

Sap flow and water transfer in the Garonne River riparian woodland, France: first results on poplar and willow

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Abstract – This work is the first attempt at using Granier sap sensors on *Populus nigra*, *Populus x euramericana* cv I45/51 and *Salix alba* for the monitoring of sap flows in an active floodplain over two consecutive years. The main characteristic of these diffuse porous trees is their capacity to use several tree rings for xylem sap transfer. Results showed that the sap flux densities remained homogeneous on the external 4 cm of the trunk, then decreased with depth. For young trees, the active sapwood can represent half of the trunk. Results indicated that in the same environment and at the same age, daily differences existed between the two major native riparian tree species, the black poplar and the white willow. Their maximal sap flux density ($2.6\text{--}3.6\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$) was similar to other fast growing trees. The influence of age was the third important screened factor. Sap flow measurements over several months indicated that water uptake was variable throughout the season, depending on water availability, and was more pronounced for older trees. The sap flux densities for the planted poplar (I45/51) ranged from $2.2\text{--}2.6\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$ (about $90\text{ dm}^3\text{ day}^{-1}$) in the wetter spring conditions and dropped to $1.6\text{--}1.7\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$ (about $60\text{ dm}^3\text{ day}^{-1}$) in less favourable conditions. Under the worst conditions, e.g., the especially long drought in the summer of 1998, these values dropped to $1.0\text{--}1.2$ (about $40\text{ dm}^3\text{ day}^{-1}$), and even to $0.35\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$ (about $12\text{ dm}^3\text{ day}^{-1}$) for a few days. Complementary long-term studies are needed to better understand the complex sap flow changes and to be able to relate them to significant environmental factors. Priority should be given to the long-term monitoring of sap flows at different depths for a correct estimation of actual daily water uptakes by riparian softwood trees.

sap flow / riparian forest / water cycle / poplar / willow

Résumé – Mesure des flux de sève et des transferts hydriques dans les ripisylves le long de la Garonne ; premiers résultats pour les peupliers et les saules. Ce travail est le premier essai d'utilisation des capteurs de sève de type Granier sur du *Populus nigra*, du *Populus x euramericana* cv I45/51 et du *Salix alba* pour la mesure de flux de sève dans une plaine inondable sur deux années consécutives. La caractéristique principale de ces bois tendres est leur capacité d'utiliser plusieurs cernes annuels pour le transfert de la sève brute. Les résultats montrent que les densités de flux de sève restent homogènes sur les quatre premiers centimètres du tronc, puis décroissent avec la profondeur. Pour les jeunes arbres, la partie active de bois d'aubier peut représenter la moitié du tronc. Les données montrent que pour un même environnement et pour le même âge, des différences journalières existent entre les deux espèces majeures des ripisylves, le peuplier noir et le saule blanc. Leurs valeurs de densité de flux de sève maximale (de $2,6$ à $3,6\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$) sont similaires à d'autres arbres à croissance rapide. L'influence de l'âge a été le troisième facteur étudié. Des mesures pendant plusieurs mois ont montré une grande variabilité au cours de la saison, en fonction des conditions hydriques, et est plus marquée pour les arbres âgés. La densité de flux de sève pour le peuplier planté (I45/51) varie de $2,2\text{--}2,6\text{ dm}^3\text{ dm}^{-2}\text{ h}^{-1}$ (environ $90\text{ dm}^3\text{ jour}^{-1}$) dans les conditions humides de printemps,

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et diminue à 1,6–1,7 dm³ dm⁻² h⁻¹ (environ 60 dm³ jour⁻¹) dans des conditions moins favorables. Dans les conditions extrêmes, lors de la longue sécheresse de l'été 1998, ces valeurs tombent à 1,0–1,2 (environ 40 dm³ jour⁻¹), et même à 0,35 dm³ dm⁻² h⁻¹ (environ 12 dm³ jour⁻¹) pour quelques jours. Des études complémentaires sur le long terme sont nécessaires pour mieux comprendre les changements complexes des flux de sève, et pour être capable de les relier aux facteurs environnementaux significatifs. La priorité devrait être donnée à des mesures simultanées de flux de sève à plusieurs profondeurs pour avoir une meilleure estimation des consommations journalières en eau de ces arbres riverains.

flux de sève / forêt riveraine / cycle de l'eau / peuplier / saule

1. INTRODUCTION

Sap flow measurement is the only way to follow the water consumption of trees in their natural environment. This technique is precise and adaptable enough to follow the variation at a daily to seasonal scale. Many sap flow studies have been undertaken for forest trees [4, 10, 11], ring-porous trees such as oak [20], coniferous trees such as pine and spruce [5, 20] and for orchards [1, 19]. However, very few authors focused on diffuse-ring trees in wetland environments. In the literature, the latest determination of water consumption of softwood trees, as reviewed by Wullschleger et al. [25], concerned planted poplar [8, 13] and some willows [3, 8].

In alluvial conditions, where the water availability is very variable (from flood to drought), the relationship between riparian vegetation, groundwater and stream water is often complex [24]. Trees may tap water stored in riverbanks or in alluvial aquifers, which may be dependent on periodic flooding for their recharge, or may tap groundwater discharged into streams [17, 4]. Although a study has shown that riparian trees can be independent of stream water in desert conditions [7], in general, trees may switch between stream water and the nearby groundwater source.

Experiments are not very easy to design in riparian environment because periodic floods may damage the sensors and other instruments. Moreover, all species do not strictly establish in the same conditions; therefore, strict comparisons in controlled situations are difficult to make.

Other than the lysimeter, the oldest system for measuring sap flow is heat pulse velocity [15] and many improvements have been made to this system. One classic installation consists of a single thermistor upstream and downstream of a central heat probe. Heat pulse duration is about one second and the measurement is quite accurate. However, this technique requires specific

calibration. One alternative is to calculate the sap flow from the energy balance of a sector of the hydroactive xylem [2]. This measurement is independent of sapwood thickness, but no information is given on how the water flows in the tree rings. This system was applied to a willow (*Salix fragilis* L.) in a polycormic form and, to follow the tree ring activity, a stained solution was injected into the tree [3]. However, the tree must be bored at different places or cut into slices to visualize dye distribution.

The sap flow technique, as described by Granier in 1985 [9], is an efficient tool that is routinely used in forest stands and orchards. This radial sap flow meter uses a continuously heated sensor. The Granier system measures the quantity of sap moving around the sensor for a given sapwood area. In many ring-porous trees, only the last (external) tree ring conducts sap. For example, in oak (*Quercus petraea*), the sapwood thickness was about 20 mm, and 80% of the sap circulated was in the first outer centimetre of the sapwood [10]. The existing 20 mm-long needles are well adapted for these kinds of trees. In such cases, the overall water consumption by the tree can be easily calculated and the exact thickness of the sapwood can be checked by the difference in the colours of a wood core extracted with an increment borer.

For other kinds of trees, especially softwood trees, there are indications that the active sapwood is not limited to the external ring. For instance, for coniferous trees such as the Scot's Pine (*Pinus sylvestris*), the sapwood thickness is about 5 cm in a 20 cm diameter tree, with a quite constant sap flow from 0–3.6 cm. The decrease is sharp and close to the sapwood/hardwood limits [10]. Other authors have used a heat pulse velocity system at different depths [12] with sensors at 0.5, 1, 2 and 4 cm depths on a 70 cm wide poplar (*P. deltoides* Marsch.). Over this short distance, compared to the wide diameter of the tree, they observed a reduction of sap flow as a function of depth. In other studies, Granier sensors were placed at different depths on yellow poplars

(*Liriodendron tulipifera* L.), but the distance in centimetres is unknown as the increment was a function of the width of the tree ring [26].

In poplars and willows, i.e., in diffuse porous riparian trees, little is known of sapwood activity. Generally, the wood core does not give any useful information because the tree rings are not well defined [6]. Moreover, the difference in colour between the sapwood and the more internal hardwood in such small samples is not very distinct. There are also some indications that sap flow densities vary with the species and with the age of the tree [25–26]. However, little is known on how it varies with time through a growing season.

The general aim of this study was to monitor the water consumption of the two dominant European riparian trees, the black poplar (*Populus nigra* L.) and the white willow (*Salix alba* L.), in the active floodplain of the Garonne River, France. The drastic and changing soil moisture conditions, which maintain a high biodiversity in such riparian areas, probably imposed a high physiologic adaptation ability to the existing species. However, it is not clear whether a tree can regulate water uptake in the case of flood or drought. Nor is it clear whether, in the same environment, differences exist between species of the same age, or between ages, for the same species. In addition, little is known on the active sapwood depth.

Therefore, the objectives of this study were, (1) to test the active sapwood depth of the poplar, (2) to compare the differences in the sap flow of a black poplar, a white willow and a planted poplar clone of the same age, and (3) to compare the sap flows of black poplars at two distinct ages in the same environment.

2. MATERIALS AND METHODS

2.1. Site description

The field site was a 2 km-long gravel bar, 250 m wide along the Garonne River and located 50 km downstream of Toulouse, France at an elevation of 90 m above sea level. This area, about mid-length of the river, is the drier part of the whole Garonne basin. The mean rainfall is about 700 mm, which ranges from 900 mm at the Atlantic coast to 1400–2000 mm on the Pyrénées slopes. This part of the Garonne valley has a mean annual potential evapotranspiration (Penman equation) of about 850 mm, which means that the vegetation is in hydric deficit during the hottest months. The Garonne River has a mean annual discharge of about $200 \text{ m}^3 \text{ s}^{-1}$. In summer, the objective low water flood is $42 \text{ m}^3 \text{ s}^{-1}$. Normal annual floods correspond to about $1000 \text{ m}^3 \text{ s}^{-1}$ and increase the river level by about 2 m. On 11 June 2000, a 50 year flood of $2925 \text{ m}^3 \text{ s}^{-1}$ (plus 6 metres) destroyed both sensors and data loggers. The site has been progressively settled by woody vegetation over the last 15 years, with mainly black poplars and white willows. In the floodplain, there is a large plantation of hybrid poplar clones nearby (*Populus x euramerica* cv I45/51); this is one of the dominant planted poplars in the Garonne valley. Three transects were marked on this gravel bar and equipped with piezometers (p), designated from p1 to p18, to monitor the water table level [16]. Sap flow measurements were made on trees located at SF1, SF2 and SF3 on the cross-section of the third transect (the furthest downstream) as shown in *figure 1*. The plotted ground lines

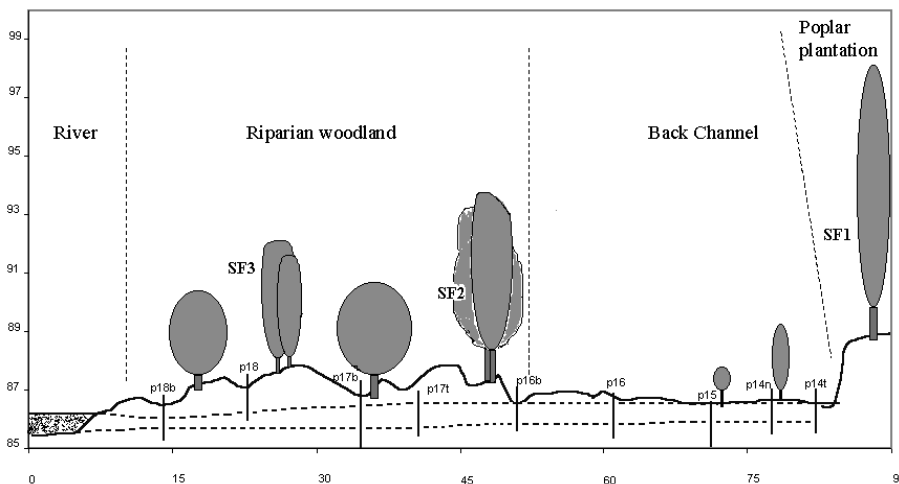


Figure 1. Field site transect on the Garonne River, 50 km downstream of Toulouse, south-west France. In abscissa, the distance is in metres from the river at low water. In ordinate, the elevation was measured in metres above sea level. The two dotted lines represent the fluctuation of the water table depths in 1998–1999. SF1, SF2 and SF3 correspond to the sap flux measurement area. The nine piezometers are shown by vertical lines.

Table I. Experimental sapflow conditions.

	Tree Type	Tree density	Elevation (m)	Age (year)	Diameter (cm)	Height (m)	Sap sensor position	Duration (week)
SF1	<i>Populus x euramerica</i> I45/51	low	2.10–2.70	10	29.0	22	2 surfaces	10
							surface / –2cm	1
							surface / –4cm	1
							surface / –6cm	1
SF2	1 <i>Populus nigra</i> 1 <i>Salix alba</i>	medium	0.80–1.50	9	21.7	12	1 surface	4
				10	14.6	10	surface / –2cm	6
							1 surface	4
SF3	1 <i>Populus nigra</i> “old” 1 <i>Populus nigra</i> “young”	high	1.46–2.00	8	18.0	10	1 surface	17
				5	9.0	8	1 surface	15
							1 surface / dendrometer	2

were obtained from a microtopographic survey using Rec Elta14, Zeiss equipment.

2.2. The sap flow sensors

In the nearby 10-year-old I45/51 poplar plantation, one tree was equipped with Granier sensors from 09/06/98 to 12/11/98, with 91 days of effective data (SF1). The heating sensors were supplied with an 80 Ah lead battery, changed every 10 days, and used to determine the depth of the active sapwood. As only 2 cm sensors were available, the problem was solved as follows: a first sensor was maintained at the surface of the sapwood with measurements at 0–2 cm and a second sensor was placed into a 10 mm-wide hole to a depth of 2 cm with effective measurements at 2–4 cm. One week later, the second sensor was inserted into a deeper hole of 4 cm with measurements at 4–6 cm. Finally, it was inserted into a 6 cm hole with measurements at 6–8 cm. In other words, measurements at each depth lasted one week and could be compared with simultaneous reference measurements at the surface (0–2 cm). All of the experimental sap flow conditions are reported in *table I*. The reported elevation corresponds to the elevation of the ground above the local water table with the seasonal fluctuation observed between 1998 and 1999.

On SF2, a black poplar and a white willow of almost the same age as the I45/51 poplar (9 and 10 years, respectively) were found very close to each other (about 3 m), i.e., in the same substrate and moisture conditions. However, in the floodplain, both spontaneous trees were located at a lower elevation than the planted poplar I45/51 (*figure 1*). Sap flow surface measurements at 0–2 cm were made on both trees, with simultaneous measurements on the I45/51 poplar. Additional deeper

measurements at 2–4 cm were also made in the black poplar. Unfortunately, following several functioning problems (e.g., sensor wires eaten away several times by rodents), the days of effective data were reduced to 42 days for the black poplar and 28 days for the white willow. However, on the black poplar, measurements at 0–2 cm and 2–4 cm were effective over 42 days. The SF2 heat sensors were supplied with two 18 W solar panels and regulated with an 80 Ah lead battery.

The same set of sensors (SF3) was installed one year later near the main channel of the Garonne River, on two nearby five- and eight-year-old black poplars separated by only 2 m. Surface measurements were made from 9/04/1999 to 07/09/1999, with 118 days of effective data. Sensors were supplied with the same 18 W solar panels and 80 Ah lead battery.

A Granier sensor (UP GmbH, Germany) consists of two cylindrical probes (20 mm long, 2 mm in diameter) that are inserted, one above the other at a distance of about 12 cm, into the sapwood after the bark is removed. Each probe contains, at mid-length, a copper-constantan thermocouple. The upper one is heated at a constant rate by the Joule effect. The lower (reference probe) is not heated and remains at wood temperature. The heads of the probes are isolated with fibreglass. Each sensor was installed on the shadiest side of the trees and isolated by a special bi-face reflective film, including expanded polystyrene, to reduce the external thermal disturbances and to avoid contact with rain. The system measures the temperature difference between the two thermocouples wired in opposition and the temperature difference decrease with an increase in sap flow. During the night, sap flow ceases, all the energy of the heating probe is dissipated by conduction in the sapwood and the maximal temperature difference $\Delta T(0)$ is observed. When the

sap circulates in the xylem, the temperature difference $\Delta T(u)$ decreases because the heater probe is cooled by the sap flow (convective heat transfer). Using the Granier calibration formula (sap flux density = $4.28 * [\Delta T(0)/\Delta T(u) - 1]^{1.231}$ in $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$), the sap flux curves are computed from the temperature differences measured between the two probes [11].

Measurements with the Granier sap sensors were made every 30 s and averaged and recorded every 5 mn (i.e. 288 values per day and per sensor) in data loggers (Datahog, Skye Instrument Ltd, UK). Data were downloaded every 10 days in the field using a portable micro-computer.

2.3 Others sensors

The water consumption of trees is very variable and depends on the tree species, tree dimension, local moisture conditions and climate. To better interpret the sap flow data, other parameters were simultaneously recorded at the same rate on data loggers. The photosynthetic active radiation (PAR) was measured under the trees with JYP gallium arsenide photodiodes (JYP 1000, SDEC, France). The JYP sensors are suitable to PAR measurements under canopies and allow high output levels with a linear response up to $5000 \mu\text{moles m}^{-2} \text{s}^{-1}$ [21]. The air temperature and air humidity (Skye Instrument Ltd, UK) were recorded under the tree canopy as well.

To monitor the trunk width variation and possible water storage by the tree, a temperature-compensated dendrometer (DEX 100, Dynamax, USA) was installed on the smallest poplar in SF3 from 13/08/99 to 7/09/99. This electronic microdendrometer used a full-bridge strain gauge attached to a flexible arm of a calliper-style device. The millivolt output signal shows both the diurnal and seasonal growth of the trunk. These data were recorded simultaneously with the sap flow measurement. Long-term tree growth can be linked to water availability using a dendrochronology approach. However, wood cores obtained from softwood trees are often not useful as the tree rings are difficult to detect and the cores are twisted. Nevertheless, some authors claim to be able to do so after special preparation with sandpaper [6]. Our experience indicates that the information is more reliable using the wood plate. In this study, dendrochronology was used on wood plates obtained in SF1 from a nearby planted poplar (i.e., a clone of exactly the same age), in SF3 from another 10-year-old black poplar established at about the same time, and from various other planted poplars growing along the Garonne

River. Two perpendicular lines were drawn on each sandpapered wood plate, with their intersection in the centre of the deeper (older) ring. On each line, the tree rings were measured and the mean value for each year ring was calculated from the four obtained data sets. The rainfall values and potential evapotranspiration were obtained from the Meteo-France Company of the Tarn-et-Garonne district.

3. RESULTS

3.1. Influence of the active sapwood depth

On the I45/51 planted poplar (SF1), two sensors were initially placed at the same depth (0–2 cm) to check the homogeneity of the sap flow in the external tree rings. After a few days, data were similar and the second sensor was placed progressively deeper in the trunk with simultaneous measurements at the surface. Results of the test showed that for the I45/51 poplar the sapwood activity remained rather stable over 4 cm, then decreased with wood depth (*figure 2*). At the surface (0–2cm), the sap flux density (SFD) was taken as the reference and the corresponding index of sapwood activity was 100%. Surprisingly, at 2–4 cm, the sapwood activity remained high ($107 \pm 7 \text{ dm}^3 \text{dm}^{-2} \text{h}^{-1}$), then progressively decreased to $77 (\pm 6)$ at 4–6 cm and to $27 (\pm 5)$ at 6–8 cm.

As the diameter of the tree was 29 cm, the collected data concerned more than half of the tree rings (i.e. the last five years of the 10-year-old poplar). In other words,



Figure 2. The sap flux density index (SFD %) is the ratio of the maximal SFD value obtained at given depth (2–4cm, 4–6cm or 6–8 cm) by the maximal SFD value at the surface (0–2 cm) obtained on the same day. The mean values obtained over one week of measurements were plotted with the standard deviation at each depth.

these fast growing trees are characterized by a wide active sapwood and not by just the very external rings. In the wood plates, a slight colour change could be observed at 8–10 cm and may correspond to a change in sapwood activity. The diameter of the black poplar (SF2) was smaller (21.7 cm) and the sap activity was checked in only the first 4 cm. The results were similar, with a high value for the sapwood activity at 2–4 cm ($102 \pm 8 \text{ dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$). The measured wood plates of nearby black poplars of identical diameter showed a difference in colour at 6 cm. This test showed that the external surface of the sapwood of poplar is characterized by almost the same sap activity over about 4 cm and that, deeper in the trunk, the activity progressively decreased, but could still exist at 8 cm.

3.2. Species influence

Three kinds of tree of nearly the same age (9–10 years old) were compared. The planted poplar clone I45/51 (SF1 in *figure 1*), was located in a more elevated position in the floodplain than the natural riparian woodland. For this reason, it was less frequently flooded than the black poplar and the white willow, which were both located at the border of the riparian woodland (SF2) under the same moisture conditions. *Figure 3* gives an example of sap flow density curves observed over three contrasted consecutive days from 24/06/98 to 26/06/98. The first day was both sunny and dry, the second day was rainy and the third densely cloudy. Results showed that the sap flow followed the daylight with a time lag. In the morning the increase is rapid, and when the weather is sunny the sap

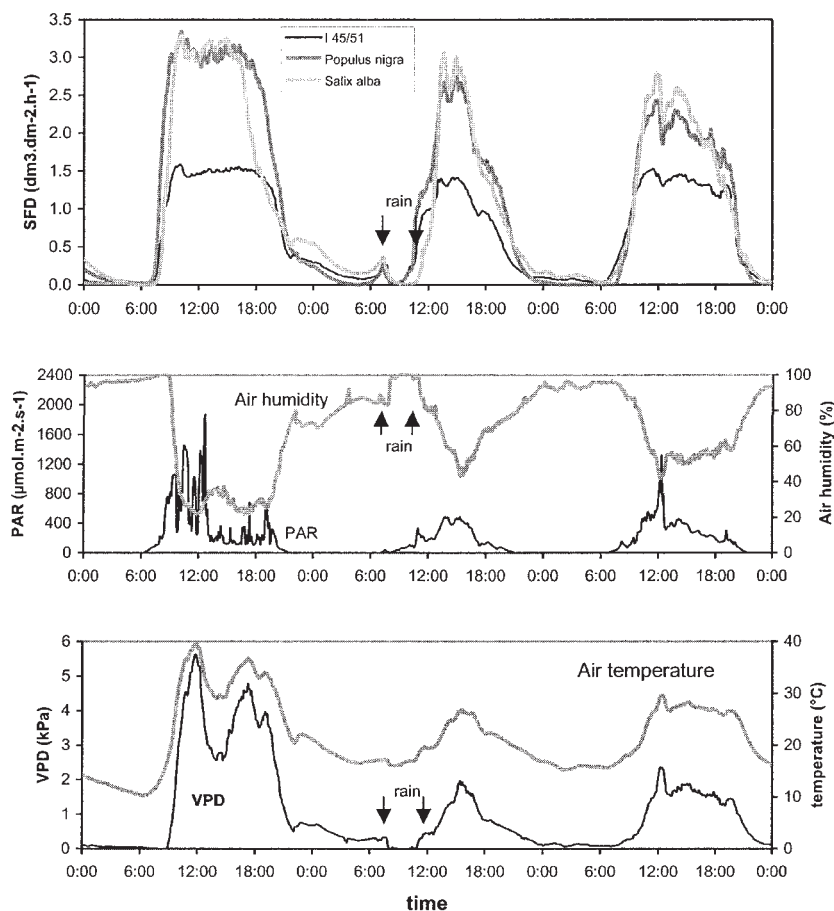


Figure 3. Comparison of the sap flux density of the planted poplar clone (heavy line), the black poplar (fine black line) and the willow (grey line) for 24, 25 and 26 June 1998. The photosynthetically active radiation (PAR) under the trees, to indicate sunlight periods, is plotted in a second frame, as well as the air humidity. The last frame reports the variation of the air temperature under the canopy and the vapour pressure deficit (VPD). The rainfall period of the second day is indicated by arrows.

flow reaches a plateau about two hours later. The decrease in the evening is sharp, and the minimum value is observed late at night or early in the morning. The PAR indicates the timing of leaf activity. One part of the high frequency PAR variation during the day is due to the shadowing effect of the leaves, since the sensor was under the canopy. The air humidity is also an important factor, as the evapotranspiration is very active when the atmosphere and the leaves are dry. On the second day, this effect was especially clear. The morning rain (from 8.30 to 11.00 am) stopped the beginning of the water uptake by trees, which started again only when the air humidity became less saturated. This rain event provoked a drop in temperature of about 1°C. The calculated vapour pressure deficit (VPD) is given in *figure 3* (bottom graph). The concomitant reaction of the two poplars can be observed, but the amplitude of the flow is lower for the I45/51 because of its drier environment. The willow response is different, with a later morning increase and an earlier evening decrease, perhaps related to less access to sunlight. The diurnal length of active sap flow is, therefore, shorter for the willow than for both poplars, but the amplitude is the same as for the black poplar, probably because they developed in the same moisture environment. Results showed that each species had its own sap flow pattern and that the local water supply probably determines the daily amplitude of the sap flow.

3.3. Influence of age

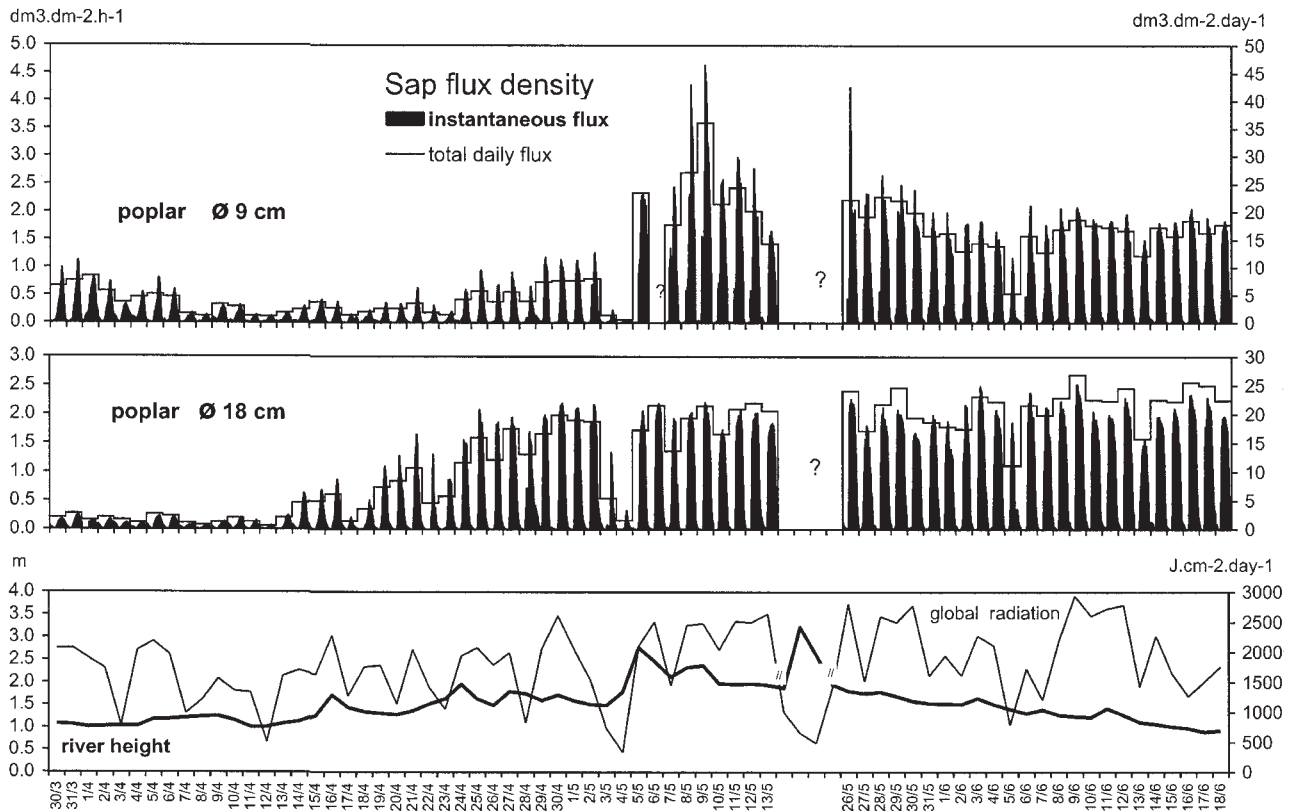
Two black poplars of different ages (five and eight years), and growing 2 m apart, were chosen on the other side of the riparian woodland close to the river (SF3 in *figure 1*). They were established on a gravel substrate covered by 80 cm of sand. *Figures 4A* and *4B* summarize the seasonal monitoring of the two poplars from the beginning of spring (end of March 1999) to the end of summer (beginning of September 1999). Two types of fluxes were plotted. The instantaneous values correspond to the sap flux densities recorded every 5 min and the total daily fluxes integrate the instantaneous values over a day and permit flux comparisons between days. Results showed that the smallest tree developed leaves first and displayed earlier and higher sap fluxes than the older poplar. As night temperatures until mid-April remained quite low (5–8 °C), the leaf development was restrained, and so the sap values did not rise. After mid-April, the older tree increased its water consumption progressively up to the rate of 2 dm³ dm⁻² h⁻¹. The smaller tree was partly shaded by the larger tree, and probably in competition at the root level, and its sap values remained lower. On very cloudy

and rainy days, such as April 22 and 23 and May 3 and 4, the daily sap fluxes were reduced for both trees. After the river flood on 05/05/99 ($h = 2.70$ m), the water absorption by the smaller poplar increased and even surpassed that of the older poplar for a period. This probably corresponded to a reduced competition for water because of the extra water availability following the flood. Unfortunately, data were missing between May 14 and 25, following a problem with the heating system during a more important flood. The peak of the flood arrived on May 18 ($h = 3.12$ m), in the middle of a four-day period of heavy rain. Local temperatures dropped from 28 °C to 15 °C during the day and from 16 °C to 9 °C at night. Both trees were flooded by about 10 cm of water above ground level, and the entire riparian woodland ground was under water for a few days. After the flood, the mean diurnal sap flux value remained around 2 dm³ dm⁻² h⁻¹ for the five-year-old poplar and for the eight-year-old poplar, with some lower values on very cloudy days such as June 5 and 13. The second part of the figure corresponds to summer, i.e., to the local low water flow. During this period, the shape of sap flux densities remained very similar for both trees and the daily sap fluxes did not appear to be affected by the lowering of the river flow during about one month. This was probably because the root system was still well connected to the water table. A decrease in the sap flux density became visible at the end of July and was more severe for the larger poplar. After a slight increase of river discharge at the end of the month, and a consecutive recharge of the water table, it seems (despite missing data) that the sap flux density increased slightly until mid-August. Then, following persistent low-water flow, the sap fluxes decreased and remained low until September. Results indicated that when the water table is high, poplars have high sap fluxes, and they decrease their water uptake when water is unavailable. Therefore, during the annual drought period, poplars are very sensitive to river discharge fluctuations. Young trees are more sensitive and vulnerable to these water table variations.

3.4. Other water transfers

3.4.1. Variation in sapwood hydration

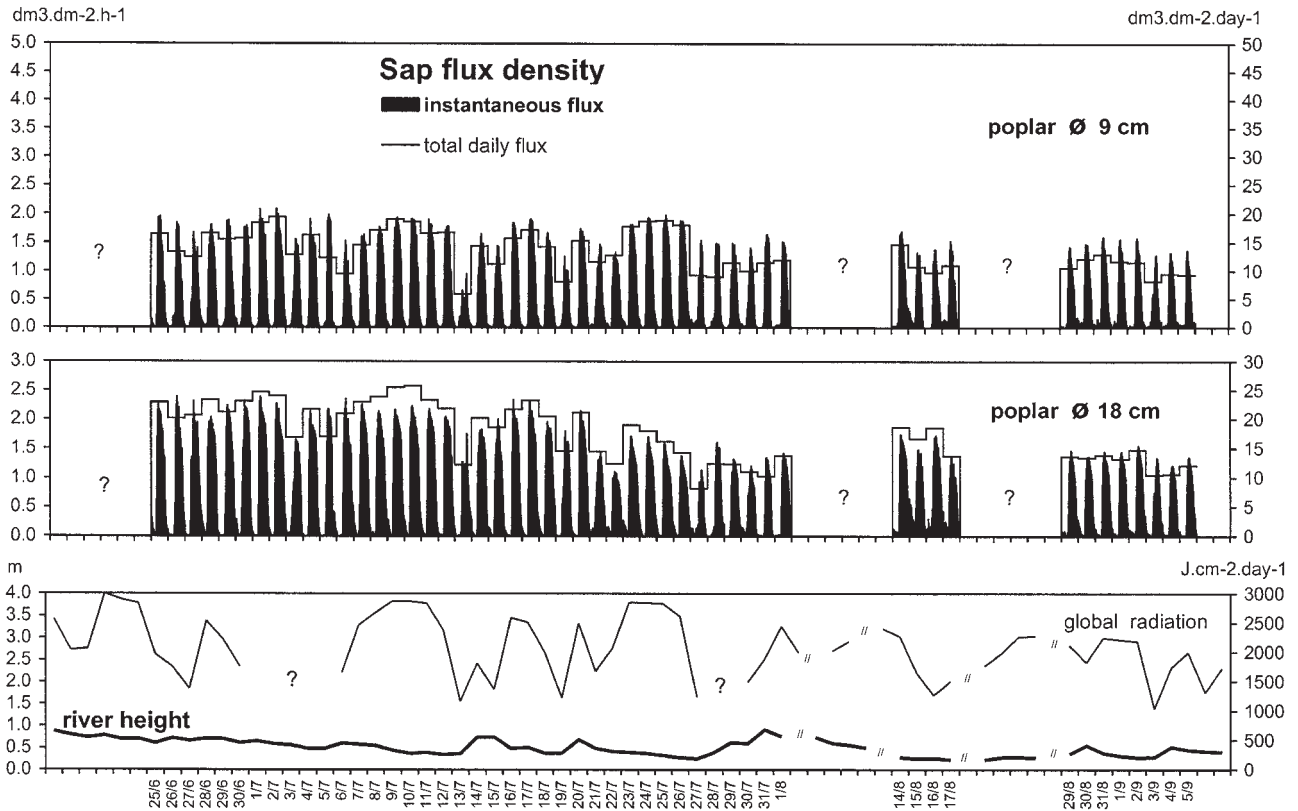
As the thermal conduction ability of the wood is influenced by its water content, the minimum night values $\Delta T(0)$ measured by the sap sensors was used as an indicator of sapwood hydration, as suggested by Granier (personal communication). Data of the planted poplar I45/51 were, therefore, re-examined in that perspective.



Figures 4A. Seasonal sap flux density of two close black poplars of different ages in function of the river height and global radiation.

In 1998 the daily maximum SFD in the first 0–2 cm ranged from 1.5–2.2 $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$ during the wet June month, then dropped to about 1.0 $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$ during the drier July month. Clearly, the summer drought was more severe for the planted poplar than for the natural woodlands situated at a lower level and closer to the river. The planted poplar had a significantly reduced water consumption and a partial leaf fall. In August, the drought was even worse and *figure 5* (top curve) reports the variation in SFD in sapwood hydration over three consecutive months. The corresponding inputs of water are reported in the second frame with the daily rainfall (histogram) and the fluctuation in river level (solid grey line). A previous study showed that at this site the ground water level closely followed the river discharge [16]. The drought remained very severe until the end of August. After local rainfalls, and an increase of the water table level at the beginning of September, the water uptake by the tree started to increase, new leaves grew and the SFD returned to its high spring value.

The second curve in the upper frame in *figure 5* represents the variation of the sapwood hydration and corresponds to the minimum night values $\Delta T(0)$ measured by the sap sensors. The two curves were very similar. However, the SFD seemed to be more sensitive to the variation in daily solar intensity and other atmospheric variations, while the sapwood hydration showed less variations. A few days' lag was also visible when the SFD started to increase at the beginning of September. After the drought, the tree probably needed some time to hydrate its tissues. Hydration curves after the drought were slightly delayed at 0–2 cm (about 2 days) and delayed by about one week at 2–4 cm. Sapwood hydration and the Garonne river level present a low correlation coefficient of 0.42. Flood waters is in part stored by the high retention capacity of local sediment; this delay has an effect on the correlation coefficient value.



Figures 4B. Seasonal sap flux density of two close black poplars of different ages in function of the river height and global radiation.

3.4.2. Daily stem width variation

Electronic microdendrometers detected an elastic reversible daily fluctuation of the stem width within the range of 0.10–0.25 mm. Figure 6 reports this variation on the small back poplar (9 cm) in SF3 on three consecutive days (28/08/99 to 30/09/99) with the simultaneous sap flow densities. The first day was very cloudy, but without rain, while the two following days were sunny. On the first day, with a high air humidity there was nearly no stem width variation, whereas during the two following sunny days the stem width decreased by 0.2 mm with a strong diurnal variation. The stem width is maximal early in the morning, just before the sap begins to flow. During the day, stem width shrinks rapidly until sap flow reaches its maximum level and until air humidity increases again. Stem width subsequently increases slowly overnight until the next morning. The minimal daily stem width is variable from one day to another, but seems to be correlated to the minimum in air humidity. A daily stem

width variation of 0.2 mm is very tiny and corresponds to only 0.2% variation in diameter, i.e. equivalent to a volume of about 1 dm³ for that tree.

3.4.3. Annual fluctuation in stem growth

Dendrochronology is a good indicator of the past hydric conditions of a given riparian woodland. In the upper frame of figure 7 the year ring width of three poplars, growing on a transect perpendicular to the river, are reported. The young black poplar growing close to the Garonne River (SF3) showed a profile different from the poplar clones growing at a higher elevation, both in the SF1 plantation (I45/51 clone) and in another nearby plantation (Robusta clone, further up the river). These trees, growing within a few hundred metres of the river, showed different growths that can only be due to the river influence and soil moisture retention ability. In contrast, other trees separated by a few kilometres, but growing on a transect along the river in similar moisture conditions

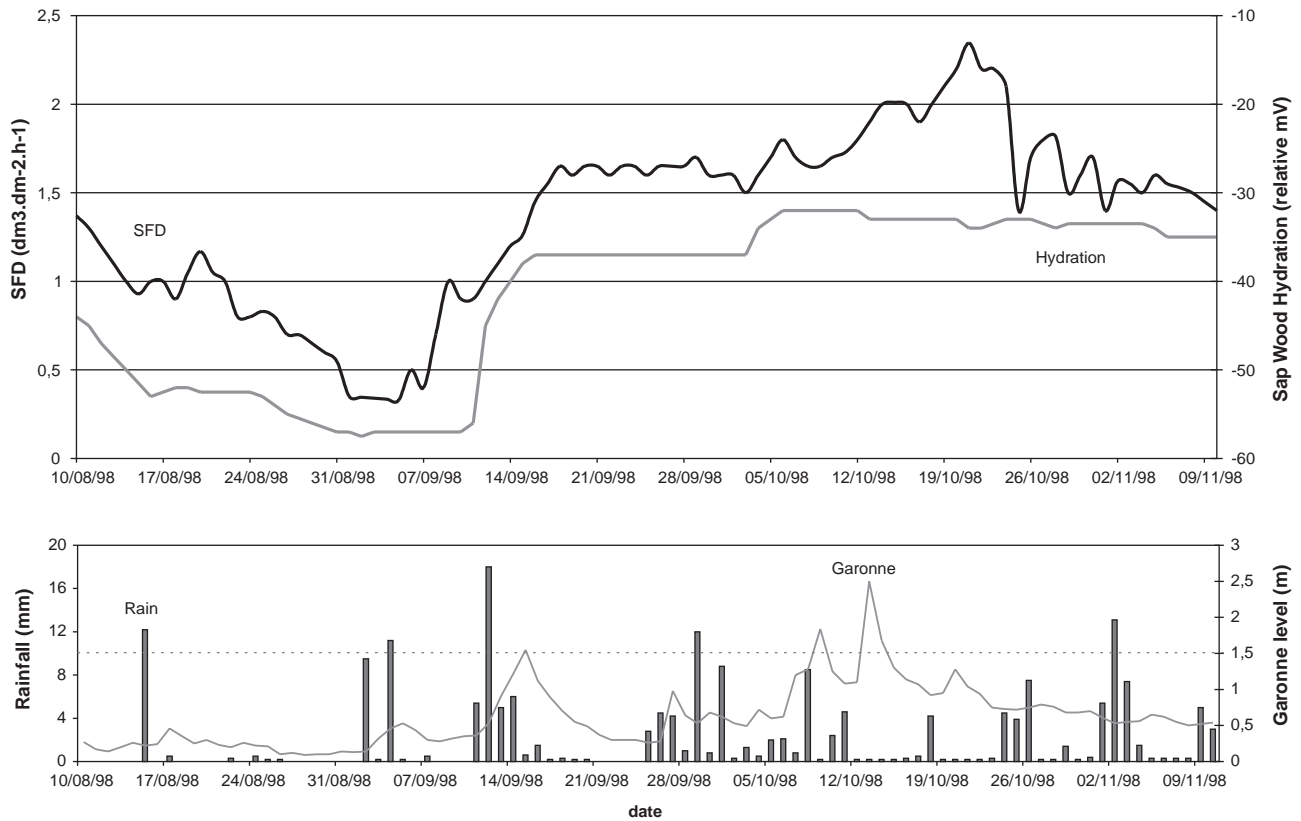


Figure 5. Comparison of the daily maximal sap flux density (SFD, in black) and the sapwood hydration index (minimum of night sap flux density values, in grey) for the planted poplar, SF1, during the 1998 drought, with the corresponding river level (continuous line) and daily rainfall (histogram). The horizontal dashed line illustrates the water height necessary for initiating back channel submersion. The back channel is located in a small depression and when the river floods above a certain level (dashed line), this pool is swamped.

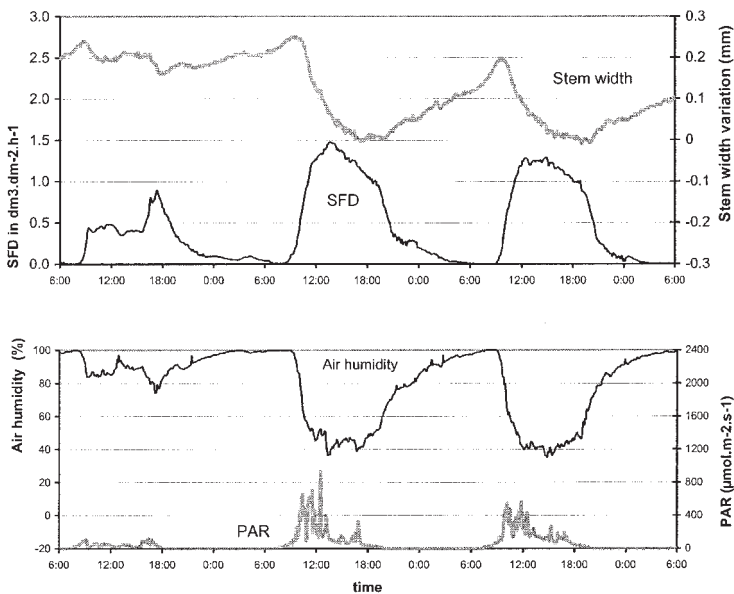


Figure 6. Comparison of the variation of the stem width (upper curve in grey) with the sap flux density (SFD, lower curve in black) on the small poplar, SF3, for three consecutive days, 28 to 30/09/99, with the corresponding air humidity (in black) and photosynthetic active radiation under the trees (in grey).

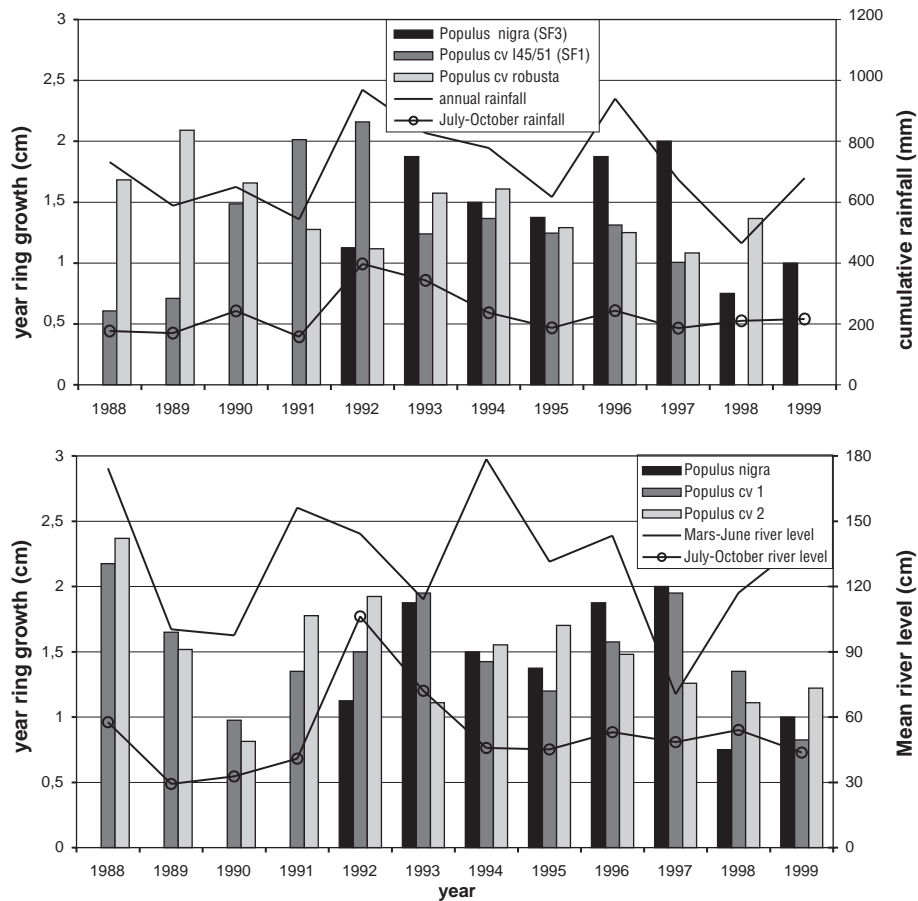


Figure 7. Dendrochronological test on poplars in the flood plain over the last 12 years. The first frame shows the variability of three trees along a few hundred metres transect perpendicular to the river (*Populus nigra*, close to the river, *Populus cv I45/51*, middle position and *Populus cv robusta*, the furthest). The solid curves report the cumulative year rainfall and July-October rainfall. The second frame summarizes the growing similarity of three poplars along a kilometre transect along the Garonne River. The solid line indicates the mean Garonne River level in March-June and July-October.

and close to the river, displayed more similar profiles (figure 7, second frame). To better understand the link between the growth and the water availability, two curves have been added to both frames. The first curve reports the variation of the annual rainfall for 12 years, with a low value of 705 ± 152 mm. The rain contribution during the hotter and drier four months of the late vegetative season (July to October) is reported on the figure. The best correlation coefficient is 0.25 between I45/51 growth and the July-October rainfall. In the second frame, the Garonne River mean level has been drawn for the two defined vegetative season parts, the first four months with high water (March to June) and the following four (July to October) with low water. The best

correlation coefficient is 0.25 for the link between the *Populus cv 2* growing and the July-October stream level.

The important water deficit for this last period during 1989 and 1990 was well synchronized with the low tree growth along the Garonne River.

4. DISCUSSION

This study on riparian woody species shows that sap flow was highly variable. At a given date it is determined by intrinsic factors such as the species, age, size of the

tree and by extrinsic factors related to the local climate and environment (evapotranspiration, rainfall and air humidity). Such results are consistent with observations made by other authors in long-term research on non-riparian trees [4, 14]. One single factor alone cannot explain the observed sap flow variation, however in riparian environments the river and the related water table determine the bulk of the water available in a location independent of the local climate. In other words, the river flow often rules the sap flow amplitude, especially in a drought period when the low river discharge becomes a limiting factor. In other seasons, when river flow has no real limitation on water, the river factor is less significant. Similar observations were made on hardwood species (e.g., oak and ash) in a Moravian floodplain [4].

Sap flux provides information on wood water content. However, in order to appreciate tree water consumption and its contribution to the water balance, radial variation of sap flow in the trunk is necessary. First, the comparison of sap fluxes on riparian softwood trees from different authors is not easy because measurements have not been made in the same conditions and there is generally little additional information to facilitate the comparisons (e.g., position of the tree in the floodplain or river discharge). Moreover, the varieties of trees are generally not the same and there are differences in local climate, season and stand density (isolated trees, natural forest, planted and pruned trees, polycormic trees and trees developed by lysimeter). Sap flow measurement techniques are often also different. Nevertheless, in *table II*, existing results on the water uptake by poplars and willows were summarized. The sap flux density is probably the best parameter to make comparisons, although there are both

diurnal and seasonal variations. Our results report a mean high flow density of about 2.6 and 3.6 $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$ for poplar and willow, respectively. These values agree well with those obtained by other authors and using different techniques (*table II*). Only two other trees have been reported as displaying higher sap values [25]: *Eucalyptus grandis* and *Larix gmelinii*, two species known for their rapid growth. This means that our diffuse-ring riparian trees display high sap density, but not at an exceptional level. The total water uptake by a diffuse-ring tree depends on the sapwood multi-ring system. The identification of radial trends along these rings provides an insight into physiological adaptations of wood water storage and movement [20]. However, it is not easy to screen deeply into the sapwood and most authors have stopped at 4 cm [12, 20] or at 5 cm [11]. We have measured to 8 cm, found high sap densities to 4 cm, a progressive decrease at 6 cm and a higher decrease at 8 cm. For the water consumption reported in *table II*, we have taken an active sapwood of 6 cm for the poplars and 4.5 cm for the willow. Our results are consistent with those obtained from measurements on the wood water content on diffuse-ring trees (*Liquidambar styraciflua*, *Populus deltoides* cv ANU 60/129 and *Populus yunnanensis*), where a decrease across the 8 cm conducting sapwood was observed [20 and references within]. Also Granier et al. [11] have found for beech, a another diffuse-ring tree (*Fagus sylvatica* L.), a maximum sap flux between 0 and 2 cm and after a decrease up to 6 cm deep. In this study, we showed that about half of the diameter of a tree may be active, which means that for these fast growing poplars, tree rings of the last 5–7 years remain conductive. For the younger black poplar, the sapwood thickness was less extended and included only the last 3–5 year rings.

Table II. Some examples of maximal sap flow density measured for different trees.

Tree	Sap flow technique	Tree diameter (cm)	Sap flow density ($\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$)	Daily water uptake ($\text{dm}^3 \text{day}^{-1}$)	References
<i>Populus x euramerica</i>	Lysimeter	14	3.41	86	Edwards 1986
<i>Populus trichocarpa x deltoides</i>	Cermak sensor	15	Not given	51	Hinckley et al. 1994
<i>Populus x eur. cv I45/51</i>	Granier sensor	29	2.64	89	Present work
<i>Populus nigra</i>	Granier sensor	22	2.68	45	Present work
<i>Salix fragilis</i>	Cermak sensor	25	2.61	103	Cermak et al. 1984
<i>Salix matsudana</i>	Lysimeter	12	5.14	48	Edwards 1986
<i>Salix alba</i>	Granier sensor	15	3.59	42	Present work
<i>Eucalyptus grandis</i>	other	18	5.44	94	Wullschleger et al. 1998

As seen from the tree trunk width, about half of the sapwood cross section is active (2×8 cm for 29 cm wide, and 2×6 cm for 22 cm wide). The high sap flow represents around one third of the tree width (2×6 cm for 29 cm, and 2×4 cm for 22 cm). But seen from the surface, the ratio between the sap wood area and the total cross section of the trunk represents respectively 75% and 55% for total sapwood and sap wood with high sap flow.

However, the active sapwood depth may change when the local hydrological constraints are modified. Therefore, more long-term experiments are needed to better understand the radial patterns of xylem sap flow in diffuse-porous trees.

Long periods of sap flow measurements are very useful for better understanding the evolution of the water pool over the growing season. Some authors have recently conducted such long-term research in boreal forests, including research on pine and spruce in Europe [4] and on the trembling aspen (*P. tremuloides* M.) in Canada [14]. The results showed that, in each year, the sap flow density evolution was different and the variability of water fluxes at the tree level remained generally high. For riparian woodlands there is often one additional parameter. Because many managed rivers have experienced vertical erosion (incision) in beds, the riverbanks are more drained and the adjacent ground water tables are now also deeper during summer drought. For example, in this study the sap flux densities for the planted poplar (I45/51) ranged from $2.2\text{--}2.6 \text{ dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$ (about $90 \text{ dm}^3 \text{ day}^{-1}$) in the wetter spring conditions and dropped to $1.6\text{--}1.7 \text{ dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$ (about $60 \text{ dm}^3 \text{ day}^{-1}$) in less favourable conditions. Under the worst conditions, e.g., the especially long drought in the summer of 1998 (figure 5), these values dropped to $1.0\text{--}1.2 \text{ dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$ (about $40 \text{ dm}^3 \text{ day}^{-1}$), and even to $0.35 \text{ dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$ (about $12 \text{ dm}^3 \text{ day}^{-1}$) for a few days. This represents a decrease of 30, 50 and 85%, respectively, of the sap flux density during the drought. Granier has also reported for oak a decrease up to 70% at the maximal drought intensity.

Low night and predawn sap flux values correspond to the low sap flow rates that prevail during the overnight rehydration of plant tissues. Therefore, night and predawn sap flux values could provide a good indication of the plant deficits that accumulated during the previous day [19, 20].

In the morning of a sunny day, water absorption lags behind the transpiration rate. Internal water deficits develop during this first phase and shrinkage processes occur, first at the leaves and then at the branches. The trunk reservoir also loses its water and its diameter, as

measured by the microdendrometer, and slightly decreases (figure 6). When the transpiration declines with solar radiation in the afternoon, absorption begins to exceed transpiration and the plant rehydrates. The process is reversed and the trunk diameter slightly increases. These internal water deficits are progressively cancelled out during the night if there is a normal water supply in the soil [1]. More information could be obtained by using microdendrometers throughout the vegetative season. The variation in stem width is not an indication of the xylem sap transfer, but of the shrinkage of the soft tissues due to root absorption lagging behind leaf evaporation. Consequently, tensions develop in the xylem, water of the nearby cells are attracted and the cells in the bark shrink. These stem variations are counterbalanced a little by the wood's thermal expansion when the ambient temperature increases [1].

Long-term dendrochronology and dendroclimatology studies [22] showed correlations between the stream flow and tree growth in a semi-desert riparian woodland. In temperate conditions, trees display a more complex and wide variation depending on the local soil moisture. However, this study on trees growing in an area directly influenced by the Garonne River level showed that there was a quite homogenous growth tendency, partly correlated with the late summer river level (figure 7). This also showed the importance of the minimal summer flow regulation of the Garonne River to maintain healthy riparian vegetation for good water quality. Interpretations and correlations are not easy to draw since it is difficult to take into account the rapid river level on the long-term growth of trees. Floods in summer are often very short and, for the strongest, the microtopography can change (deposit or digging of gravel or modification of the link with the river), which could modify moisture conditions.

In New Zealand, rapidly growing poplars were used for wood production and for the drying of isolated wetlands. In a poplar-pasture system, evapotranspiration of the poplar stand was 20–35% higher than that of the open pasture, but the tree density was low [12]. In Florida in a wide cypress-pine flatwoods, the water table rose from 32–42 cm after the trees were removed [23]. The water table was isolated and disconnected from any river system. In riparian woodlands, large trees can uptake 100–150 L a day when the available water pool between ground water and river water is enough to sustain the trees, i.e., outside low water flow [17]. Water taken up by the trees is mainly evaporated, which positively influences the surrounding area due to oasis effects [18]. In addition, the dew intercepted by the riparian trees is an additional water input for the trees.

5. CONCLUSION

This study is the first one using the Granier sap flow technique to measure the water consumption of poplar, and to a lesser extent willow, in an active floodplain. It was difficult to obtain continuous long-term data following problems with instrument damage during floods, with humidity on electronic components and with the destruction of wire by rodents. The first results obtained over a monitoring period of two years showed that sap flows varied with both species and age. They also showed that the high temporal variability of water consumption and the multi-ring sap transfers are major characteristics of poplars and willows and do not facilitate simple statements on water uptake.

During periods of flood the evaporation process did not stop, and sap fluxes could even be enhanced, whereas during the summer drought, the sap fluxes were drastically reduced, certainly by stomatal closing. The black poplar lost leaves that were probably in excess for the available soil moisture and recovered new ones a few weeks later when the available soil moisture increased.

Complementary long-term studies are clearly needed to better understand the complex sap flow changes and to be able to relate them to significant environmental factors, to leaf area and to physiological parameters such as stomatal conductance and water potential. Comparison of the same species at the same age between floodplains under different climates and regimes would facilitate such approach. One major difficulty comes from the fact that it is not clear whether the contribution of the sapwood activity at different depths remain stable throughout the season or, most probably, if it varies with climatic and hydrologic constraints and how. Therefore the priority of future researches should be both long-term monitoring and simultaneous measurements of sap flows at different depths. Such studies are prerequisites to the modelling of water transfer and water balance in riparian woodlands at the tree and at the stand scales. They should be facilitated in the future using the newly manufactured Granier sensors with 2 cm-long probes fixed at the extremity of needles of 2, 4, 6 and 8 cm.

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REFERENCES

- [1] Ameglio T., Cruiziat P., Daily variations of stem and branch diameter: short overview from a developed example. NATO ASI series, Vol. H64. Mechanics of swelling: from clays to living cells and tissues, edited by T. Karalis, Springer-Verlag Berlin Heidelberg, 1992, pp. 193–204.
- [2] Cermak J., Deml M., Penka, A new method of sap flow rate determination in trees, *Biol. Plant* 15 (1973) 171–178.
- [3] Cermak J., Jenik J., Kudera, J., Zidek V., Xylem water in a crack willow (*Salix fragilis* L.) in relation to diurnal changes of environment, *Oecologia* 64 (1984) 145–151.
- [4] Cermak J., Prax A., Water balance of a southern Moravian floodplain forest under natural and modified soil water regimes and its ecological consequences, *Ann. For. Sci.* 58 (2001) 15–29.
- [5] Cienciala E., Kucera J., Lindroth, A., Long-term measurements of stand water uptake in Swedish boreal forest, *Agric. Forest Meteorol.* 98–99 (1999) 547–554.
- [6] Clark S., A new method of examining cottonwood cores, *Proc. of the Int. Symp. on Ecological Aspects of Tree Ring Analysis*, 1987, pp. 695–698.
- [7] Dawson T.E., Ehleringer J.R., Streamside trees that do not use stream water, *Nature* 350 (1991) 335–337.
- [8] Edwards W.R.N., Precision weighing lysimetry for trees using a simplified tare-balance design, *Tree Physiol.* 1 (1986) 127–144.
- [9] Granier A., A new method to measure the raw sap flux in the trunk of trees, *Ann. Sci. For.* 42 (1985) 193–200.
- [10] Granier A., Biron P., Breda N., Pontallier J.-Y., Saugier B., Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods, *Glob. Change Biol.* 2 (1996) 265–274.
- [11] Granier A., Biron P., Lemoine D., Water balance, transpiration and canopy conductance in two beech stands, *Agric. Forest Meteorol.* 100 (2000) 291–308.
- [12] Guevara-Escobar A., Edwards W.R.N., Morton R.H., Kemp P.D., Mackay A.D., Tree water use and rainfall partitioning in a mature poplar-pasture system, *Tree Physiol.* (2000) 97–106.
- [13] Hinckley T.M., Brooks J.R., Cermak J., Ceulemans R., Kucera J., Meinzer F.C., Roberts D.A., Water flux in a hybrid poplar stand, *Tree Physiol.* 14 (1994) 1005–1018.

- [14] Hogg E.H., Hurdle P.A., Sap flow in trembling aspen: implication for stomatal responses to vapor pressure deficit, *Tree Physiol.* 17 (1997) 501–509.
- [15] Hübert B., Schmidt E., Eine Kompensations Methode zur thermoelektrischen Messung langsamer Stafströme, *Bericht der Deutschen Botanischen Gesellschaft* 55 (1937) 514–529.
- [16] Lambs L., Correlation of conductivity and stable isotope ^{18}O for the assessment of water origin in river system, *Chem. Geol.* 164 (2000) 161–170.
- [17] Le Maitre D.C., Scott D.F., Colvin C., A review of information on interaction between vegetation and groundwater, *S.A. Water* 25 (1999) 137–152.
- [18] Malanson G.P., *Riparian Landscapes*, Cambridge study in Ecology, Cambridge University Press, UK, 1993, 296 p.
- [19] Nadezhdina N., Sap flow index as an indicator of plant water status, *Tree Physiol.* 19 (1999) 885–891.
- [20] Phillips N., Oren R., Zimmerman R., Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species, *Plant Cell Environ.* 19 (1996) 983–990.
- [21] Pontailier J.-Y., A cheap quantum sensor using a gallium arsenide photodiode, *Functional Ecology* 4 (1990) 591–596.
- [22] Stromberg J.C., Patten D.T., Riparian vegetation instream flow requirements: a case study from diverted stream in the eastern Sierra Nevada, California, USA, *Environ. Manage.* 14 (1990) 185–194.
- [23] Sun G., Riekerk H., Kornhak L.V., Ground-water-table rise after forest harvesting on cypress-pine flatwoods in Florida, *Wetlands* 20 (2000) 101–112.
- [24] Tabacchi E., Lambs L., Guilloy H., Planty-Tabacchi A.M., Muller E.H., Décamps H., Impact of Riparian vegetation on hydrological processes, *Hydrol. Process. Special Issues* 14 (2000) 2959–2976.
- [25] Wullschleger S.D., Meinzer F.C., Vertessy R.A., A review of whole-plant water use studies in trees, *Tree Physiol.* 18 (1998) 449–512.
- [26] Wullschleger S.D., King A.W., Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees, *Tree Physiol.* 20 (2000) 511–518.