; Yasue et al. 2000).

$S_{AP_{after}}$ ,  $S_{AP_{before}}$ ,  $S_{BP_{after}}$  are dummy variables:

- $S_{AP_{after}}$  is equal to 1 in stand A and in the period after the onset of poplar decline at site B (1978–1996) and 0 otherwise.
- $S_{AP_{before}}$  is equal to 1 in stand A and in the period before the onset of poplar decline at site B (1973–1977) and 0 otherwise.
- $S_{BP_{after}}$  is equal to 1 in stand B and in the period after the onset of poplar decline at site B (1978–1996) and 0 otherwise.

The lower limit of the time period “before” was defined as being the year 1973 to exclude the juvenile years characterized by narrower vessels (Peszlen 1994) from statistical analyses. In order to allow comparison with vessel diameter studies, all analyses were carried out for vessel lumen area and vessel diameter. The coefficients of the model ( $a_0$ – $a_3$ ,  $b_1$ – $b_8$  and  $c_1$ – $c_9$ ) were estimated using stepwise regression to test all possible hypotheses. The analyses were performed using STAT-Graphics 4+.

## Results

### Increment

Average tree-ring widths were markedly reduced with the operational start of the power plant in 1976, especially at site B (Fig. 2a, Table 2). ANOVA revealed a highly significant stand–period interaction for RI and for BAI: after 1977 the average RI was 62.2% lower at site B than at site A and BAI was reduced by 65.6% (Tables 2, 3).

Comparing the mean BAIs of the two stands with annual precipitation shows that in years with less than 450 mm of precipitation, local minima in the increment curve can be observed for stand B, while in years with more than 600 mm of precipitation local maxima occur (Fig. 2b).

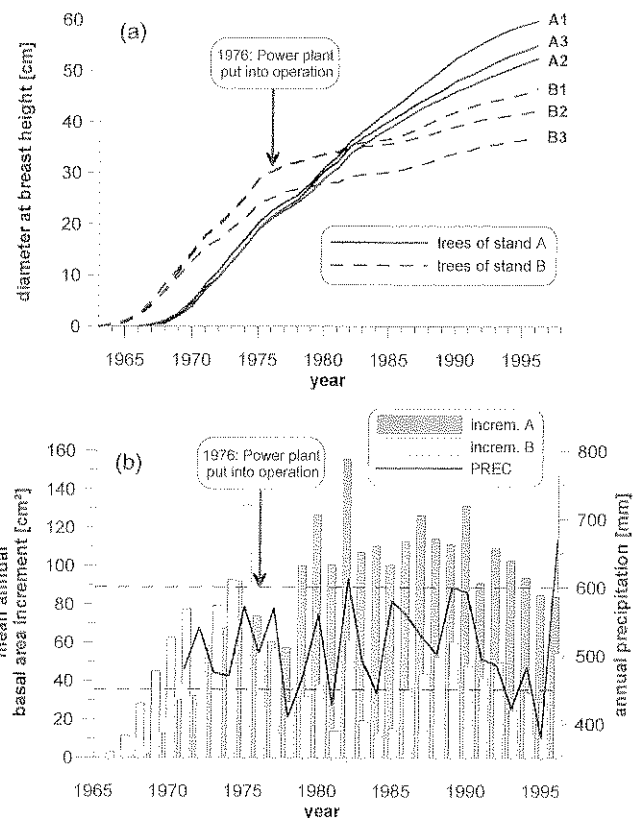


Fig. 2 a Development of tree diameters at breast height over time for all six experimental trees. b Mean annual basal area increment in relation to open field precipitation. Dashed lines mark the 450 and 600 mm precipitation thresholds referred to in the text

### Annual means of vascular properties

An acclimation of the conductive xylem to the drier site conditions can be recognized at site B after 1977 (Fig. 3). Vessel density (VD) was the feature that reacted first and most significantly to the changed site hydrology (Table 1).

With respect to vessel properties, neither of the main effects “stand” and “period” turned out to be significant at the 5% level or better in ANOVA (Table 3). The stand–

Table 2 Mean vascular properties and stem growth characteristics before and after the occurrence of poplar decline at site B by stands

	Stand A				Stand B			
	Period before (1973–77)		Period after (1978–96)		Period before (1973–77)		Period after (1978–96)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<b>Vessel properties</b>								
Diameter ( $\mu\text{m}$ )	85.8	6.8	94.7	3.9	88.8	4.9	87.1	3.0
Lumen area ( $\mu\text{m}^2$ )	6,218	1,018	7,575	649	6,718	758	6,463	438
Density (no. $\text{mm}^{-2}$ )	45	5	42	3	44	4	60	5
Percentage of lumen area	27.7	2.0	31.4	0.2	29.1	3.7	37.5	3.8
<b>Growth characteristics</b>								
Radial increment (1/100 mm)	1,344	19	852	77	1,087	137	322	60
Basal area increment ( $\text{cm}^2$ )	70.5	3.8	106.4	15.8	83.9	17.9	36.6	10.0

**Table 3** Results of the two way analysis of variance (ANOVA)

	Stand			Period			Stand–period interaction		
	<i>F</i>	<i>P</i>	Sign <sup>a</sup>	<i>F</i>	<i>P</i>	Sign <sup>a</sup>	<i>F</i>	<i>P</i>	Sign <sup>a</sup>
Vessel properties									
Diameter	0.6	0.4559	ns	0.3	0.6153	ns	5.0	0.0559	(*)
Lumen area	0.5	0.4830	ns	0.3	0.6154	ns	4.8	0.0591	(*)
Density	4.9	0.0588	(*)	1.0	0.3447	ns	24.5	0.0011	**
Percentage of lumen area	1.6	0.2465	ns	2.2	0.1735	ns	16.6	0.0036	**
Growth characteristics									
Radial increment	15.7	0.0041	**	27.7	0.0008	***	196.0	0.0000	***
Basal area increment	8.0	0.0220	*	0.1	0.7673	ns	36.6	0.0003	***

<sup>a</sup> Significance

(\*) 0.05 < *P* < 0.1, \*0.01 < *P* < 0.05, \*\*0.001 < *P* < 0.01, \*\*\**P* < 0.001, *ns* not significant

period interaction however, expresses the previously mentioned anatomical acclimation of trees at site B after 1977. It was significant at the 1% level for VD and the percentage of lumen area, and on the edge of statistical significance at the 5% level for vessel size.

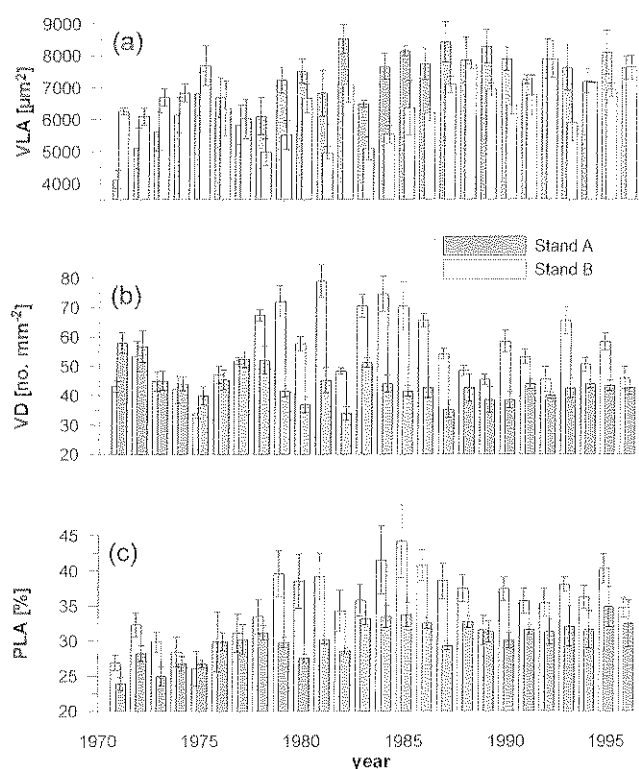
During the 19 years from 1978 to 1996, the mean annual vessel lumen area of the trees of stand B was on average reduced by 14.7% in relation to that of stand A (i.e. 8% in terms of vessel diameter). At the same time, the mean annual VD increased by 42.8% and the mean percentage of vessel lumen area increased relatively by 19.4% (Table 2). The most extreme differences occurred in 1981, when mean vessel lumen area was 27.3% smaller at site B and VD 74.8% higher. A similar relationship was observed for 1984 (−27.6% and +69.6%, respectively). In both years, precipitation was less than 450 mm. For moist years (e.g. 1982, 1989) the differences were less striking (Fig. 3, Table 1). Vessel lumen area and VD were negatively correlated to each other. This linear relation was highly significant for both stands over both periods (for stand A,  $r^2=0.59$ ,  $P<0.001$ ; for stand B,  $r^2=0.69$ ,  $P<0.001$ ).

#### Intra-annual development of vessel size

The years 1981 and 1983 serve as examples to illustrate the response of vessel size to the hydrological conditions of the current season, the latter being one of the few years, when site A remained completely without groundwater contact (Table 1). The seasons were characterized by little precipitation and initial lack of groundwater contact at both sites, causing the vessel lumen areas to decrease. While this declining trend continued in 1983, it was abruptly interrupted at site A in July 1981, when the groundwater table rose into the rooting zone of the trees (Fig. 4), an observation that was made repeatedly.

Basically, three different types of tracheograms could be distinguished (Fig. 5):

1. The trees regularly start into the season producing large vessels. The highest seasonal vessel-lumen area is usually reached in early summer. During years with abundant water supply the initial vessel sizes are more



**Fig. 3a–c** Comparison of mean annual vascular parameters by stands and years. **a** Vessel lumen area (VLA). **b** Vessel density (VD). **c** Percentage of vessel lumen area (PLA). *Errors bars* are standard errors of means

- or less retained throughout the growing season. They decrease rapidly only at the very end of the season.
2. The big vessel diameters from the early season continuously decrease with prolonged drought (see also year 1983 in Fig. 4).
3. Rising groundwater interrupts drought, which is immediately reflected by a series of distinctly larger vessels, even in the late season, as occurred for instance at site A in 1977 (Fig. 5) and in 1981 (Fig. 4).

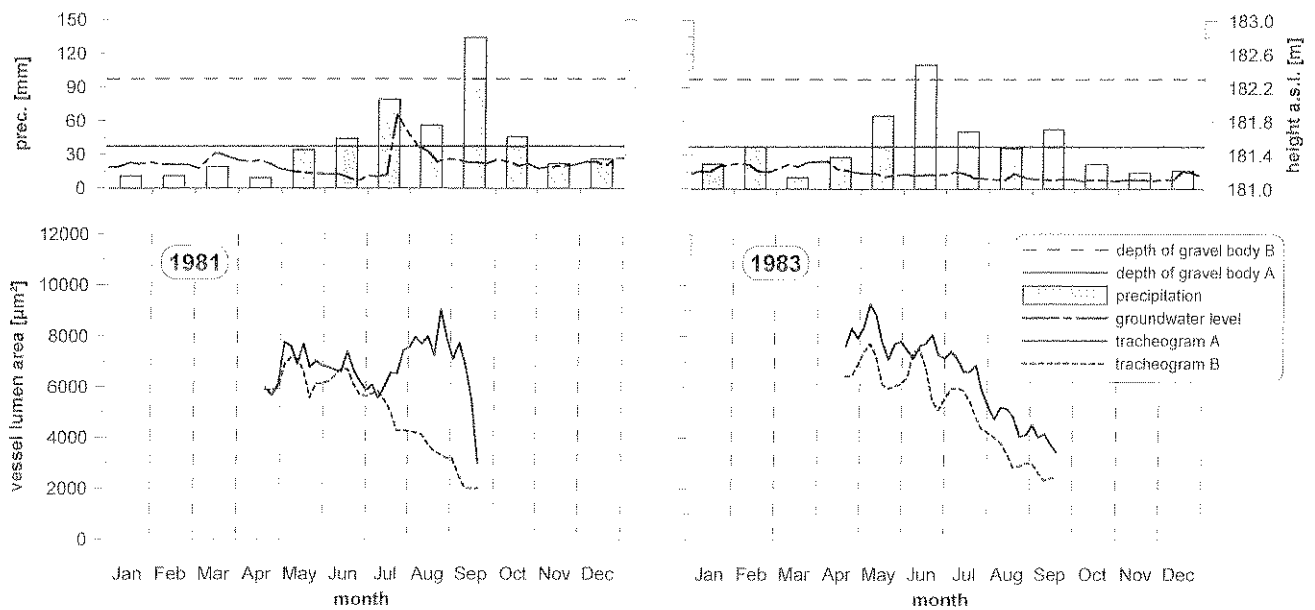


Fig. 4 Development of vessel size in 1981 and 1983 in relation to precipitation and groundwater contact

**Table 4** Coefficients for the linear regression models for estimating vessel diameter, lumen area, the percentage of lumen area as well as basal area and radial increment

Variable	Coefficient <sup>ab</sup>	Vessel properties				Growth characteristics	
		Diameter ( $\mu\text{m}$ )	Lumen area ( $\mu\text{m}^2$ )	Density ( $\text{no. mm}^{-2}$ )	Percentage of lumen area	Basal area increment ( $\text{cm}^2$ )	Radial increment ( $1/100 \text{ mm}$ )
Intercept	$a_0$	76.02	4,805.72	43.09	32.71	42.54	1,240.07
$S_A P_{\text{after}}$	$a_1$	3.32	513.05	14.35	4.44		-355.78
$S_B P_{\text{after}}$	$a_3$			31.49		-34.01	-726.06
BAI	$b_1$	0.14	21,200		-0.054		
$S_A P_{\text{after}} \times \text{BAI}$	$b_2$			-0.151			
$S_B P_{\text{after}} \times \text{BAI}$	$b_4$			-0.545	-0.160		
PREC <sup>c</sup>	$c_1$					0.081	
$S_A P_{\text{after}} \times \text{PREC}^c$	$c_2$					0.048	
$S_B P_{\text{after}} \times \text{PREC}^c$	$c_4$	0.01	1,749		0.025		
GW	$c_5$					-13.790	-202.880
GW $\times$ PREC <sup>c</sup>	$c_9$			-0.010			
	$r^2(\text{adj})$	41.4%	41.6%	76.9%	60.8%	70.3%	61.9%

<sup>a</sup> All mentioned coefficients are significant at the 5% level or lower

<sup>b</sup> The coefficients  $a_2$ ,  $b_3$ ,  $b_5$ - $b_8$ ,  $c_3$ ,  $c_6$ - $c_8$  were never significant

<sup>c</sup> The unit of precipitation is the millimeter

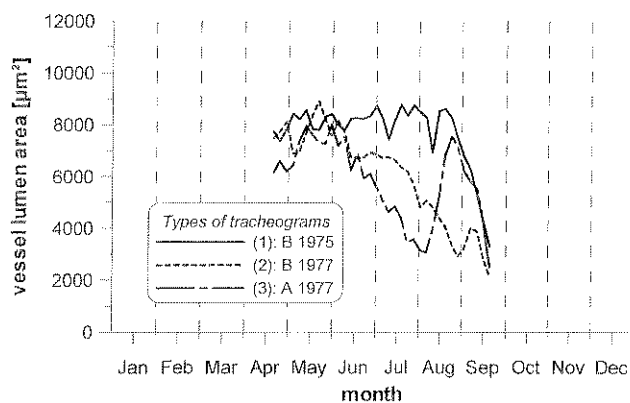


Fig. 5 Examples of the three basic types of tracheograms

#### Relationship between water supply, stem growth and vessel properties

Both lack of groundwater contact and reduced precipitation had a significant negative effect on the annual BAI of all experimental trees regardless of the period (Tables 4, 5). Precipitation was not included in the model for RI, which did not explain as much of the variations, as did the model for BAI (62% versus 70%).

According to the model for BAI, an increase in precipitation from 400 to 600 mm enhanced BAI by 22% in both stands between 1973 and 1977. Afterwards the positive effect of the extra 200 mm of precipitation on BAI was 27% for stand A (usually with groundwater contact), but 60% for stand B (usually without ground-

**Table 5** Modeled basal area increment ( $\text{cm}^2$ ) before and after the onset of poplar decline at site B under different hydrological scenarios, including relative changes

	Stand	Period			
		"Before" (1973–1977)		"After" (1978–1996)	
		Groundwater	No groundwater	Groundwater	No groundwater
Precipitation 400 mm	A	74.7		94.0	80.2
	B	74.7	61.0		26.9
Precipitation 600 mm	A	90.8		119.7	105.9
	B	90.8	77.1		43.0
Increase	A	22%		27%	32%
	B	22%	26%		60%

water contact), substantiating the transition of stand B from a groundwater supplied stand to a stand exclusively covering its water demand from precipitation. In the exceptional seasons, when stand B was without groundwater supply in period "before" and stand A in period "after", the relative effect of increasing precipitation was, however, only slightly enhanced relative to groundwater contact (Table 5).

Increasing BAI had a significant positive influence on vessel size at both sites and in both periods. For stand B trees this positive effect was reinforced by increasing precipitation in period "after" (Table 4).

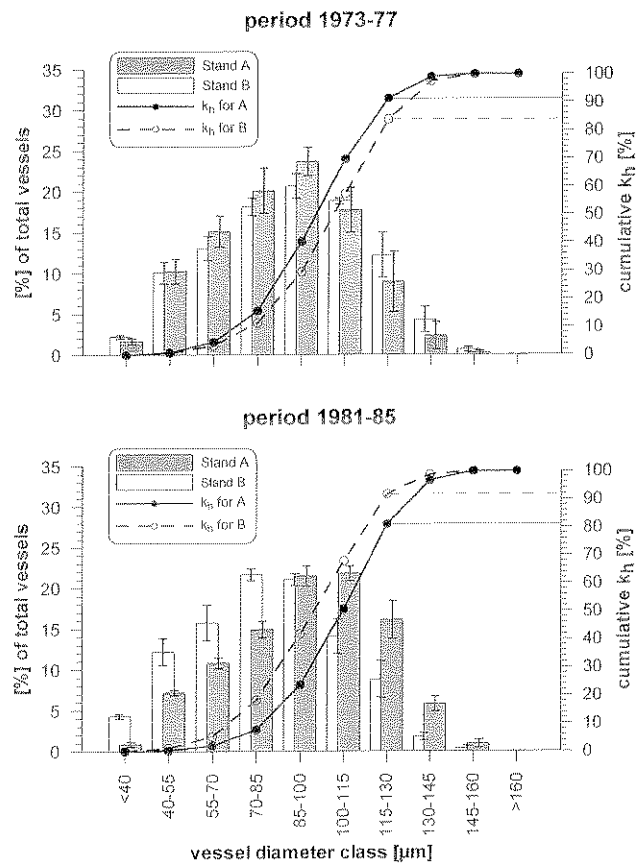
VD on the other hand was negatively correlated with BAI after 1977. In years without groundwater contact, a direct negative influence of precipitation on VD was detected. VD was the vascular parameter that could be best explained by the regression model [ $r^2(\text{adj})=77\%$ ].

The PLA proved to be negatively correlated with annual BAI. For stand B and period "after", PLA was found to be best described by a linear combination of BAI and precipitation. In the model, the negative effect of increasing BAI on PLA is balanced by the effect of precipitation for moist years, but overcompensated for dry years. So for stand B and period "after", PLA was more or less equal to the intercept value of 33% in moist years, but was higher in dry years.

#### Water transport efficiency

Figure 6 shows the mean frequency distributions of vessel diameter classes for the period before poplar decline at site B (1973–1977) and for the period 1981–1985, when the most pronounced differences between the stands regarding BAI and vessel properties were observed.

Between 1981 and 1985 the vessel diameter distribution for stand B shifted significantly towards smaller diameter classes in comparison with stand A (chi-square test for period 1973–1977 gives  $P=0.715$ ; for period 1981–1985,  $P<0.001$ ). During this time, the three diameter classes over  $130 \mu\text{m}$ , for instance, comprised 7% of the total vessel number in stand A, while in stand B only 2% of the vessels fell into this category. Their contribution to  $k_h$  was 19% and 8% for stands A and B, respectively (Fig. 6). The smaller 50% of the vessels, on the other hand, contributed 18% (A) and 14% (B) to the



**Fig. 6** Mean frequency distributions of vessel diameter classes (error bars indicate the standard error of the mean) and cumulative theoretical hydraulic conductivities  $k_h$  by stands and periods. Horizontal lines serve to illustrate the example given in the text

hydraulic conductivity, underlining the significance of large vessels for water transport.

#### Discussion

Riparian trees are known to be sensitive to reductions in stream flow or groundwater availability. Recent studies on poplar decline show that xylem cavitation is a key process, underlying most decline symptoms (Tyree et al. 1994b; Rood et al. 2000). Depending on the degree of xylem dysfunction, consequences range from earlier



stomatal closure (Tyree et al. 1994b; Horton et al. 2001), leaf shedding or branch sacrifice to the death of the entire individual (Scott et al. 1999; Rood et al. 2000). Each of those effects diminishes net assimilation and thus branch growth (Willms et al. 1998; Horton et al. 2001) or stem growth (Hager et al. 1999).

In this study, circumferential stem growth of hybrid poplar was also positively correlated with site water supply. BAI, a direct measure of the relative enlargement or reduction of the sapwood area, proved to be a more suitable parameter for the characterization of a tree's water transport system than RI. Variations in BAI could be better explained by water supply in the linear regression model, including the effect of precipitation (Table 4), which became especially meaningful at site B after 1977 (Table 5). In addition, BAI does not suffer from a declining age-related trend as RI does (highly significant period effect in ANOVA for RI, which was not given for BAI). Accordingly BAI entered all linear regression models for vascular properties instead of RI.

Vessel properties were all correlated with BAI, and were thus implicitly controlled by water supply. The importance of precipitation in years without groundwater contact is emphasized by the direct entry of precipitation into the regression models for vascular features (Table 4). Higher BAI in moist years was associated with the production of wider vessels, but at a much lower density.

Water may have direct and indirect influences on the formation of vessels and, finally, vessel size. The first vessels formed within a tree-ring integrate the water conditions from the preceding late summer up to the current spring (Sass and Eckstein 1995). This water is operative through storage materials in the plant, shoot and root growth or the formation of buds in the previous year (Fritts 1976). Moreover, dormant-season precipitation recharges the soil water storage. The effects of growth-limiting or -enhancing conditions are thus carried over from one growing season to the next, an aspect that was considered by calculating the annual precipitation for a modified hydrological year [July<sub>(preceding)</sub> until June<sub>(current)</sub>]. A direct influence of water on vessel size is via turgor pressure (Ray et al. 1972; Tyree and Sperry 1989), whereby abundant water supply during the growing season promotes the formation of large cells by a high turgor and rapid cell expansion.

The vessel sizes observed in this study are large compared to values for poplar reported in literature and to other tree species (e.g. Wagenführ and Scheiber 1985; Hacke and Sperry 2001), but very similar to those measured by Peszlen (1994). In her investigation, vessel-lumen diameters of I-214 poplars stabilized at an average value around 90  $\mu\text{m}$ , after a juvenile phase of 6–10 years, which was characterized by narrower conduits. Better site conditions accelerated maturation (Mátyás and Peszlen 1997). The vessel diameters of the control trees (stand A) started to level off after 6–7 juvenile years and finally reached average annual values around 95  $\mu\text{m}$ .

Large vessels are very efficient regarding water transport capacity (Fig. 6), but at the same time their vulnerability to drought-induced embolism and subsequent cavitation is enhanced within a species (e.g. Sperry and Tyree 1988; Tyree and Sperry 1989; Lo Gullo and Saleo 1993; Lo Gullo et al. 1995). Pores in the interconduit pit membranes have been identified as big enough to allow the aspiration of air from outside into a water-filled vessel at water potentials occurring in trees ("air-seeding"). Larger pores allow air-entry at less negative water potentials (Zimmermann 1983; Tyree et al. 1994a; Hacke and Sperry 2001). Tyree and Sperry (1989) explain the higher porosity of the pit membrane in large vessels on a developmental basis: rapid cell expansion under turgor pressure stretches the cellulose fibers in the primary cell wall, increasing pore size and effective porosity.

Therefore the relation between water supply, growth and vessel size outlined above can be extended by the safety aspect: the trees of stand B responded to groundwater draw-down with a significantly reduced BAI and the formation of narrower, hydraulically less efficient vessels, but with a lower risk of embolism and cavitation. This mechanism would help to explain the acclimation of a species to different sites, as described by Sparks and Black (1999). They investigated cuttings of *P. trichocarpa* sampled along a humidity and temperature gradient and measured more negative vulnerability thresholds and better stomatal control in populations from dry environments.

In comparison to the control trees, the mean vessel diameter decreased by 8%, while mean VD increased by 43%. Corresponding to the Hagen-Poiseuille law, this small reduction in vessel diameter causes a considerable decrease in hydraulic efficiency. The necessity to compensate for this efficiency drop by a disproportionate increase in VD makes VD the most sensitive indicator of site hydrologic alterations. VD responded first and most pronouncedly to the loss of groundwater contact (Table 1), the stand-period interaction in ANOVA was highly significant for VD (Table 3) and its variations could be better described by circumferential stem growth and water supply in a linear regression model than those of any other vascular parameter (Table 4). Integrating the small decrease of vessel size and the massive increase in density, the PLA was intermediate between these two features, though more similar to VD. The hypothesis that poplar would respond to the loss of groundwater access with a modified xylem anatomy was confirmed.

Intra-annual development of vessel size indicates a rapid response to the prevailing hydrological conditions (Fig. 4). In spring, when evaporative demand is lower and water is readily available, trees regularly form large vessels. After that, vessel size is closely linked to the existence of groundwater access or the amount of precipitation, because turgor pressure as driving force of cell expansion (Tyree and Sperry 1989) depends on water availability. This tight coupling of vessel size to site water supply seems to be a particular feature of diffuse-porous

tree species. In contrast to ring-porous trees, the transition between different vessel sizes is gradual, and the formation of wide or narrow vessels is not bound to seasonality (Bosshard 1982; Schweingruber 2001). In the study of Villar-Salvador et al. (1997), the diffuse-porous evergreen oaks, *Q. coccifera* and *Q. ilex*, showed a significant correlation between mean annual vessel size and annual precipitation, while *Q. faginea*, a deciduous ring-porous species, did not. The tendency of European beech to develop a semi-ring-porous wood structure under severe drought stress (Bosshard 1982) may be interpreted as a continuous decrease of vessel size with persisting drought, as we observed for poplar (Fig. 4).

Unlike the case in ring-porous trees, which transport almost all the water in the large earlywood vessels of the outermost tree-ring (e.g. Hacke and Sperry 2001), the influence of the last tree-ring on the total conductivity of a stem or the safety of the tree's hydraulic system is limited in diffuse-porous trees. Their conductive sapwood consists of several tree-rings, each of them reflecting the hydrological conditions of the year of its formation in ring width and vessel sizes. So despite the immediate response of vessel size to a varying site water supply, this buffered hydraulic system is likely to react too slowly on the whole-tree level and is in danger of failing in case of sudden and severe changes in site hydrology.

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## References

- Braatne JH, Hinckley TM, Stettler RF (1992) Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F<sub>1</sub> hybrids. *Tree Physiol* 11: 325–339
- Braatne JH, Rood SB, Heilmann PE (1996) Life history, ecology and conservation of riparian cottonwoods in North America. In: Stettler RF, Bradshaw HD Jr, Heilmann PE, Hinckley TM (eds) *Biology of Populus and its implications for management and conservation*. NRC Research Press, Ottawa, pp 57–85
- Bosshard HH (1982) *Holzkunde Band 1: Mikroskopie und Makroskopie des Holzes*. Birkhäuser, Basel
- Busch DE, Ingraham NL, Smith SD (1992) Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecol Appl* 2:450–459
- Chen S, Wang S, Altman A, Hüttermann A (1997) Genotypic variation in drought tolerance of poplar in relation to abscisic acid. *Tree Physiol* 17:797–803
- Eckmüllner O, Sterba H (2000) Crown condition, needle mass, and sapwood area relationships of Norway spruce (*Picea abies*). *Can J For Res* 30:1646–1654
- Fritts HC (1976) *Tree rings and climate*. Academic, London
- Gartner BL (1995) Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. In: Gartner BL (ed) *Plant stems—physiology and functional morphology*. Academic, San Diego
- Gerlach D (1984) *Botanische Mikrotechnik*. Thieme, Stuttgart
- Günzel L (1954) Ergebnisse der österreichischen Pappelsortenprüfung 1949–1952. *Allg Forstz* 65:125–131
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol Evol Syst* 4:97–115
- Hager H, Haslinger R, Schume H (1999) Productivity and LAI of floodplain forest sites in relation to water supply. *Ekológia (Bratislava)* 18[1/1999]:5–14
- Hinckley TM, Braatne JH, Ceulemans R, Clum P, Dunlap J, Newman D, Smit B, Scarascia-Mugnozza G, van Volkenburgh E (1992) Growth dynamics and canopy structure of fast growing trees. In: Mitchell PK, Sennery-Forsee L, Hinckley TM (eds) *Ecophysiology of short rotation forest crop*. Elsevier, London, pp 1–34
- Horton JL, Kolb TE, Hart SC (2001) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant Cell Environ* 24:293–304
- Huber B (1928) Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. *Jahrb Wiss Bot* 67:877–959
- Hydrographischer Dienst in Österreich (1994) *Die Niederschläge, Schnee- und Verhältnisse und Lufttemperaturen in Österreich im Zeitraum 1981–1990. Beiträge zur Hydrographie Österreichs, Heft 52*. Hydrographisches Zentralbüro im Bundesministerium für Land- und Forstwirtschaft
- Kozłowski TT, Pallardy SG (1997) *Physiology of Woody Plants*, 2nd edn. Academic, San Diego
- Lo Gullo MA, Salleo S (1993) Different vulnerabilities of *Quercus ilex* L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation. *Plant Cell Environ* 16:511–519
- Lo Gullo MA, Salleo S, Piaceri EC, Rosso R (1995) Relations between vulnerability to xylem embolism and conduit dimensions in young trees of *Quercus cerris*. *Plant Cell Environ* 18:661–669
- Mader K (1989) Forstökologische Veränderungen durch das Donaukraftwerk Altenwörth. In: Hary N, Nachtnebel HP (eds) *Ökosystemstudie Donaustau Altenwörth—Veränderungen durch das Donaukraftwerk Altenwörth. Veröffentlichungen des österr. MAB-Programms, vol 14*. Universitätsverlag Wagner, Innsbruck, pp 267–340
- Mátyás C, Peszlen I (1997) Effect of age on selected wood quality traits of poplar clones. *Silvae Genet* 46:2–3, 64–72
- Nachtnebel HP (1989) Hydrologische Veränderungen durch das Donaukraftwerk Altenwörth. In: Hary N, Nachtnebel HP (eds) *Ökosystemstudie Donaustau Altenwörth—Veränderungen durch das Donaukraftwerk Altenwörth. Veröffentlichungen des österr. MAB-Programms, vol 14*. Universitätsverlag Wagner, Innsbruck, pp 30–93
- Pallardy SG, Kozłowski TT (1979) Frequency and length of stomata of 21 *Populus* clones. *Can J Bot* 57:2519–2523
- Peszlen I (1994) Influence of age on selected anatomical properties of *Populus* clones. *IAWA J* 15:311–321
- Rasband W (1996) NIH Image (release 1.61)—a public domain image processing and analysis program for Macintosh computers. Developed at the Research Services Branch (RSB) of the National Institute of Mental Health (NIMH), part of the National Institutes of Health (NIH), USA
- Ray PM, Green PB, Cleland R (1972) Role of turgor in plant cell growth. *Nature* 239:163–164
- Rood SB, Mahoney JM (1990) Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environ Manage* 14:451–464
- Rood SB, Patino S, Coombs K, Tyree MT (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* 14:248–257
- Sass U, Eckstein D (1995) The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. *Trees* 9:247–252
- Schweingruber FH (2001) *Dendroökologische Holz-anatomie: anatomische Grundlagen der Dendrochronologie*. Paul Haupt, Bern
- Scott ML, Shafroth PB, Auble GT (1999) Responses of riparian cottonwoods to alluvial water table declines. *Environ Manage* 23:347–358
- Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form—the pipe model theory. II. Further

- evidence of the theory and its application in forest ecology. *Jpn J Ecol* 14:133–139
- Sparks JP, Black RA (1999) Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. *Tree Physiol* 19:453–459
- Sperry JS, Tyree MT (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiol* 88:581–587
- Taize L, Zeiger E (1998) *Plant Physiology*, 2nd edn. Sinauer, Sunderland, Mass.
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Physiol Mol Biol* 40:19–38
- Tyree MT, Davies SD, Cochard H (1994a) Biophysical perspectives of xylem evolution. Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA J* 15:335–360
- Tyree MT, Kolb KJ, Rood SB, Patino S (1994b) Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiol* 14:455–466
- Vaganov EA (1990) The tracheidogram method in tree-ring analysis and its application. In: Cook ER, Kairiukstis LA (eds) *Methods of dendrochronology: applications in the Environmental Sciences*. Kluwer, Dordrecht, pp 63–76
- Villar-Salvador P, Castro-Díez P, Pérez-Rontomé C, Montserrat-Martí G (1997) Stem xylem features in three *Quercus* (*Fagaceae*) species along a climatic gradient in NE Spain. *Trees* 12:90–96
- Wagenführ R, Scheiber C (1985) *Holzatlas*. 2. Auflage. VEB Fachbuchverlag, Leipzig
- Willms J, Rood SB, Willms W, Tyree M (1998) Branch growth of riparian cottonwoods: a hydrologically sensitive dendrochronological tool. *Trees* 12:215–223
- Yasue K, Funada R, Kobayashi O, Ohtani J (2000) The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. *Trees* 14:223–229
- Zimmermann MH (1978) Hydraulic architecture of some diffuse porous trees. *Can J Bot* 56:2286–2295
- Zimmermann MH (1983) *Xylem Structure and the Ascent of Sap*. Springer, Berlin Heidelberg New York