

Hydrological properties of bark of selected forest tree species. Part 2: Interspecific variability of bark water storage capacity

Anna Ilek ✉, Jarosław Kucza, Karolina Morkisz

University of Agriculture in Krakow, Faculty of Forestry, Institute of Forest Ecosystem Protection,
Department of Forest Engineering, al. 29 Listopada 46, 31-425 Kraków, Poland, phone: 48 12 6625313,
fax: 48 12 4119715, e-mail: a.ilek@wp.pl

ABSTRACT

The subject of the present research is the water storage capacity of bark of seven forest tree species: *Pinus sylvestris* L., *Larix decidua* Mill., *Abies alba* Mill., *Pinus sylvestris* L., *Quercus robur* L., *Betula pendula* Ehrh. and *Fagus sylvatica* L. The aim of the research is to demonstrate differences in the formation of bark water storage capacity between species and to identify factors influencing the hydrological properties of bark. The maximum water storage capacity of bark was determined under laboratory conditions by performing a series of experiments simulating rainfall and by immersing bark samples in containers filled with water. After each single experiment, the bark samples were subjected to gravity filtration in a desiccator partially filled with water. The experiments lasted from 1084 to 1389 hours, depending on the bark sample. In all the studied species, bark sampled from the thinnest trees is characterized by the highest water storage capacity expressed in $\text{mm H}_2\text{O} \cdot \text{cm}^{-3}$, while bark sampled from the thickest trees – by the lowest capacity. On the other hand, bark sampled from the thickest trees is characterized by the highest water storage capacity expressed in $\text{H}_2\text{O} \cdot \text{cm}^{-2}$ whereas bark from the thinnest trees – by the lowest capacity.

In most species tested, as the tree thickness and thus the bark thickness and the coefficient of development of the interception surface of bark increase, the sorption properties of the bark decrease with bark depth, and the main role in water retention is played by the outer bark surface. The bark of European beech is an exception because of the smallest degree of surface development and because the dominant process is the absorption of water. When examining the hydrological properties of bark and calculating its parameters, one needs to take into account the actual surface of the bark of trees. Disregarding the actual bark surface may lead to significant errors in the interpretation of research results.

KEY WORDS

bark surface, bark water storage capacity, forest hydrology, forest tree bark

INTRODUCTION

Bark is structurally much more complex than wood. Bark includes all tissues outside the cambium, including the inner living phloem and dead outer tissue (rhytidome) (Pallardy 2010). The outer bark is affected by external weathering processes and tangential strain, which produce fissures and ridges of the surface (Whitmore 1962). The periderm and weathering processes control the sloughing of the bark and hence also its surface texture and colour. Bark is an effective defence against fire (Harmon 1984). Bark thickness is often an important factor, decisive about the survival of a tree in a fire (Hengst and Dawson 1994; Pinard and Huffman 1997; Barlow et al. 2003; Hoffmann et al. 2003; Bauer et al. 2010). The periderm provides protection from mechanical injury (Pallardy 2010). Bark limits the diffusion of water, oxygen and CO₂ between the vascular cambium and the atmosphere. The strength of this limitation can increase with the thickness of bark and the degree to which bark is impregnated with suberin, lipids and waxes (Lendzian 2006; Teskey et al. 2007). Bark is rich in organic nutrients and is a target of many different organisms, including insects, vertebrates, fungi and bacteria (Franceschi et al. 2005).

Plant interception is a significant component of the water balance of forest ecosystems. The ability of plants to retain water, amounting to 10–30% of the entire rainfall, has been indicated by Blake (1975) and Webb (1975), while Calder (1999) states the interception value even amounting to 50%. Similarly, Tsiko et al. (2012) indicate that the interception of water on the surface of plants and litter can constitute a total of 37 to 50% of all rainfall. According to Keim et al. (2006), rainwater retention is influenced by the morphological properties of plants. Crockford and Richardson (2000) regard the ability of the crown to retain water as the key feature affecting the size of interception.

A small number of studies have shown that the bark of trees plays a significant role in the interception of rainfall (Levia and Herwitz 2005; Valová and Bielešzová 2008). The water capacity of stems and branches depends on bark tissue properties, such as its thickness, texture and surface roughness, which change along with tree age (Liu 1998; Pypker et al. 2011). Van Stan et al. (2016) studied the bark structure of beech

and oak trees showing that, while a difference between species could be found, intraspecific differences in bark structure were statistically not detectable. Differences in water capacity and roughness of the bark of different species of forest trees affect the amount of stemflow production (Návar 1993; Aboal et al. 1999; Levia et al. 2010; Van Stan and Levia 2010).

Herwitz (1985) indicates that the bark surface, regardless of its structure, may provide from 50 to 80% of the total plant interception capacity. Llorens and Gallart (2000) studied Scots pine *Pinus sylvestris* L. in order to estimate that the needles can retain from 0.043 to 0.104 mm of water, while the surface of branches and stems may intercept about 0.620 mm of it. Liu (1998) also showed that the bark of *Taxodium ascendens* Brongn. and *Pinus elliottii* Engelm. has a higher water capacity than the leaves. Levia and Wubbena (2006), who studied eastern white pine (*Pinus strobus* L.), also found the vertical variation in the bark water capacity: in the lower part of the stem the bark retains approximately twice as much water as in the upper part.

Given the significant share of bark of trees in the interception of rainwater, the subject of present research are the hydrological properties of bark of selected species of forest trees. The aim of this study is to determine the maximum water capacity of the bark of stem at breast height (1.3 m) for various species of forest trees, and to attempt to answer the following questions: (a) does the ability to retain rainwater by tree bark vary significantly between different species? (b) do the changes concerning bark surface and thickness and progressing with an increase in breast height diameter of a tree affect the bark water storage capacity?

MATERIAL AND METHODS

The research area

Bark samples were collected in the Trzebnia Forest Subdistrict, located in the area of Myślenice Forest District (Regional Directorate of the State Forests in Krakow), situated in the southern Beskid Makowski in southern Poland. The samples were obtained from the bark of the trees growing on the mixed mountain forest habitat, on an eastern slope within the altitudes from 650 to 700 m.

The scope of research

The study included seven species of forest trees: *Pinus sylvestris* L., *Larix decidua* Mill., *Abies alba* Mill., *Pinus sylvestris* L., *Quercus robur* L., *Betula pendula* Ehrh. and *Fagus sylvatica* L. The bark samples were obtained during the summer of 2011. The samples were collected using a chisel, a saw and a knife from the stems of living trees at the breast height (1.3 m) by cutting possibly rectangular pieces of bark. The bark samples were collected for each species from trees with thickness ranging from 5 to 60 cm. Because the bark samples were obtained from trees growing under the same site conditions, the elaboration of the results was based on the assumption that tree thickness is the measure of their age. A total of 71 bark samples were tested, including 43 samples of bark of conifers and 28 deciduous tree bark samples. The number of samples of individual tree species was given in a study by Ilek and Kucza (2014).

Preparation of samples for analysis

Prior to testing, the bark samples were dried at 35°C. During the drying, the samples were control weighed every 4 hours until the time when drying no longer resulted in weight loss of individual bark samples. The weight of samples after drying at 35°C was the initial weight of the bark m_s . Then, all side surfaces and the inner surface of the samples were covered with a layer of silicon, applied in such a way that, during the experiments, water was absorbed only by the outer layer of the bark. Next, the samples were dried again at 35°C until the silicone dried and they were reweighed to determine the dry weight of the insulating layer of individual samples.

Determination of the maximum water storage capacity of the bark under laboratory conditions

Experiments designed to determine the maximum water storage capacity of the bark of forest trees were divided into two successive stages. The first stage consisted of several series of experiments which involved spraying the bark samples with simulated rain. The simulation was carried out using a pressure sprayer with the smallest possible droplet size, over a period of one hour. The second stage was the continuation of the first one, and consisted of several series of experiments involving the

immersion of bark samples in containers with water for a period lasting from 10 to 72 hours.

The experiment showed that the maximum water storage capacity would be easier to obtain by performing, in the first stage of the experiments, a gradual soaking of the bark samples by means of spraying and drainage. The external conditions of those experiments allowed free and natural absorption of water by the bark. When the amount of water absorbed by the samples after a single rainfall simulation was no longer significant, the second stage of the experiments was launched.

Every single experiment (simulation or immersion) with number i started by weighing the bark samples in order to determine the initial sample mass m_i . Then, in the first stage of the experiments, the samples were set vertically on a rack and subjected to an hour of rainfall simulation; whereas in the second stage, the samples were inserted into containers filled with water for a period lasting from several to several dozens of hours. The vertical position of the samples during the rainfall simulation allowed gravity drainage of excess water from the surface of the bark. After completion of a single experiment (simulation or immersion) and wiping the silicon-sealed bark surfaces, the samples were placed in a desiccator partially filled with water, in which the relative air humidity was about 100%. In the desiccator, the samples were placed vertically and subjected to gravity filtration. Storing the samples in a desiccator ensured the elimination of evaporation of water from the surface of the bark between successive experiments and its absorption into the bark tissue. After gravity filtration, the bark samples were weighed to determine their final weight M_i , which was also the initial weight of the bark m_{i+1} before the next experiment $i+1$. Disregarding gravity filtration in the calculation of increase in water reserve could make the obtained measurement results significantly higher due to temporary detention of water on the surface of bark samples after a single experiment. The increase of permanent water reserve in the bark after a single experiment was calculated by means of the formula:

$$\Delta S_i = M_i - m_i \quad (1)$$

where:

ΔS_i – the increase of permanent water storage in the bark following the i -th experiment (g);

- M_i – the final mass of samples of bark following the i -th experiment and gravity filtration (g);
 m_i – the initial mass of bark samples before the i -th experiment (g).

The experiments lasted until further immersing of the samples in water no longer caused bark weight gain in comparison with the previous experiments, i.e. until the bark reached the state of maximum filling with water.

The total water reserve in the bark after a series of experiments of rainfall simulation and immersion of the samples in water was calculated using the formula:

$$\Delta S = S_0 + \sum_{i=1}^n S_i \quad (2)$$

where:

- S – the total water reserve in the bark (g);
 S_0 – the initial reserve of water in the bark after the samples were dried at 35°C (g);
 ΔS_i – an increase of the permanent water reserve in the bark following the i -th experiment (g).

The initial reserve of water S_0 (g) in each bark sample prior to the beginning of the experiments was calculated using the formula:

$$S_0 = m_s - M_s \quad (3)$$

where

- m_s – the initial mass of the bark sample after drying at 35°C (g);
 M_s – the dry mass of the bark sample after drying at 105°C (g).

Calculation of the parameters of bark

Analysis of the maximum water capacity of bark of the selected species of forest trees was based on the parameters of individual samples of bark, which included the actual surface A_d and the model surface A , volume V and bark thickness H .

The actual surface A_d (cm²) of the bark includes all irregularities, cracks and cavities of bark sample and can be calculated according to the formula (Ilek and Kucza 2014):

$$A_d = A \cdot C_{sd} \quad (4)$$

where:

- A – the model surface of a bark sample (cm²), corresponding to the surface of the cylinder slice;
 C_{sd} – the coefficient of development of the interception surface, describing the level of development of the outer bark layer of the trees.

The method of calculation of the model surface A and the coefficient of development of the interception surface of the bark C_{sd} was presented by Ilek and Kucza (2014).

Bark volume V (corresponding to maximum water storage capacity) was determined using the method of instantaneous displacement of water in a measuring cylinder.

Bark thickness H (cm), which takes into account the degree of irregularity of the outer surface of the bark, was calculated using the following formula:

$$H = \frac{V}{A_d} \quad (5)$$

where:

- V – the volume of a bark sample (cm³);
 A_d – the actual surface of a bark sample (cm²).

Measurements of the maximum water storage capacity of bark

For the comparison of water retention capability of the bark of various species of forest trees, we used three measures describing the total water reserve in the bark obtained after the experiments:

- a) the maximum water storage capacity S_v expressed in millimetres of water in 1 cm³ of a bark sample calculated using the equation:

$$S_v = \frac{S}{V} \cdot 10 \quad (6)$$

where:

- 10 – a factor of conversion into mm of H₂O.
 b) the maximum water storage capacity S_{Ad} expressed in millimetres of water per 1 cm² of the actual bark surface, calculated using the equation:

$$S_{Ad} = \frac{S}{A_d} \cdot 10 \quad (7)$$

- c) the maximum water storage capacity S_A expressed in millimetres of water per 1 cm² of the model sur-

face of individual bark samples, calculated using the formula:

$$S_A = \frac{S}{A} \cdot 10 \quad (8)$$

Data analysis

All statistical analyses were conducted with STATISTICA 10 (StatSoft 2011). The analysis of significance of differences in the bark water storage capacity S_v and S_{Ad} between different species was performed using one-way variance analysis ANOVA and Tukey's *post-hoc* analysis, on the significance level $\alpha = 0.05$.

The study examined the relationship of breast height diameter, bark thickness and tree species with maximum water capacity of bark S_v and S_{Ad} . Analyses were performed using the multiple regression method. For the purposes of calculations, in the water capacity models S_v (Eq. 10 and 11) and S_{Ad} (Eq. 12 and 13), individual species were introduced as dummy variables, converting them into six zero-one variables: *Pine*, *Larch*, *Fir*, *Oak*, *Birch* and *Beech*. Spruce bark was adopted as the auxiliary group, constituting the reference group in the interpretation of the model parameters. Collinearity of the variables was assessed using the variance inflation factor (VIF):

$$VIF_j = \frac{1}{1 - R_j^2} \quad (9)$$

where:

R_j^2 – the coefficient of determination of the variable X_j for the other explanatory variables included in the model.

The selection of best model was based on the standard error of estimation, the share of variance explained by the regression model (R_{adj}^2), the distribution of residual values and the scatter of residual values versus values predicted by the equation of regression.

RESULTS

The duration of experiments designed to determine the maximum water capacity of the bark of forest trees ranged from 1084 to 1389 hours, depending on the bark sample, wherein the total rainfall simulation time and the time of sample immersion in water ranged from 598

to 812 hours, and the overall time of draining the samples lasted from 486 to 577 hours.

The maximum water storage capacity S_v

Norway spruce and European beech are characterized by the highest average water storage capacity of bark S_v , expressed in $\text{mm H}_2\text{O} \cdot \text{cm}^{-3}$ whereas Scots pine, European larch and common birch – by the lowest capacity (Fig. 1). Based on the analysis of variance and Tukey's *post hoc* analysis, significant differences were found in the mean values of capacity S_v between spruce and pine ($p < 0.01$), spruce and larch ($p < 0.01$), spruce and birch ($p < 0.01$), beech and pine ($p < 0.01$), beech and larch ($p < 0.01$), beech and birch ($p < 0.01$) and between oak and larch ($p = 0.04$).

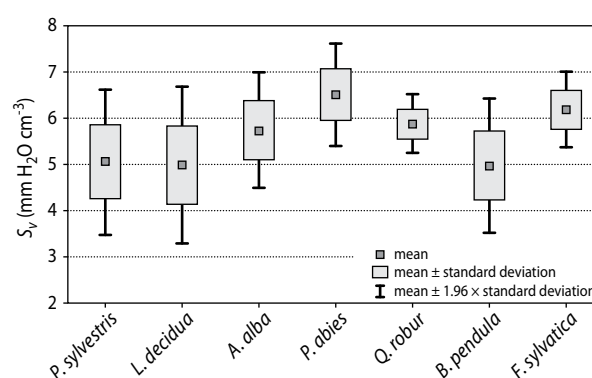


Figure 1. The maximum water storage capacity of bark S_v of particular species of forest trees

The maximum water storage capacity of bark S_v shows a clear relationship with the tree diameter at breast height (Fig. 2). Among all species tested, the highest water storage capacity S_v characterized the bark obtained from the thinnest trees and the lowest – the bark obtained from the thickest trees. The equation describing the dependence of maximum water capacity of bark S_v ($\text{mm H}_2\text{O} \times \text{cm}^{-3}$) on the tree diameter at breast height (cm) as well as on the tree species explains about 88% of the variability of this trait (Table 1):

$$S_v = 7.41 - 0.03 \cdot DBH + \sum_{i=1}^n \delta_i \cdot SPECIES_i \quad (10)$$

where:

δ_i – a parameter for the *i*-th species, and species variables assume the value 0 or 1 depending on the species for which the water capacity is calculated.

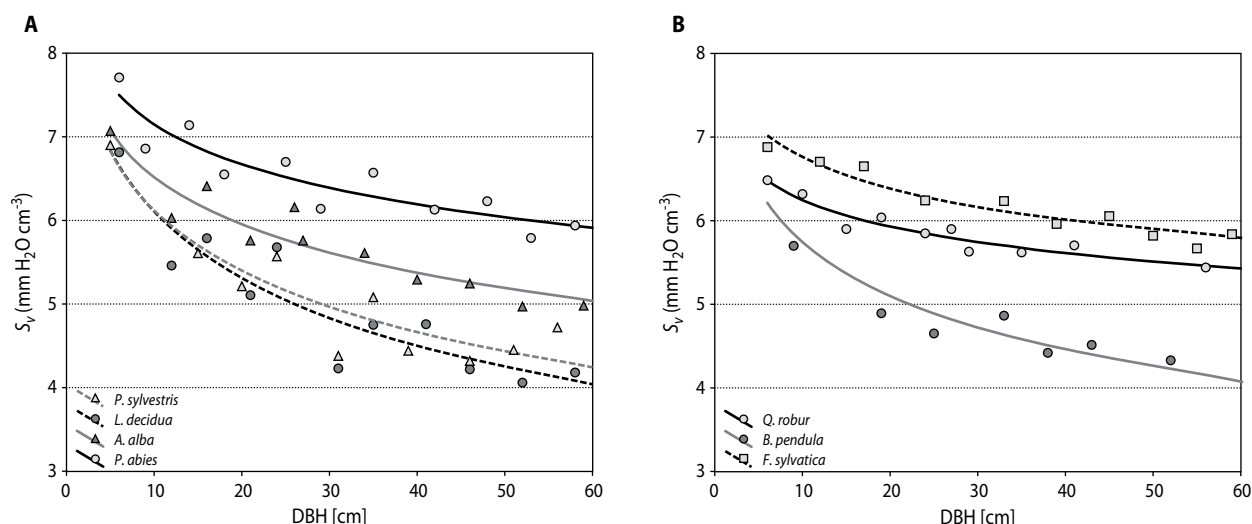


Figure 2. Dependence of the maximum water storage capacity S_v on the tree diameter at breast height (DBH) of conifers (A) and deciduous trees (B)

Similarly, the dependence of water storage capacity S_v ($\text{mm H}_2\text{O} \cdot \text{cm}^{-3}$) on bark thickness H (cm) and the tree species was described by an equation that explains 88% of variability of this trait:

$$S_v = 7.61 - 2.44 \cdot H + \sum_{i=1}^n \delta_i \cdot \text{SPECIES}_i \quad (11)$$

The values of δ parameters for particular species, together with estimation of their significance, are presented in Table 1 (Eq. 10) and in Table 2 (Eq. 11). Based

on the t statistics, it was found that the parameters of the analysed regression models differ significantly from 0 (Tab. 1 and 2). Partial correlation values confirm that a large part of the variability of water storage capacity S_v is explained by tree species as well as by the tree diameter at breast height (Eq. 10) and bark thickness (Eq. 11). Based on the variance inflation factor (Tab. 1 and 2), it can be concluded that the independent variables applied in equation 10 and 11 are not redundant, which confirms their direct relationship with the bark water storage capacity S_v .

Table 1. The parameters of equation 10 and evaluation of their significance

Variable	Parameter value	Standard error	The value of t-statistics	Probability level	Partial correlation	VIF	R^2_{adj}	Std error of estimation
Free term	7.41	0.11	65.53	0.00	—	—	0.88	0.30
DBH	-0.03	0.00	-12.79	0.00	-0.85	1.04		
Pine	-1.53	0.13	-11.44	0.00	-0.83	1.59		
Larch	-1.61	0.13	-12.47	0.00	-0.85	1.64		
Fir	-0.77	0.13	-6.09	0.00	-0.61	1.68		
Beech	-0.22	0.13	-1.70	0.09*	-0.21	1.64		
Oak	-0.76	0.13	-5.89	0.00	-0.60	1.64		
Birch	-1.61	0.14	-11.73	0.00	-0.83	1.53		

* not significant at $\alpha = 0.05$.

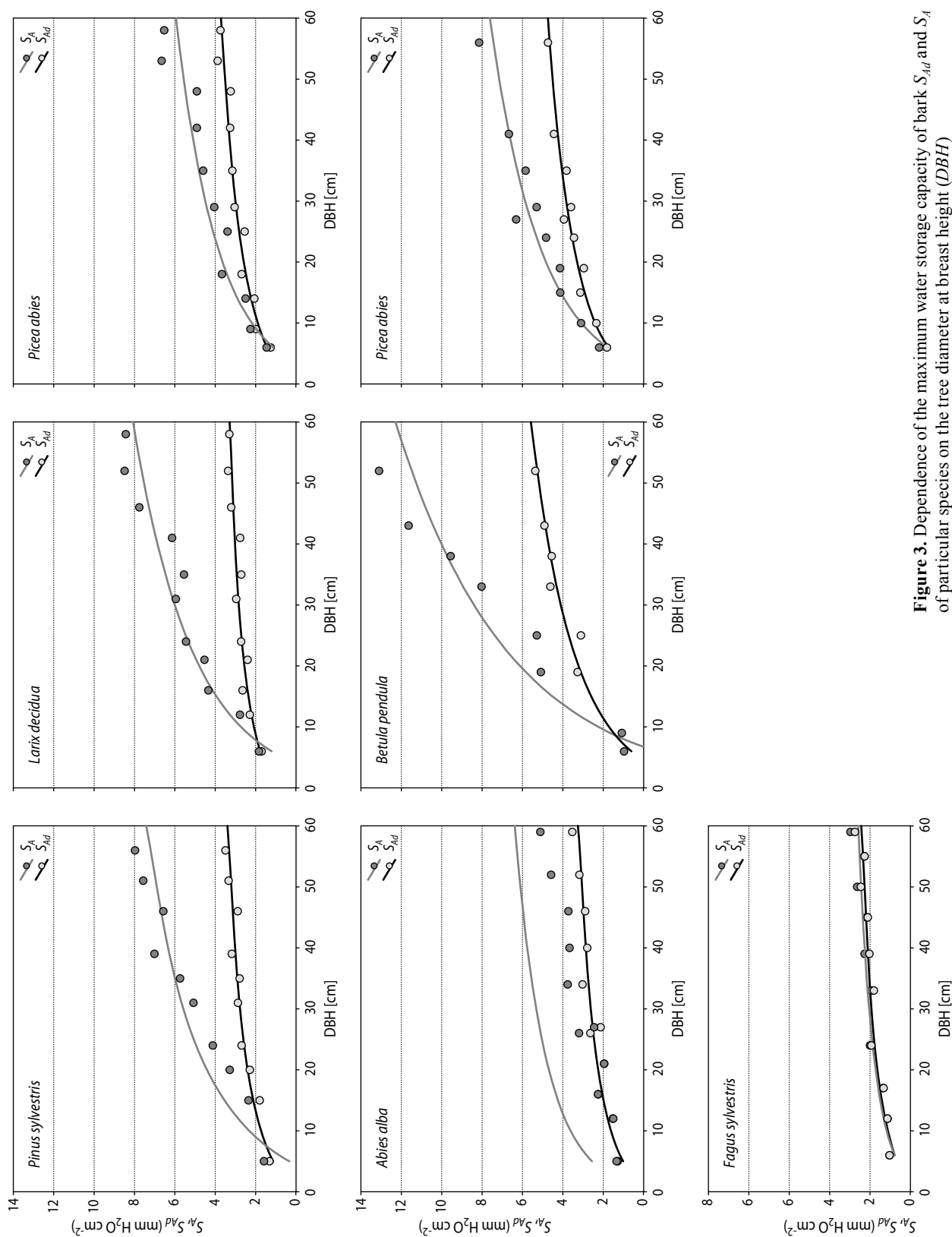


Figure 3. Dependence of the maximum water storage capacity of bark S_{Ad} and S_A of particular species on the tree diameter at breast height (DBH)

Table 2. The parameters of equation 11 and evaluation of their significance

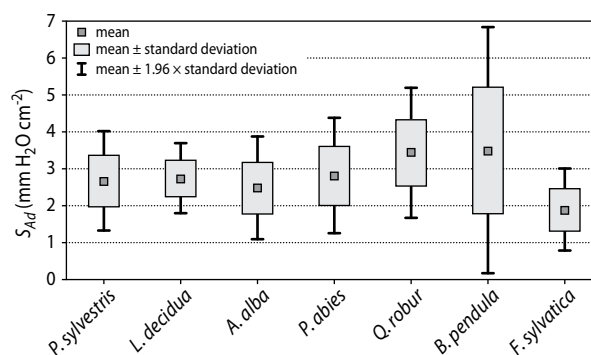
Variable	Parameter value	Standard error	The value of t-statistics	Probability level	Partial correlation	VIF	R_{adj}^2	Std error of estimation
Free term	7.61	0.12	64.03	0.00	—	—	0.88	0.29
H	-2.44	0.18	-13.32	0.00	-0.86	1.47		
Pine	-1.30	0.13	-9.85	0.00	-0.78	1.65		
Larch	-1.31	0.13	-10.14	0.00	-0.79	1.72		
Fir	-0.77	0.12	-6.29	0.00	-0.63	1.68		
Beech	-0.65	0.13	-5.05	0.00	-0.54	1.70		
Oak	-0.28	0.13	-2.21	0.03	-0.27	1.70		
Birch	-0.80	0.14	-5.54	0.00	-0.58	1.79		

The maximum water capacity S_{Ad} and S_A

The maximum water capacity of bark S_{Ad} and S_A expressed in $\text{mm H}_2\text{O} \cdot \text{cm}^{-2}$ of the developed bark surface A_d and the model bark surface A in all the examined tree species are also related to the breast height diameter (Fig. 3). The largest values of water capacity S_{Ad} and S_A characterize the bark obtained from the thickest trees while the smallest values – the bark obtained from the thinnest trees. It is worth noting that the bark water capacity S_A assumes very large values as compared with the capacity S_{Ad} , which takes into account the actual surface of the bark of individual samples. These differences are particularly evident among species with high dynamics of changes of the coefficient of development of the interception surface of bark C_{sd} along with the thickness of the trees (Ilek & Kucza 2014), which include Scots pine, European larch and common birch. In the case of European beech, in which the coefficient C_{sd} of the bark does not undergo large changes with the growth of tree thickness, the differences between water capacity S_{Ad} and S_A are small. In our opinion, the use of the actual bark surface in this type of research is more correct methodologically and that is why further description of the results concerns only the maximum water storage capacity S_{Ad} .

The highest average value of water capacity S_{Ad} characterizes the bark of common birch and pedunculate oak, while the lowest – the bark of European beech (Fig. 4). On the basis of the analysis of variance and Tukey's *post hoc* analysis, significant differences were found in the mean water capacity of bark S_{Ad} between beech and oak ($p < 0.01$), as well as beech and birch ($p = 0.03$). Among other species, there was no significant

difference in the mean values of the maximum water capacity S_{Ad} .

**Figure 4.** The maximum water storage capacity of bark S_{Ad} of particular species of forest trees

The equation which describes the dependence of water storage capacity S_{Ad} ($\text{mm H}_2\text{O} \cdot \text{cm}^{-2}$) on the diameter at breast height (cm) and the tree species explains about 89% of variability of this trait (Tab. 3):

$$S_{Ad} = 1.61 + 0.04 \cdot DBH + \sum_{i=1}^n \delta_i \cdot SPECIES_i \quad (12)$$

where:

δ_i – the parameter for the i -th species, and species variables assume the values 0 or 1 depending on the species for which the bark water storage capacity S_{Ad} is calculated.

Similarly, the dependence of water capacity S_{Ad} ($\text{mm H}_2\text{O} \cdot \text{cm}^{-2}$) on bark thickness H (cm) and the tree

Table 3. The parameters of equation 12 and evaluation of their significance

Variable	Parameter value	Standard error	The value of t-statistics	Probability level	Partial correlation	VIF	R^2_{adj}	Std error of estimation
Free term	1.61	0.12	13.61	0.00	—	—	0.89	0.31
DBH	0.04	0.00	16.46	0.00	0.90	1.02		
Pine	−0.20	0.14	−1.48	0.14 ^a	−0.19	1.63		
Larch	−0.09	0.13	−0.68	0.50 [*]	−0.09	1.68		
Fir	−0.34	0.13	−2.54	0.01	−0.31	1.68		
Beech	−1.05	0.14	−7.72	0.00	−0.70	1.64		
Oak	0.79	0.14	5.78	0.00	0.59	1.64		
Birch	1.33	0.16	8.39	0.00	0.73	1.42		

^{*} not significant at $\alpha = 0.05$.

Table 4. The parameters of equation 13 and evaluation of their significance

Variable	Parameter value	Standard error	The value of t-statistics	Probability level	Partial correlation	VIF	R^2_{adj}	Std error of estimation
Free term	0.98	0.08	12.87	0.00	—	—	0.96	0.19
H	4.12	0.11	36.19	0.00	0.98	1.39		
Pine	−0.58	0.08	−7.03	0.00	−0.66	1.68		
Larch	−0.60	0.08	−7.42	0.00	−0.68	1.75		
Fir	−0.33	0.08	−4.18	0.00	−0.47	1.69		
Beech	−0.37	0.08	−4.41	0.00	−0.49	1.70		
Oak	0.02	0.08	0.26	0.79 ^a	0.03	1.71		
Birch	−0.57	0.09	−6.11	0.00	−0.61	1.77		

^{*} not significant at $\alpha = 0.05$.

species was described by an equation which explains 96% of variability of this trait (Tab. 4):

$$S_{Ad} = 0.98 + 4.12 \cdot H + \sum_{i=1}^n \delta_i \cdot SPECIES_i \quad (13)$$

The values of the δ parameters for particular species, together with estimation of their significance, are presented in Table 3 (Eq. 12) and in Table 4 (Eq. 13).

DISCUSSION

In the course of experiments on the water storage capacity of forest trees, the total time of contact of bark samples with water ranged from 24 to 35 days, disregarding any breaks between subsequent experiments. Although that time may seem to be long, it was necessary in or-

der to achieve the state of maximum water capacity by particular bark samples. The long time of experiments indicates the complexity of the processes of filling the bark retention container.

Paine et al. (2010) showed that total bark thickness is dependent on rhytidome thickness. Given the strong dependence of bark thickness H on the breast height diameter of trees for particular species (Fig. 5), the decrease of maximum capacity of the bark S_v with the thickness (age) of trees may be caused by a decrease in the absorption capacity of the bark along with its increment in thickness. In the early years of tree life, bark probably has great sorption potential and water can be absorbed by the whole volume of the bark. However, in a certain period of life of the trees, the bark sorption capabilities decrease deeper inside, or even disappear completely, and the central role in rainfall retention is

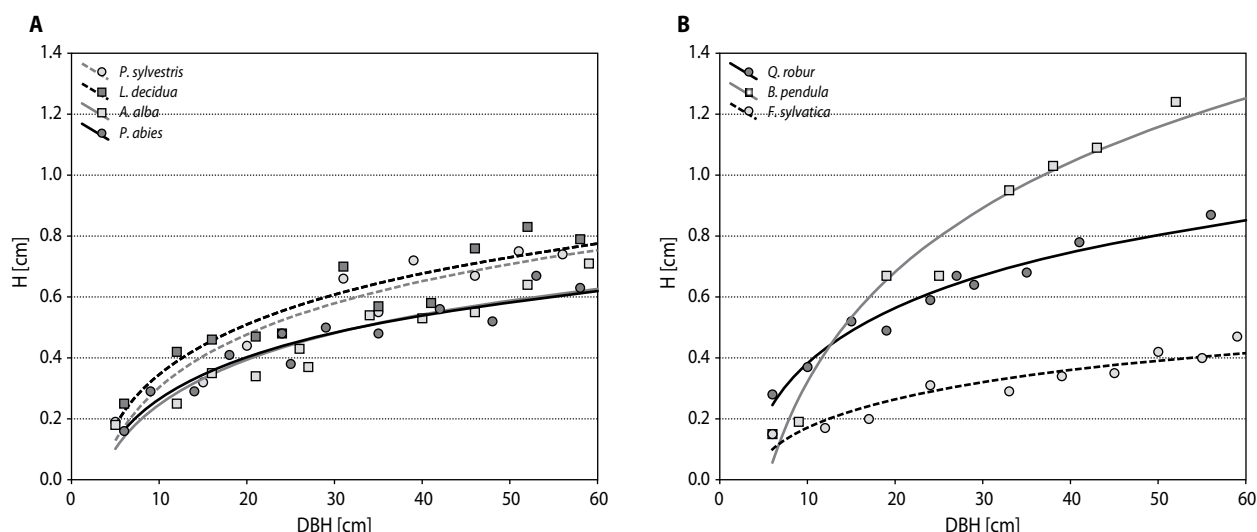


Figure 5. Dependence of bark thickness (H) on the tree diameter at breast height (DBH) of conifers (A) and deciduous trees (B)

played by the outer bark layer. In connection with an increase of bark thickness H along with increasing thickness of the tree, thereby increasing the bark volume, the maximum water storage capacity, expressed in units of volume, results in values decreasing with the breast height diameter of trees.

Interspecies differentiation of bark water storage capacity has also been shown by Valová and Bielešová (2008). They noted that the bark of apple-tree (*Malus* sp.) with the stem circumference of 100 cm retained 0.886 g/cm^3 whereas birch (*Betula pendula* Ehrh.) with the same circumference was able to retain only 0.342 g/cm^3 . Similarly, Levina and Herwitz (2005) showed differences between the bark water storage capacity of birch (*Betula lenta* L.), hickory (*Carya gabra* Mill.) and oak (*Quercus rubra* L.). Some authors point to differences in the anatomical structure of bark, both between different tree species (Chattaway 1953; Howard 1977; Franceschi et al. 2005) and within a single species (Quilhó et al. 2000). Yáñez-Espinosa et al. (2001) state that certain anatomical features of bark may be related to the adaptation of plants to the life conditions in a given environment. The anatomical structure of the bark of different tree species may be a very important factor affecting its water storage capacity as well.

In our opinion, a study of water storage properties of bark should take into account its actual surface A_d . Not taking into account the actual surface in such

considerations may cause large errors in the interpretation of research results, especially for bark with large values of coefficient C_{sd} . For example, the water capacity S_A of larch bark sampled from a tree with the breast height diameter of 58 cm is $8.44 \text{ mm} \cdot \text{cm}^2$ while the water capacity S_A of oak bark (DBH = 56 cm) is $8.15 \text{ mm} \cdot \text{cm}^2$; therefore, when interpreting the results, we find that larch bark has a larger capacity of rainfall retention (Fig. 3). However, if the calculation of the water storage capacity takes into account the actual bark surface, it appears that the maximum water capacity of larch bark S_{Ad} is $3.30 \text{ mm} \cdot \text{cm}^2$, whereas for oak bark it is $4.74 \text{ mm} \cdot \text{cm}^2$; therefore, it is oak bark that has a higher water retention capacity than larch bark.

As trees age, subsequent periderms may arise at successively greater depths, thus causing accumulation of dead tissues on the surface of the stem and contributing to the formation of rhytidome on rough-barked species or simple outer bark on smooth-barked species (Biggs 1992). Given the increase of coefficient of development of the interception surface of bark C_{sd} along with thickness of the trees (Ilek and Kucza 2014), the increase in bark water storage capacity S_{Ad} (Fig. 3) with the diameter at breast height of trees in all the examined species may confirm the importance of outer bark surface in rainwater retention. Since the thinnest trees have a relatively lower level of development of their bark surface (Ilek and Kucza 2014), they have the lowest water

capacity S_{Ad} and the main role in rainwater retention is played by sorption into the bark tissue. The thickest trees, characterized by high values of coefficient C_{sd} (Ilek and Kucza 2014), have the highest water capacity of bark S_{Ad} where a large role in rainwater retention is also played by the very surface of the bark, apart from water sorption deeper inside. Bark roughness and the presence of numerous cracks with a high coefficient C_{sd} mean that much of the retained water can be adsorbed directly on the surface of the outer bark.

The large differentiation in the water capacity of birch bark (Fig. 4) is probably due to the greatest dynamics of changes in the coefficient of development of bark surface (Ilek and Kucza 2014) and bark thickness (Fig. 5) along with tree age, found among all the examined species. The low water storage capacity of bark S_{Ad} and the high water storage capacity S_v of European beech bark may also confirm the importance of the outer bark surface in rainwater retention. In the case of beech bark, which has the lowest coefficient of development of the interception surface of bark C_{sd} in comparison with other species (Ilek and Kucza 2014), a major role in water retention is probably played by the sorption of water deeper inside, while only a small amount of it is adsorbed on the outer bark surface.

SUMMARY AND CONCLUSIONS

When studying the water storage properties of the bark of forest trees and calculating its parameters, one should take into account the degree of development of the outer bark surface of trees. Disregarding the actual bark surface may cause significant errors in the interpretation of research results.

The results of the present study indicate that the absorption of water into the bark tissue decreases with an increase in tree thickness, and thus with bark thickness, and that an increasingly important role in retaining rainwater is played only by the outer surface of the bark, the development of which is dynamic and progresses with tree age. The calculations of total water retention in the bark per unit of the actual bark surface of individual samples indicate no significant differences in the water capacity between the different species, which may also confirm the importance of outer bark surface in water adsorption. European beech is an exception, as it has

the lowest degree of surface development and because the absorption of water into the bark tissue is probably the dominant process in this species.

The results of the present research show changes in water storage capacity of the bark occurring with an increasing age of trees. This suggests that the water storage capacity of the bark will also vary along a single tree stem, similarly to the differentiation of bark thickness and the degree of surface development. Therefore, the verification of relationships described in this study should be conducted for each species along the entire length of the stem, with more numerous samples. At the same time, research should be carried out on bark samples obtained from trees growing under optimal habitat conditions for a given species.

ACKNOWLEDGMENTS

These investigations were supported by a grant for young scientists from Polish Ministry of Science and Higher Education (No. BM/4419/KIL/12).

The authors would like to thank two anonymous reviewers for the thorough assessment of the present paper and for their many valuable and helpful suggestions.

REFERENCES

- Aboal J.R., Morales D., Hernández M., Jiménez M.S. 1999. The measurement and modelling of the variation of stemflow in a laurel forest in Tenerife, Canary Islands. *Journal of Hydrology*, 221 (3), 161–175.
- Barlow J., Lagan B.O., Reres C.A. 2003. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, 19, 291–299.
- Bauer G., Speck T., Blömer J., Bertling J., Speck O. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Materials Science*, 45 (21), 5950–5959.
- Biggs A.R. 1992. Anatomical and physiological responses of bark tissues to mechanical injury. In: Defense mechanisms of woody plants against fungi (eds.: R. Blanchette, A. Biggs). Springer, Berlin Heidelberg, 13–40.

- Blake G.J. 1975. The interception process. In: Prediction in Catchment Hydrology (eds.: T.G. Chapman, R.X. Dunin). Australian Academy of Science, Netley, 59–81.
- Calder I.R. 1999. Dependence of rainfall interception on drop size – a replay to the comment by Uijlenhoet and Sticker. *Journal of Hydrology*, 217, 164–165.
- Chattaway M.M. 1953. The anatomy of bark. I. The genus *Eucalyptus*. *Australian Journal of Botany*, 1 (3), 402–433.
- Crockford R.H., Richardson D.P. 2000. Partitioning of rainfall into throughfall, stemflow and interception: Effect of forest type, ground cover and climate. *Hydrological Processes*, 14, 2903–2920.
- Franceschi V.R., Krokene P., Christiansen E., Krekling T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, 167 (2), 353–376.
- Harmon M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology*, 65, 796–802.
- Hengst G.E., Dawson J.O. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research*, 24 (4), 688–696.
- Herwitz S.R. 1985. Interception storage capacities of tropical rainforest canopy trees. *Journal of Hydrology*, 77, 237–252.
- Hoffmann W.A., Orthen B., do Nascimento P.K.V. 2003. Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology*, 17, 720–726.
- Howard E.T. 1977. Bark structure of southern upland oaks. *Wood and Fiber Science*, 9 (3), 172–183.
- Ilek A., Kucza J. 2014. Hydrological properties of bark of selected forest tree species. Part I: the coefficient of development of the interception surface of bark. *Trees*, 28, 831–839.
- Keim R.F., Skaugset A.E., Weiler M. 2006. Storage of water on vegetation under simulated rainfall of varying intensity. *Advances in Water Resources*, 29, 974–986.
- Lendzian K.J. 2006. Survival strategies of plants during secondary growth: barrier properties of phelloms and lenticels towards water, oxygen, and carbon dioxide. *Journal of Experimental Botany*, 57, 2535–2546.
- Levia D.F., Herwitz S.R. 2005. Interspecific variation of bark water storage capacity of three deciduous tree species in relation to stemflow yield solute flux to forest soils. *Catena*, 64, 117–137.
- Levia D.F., Van Stan J.T., Mage S.M., Kelley-Hauske P.W. 2010. Temporal variability of stemflow volume in a beech-yellow poplar forest in relation to tree species and size. *Journal of Hydrology*, 380 (1), 112–120.
- Levia D.F., Wubbena N.P. 2006. Vertical variation of bark water storage capacity of *Pinus strobus* L. (eastern white pine) in Southern Illinois. *North-eastern Naturalist*, 13 (1), 131–137.
- Liu S. 1998. Estimation of rainfall storage capacity in the canopies of cypress wetlands and slash pine uplands in North-Central Florida. *Journal of Hydrology*, 207, 32–41.
- Llorens P., Gallart F. 2000. A simplified method for forest water storage capacity measurement. *Journal of Hydrology*, 240, 131–144.
- Návar J. 1993. The causes of stemflow variation in three semi-arid growing species of northeastern Mexico. *Journal of Hydrology*, 145 (1), 175–190.
- Paine C.E.T., Stahl C., Courtois E.A., Patiño S., Sarmiento C., Baraloto C. 2010. Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology*, 24, 1202–1210.
- Pallardy S.G. 2010. Physiology of woody plants. Academic Press.
- Pinard M.A., Huffman J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology*, 13 (5), 727–740.
- Pypker T.G., Levia D.F., Staelens J., Van Stan J.T. 2011. Canopy structure in relation hydrological and biogeochemical fluxes. *Forest Hydrology and Biogeochemistry, Ecological Studies*, 216 (4), 371–388.
- Quilhó T., Pereira H., Richter H.G. 2000. Within-tree variation in phloem cell dimensions and proportions in *Eucalyptus globulus*. *IAWA Journal*, 21 (1), 31–40.
- StatSoft, Inc. 2011. STATISTICA (data analysis software system), version 10. www.statsoft.com
- Teskey R., Saveyn A., Steppe K., McGuire M. 2007. Origin, fate and significance of CO₂ in tree stems. *New Phytologist*, 177, 17–32.

- Tsiko C.T., Makurira H., Gerrits A.M.J., Savenije H.H.G. 2012. Measuring forest floor and canopy interception in a savannah ecosystem. *Physics and Chemistry of the Earth, Parts A/B/C*, 47, 122–127.
- Valová M., Bielešzová S. 2008. Interspecific variations of bark's water storage capacity of chosen types of trees and the dependence on occurrence of epiphytic mosses. *GeoScience Engineering*, 54 (4), 45–51.
- Van Stan J.T., Hildebrandt A., Rebmann C., Friesen J. 2016. Impact of interacting bark structure and rainfall conditions on stemflow variability in a temperate beech-oak forest, central Germany. *Hydrological Sciences Journal*, 61 (11), 2071–2083.
- Van Stan J.T., Levia D.F. 2010. Inter- and intraspecific variation of stemflow production from *Fagus grandifolia* Ehrh. (American beech) and *Liriodendron tulipifera* L. (yellow poplar) in relation to bark microrelief in the eastern United States. *Ecohydrology*, 3 (1), 11–19.
- Webb E.K. 1975. The interception process. In: Prediction in Catchment Hydrology (eds.: T.G. Chapman, R.X. Dunin). Australian Academy of Science, Netley, 203–236.
- Whitmore T.C. 1962. Studies in systematic bark morphology. *New Phytologist*, 61 (2), 191–207.
- Yáñez-Espinosa L., Terrazas T., López-Mata L. 2001. Effects of flooding on wood and bark anatomy of four species in a mangrove forest community. *Trees*, 15, 91–97.