

Seasonal changes in water absorbability of some litterfall components in Scots pine stands differing in age

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Abstract Understanding the water-holding capacity of the litter layer is of interest when constructing forest hydrology models, where the presence of litter affects soil moisture content and fire behavior. However, to understand the process of water storage in the litter layer it is not only important to know (i) how much water the litter layer can store, but also (ii) how much water particular litter components can store. Little is known about the role of organic matter chemistry in water absorption and saturation of its internal capillarity. We hypothesized that water absorption of freshly fallen organic matter changes with stand age and during the year, i.e. the term when organic matter falls (month of the year or season) affects its water absorbability. Thus, we determined seasonal changes in water absorption time, carbon and nitrogen contents, and the C/N ratio of bark and needles taken from Scots pine stands of different ages during laboratory tests. Pine needles and bark were collected every month for one year in five stands in north-western Poland. The time of water absorption for bark was about 30% shorter than that of needles. The age of the stand did not affect the time of water absorption in the litterfall components. We observed that the term when litter falls (month of the year or season) significantly affected the water absorption time. It indicates that organic matter reaching the forest floor and forming the litter layer is characterized by different output properties affecting the water storage capacity of the litter layer.

Keywords: forest hydrology, water absorbability, internal capillarity, litterfall, litter layer, *Pinus sylvestris*

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Introduction

During a storm event, water is temporarily intercepted and stored on vegetation surfaces, evaporates into the atmosphere, or drains to the soil surface afterwards as either throughfall and stemflow (Li et al. 2017). Throughfall is the portion of precipitation that falls through or drips from the canopy (Sadeghi et al. 2020) and may be intercepted by the organic horizon of forest soils, designated as ‘forest floor’ in forestry literature. The forest floor is usually divided into three sub-horizons, i) the uppermost layer of fresh organic residues (it is the first forest soil layer that intercepts water), ii) the middle partially decomposed layer, iii) the completely decomposed organic layer, and they are correspondingly called litter (L), fermented (F), and humus layers (H) (Osman 2013a). Although forest floor interception is often considered a minor process due to the lack of radiation under the canopy (Gerrits & Savenije 2011), Li et al. (2017) found that litter interception in a *Pinus elliotii* stand can consistently and significantly reduce throughfall (9–46%) reaching the soil surface. Similarly, Thurrow et al. (1987) reported that litter interception under oaks was ~21% of the annual rainfall, while Brye et al. (2000) reported for prairie litter that interception loss may even reach ~70% of gross rainfall. Thus the presence of forest litter can alter the quantities of water available for soil infiltration and runoff (Guevara-Escobar et al. 2007).

Litter interception loss is controlled by amounts of litter on the forest floor, water storage capacity, and the local climate, which controls wetting and drying (Helvey & Patric 1965, Pitman 1989, Putuhena & Cordery 1996). Water storage capacity of the litter layer depends, among others, on its total mass, thickness, porosity, hydrophobicity of litter components, rainfall intensity, rainfall duration and slope (Du et al. 2019, Fernald 2012, Ilek et al. 2015, Leuschner 1998, Tsiko et al. 2012, Ogée & Brunet 2002, Xing et al. 2018, Zhang et al. 2006). Litter interception differs

depending on the stand species composition and litter type (leaf litter usually intercepts more water than needle litter). Walsh & Voigt (1977) found that pine litter (*Pinus sylvestris*) may intercept 0.6-1.7 mm of water, while beech litter (*Fagus sylvatica*) may intercept 0.9-2.8 mm, which correlates with the study of Gerrits et al. (2010).

Research showed that bracken litter (*Pteridium aquilinum*) intercepted 1.67 mm of water (Pitmann 1989), while *Pinus radiata* and eucalyptus litter intercepted 2.78 mm and 1.78 mm, respectively (Putuhena & Cordery 1996). Sato et al. (2004) stated that litter of *Cryptomeria japonica* and *Lithocarpus edulis* might intercept 0.27-1.72 and 0.67-3.05 mm of water. However, to understand the process of water storage in the litter layer it is not only important to know (i) how much water the litter layer can store, - we must also understand (ii) how much water the particular components of litter can store, (iii) how long water can be stored in litter layer, and (iv) how much of the litter water storage capacity is available for the interception before the storm event. Understanding the water holding capacity in the litter layer is thus of interest when constructing models of forest hydrology, where the presence of litter affects soil moisture content and fire behavior (Ogée & Brunet 2002).

According to Kucza (2007), soil horizons containing organic matter are characterized by double capillarity: between and inside organic matter debris. It means that on the forest floor water can be stored in pores created between organic matter debris and in pores inside dead tissues. Due to a loose structure of the litter layer, low density, high total porosity and high macroporosity (Ilek et al. 2017; Osman 2013b), water holding capacity in litter mainly consist of water adsorption on the surface of organic debris and water absorption to the inside of dead debris.

Water in the litter layer may also be present as water vapor in its air spaces (Matthews 2005). The ability to adsorb water on the

plant's surface is mainly dependent on its morphological characteristics (Fernández et al. 2014). Broad-leaf litter is generally large and curved and can easily capture rainwater (Li et al. 2020), but on a slope the needle-leaf litter may intercept more rainwater than the broad-leaf litter (Zhao et al. 2019). Yan et al. (2021) stated that the adsorption ability of water was strong in the case of broadleaved tree species having papery leaves and trichomes on leaves, while it was weak for evergreen tree species having leathery leaves and no trichomes on leaves. Variation in water adsorption is attributed to physical differences across species, specific leaf area, as well as hydrophobic lignin concentrations, lipid biomolecules, element concentrations and carbon oxidation state (Talhelm & Smith 2018). The process of filling up the internal capillarity of dead plant debris during water absorption is relatively poorly understood. Kucza & Urbaś (2005) stated that the time of water absorption by organic matter might indicate its current state of decomposition. Ilek et al. (2019) also reported that water absorption time depended on the botanical origin of organic matter and its state of decomposition. Those authors indicated that water absorption time increased with European beech organic matter decomposition and decreased with silver fir organic matter decomposition. Decreasing water absorption time with the degree of decomposition has also been stated for organic matter of the forest floor in Norway spruce stands (Kucza 2007, Kucza & Urbaś 2005). Although some research indicated that litter morphology might affect the moisture content dynamic of the litter layer (Sato et al. 2004), the role of organic matter chemistry in water absorption and filling up its internal capillarity received little attention. Thus, to better understand factors affecting the water storage capacity of the litter layer we determined water absorbability of some components in litterfall (needles and bark) collected every month for one year in Scots pine stands (*Pinus sylvestris*

L.) differing in age.

The main aim of the study was to demonstrate the role of needles and bark of Scots pine in water storage in forest ecosystems. The null hypotheses tested in this study include: (i) water absorption of particular components of litterfall (leaves and bark) is constant for the tree species it comes from and does not change with the age of trees; (ii) water absorption of freshly fallen organic matter is constant during the year, i.e. the time when organic matter falls (month of the year or season) does not affect its water absorbability.

Rejection of the null hypotheses will suggest that water absorption depends not only on the botanical characteristics of organic matter, but also on the chemical composition changes due to the physiological processes of trees occurring with varying intensity throughout the year. It will also suggest that organic matter reaching the forest floor and forming the litter layer is characterized by different output properties affecting the litter water storage capacity, thus meriting further research.

Methods

Study area and litterfall sampling

We collected the research material in Scots pine stands (*Pinus sylvestris* L.) in the Szczecin Lake District within the area administered by the State Forests (the Czarnobór Forest District) and situated in northwestern Poland at the height of about 140 m asl (Fig. 1, Table 1). The study site is situated in a temperate climate zone. The average annual temperature is 7.5°C and the average annual precipitation is 615 mm. The average temperature and precipitation within the growing season are 14.5°C and 200 mm, respectively (www.bdl.lasy.gov.pl/portal/en).

We selected five Scots pine stands of different ages (from 22 to 97 years) (Table 1), dominated by Albic Brunic Arenosols (World Reference Base 2015) with a uniform soil texture (sand). The 100-meter-long transect was delineated

in each stand, where we placed five litterfall traps every 25 m (Fig. 1c). Litterfall traps had an entry diameter of 50 cm and were placed 1 m above the ground. The litterfall traps had a perforated bottom, which made it impossible for the rainwater to remain inside. The falling organic matter stopped on the permeable mesh placed inside each litterfall trap (Fig. 1c). We installed the litterfall traps in all pine stands on 19th April 2019, i.e. around the term when the growing season usually starts in this region. Then we collected litter from the litterfall traps once a month in each experimental plot (12 sampling periods) (Table 2).

Laboratory tests

We determined seasonal changes in water absorbability of bark and needles taken from

Scots pine stands of different ages during laboratory tests. First, we separated pine bark and collected a sample of pine needles from the litter gathered from each litterfall trap in a given month. Needle and bark samples separated from all the five litterfall traps in a particular experimental plot were mixed to form aggregate samples of bark and needles for each Scots pine stand, and then all the samples were dried at 35°C to constant mass.

The determination of water absorbability consisted in measuring the time of water absorption by pine needles and bark and the minimum time needed to fill their internal capillarity (Ilek et al. 2019). After drying the needles and bark at 35°C, each sample was submerged in distilled water. We measured the water

absorption time from the moment particular bark pieces and needles were submerged in water until they reached a density $>1 \text{ g cm}^{-3}$, i.e. until bark and needles fell to the bottom of the container (Ilek et al. 2019, Kuczka 2007, Kuczka & Urbaś 2005). Samples were submerged in water for no longer than 14 days and those bark pieces and needles which did not sink to the bottom of the container after 14 days were considered unable to achieve the desired absorbability, i.e. density greater than 1 g cm^{-3} (Ilek et al. 2019). All samples were covered from above with a wet textile during the immersion process. We were removing sunk bark pieces and needles from the containers at least once a day and at that time we also replaced water in the containers. The sunk needles and bark pieces were gently dried using a moist paper towel

Table 1 Characteristics of Scots pine stands.

Plot	Age [yr]	Location	Alt [m asl]	Dbh [cm]	H [m]
P_100	97	53°42'49.3"N 16°52'44.9"E	140	35	24
P_80	77	53°42'22.0"N 16°53'07.9"E	139	26	21
P_60	60	53°42'17.8"N 16°52'16.3"E	137	23	21
P_40	41	53°42'13.8"N 16°52'37.0"E	138	16	13
P_20	22	53°42'20.3"N 16°52'21.4"E	138	10	9

Plot: Plot symbol; Age: Age of stand; Alt: Altitude; Dbh: Breast height diameter; H: Average height of stand

Table 2 Detailed information on sampling date of needles and bark.

Sampling period	Month	Time of litterfall collection	Season
I	January	20-12-19 – 19-01-20*	Winter
II	February	20-01-20 – 19-02-20*	
III	March	20-02-20 – 19-03-20*	
IV	April	20-03-20 – 19-04-20*	Spring
V	May	19-04-19** – 19-05-19*	
VI	June	20-05-19 – 19-06-19*	
VII	July	20-06-19 – 19-07-19*	Summer
VIII	August	20-07-19 – 19-08-19*	
IX	September	20-08-19 – 19-09-19*	
X	October	20-09-19 – 19-10-19*	Autumn
XI	November	20-10-19 – 19-11-19*	
XII	December	20-11-19 – 19-12-19*	

where * is the term when litter samples were collected from litterfall traps in a given month, ** is the term when litter traps were placed inside experimental plots.

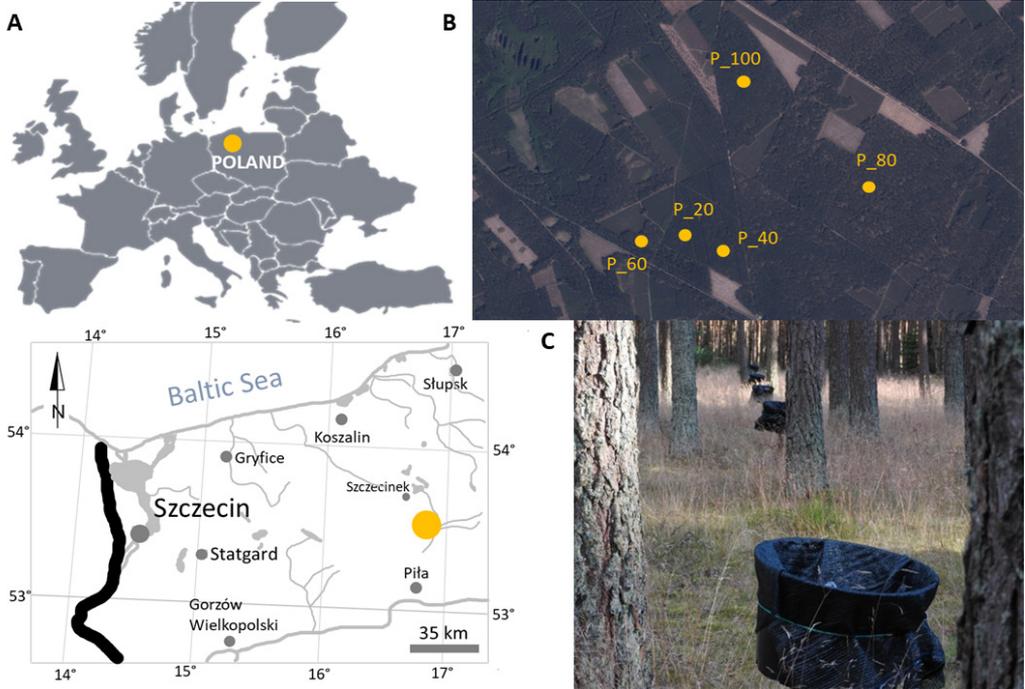


Figure 1 Location of the study area (A) with a view of particular Scots pine stands where organic matter was collected (B), and a view of the transect with litterfall traps placed within the P_100 stand (C).

to remove excess water from their surface. Then we determined the wet mass m_w [g] of bark pieces and needles, volume v [cm³] with a standard displacement method in a graduated cylinder and their dry mass m_s [g] after drying of individual samples at 105°C. Based on the m_w , m_s , and v we calculated the moisture content MC [%] and bulk density BD [g cm⁻³] of bark and needles according to the formulas:

$$MC = \frac{(m_w - m_s)}{m_s} \times 100 \quad (1)$$

$$BD = \frac{m_s}{v} \quad (2)$$

We calculated the average time of water absorption T_A [days] by bark and needles collected in a given month and the pine stand according to the formula:

$$T_A = \frac{\sum_{i=1}^n m_{Si} \times t_i}{\sum_{i=1}^n m_{Si}} \quad (3)$$

where t is the time, after which the i -th batch of needles or bark fell to the bottom of the container and reached a density greater than 1 g cm⁻³ [days].

The minimum time T_{MIN} needed to fill the internal capillarity is the time when 75% of the needles or bark pieces from a given month and pine stand reached a density greater than 1 g cm⁻³. We determined this time based on the cumulative percentage of all needles or bark pieces that sank after a given soaking time during 14 days of the immersion process (Ilek et al. 2019).

We analyzed contents of organic carbon (C) and total nitrogen (N) in needles and bark

collected in a given month of the year from each Scots pine stand. Contents of total nitrogen and organic carbon were measured using a LECO CNS True Mac Analyzer (Leco, St. Joseph, MI, USA), including the C/N ratio calculation.

Statistical analysis

The statistical analysis and associated graphics were performed in the Statistica 13.3 PL software (StatSoft Inc.). We used the Mann-Whitney U test to compare physical, chemical and hydrological properties of pine needles and pine bark collected from all litterfall traps during the 12-month study period. Significant differences in the mean water absorption time, the minimum time of filling the internal capillarity of pine needles and bark, carbon and nitrogen contents in needles and bark between individual stands, months and seasons were tested by the non-parametric Kruskal-Wallis test and one-way ANOVA with the post-hoc Tukey test. Normality and equality of variance were checked by the Shapiro-Wilk and Levene's tests, respectively. We adopted a general linear model (GLM) to investigate the

effect of age of Scots pine stands and the effect of sampling date (month of the year or season) on bark and needles characteristics. All the tests were performed at a significance level of 0.05.

Results

Hydro-physical and chemical properties of pine bark and needles

Bark and needles collected during the entire 12-month study period in all the pine stands differed in terms of their physical, chemical and hydrological properties (Fig. 2). The bulk density of bark was significantly greater than that of needles ($p = 0.039$). Bark contained significantly less organic carbon and total nitrogen than needles ($p < 0.001$), on average by 2.3 and 63.0%, respectively. The C/N ratio in needles was significantly lower than the C/N ratio in bark ($p < 0.001$), on average by 65.3%. No significant differences were observed in the moisture content between bark and needles ($p = 0.397$). Still, T_A and T_{MIN} were significantly lower for bark than needles, on average by 31.1 and 34.5%, respectively ($p < 0.001$).

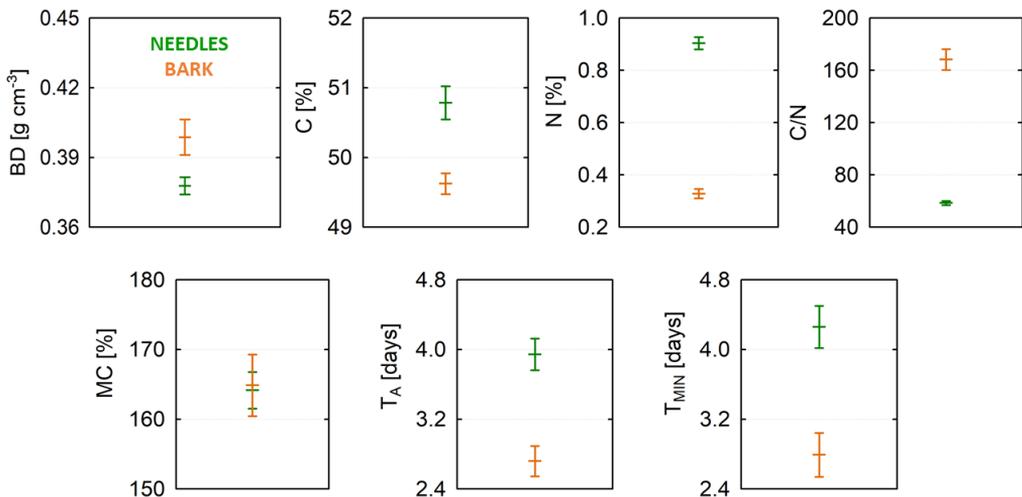


Figure 2 General characteristics of pine needles and bark collected during 12 months in all examined Scots pine stands, where BD is bulk density, C is organic carbon content, N is total nitrogen content, C/N is the ratio of organic carbon content to total nitrogen content, MC is moisture content at the moment when needles and bark reached the density of 1 g cm^{-3} , T_A is the mean time of water absorption, T_{MIN} is the minimal time of filling the internal capillarity (mean±SE).

Water absorbability and chemical properties of litter components collected in Scots pine stands of different ages

The mean time of water absorption (T_A) by pine needles ranged from 2.2 days (P_60) to 9.5 days (P_20), while that for pine bark ranged from 1.0 days (P_20, P_40, and P_80) to 7.2 days (P_20). Both needles and bark collected from the P_20 plot were characterized the highest variability in T_A among all the pine stands ($CV = 49\%$ and 74% , respectively). No significant differences were observed in T_A of needles and bark among individual pine stands, but T_A of needles collected from the younger stands (P_20 and P_40) was $\sim 11\%$ higher than T_A of needles from older stands (P_60-100) (Table 3). Similarly, no differences were found in the T_{MIN} of needles and bark between the pine stands, but T_{MIN} of needles taken from the younger stands (P_20 and P_40) was $\sim 12\%$ higher than T_{MIN} of needles from the other stands (Table 3).

Carbon content in pine needles ranged from

43.7% (P_40) to 61.4% (P_60) and in pine bark ranged from 47.7% (P_20) to 53.0% (P_60). Needles from the P_20 stand contained significantly less carbon than needles from the P_80 stand ($p = 0.043$). No significant differences were found in bark carbon contents between the stands (Table 3). Nitrogen content in pine needles ranged from 0.60% (P_100) to 1.27% (P_40) and in pine bark ranged from 0.14% (P_80) to 0.70% (P_100). No significant differences were found in needles and bark nitrogen contents between the stands (Table 3). The C/N ratio in pine needles ranged from 40.0 (P_40) to 85.4 (P_100), while in pine bark it ranged from 71.0 (P_100) to 343.6 (P_80). The C/N ratio in needles and bark did not differ between the Scots pine stands, but the C/N ratio in bark collected in the older stands (P_80 and P_100) was on average $\sim 15\%$ higher than that in bark from the other stands.

The GLM analysis confirmed that the age of the stand did not affect T_A , T_{MIN} , C, N, and the C/N ratio of bark and needles (Table 4).

Table 3 Statistics of the mean water absorption time and the minimum time of filling the internal capillarity of pine needles and bark and carbon content, nitrogen content and the C/N ratio in needles and bark collected in Scots pine stands of different ages, where different letters denote significant differences between pine stands based on * the Kruskal-Wallis test and ** one-way ANOVA (with the post-hoc Tukey test) ($p < 0.05$).

Organic matter type	Exp. plot	Mean time of water absorption [days]		Minimum time of filling the internal capillarity [days]		Carbon content [%]		Nitrogen content [%]		C/N	
		Mean	Median*	Mean	Median*	Mean	Median*	Mean	Median*	Mean	Median
		\pm Std error		\pm Std error		\pm Std error		\pm Std error**		\pm Std error**	
Pine needles	P_20	4.2 \pm 0.6	3.5 ^a	4.4 \pm 0.8	3.4 ^a	50.1 \pm 0.3	50.3 ^a	0.84 \pm 0.04 ^a	0.85	60.9 \pm 3.0 ^a	57.2
	P_40	4.3 \pm 0.4	4.3 ^a	4.7 \pm 0.6	4.8 ^a	50.4 \pm 0.7	50.8 ^{ab}	0.91 \pm 0.06 ^a	0.94	58.4 \pm 4.0 ^a	54.0
	P_60	3.7 \pm 0.3	3.6 ^a	4.0 \pm 0.4	3.8 ^a	51.6 \pm 0.9	50.7 ^{ab}	0.90 \pm 0.05 ^a	0.90	59.1 \pm 3.5 ^a	55.8
	P_80	3.7 \pm 0.3	3.6 ^a	4.0 \pm 0.4	3.8 ^a	51.0 \pm 0.2	51.0 ^b	0.91 \pm 0.05 ^a	0.89	58.1 \pm 3.2 ^a	57.6
	P_100	3.9 \pm 0.4	3.3 ^a	4.2 \pm 0.5	3.4 ^a	50.8 \pm 0.1	50.8 ^{ab}	0.95 \pm 0.06 ^a	0.99	56.1 \pm 4.0 ^a	52.3
Pine bark	P_20	3.0 \pm 0.6	2.6 ^a	3.3 \pm 0.9	2.2 ^a	49.4 \pm 0.4	49.6 ^a	0.33 \pm 0.06	0.37 ^a	150.3 \pm 20.4 ^a	124.1
	P_40	2.9 \pm 0.3	2.7 ^a	3.1 \pm 0.5	2.5 ^a	50.3 \pm 0.5	49.7 ^a	0.35 \pm 0.03	0.34 ^a	157.4 \pm 14.8 ^a	145.0
	P_60	2.6 \pm 0.3	2.3 ^a	2.5 \pm 0.4	2.0 ^a	49.9 \pm 0.3	49.5 ^a	0.35 \pm 0.04	0.33 ^a	160.5 \pm 17.2 ^a	152.4
	P_80	2.8 \pm 0.3	2.6 ^a	3.0 \pm 0.5	2.6 ^a	49.3 \pm 0.2	49.5 ^a	0.29 \pm 0.03	0.27 ^a	187.2 \pm 19.7 ^a	187.1
	P_100	2.3 \pm 0.3	2.1 ^a	2.0 \pm 0.4	1.5 ^a	49.2 \pm 0.2	49.2 ^a	0.32 \pm 0.05	0.28 ^a	181.0 \pm 18.2 ^a	180.7

Table 4 GLM analysis for needles and bark characteristics. Significant effects ($p < 0.05$) are shown in bold.

		T_A		T_{MIN}		C		N		C/N	
		F	p	F	p	F	p	F	p	F	p
Needles	Age of stand	1.973	0.115	1.740	0.158	0.842	0.506	2.240	0.080	0.996	0.420
	Sampling date	18.122	0.000	20.551	0.000	0.270	0.988	19.777	0.000	20.770	0.000
		25.296	0.000	25.659	0.000	0.435	0.729	22.519	0.000	25.052	0.000
Bark	Age of stand	0.662	0.622	0.991	0.421	2.030	0.106	1.452	0.236	1.003	0.416
	Sampling date	3.937	0.001	3.859	0.001	1.198	0.321	2.080	0.047	1.155	0.349
		3.827	0.015	2.735	0.053	1.560	0.212	3.019	0.039	2.387	0.081

Seasonal variation in hydrological and chemical properties of pine bark and needles

T_A and T_{MIN} of pine needles changed over the year (Fig. 3A, B). The greatest variation in T_A and T_{MIN} of needles was observed in February (CV = 26 and 36%, respectively), while the lowest variation in November for T_A (CV = 8%) and in January for T_{MIN} (CV = 10%). We found the lowest mean values of T_A and

T_{MIN} of needles in March (2.5 ± 0.2 days and 2.4 ± 0.3 days), and the highest mean values in August (6.9 ± 0.7 days and 8.4 ± 0.8 days, respectively). We observed an upward trend in the water absorption time (both T_A and T_{MIN}) from January to August and a downward trend from August to December. From January to August T_A and T_{MIN} of needles increased on average by 61.4 and 67.5%, and from August to December T_A and T_{MIN} decreased on average by 56.8 and 66.5%, respectively (Fig. 3).

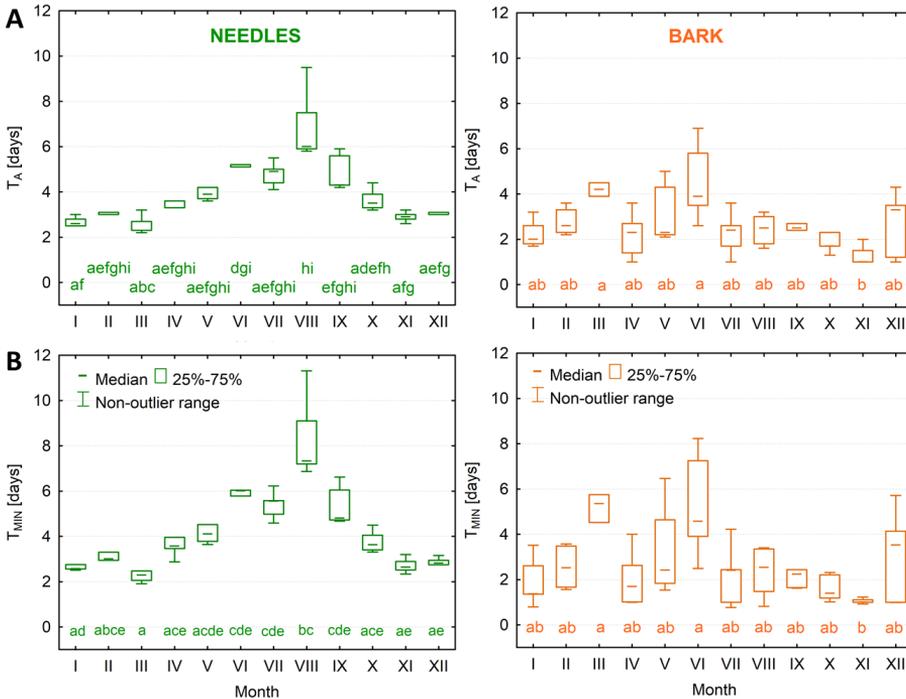


Figure 3 Seasonal variations in (A) the mean time of water absorption T_A and (B) minimum time of filling the internal capillarity T_{MIN} of pine needles and bark collected in individual months of the year. Different letters denote significant differences between months based on the Kruskal-Wallis test ($p < 0.05$).

We observed the greatest variation in T_A and T_{MIN} of pine bark in December (CV = 55 and 67%, respectively), and the lowest variation in February for T_A (CV = 22%) and in November for T_{MIN} (CV = 11%). We found the lowest mean values of T_A and T_{MIN} of bark in November (1.3 ± 0.2 days and 1.1 ± 0.1 days), while the highest mean values were recorded in March (4.5 ± 0.7 days) and June (4.5 ± 0.8 days) for T_{MIN} , and in March (5.5 ± 1.2 days) and June (5.3 ± 1.1 days) for T_A (Fig. 3). Significant differences in T_A of bark were observed between March and November ($p = 0.005$) and between June and November ($p = 0.011$). Similarly, T_{MIN} of bark collected in November was significantly lower than T_{MIN} of bark collected in March ($p = 0.016$) and June ($p = 0.017$) (Fig. 3).

The greatest variation in carbon contents in pine needles was found in September (CV = 12%) and the lowest in June (CV = 0.05%). Needles collected in July contained the least carbon ($50.1 \pm 0.1\%$ on average), whereas needles collected in February and March contained the highest carbon levels ($51.3 \pm 0.1\%$ and $51.4 \pm 0.2\%$, respectively) (Fig. 4). The greatest variation in nitrogen contents in pine needles was found in August (CV = 21%) and the lowest in June (CV = 2%). From October to April the nitrogen content in needles increased on average by 44.7% and from April to September decreased on average by 38.3%. No significant differences were observed in carbon and nitrogen contents in pine bark between individual months over the year (Fig. 4). The C/N ratio in needles changed over the year. We observed an upward trend in the C/N ratio in needles from April to October and a downward trend from October to March. From April to October the C/N ratio in needles increased on average by 44.8%, whereas from October to March the C/N ratio decreased on average by 39.3% (Fig. 4c). No significant differences were observed in the C/N ratio in pine bark between individual months over the year. Still, the lowest average C/N ratio in bark was found in January (102 ± 24), while it was highest in June (213 ± 23) and May (195 ± 23) (Fig. 4).

The GLM analysis confirmed the importance

of sampling date in determining the N content, C/N ratio, T_A , T_{MIN} of needles and T_A , T_{MIN} and N content of bark (Table 4).

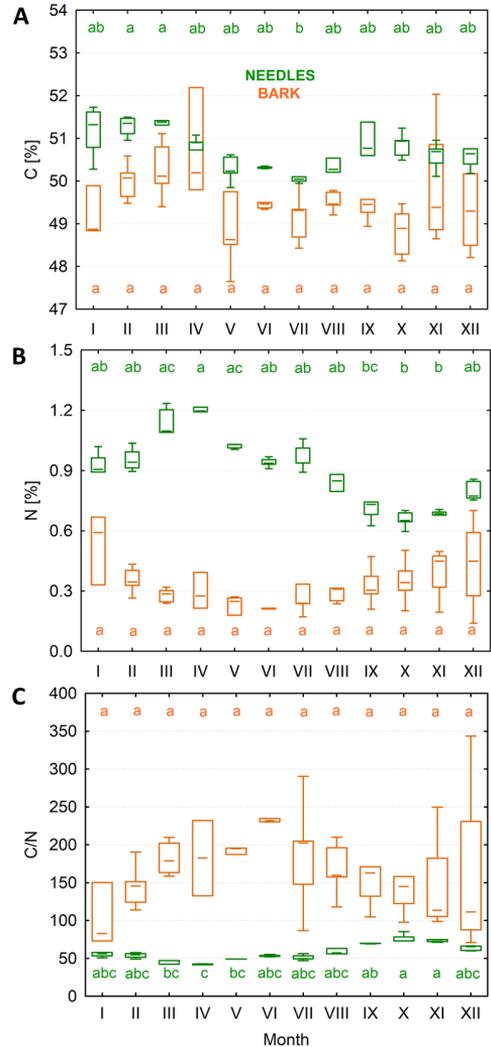


Figure 4 Seasonal variations in (A) carbon content C, (B) nitrogen content N and (C) the C/N ratio in pine needles and pine bark collected every month over one year. Different letters denote significant differences between months based on the Kruskal-Wallis test ($p < 0.05$) (median, 25-75%, non-outlier range).

T_A and T_{MIN} of pine needles and bark differed between the seasons (Fig. 5). The greatest variation in T_A of needles was observed in summer (CV = 26%) and T_{MIN} in winter and summer (CV = 30 and 29 %). The lowest variation in T_A and T_{MIN} was observed in autumn (CV = 15 and 20%). T_A of needles collected in summer was higher than T_A of needles collected in autumn, winter and spring, on average amounting to 42.3, 48.9, and 23.3%, respectively (Fig. 5). Similarly, T_{MIN} of needles collected in summer was by 51.4, 55.2, and 26.3 higher than T_{MIN} of needles collected in autumn, winter and spring. We found the lowest mean values of T_A and T_{MIN} of bark in autumn (1.9 ± 0.3 days and 1.9 ± 0.4 days), and the highest mean values in spring (3.3 ± 0.4 days and 3.6 ± 0.6 days, respectively). T_A of bark collected in spring was higher than that of bark collected in summer, autumn and winter, on average amounting to 26.0, 41.3, and 3.6%, respectively (Fig. 5). Similarly, T_{MIN} of bark collected in spring was by 35.1, 46.4,

and 6.6% higher than T_{MIN} of needles collected in summer, autumn and winter.

We found significant differences in carbon contents between needles collected in winter and spring ($p = 0.002$) and between winter and summer ($p = 0.001$) (Fig. 6). No differences were recorded in bark carbon contents between the seasons. Needles collected in autumn contained significantly less nitrogen than those collected in spring ($p < 0.001$), summer ($p = 0.011$) and winter ($p < 0.001$). No significant differences were found in nitrogen contents and the C/N ratio in bark between the seasons. The C/N ratio in needles collected in autumn was significantly higher than the C/N ratio in spring ($p < 0.001$) and winter ($p < 0.001$). The C/N ratio in needles collected in summer was ~15% higher than the C/N ratio in spring and lower than the C/N ratio in needles collected in winter and autumn, on average by 16.1% and 23.8%, respectively.

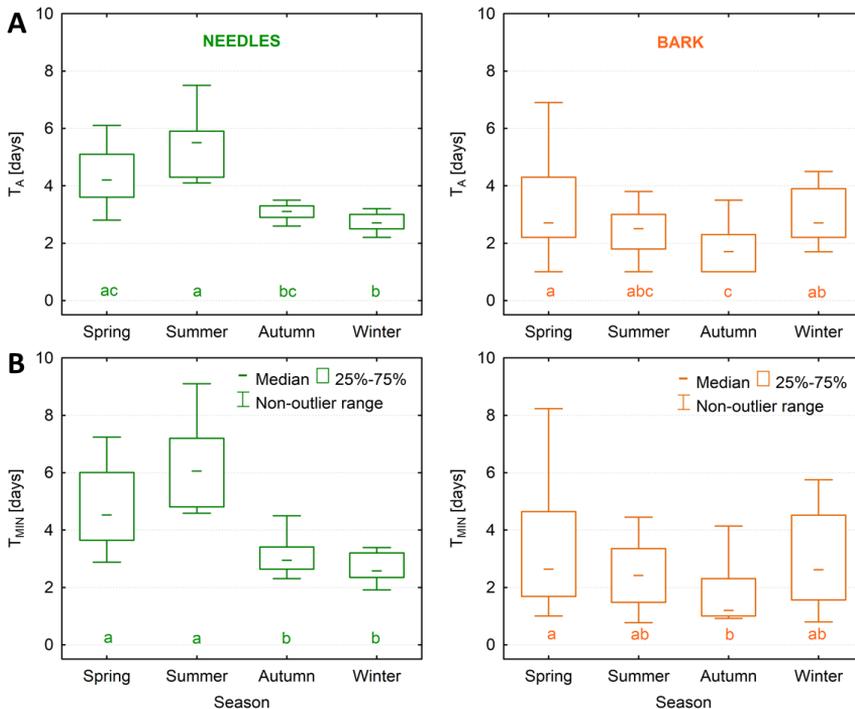


Figure 5 Seasonal variations in (A) the mean time of water absorption T_A and (B) minimum time of filling the internal capillarity T_{MIN} of pine needles and bark collected in spring, summer, autumn and winter. Different letters denote significant differences between the seasons based on the Kruskal-Wallis test ($p < 0.05$).

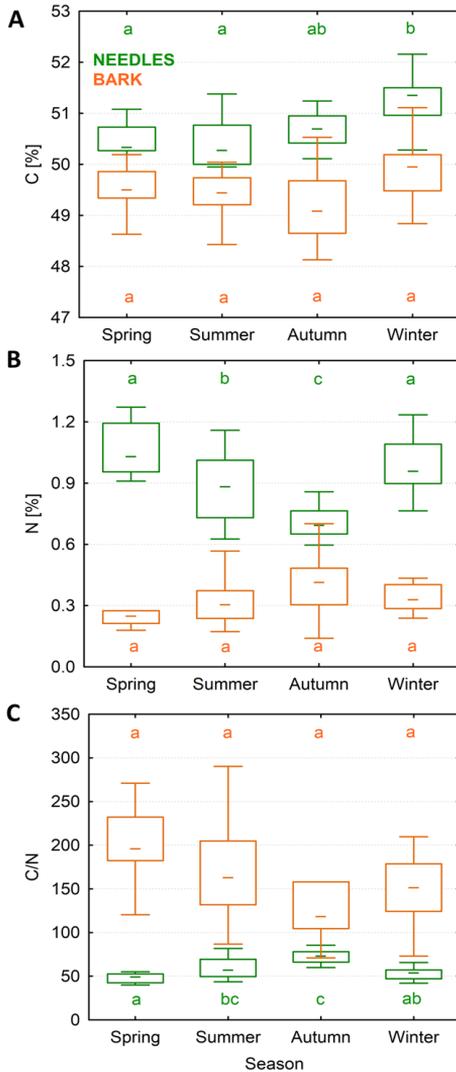


Figure 6 Seasonal variations in the content of organic carbon C (A), total nitrogen N (B), and the C/N ratio (C) in pine needles and pine bark collected in spring, summer, autumn and winter. Different letters denote significant differences between the seasons based on the Kruskal-Wallis test ($p < 0.05$) (median, 25-75%, non-outlier range).

Discussion

We stated that the T_A for all pine needles collected over one year amounted on average to 3.3 days. This time was similar to T_A of silver fir

needles (3.2 days) and higher than of Norway spruce needles and European beech leaves, on average by ~ 21 and $\sim 73\%$, respectively (Kucza & Urbaś 2005, Ilek et al. 2019). These differences indicate that the time of water absorption may depend on the botanical origin of the organic debris, which probably is related to its chemical composition and morphology. The organic chemical composition of tree litter seems to vary with tree species. Berg & Wessen (1984), who compared the chemical composition of needle and leaf litter from Scots pine and white birch, stated that birch leaf litter had higher concentrations of water solubles and lower levels of cellulose and lignin than the pine needle litter. Pine needles have embedded stomata and a waxy layer on their thick-walled epidermis to protect them from water loss (Krakau et al. 2013), hindering water absorption to the inside of undecomposed needles. To our best knowledge, no previous studies are available on the water absorption time by bark being a component of litterfall. The approximately 30% lower T_A and T_{MIN} of bark compared to T_A and T_{MIN} of needles may be associated with a higher bulk density of bark (Fig. 2), as a result of which bark needs to absorb less water to achieve a density $> 1 \text{ g cm}^{-3}$ (assuming the same rate of water absorption by bark and needles). Bark and needles were characterized by significant differences in their contents of C and N and the C/N ratio, which may have an impact on the v and T_{MIN} . A 3-fold greater C/N ratio was recorded in bark than needles; thus, it may be assumed that this is reflected in the rate of bark decomposition and, consequently, the time of water absorption. Previous studies have shown that nitrogen concentration in the litter and the C/N ratio are strongly related to the rate of litter decomposition (Krishna & Mohan 2017).

We observed no significant effect of the stand age on T_A and T_{MIN} of pine bark and needles (i.e. hypothesis 1 was not rejected) (Table 3-4). We did not also confirm the influence of stand age on the C and N contents in litterfall in a pine forest. Only in the case of needles in the

80-year-old stand a statistically significantly higher C content was recorded. The lack of differences in T_A and T_{MIN} and the chemical composition of needles between the stands may be associated with a similar age of falling needles (2-3 years), especially that Scots pine sheds one needle cohort at a time (Muukkonen 2005). The inputs of C and N in the litterfall depend on several ecological factors and forest management activities such as forest type, climate, site quality, stand increment, stand age, stand density, fertilization and thinning (Cuveas & Lugo 1998, Kim et al. 2009). In the case of bark, there was a downward trend in the N content with the age of stand. The decrease in nitrogen content is the result of the bark aging process. The bark of trees comprises dead outer bark (periderm) and living inner bark, i.e. non-lignified phloem, including conducting and non-conducting phloem and parenchyma (Oberhuber et al. 2020). Needle and bark biomass usually increases with the age of Scots pine trees (Vanninen et al. 1996), which affects litterfall, i.e. the amount of litterfall usually increases with the age of stand (Małek & Grabowski 2010). As the litter horizon usually has low density and high porosity (Osman 2013a), water at this horizon is retained mainly on the surface of individual litter fractions and is absorbed into their inside (Ilek et al. 2015). Thus, despite the lack of differences in the water absorption time of bark and needles between stands, stand age may affect the total water storage capacity of the forest floor.

We confirmed a significant effect of the term when litter falls (month and season) on T_A and T_{MIN} of needles and bark (i.e. hypothesis 2 was rejected). Seasonal variability of T_A and T_{MIN} may be caused by the seasonal variability of the N content in pine needles and bark. Seasonal variability in the case of C content was not confirmed. The lowest amounts of C and N in needles are delivered to the soil in summer. In this season T_A and T_{MIN} of needles were the highest (Fig. 5), which could also be related with the fact that Scots pines shed their oldest

needles during August-October (Ukonmaanaho et al. 2008). In the case of C, an increase was recorded in autumn and winter, while in the case of nitrogen it was in winter. In these seasons T_A and T_{MIN} of needles was the lowest (Fig. 5). According to Helmisaari (1990), concentrations of the mobile nutrients N, P and K decreased in spring and early summer during shoot and needle elongation and increased in late summer and autumn during needle senescence and litterfall. Nutrients are retranslocated from aging needles and stored in the tree over winter and used by the growing tissues in spring. Nutrient concentrations in needles of coniferous species are associated with the course of the annual physiological cycle (Fife & Nambiar 1984). According to Blanco et al. (2008), seasonal changes in nutrient concentrations, which are buffered by resorption, but can also be reflected in needle litter, are mainly caused by changes in the flow rates of carbohydrates, N and P in (i.e. xylem sap) and out (i.e. resorption and leaching) of green needles.

In our research we proved that litterfall in pine stands is important for increasing the carbon and nitrogen reserves in forest soils. Our study confirmed that litterfall is highly significant in the functioning of ecosystems, as it is a major element in the recycling of nutrients, especially carbon and nitrogen in the ecosystem. According to Kim et al. (2010), litterfall inputs and litter decomposition represent important components of the carbon and nitrogen cycles in forest ecosystems. Jasińska et al. (2020) discovered that even the litterfall categories of relatively low mass were important for the total return of nutrients to the topsoil. In the case of pine needles we noted over 50 times more C returning to the soil compared to N. In the case of pine bark 150 times more C is transferred to the soil compared to N. Litterfall in West European forests was the greatest source of soil carbon, providing about 70-80% of total C (Liski et al. 2002). In our study we confirmed that different categories of litterfall (bark and needles) have different chemical composition,

which in turn is reflected in the properties of litter and its decomposition in the soil surface horizons. The C content in pine needles and bark was comparable. In the case of bark a significantly lower N content was recorded, being 3-fold lower, which consequently resulted in a significantly higher C/N ratio and probably a slower decomposition rate. According to Melillo et al. (1982), leaf litter decomposition can be calculated from the C/N ratio. In general the decomposition rate is high in materials with extreme ash and nitrogen contents.

In pine stands the litterfall fractions are usually homogeneous, with low ash content and acidic reaction. This litterfall contains compounds that are difficult to access for soil fauna, so they are slowly mineralized (Gonet et al. 2007). Scots pine forests characteristically grow on sandy, dry soils and usually in nutrient-poor sites (Richardson 2000). Poor habitat and hardly decomposable organic debris result in a thick forest floor often formed in Scots pine stands, which plays a crucial role in rainfall retention. However, water retention in the pine forest floor and factors that influence this process are still poorly understood. Greiffenhagen et al. (2006) found that the forest floor in pine stands may contain over 20% of the total amount of water available to plants. On the other hand, Leuschner (1998) reported that the amount of water available to plants in the forest floor of pine stands is about 20% lower than in the forest floor of beech and oak stands. In our research we took into account only some components of litterfall, i.e. needles and bark. However, other categories of litterfall from various parts of trees, such as branches, cones, seeds, fruits, etc., are also important in the nutrient cycling dynamics, because they change the quality of annual litterfall (Cuevas & Lugo 1998). Annual litter production in Scots pine stands may vary from 1.3 to 5.3 t ha⁻¹ (Maddelein & Lust 1992, Ukonmaanaho et al. 2008). The average proportion of needle litter to the total litter production in these stands may vary from 34 to 80% (Pausas 1997,

Berg & Meentemeyer 2001), the non-needle part amounts to about 30-40 %, while cones and branch bark have about equal shares in the total litter (15 to 20 %) (Maddelein & Lust 1992). Santa Regina & Tarazona (2001) reported annual branch litterfall of 1.8 t ha⁻¹, which made up about 30% of the total litterfall in Spain. Thus, to gain insight into complete hydrological properties of the forest floor further research is needed on water absorption of individual litterfall components and its variability over the year.

Conclusions

We evaluated the water absorption time of freshly fallen litterfall components (needles and bark) collected every month over one year in Scots pine stands of different ages. The water absorption time (the time needed to fill the internal capillarity of organic particles) differed between pine bark and needles. We observed no significant effect of stand age on the water absorption time of bark and needles, but the term when litter falls (month of the year or season) significantly affected the water absorption time. Seasonal variability of the water absorption time was probably caused by the seasonal variability in the chemical composition of needles and bark. It indicates that organic matter reaching the forest floor and forming the litter layer is characterized by different output properties affecting the litter water storage capacity, thus meriting further research. In summary, litterfall (bark and needles) in pine stands is important for increasing the carbon and nitrogen reserves in forest soils. This implies that the selected species composition of a stand can significantly influence carbon and nitrogen contents in soil.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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