Received: 20 April 2021 | Revised: 19 July 2021 | Accepted: 19 August 2021

DOI: 10.1002/eco.2349

RESEARCH ARTICLE

WILEY

The effect of plant size and branch traits on rainfall interception of 10 temperate tree species

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Funding information
Horizon 2020 Framework Programme, Grant/Award Number: 641739

Abstract

Rainfall interception by vegetation plays an important role in the hydrological cycle. Next to rainfall characteristics, interception is influenced by tree size, crown structure and bark morphology. How tree traits determine interception across functionally and morphologically wide-ranging tree species is poorly understood. We determined interception ratios (interception:gross precipitation) and canopy storage capacities of seven temperate deciduous broadleaved (*Acer pseudoplatanus* L., *Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Populus tremula* L., *Sorbus aucuparia* L.) and three evergreen coniferous tree species (*Picea abies* (L.) Karsten, *Pinus sylvestris* L., *Pseudotsuga menziesii* (Mirb.) Franco) as well as the influence of various tree traits on interception parameters. Interception was measured directly with natural rainfall by means of gravimetry on potted trees, 2–8 m tall, for seven consecutive months. Our results show that (a) the coniferous species had larger canopy storage capacities and larger interception ratios than the broadleaved species both during (summer) and outside the growing season (winter); (b) the absolute tree interception (in kg) of the broadleaved species was positively related to stem diameter at breast height, tree and crown height, maximum branch length, the total branch surface area and above ground dry weight; and (c) interception per unit crown projected area (in mm) of all species was positively related to branch length and branch surface area per unit crown projected area. These results can be used to estimate interception parameters from plant traits and to simulate interception losses of trees in a more reliable manner.

KEYWORDS
deciduous, evergreen, forest hydrology, gravimetry, plant traits, precipitation partitioning

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Abbreviations: (*BA*), mean branch angle; (*BC*), total branch count; (BC_{CPA}), branch count per CPA; (*BD*), mean distance between branches at the trunk; (BL_{CPA}), branch length per CPA; (BL_{max}), maximum branch length; (BL_{tot}), total branch length; (*BSA*), total branch surface area; (BS_{CPA}), branch surface area per CPA; (*CH*), crown height; (*CPA*), crown projected area; (*CPM:CPA*), ratio crown perimeter:crown projected area; (CW_{max}), maximum crown width; (*DBH*), diameter at breast height; (DW_B), total branch dry weight; (DW_{CPA}), branch dry weight per CPA; (DW_{tot}), total aboveground wood dry weight; (*H*), tree height; (*I*), interception; ($I{:}G_P$), interception ratio; (I_{cum}), cumulative interception; (*S*), canopy storage capacity.

1 | INTRODUCTION

Rainfall interception by vegetation is defined as the fraction of precipitation which is retained by vegetation during and after a precipitation event and which subsequently evaporates from this surface (Crockford & Richardson, 2000). The part of the precipitation reaching the soil either passes through the canopy (throughfall) or is diverted from the branches down the stem (stemflow). Intercepted precipitation directly re-enters the atmosphere as water vapour where it forms part of the moisture feedback to support continental precipitation (van Der Ent et al., 2010). Globally, interception is estimated to be 19% of the gross precipitation for broadleaved and 22% for coniferous forests (Miralles et al., 2010). The intercepted part of the precipitation is not available for soil moisture and groundwater replenishment or run-off, which can lead to a decreased water resource availability and to a possible scarcity of water for, for example, drinking, agricultural or industrial purposes (e.g., van Huijgevoort et al., 2020). Water scarcity is of increasing relevance in the course of current and predicted climate change, where meteorological patterns are changing to wetter winters and drier and hotter summers in many temperate and boreal regions (IPCC, 2014). For this reason, knowledge of determinants of interception losses, especially of trees, can be useful to align land use with current and foreseen water needs.

Rainfall interception is influenced by both abiotic and biotic factors and the interaction within and between them (Bartholomeus et al., 2015). The specific combination of the biotic and abiotic factors determines how the rain drops hit and travel through the canopy. For example, the vegetation can be wetted directly by incoming rain drops and/or indirectly by dripping from other leaves or branches (see Klamerus-Iwan et al., 2020). As the drops travel through the canopy, their size and velocity change, which influences the interception processes (Zabret et al., 2017). Especially high intensity rain events lead to splashes when the rain drops hit a leaf or branch. These splash droplets can then end up as throughfall, land on other plant parts, thereby adding to interception or initiating dripping, or evaporate immediately when the droplets are small enough (splash droplet evaporation, Murakami, 2006). Next to the evaporation of splash droplets, intercepted water can evaporate during the rain event and, lastly, after the rain event. The rate of interception evaporation is determined by air temperature, solar radiation, wind speed and air humidity (Allen et al., 1991). Below, the main abiotic and biotic factors influencing interception are briefly introduced. The most important abiotic factors are precipitation amount (Llorens et al., 1997; Rutter, 1963) and intensity (Li et al., 2016; Toba & Ohta, 2005). Duration and frequency of rainfall events (Rutter & Morton, 1977), wind speed (Staelens et al., 2008) and direction (Zabret et al., 2018) during and after the event as well the precipitation type (rain or snow) (Lundberg & Halldin, 2001) also influence interception.

The key biotic factors are the structural properties of the intercepting vegetation, from the traits of the individual leaf to the bark structure to the canopy architecture including the three-dimensional arrangement of its foliage. Individual leaf area (Yang et al., 2019), the presence and density of trichomes ('leaf hairs') (Brewer et al., 1991) and leaf hydrophobicity (Holder & Gibbes, 2017) influence the interception process. Coniferous (needle-like) leaves intercept more rain than broad leaves (as a percentage of total rain; Horton, 1919; Barbier et al., 2009). Depending on the thickness and texture of the bark, the bark can either increase flow along the stem or serve as a water storage organ (Carlyle-Moses & Schooling, 2015; Crockford & Richardson, 2000). Naturally, the actual size of the canopy has a large impact on rainfall interception. Traits such as total leaf area (Aston, 1979; Klimenko et al., 2019; Li et al., 2016), leaf area index (*LAI*) (Deguchi et al., 2006; Fathizadeh et al., 2017), canopy openness (in a negative relation; Llorens & Gallart, 2000; Soto-Schönherr & Iroumé, 2016; Wei et al., 2017) and the projected surface area of a tree (i.e., branches and leaves) (Baptista et al., 2018) can be used to estimate interception loss (i.e., the ratio of interception to gross precipitation) and canopy storage capacity (i.e., the maximum amount of water a plant can hold). Since stem diameter at breast height (*DBH*) tends to be positively related to tree height (Sharma & Parton, 2007) and to total leaf area (Vertessy et al., 1995), both *DBH* (Ahrends & Penne, 2011; Fathizadeh et al., 2017; Soto-Schönherr & Iroumé, 2016) and tree height (Calvo-Alvarado et al., 2018; Llorens & Domingo, 2007; Wani & Manhas, 2012) have been shown to correlate with interception loss and storage capacity. Less well studied are the effects of branch dimensions, angles and density of the whole tree on interception. For individual branches, positive relationships between storage capacity and branch diameter (Liu, 1998; Llorens & Gallart, 2000) as well as total leaf area of the branch (Klimenko et al., 2019) have been observed. The effect of various branch traits on whole-tree interception of four different trees was studied by Li et al. (2016). For this, trees were placed on weighing balances and subjected to artificial rainfall. After the experiment, the tree was cut into parts to determine branch lengths and woody surface area. Their results showed that the total branch length, branch number, branch density (i.e., the number of branches per unit crown volume) as well as the woody surface area were positively related to canopy storage capacity. In our study we want to further explore the relationships between tree properties and interception parameters by including species with a wider range of tree architectures and foliage phenologies representative for temperate and boreal forests under natural rainfall conditions.

In this study we aim to answer the following research question: How do tree size and branch traits affect interception amounts of 10 common temperate tree species of wide-ranging morphology and foliage phenology? These species included seven broadleaved deciduous and three coniferous evergreen species. To answer our research question, we set up an outdoor experiment where each tree was planted in a container, permanently placed on a weighing balance. The weight increases during interception and the meteorological conditions were recorded continuously. Trait measurements were done non-destructively during the experiment and destructively after 7 months at the end of the experiment. We show the canopy storage capacity of the individual trees, the interception ratios for summer and winter, as well as their relationships with tree traits.

2 | MATERIALS AND METHODS

2.1 | Location and tree arrangement

For the interception measurements, 10 potted trees of 10 different species (Table 1) were positioned within a group of other trees of the same species and sizes as part of a large outdoor experiment to study plant traits in relationship to transpiration and interception in Nieuwegein, The Netherlands (52°01′N, 5°06′E, 1 m.a.s.l), in 2017. The trees were purchased from commercial tree growers: Huverba B.V. (Opheusden, The Netherlands) and Boomkwekerij 't Kempke (Opheusden, The Netherlands). The plant containers were arranged in a way to ensure at least 1 m of space between the edges of the canopy of the neighbouring trees. The species differed in their heights and to minimize shading, the 10 species were divided into three size groups, each containing three to four species. The trees were arranged in rows with the largest species to the North, the smallest species to the South and the medium-sized species in between. The position of the species was randomized within each size class. The outer edge of the experiment contained an additional row of trees of the respective species in the neighbouring row to avoid edge effects.

2.2 | Plant container preparation

For a detailed description of the plant container preparation, the soil mixture and fertilization, see Section 2.3 in Pflug et al. (2020). In short, the trees were planted individually in 220-L containers (976 mm high and 590 mm wide at their widest point) in a mixture of peat, coconut and bark (70, 20 and 10 vol%). The containers had no drainage holes. The bottom of each container was filled with 26 L of basalt gravel (gravel size 2–5 mm) into which a vertical watering pipe extended. The water level was set to 19 cm above the bottom of the container and watering occurred from below through the aforementioned pipe. This was done to create similar soil moisture and watering conditions as the other trees in the experiment, which were not placed on balances (Pflug et al., 2020). Each container was refilled manually every day until the water level in the bottom of the container was back at its original level, which was visible through a transparent tube attached to the soil container. Rain exclusion from the container was facilitated by a cone-shaped rain cape made from watertight sailcloth which was installed around the tree stem and rim of the container (Figure 1). It contained two covered areas with ventilation holes (opposite each other). Holes drilled below the rim of the container (around 10 holes per container, 20-mm diameter) further aided air circulation.

2.3 | Plant material

The 10 most common species of the Veluwe region, a sandy nature reserve in the centre of the Netherlands, all also common trees of NW Europe in general and together ranging widely in morphology and phenology, were selected to improve understanding of the broader role of tree traits in the hydrological cycle and of local hydrology in particular. The selection consisted of seven broadleaved deciduous and three coniferous evergreen species (Table 1). A number of traits were measured non-destructively (August/September 2018) and destructively (February/March 2019). We assumed that tree and canopy growth in the 2018 season had stopped by the time the traits were measured in August and September 2018. Possible effects of canopy growth on interception amounts were therefore not accounted for in the analysis. In August 2018, tree height (*H*) and crown height (*CH*) were measured by means of an extendable pole. Tree height is defined as the distance from the base of the stem to the highest point in the canopy and crown height is the distance from

TABLE 1 Species, leaf habits and canopy storage capacities of the 10 trees measured

Tree	Leaf habit	S_{kg}	S_{mm}	Coefficient a_{mm}
Acer pseudoplatanus L.	BL deciduous	2.68	1.5	0.43
Betula pendula Roth	BL deciduous	4.01	1.4	0.49
Carpinus betulus L.	BL deciduous	4.18	1.3	0.38
Fagus sylvatica L.	BL deciduous	3.45	0.8	0.24
Populus tremula L.	BL deciduous	6.71	1.5	0.43
Quercus robur L.	BL deciduous	2.86	0.8	0.27
Sorbus aucuparia L.	BL deciduous	5.61	1.2	0.38
Picea abies (L.) Karsten	C evergreen	5.05	3.1	0.81
Pinus sylvestris L.	C evergreen	6.66	2.4	0.70
Pseudotsuga menziesii (Mirb.) Franco	C evergreen	7.33	2.6	0.72
Mean broadleaved trees (±SD)			1.2 ± 0.3	0.37 ± 0.09
Mean coniferous trees (±SD)			2.7 ± 0.4	0.74 ± 0.06

Note: BL = broadleaved; C = coniferous. Canopy storage capacity *S* (highest cumulative interception of the 12 distinct rain events) per tree (in kg and mm) and the coefficient a_{mm} of the model $I = a_{mm} * \ln(G_P + 1)$ with *I* being the rainfall interception (mm) and G_P being the gross precipitation (mm) per distinct rain event.

FIGURE 1 Experimental set up: Weighing balance (a), tree on balance with white rain cape (b)

the lowest leaf to the highest point in the canopy. In September 2018 (before the start of leaf fall), aerial photographs (spatial resolution 3.5 cm) of the experiment were taken with a Remotely Piloted Aircraft System (RPAS). After geo-referencing, these were used to create an orthomosaic to measure the canopy dimensions. The tree crowns were traced manually in ArcMap 10.7 (ArcGIS, ESRI, Redlands, USA) to measure the widest point of the crown (CW_{max}), the crown perimeter (*CPM*) and the crown projected area (*CPA*). From the latter two the ratio crown perimeter:*CPA* was calculated (*CPM*:*CPA*). *LAI* was not measured since we assessed the crown projected areas to be too small to retrieve reliable results with standard methods for determining *LAI*.

In February and March 2019, the trees were harvested. In the process, the diameter at breast height (*DBH*) and the branch traits were measured. We assumed that there had not been any growth during the winter period, that is, that these branch traits were representative of those in the 2018 growing season. The following steps were applied to each primary branch: (1) measurement of the branch angle in relation to the stem section above the node (*BA*) and (2) cutting off the branch and measuring branch basal diameter and length (*BL*). The total length of all branches of one tree yields the total branch length (BL_{tot}). The longest branch of a tree is denoted as BL_{max}. The branch diameter and length were used to calculate its surface area by approximating a cone shape (surface area $= \pi \times r \times \sqrt{[r^2 + h^2]}$, where r is the branch basal radius and h the branch length). Next, the surface areas of all primary branches were added up per tree (*BSA*). The crown height divided by the total number of branches (BC_{tot}) yields the mean vertical distance between the branches (*BD*). The fresh weights of the stem and of all branches were measured and samples of stem and branches were taken for the determination of their oven-dry weight (dried at 103°C for 3 days). The ratio of dry to fresh weight was used to calculate the branch dry weight (DW_B) and the total dry weight of stem and branches (DW_{tot}). Total branch count, length, branch surface area and branch dry weights were also divided by *CPA* to correct for the tree size (BC_{CPA}, BL_{CPA}, BSA_{CPA}, DW_{CPA}).

2.4 | Interception measurements

In total 10 trees (Table 1) of 10 different species were placed permanently on separate weighing balances (bench scale, series WPT-K, division = 10 g, maximum load = 250 kg, Henk Maas Weegschalen B.V., Veen, The Netherlands), to measure and record the weights every minute. The values were stored automatically on a computer. The weighing balances were placed on a frame made of scaffolding pipe which extended about 70 cm into the soil (Figure 1). The pan of the balance had the same shape and dimensions as the bottom of the plant container. The trees were fixed at two points on the stem about 1 m apart to horizontal wires with elastics to prevent tipping over of the containers during storms. Tests showed that this did not impact accurate weight recordings. The canopies of the trees on the balances were not overlapping with the canopies of the neighbouring trees.

2.4.1 | Measurement period

We measured interception from 21 May 2018 up until 31 December 2018 (referred to as 'entire measurement period'). In the period from 21 May 2018 until 5 October 2018 all 10 trees had a full canopy (referred to as 'summer'). In the period from 15 November until 31 December 2018 ('winter'), most broadleaved trees had shed all of their leaves. *Carpinus betulus* and *Fagus sylvatica* retained most of their dead leaves and *Quercus robur* retained a small part of its dead leaves.

2.5 | Meteorological measurements

The meteorological parameters solar radiation, relative humidity, air temperature, air pressure, wind direction and wind speed were measured on-site by a WS501 smart weather sensor (G. Lufft Mess-und Regeltechnik GmbH, Fellbach, Germany). These parameters were measured every 100 s and averaged to 5-min values. Precipitation was measured with a tipping-bucket with a resolution of 0.2 mm (ARG100, Campbell Scientific, Logan, USA) and summed over 5 min.

2.6 | Data analysis

2.6.1 | Interception data

The weight data obtained from the balances was first smoothened by the AWAT filter to eliminate the noise (Peters et al., 2014). An increase of the smoothened signal was considered interception if it occurred within 20 min before or after a tip recorded by the tipping bucket rain gauge. This time frame was chosen since it takes time to fill up the tipping bucket before it tips and empties. Manual water additions (watering of the trees) were characterized by a larger and faster increase in weight than typical for interception and were removed by automation. This resulted in an output file containing the weight increase per min: 0 kg in the case of no interception, >0 kg in the case of interception.

Two measures for rainfall interception (*I*) and gross precipitation (G_P) were used: (1) cumulative values, that is, totals over longer time periods, such as summer and winter (disregarding separate rain events during these seasons). (2) *I* and G_P for distinct rain events. We defined a distinct rain event by two criteria: a dry canopy at the start of the event and a low cumulative evapotranspiration during the event. To fulfil these criteria, the period preceding the rain event should have a cumulative reference evapotranspiration (ET_{ref}) according to the ASCE-EWRI (2005) definition (calculated from meteorological parameters) of at least 5 mm with no rain, and the cumulative ET_{ref} during the rain event should not exceed 0.05 mm. This means that a rain event 'ended' when the threshold for the cumulative ET_{ref} during the event was reached. This was done to be able to determine the largest amount of rain a canopy can hold for a given amount of precipitation without having the effect of re-wetting a drying canopy.

Furthermore, interception is given in two units: in kg, as measured directly by the weighing balances, and in mm (*I* in kg divided by *CPA*). The interception ratio is defined as the ratio of interception (mm): gross precipitation (mm), I:G_P. Lastly, the largest cumulative interception (in mm and kg) of all distinct rain events is given as canopy storage capacity *S* (Klaassen et al., 1996). *S* is defined as the maximum amount of precipitation a canopy can hold at a moment in time, measured when the canopy is fully developed. The (logarithmic) relationships between interception amount or interception ratio and G_P for distinct rain events were analysed by means of non-linear regression with a starting value of 0 (nls function, R Core Team, 2019).

Of the 97 rain days in the measurement period (total rain $=$ 397 mm), 33 days were excluded from the analysis of the seasonal cumulative interception (total rain excluded $=$ 27 mm), as daily rain (intensity) was too low to generate measurable interception data in some of the trees. Only rain days with interception data for all 10 trees ($n = 64$) were used for the calculation of the seasonal sums.

2.6.2 | Plant traits

The trait data was distributed normally so no data transformation prior to analysis was needed. A Pearson correlation analysis was done for all measured tree traits. The relationships between interception parameter and individual tree trait were analysed with linear regressions. A significance threshold of $\alpha = 0.05$ was used throughout.

3 | RESULTS

3.1 | Relationship between gross precipitation and interception

Total precipitation (G_P) during the entire measurement period (21 May 2018–31 December 2018) was 397 mm and the average daily temperature was 14.7°C (Figure 2). The highest recorded temperature was 37°C and the lowest −1.3°C. The highest total precipitation on one day was 35.5 mm. In 'summer' (21 May to 5 October 2018), total G_P was 236 mm and in 'winter' (15 November to 31 December 2018), total G_P was 100 mm.

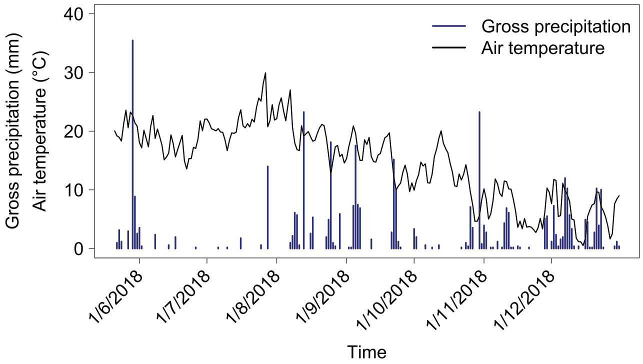

FIGURE 2 Daily gross precipitation G_P (mm) and mean air temperature (°C) at the experimental site during the measurement period

Total precipitation of the entire year 2018 was 656 mm as compared to the 50-year average of 820 mm of a nearby weather station (weather station De Bilt of the Royal Netherlands Meteorological Institute KNMI).

Figure 3 shows the interception ratio (I:G_P, mm mm^{-1}) of each tree for summer, winter and the total period. The summer interception ratio ranged from 0.07 (*F. sylvatica*) to 0.16 (*B. pendula*) for the broadleaved species (average 0.12 ± 0.03 *SD*). The three coniferous species had very similar summer interception ratios: 0.21 for *P. sylvestris* and *P. menziesii* and 0.22 for *P. abies* (average 0.21 ± 0.01 *SD*). The winter interception ratio ranged from 0.04 (*S. aucuparia*) to 0.12 (*C. betulus*) for the broadleaved species (average 0.08 ± 0.03 *SD*). The coniferous species had winter interception ratios of 0.24 (*P. abies*) and 0.25 (*P. menziesii* and *P. sylvestris*) (average 0.24 ± 0.01 *SD*).

The broadleaved species had a higher interception in summer than in winter due to leaf loss in autumn. The exceptions were *C. betulus* and *F. sylvatica*. These two species had very similar interception rates both in summer and winter since they retained most of their dead leaves in the autumn and winter period. The winter interception ratio of the broadleaved species that shed (almost) all of their leaves in autumn (*A. pseudoplatanus*, *B. pendula*, *P. tremula*, *Q. robur* and *S. aucuparia*) was on average 56% of their average summer interception ratio.

The measurement period from May 2018 until December 2018 contained 14 distinct rain events, of which 12 were in the summer period. Only the 12 events in summer were used for the analysis. Gross precipitation per distinct event in the summer ranged from 0.4 to 35.5 mm. Most rain events ($n = 9$) were <5 mm (<1 mm: $n = 4$, >1 and <5 mm: $n = 5$); three rain events were >5 mm (7.5, 7.9 and 35.5 mm). Rain duration ranged from 33 to 312 min (mean 118 min ± 81 SD). Mean rain intensities of the events ranged from 0.15 to 19 mm h^{-1} (mean 3.4 mm h^{-1} ± 5.7 SD), with 10 out of 12 events having a mean rain intensity of <5 mm h^{-1}.

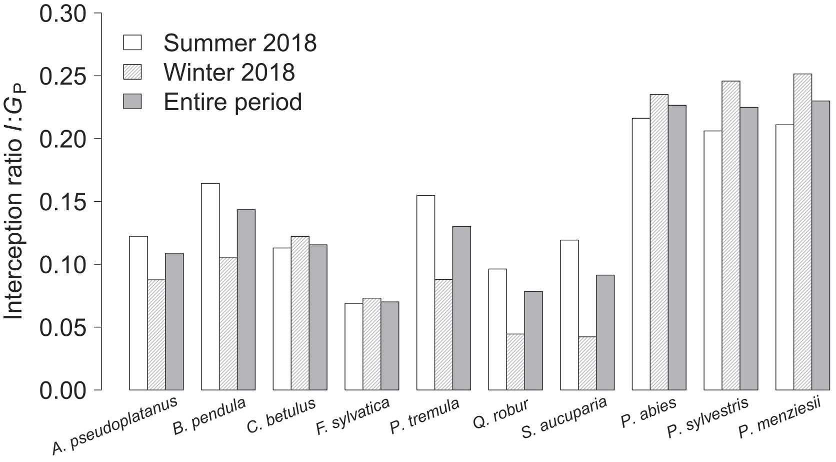

FIGURE 3 Interception ratio (interception: gross precipitation, $I:G_P$, mm mm^{-1}) of each species for summer, winter and the entire measurement period

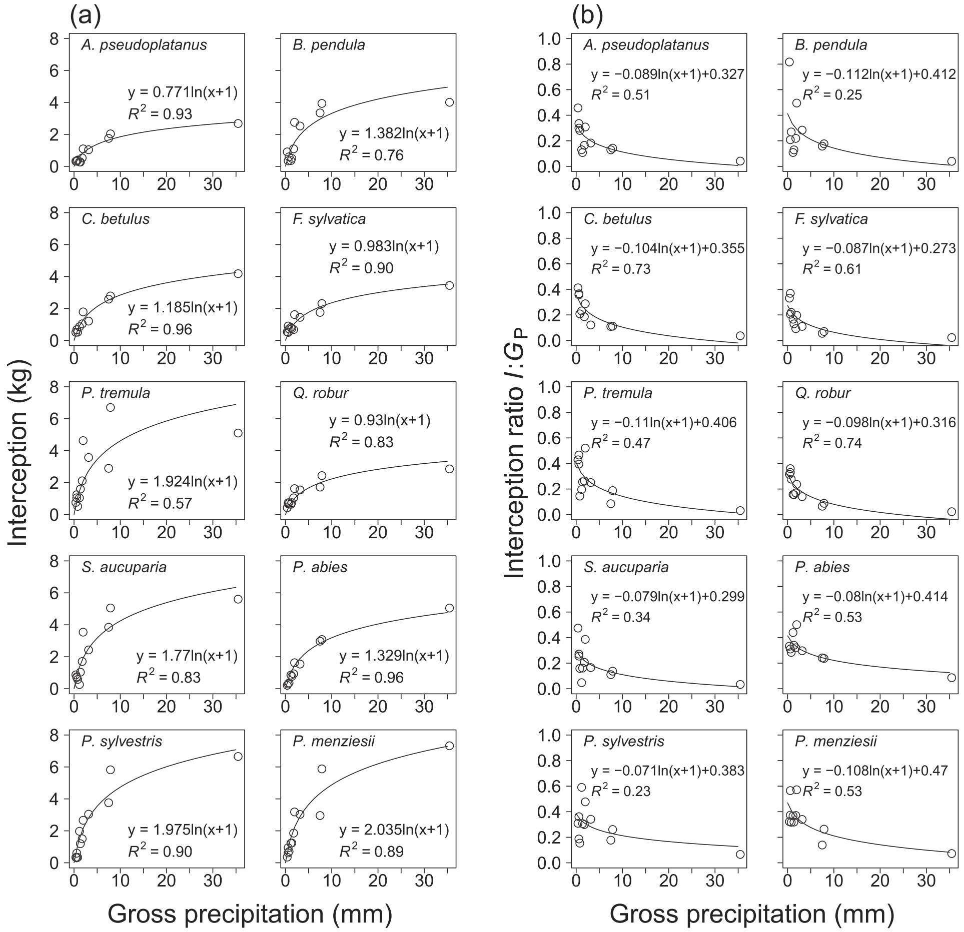

FIGURE 4 Relationship of (a) interception (kg) and (b) interception ratio (mm mm^{-1}) with gross precipitation for each tree during the distinct rain events in summer ($n = 12$)

Figure 4a shows the non-linear relationship between gross precipitation (mm) and interception (kg) for the distinct rain events. Noticeable are the high interception values for larger precipitation events of the two coniferous species *P. sylvestris* and *P. menziesii* which were similar to that for the broadleaved species *P. tremula*, even though the latter was much taller (Table 2). The fit of the curves for the absolute interception was generally good ($R^2 \geq 0.76$; except for *P. tremula*, $R^2 = 0.57$). To determine whether canopy saturation had been achieved during the distinct events, the cumulative interception was plotted against the cumulative precipitation for each tree individually (data not shown). When the cumulative interception no longer increased with increasing rainfall, the canopy saturation had been achieved. This was the case for the 35.5 mm rain event for all trees, and for the 7.5 mm rain event for all trees except *P. tremula*.

Figure 4b shows the non-linear relationship between gross precipitation (mm) and interception ratio (mm mm^{-1}) for the distinct rain events. The largest interception ratio was measured for *B. pendula* ($I{:}G_P = 0.82$) at a G_P of 0.4 mm (the event with the lowest G_P). The mean interception ratio at this event was 0.46 (±0.17 *SD*) for the broadleaved and 0.32 (±0.01 *SD*) for the coniferous trees.

The average interception ratio for rain events <1 mm G_P ($n = 4$) were very similar for both broadleaved and coniferous species. However, from a G_P > 1 mm, the average interception ratio of the coniferous species was about twice as high as the average interception ratio of the broadleaved species. For example, for a G_P of >1 and <2 mm ($n = 4$), the average interception ratios were 0.21 (±0.10 *SD*) for the broadleaved species and 0.41 (±0.10 *SD*) for the coniferous species.

The mean interception ratio for the largest rain event ($G_P = 35.5$ mm) was 0.03 (± 0.01 *SD*) for the broadleaved trees and 0.08 (±0.01 *SD*) for the coniferous trees.

Table 1 shows the canopy storage capacity *S* for each tree as well as the coefficient of the logarithmic model with gross precipitation G_P (mm) as a predictor of the intercepted amount of water *I* (mm): $I = a_{mm} * \ln(G_P + 1)$, where a_{mm} is a fitting parameter. The *S* measured for all trees except *P. tremula* was at a G_P of 35.5 mm (G_P for *P. tremula*: 7.9 mm) (see also Figure 4a). The mean canopy storage capacity was larger for the coniferous trees (2.7 ± 0.4 *SD*) than the broadleaved trees (1.2 ± 0.3 *SD*).

The coefficient a_{mm} ranged from 0.24 to 0.49 for the broadleaved trees and from 0.70 to 0.81 for the coniferous trees. It was used to establish general equations for precipitation-dependent interception (mm) for the two groups of species:

$$\text{Broadleaved trees}: I_{mm} = 0.371^{*}\ln(G_P + 1)\ R^2 = 0.70 \tag{1}$$

$$\text{Coniferous trees}: I_{mm} = 0.741^{*}\ln(G_P + 1)\ R^2 = 0.91 \tag{2}$$

Figure 5 shows the relationship between the cumulative summer interception (kg, mm) and the coefficients (a_{kg}, a_{mm}) of the model $I = a * \ln(G_P + 1)$ (p < 0.001). This shows that the coefficients a_{kg} and a_{mm} obtained from the 12 distinct rain events (no re-wetting of a drying canopy) have a positive linear relationship with the cumulative interception (including rewetting of a drying canopy) of the summer period. They can therefore be used interchangeably in the analysis of the effect of tree traits on interception parameters (see section on traits).

3.2 | Relationship between tree traits and interception

Table 2 shows the measured tree traits and Table 3 shows the correlations between them. Tree-size related traits such as *DBH*, tree height,

TABLE 2 Measured and calculated tree traits of the 10 species

Tree	DBH cm	H m	CH m	CPA m^2	CW_{max} m	*CPM:CPA* m m^{-2}	BA °	BD m	BC *n*	BL_{tot} m	BL_{max} m	BSA cm^2	DW_B kg	DW_{tot} kg	BC_{CPA} *n* m^{-2}	BL_{CPA} m m^{-2}	BSA_{CPA} cm^2 m^{-2}	DW_{CPA} kg m^{-2}
A. pseudoplatanus	5.1	4.9	2.96	1.81	2.36	6.9	39	0.093	32	16.1	2.17	4892	1.36	4.83	17.7	8.9	2707	0.75
B. pendula	6.7	7.3	6.28	2.82	3.26	7.3	53	0.098	64	69.1	2.75	13234	2.77	9.00	22.7	24.5	4687	0.98
C. betulus	5.8	5.0	4.27	3.16	2.83	5.9	83	0.044	97	49.1	1.90	8027	1.48	6.01	30.7	15.5	2541	0.47
F. sylvatica	5.8	4.7	3.76	4.16	3.55	6.9	71	0.065	58	42.8	2.23	11781	3.18	7.57	13.9	10.3	2833	0.76
P. tremula	9.9	8.4	6.54	4.52	3.16	5.8	65	0.142	46	55.4	4.79	20990	5.57	16.81	10.2	12.3	4647	1.23
Q. robur	6.5	5.2	3.68	3.48	2.94	5.4	63	0.058	64	29.6	1.74	7121	2.06	8.64	18.4	8.5	2045	0.59
S. aucuparia	6.8	6.3	5.42	4.65	3.51	6.7	45	0.155	35	43.0	3.74	13199	4.88	11.22	7.5	9.2	2838	1.05
P. abies	2.3	2.1	2.11	1.65	1.84	6.0	77	0.023	90	42.0	1.07	6566	1.62	2.85	54.7	25.5	3989	0.98
P. sylvestris	6.0	2.9	2.89	2.83	2.47	4.2	67	0.050	58	31.7	1.42	9562	3.16	6.30	20.5	11.2	3377	1.12
P. menziesii	5.3	3.6	3.64	2.83	2.48	6.6	65	0.044	83	58.0	1.38	12643	2.90	6.06	29.3	20.5	4468	1.03

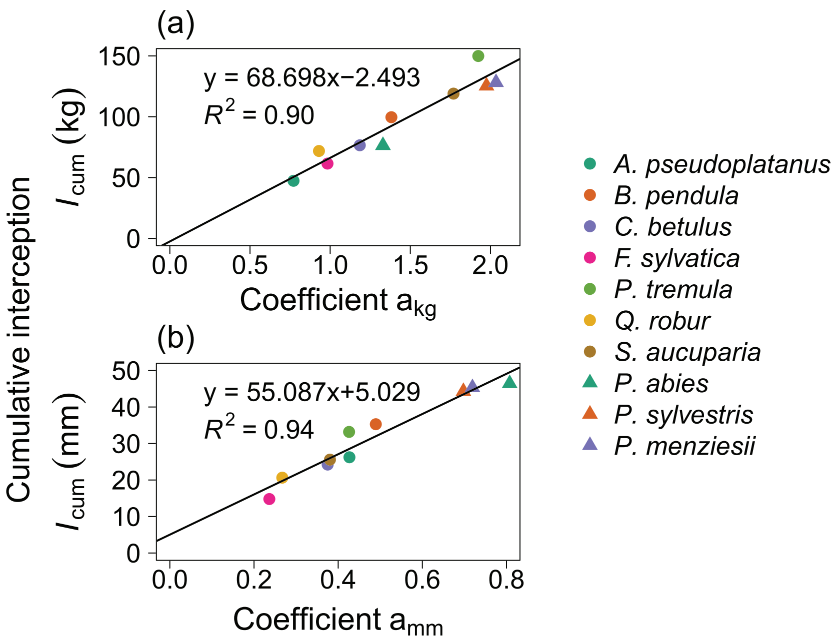

FIGURE 5 Relationship between cumulative interception in the summer period ((a)—kg, (b)—mm) and the respective coefficient a of the model $I = a^*\ln(G_P + 1)$ (I—rainfall interception in kg or mm; G_P—gross precipitation in mm)

crown height, *CPA*, maximum crown width, maximum branch length and branch surface area and branch dry weight were positively related to each other. The coniferous trees were characterized by a relatively small *CPA*, a large branch count per *CPA*, a large branch length per *CPA* (except for *P. sylvestris*) and a small distance between the branches, therefore a small and dense canopy. Conversely, the larger broadleaved trees had a larger BL_{max}, mostly a lower branch count per *CPA*, a larger distance between the branches and a similar total branch count as the coniferous species, therefore a more open canopy. The relationships between total branch count, branch angle and distance between the branches show that trees with more horizontal than steep-angled branches (e.g., *C. betulus* and *P. abies*) also had more branches and smaller distances between them.

Figure 6a and Table 4 show the relationships between the cumulative interception (kg) in the summer and the tree traits. The tree traits *DBH*, tree height, crown height, maximum branch length and total aboveground dry weight were positively related to I_{cum} (kg) for the broadleaved species only. The total branch surface area and the total branch dry weight were significant predictors of I_{cum} for both broadleaved trees only and all 10 trees. There was no relationship of I_{cum} with *CPA* or any of the other measured traits for either broadleaved trees only or all trees.

Figure 6b and Table 5 show the relationships between the cumulative interception (mm) in the summer and the tree traits. As opposed to the I_{cum} (kg), there were no effects when the broadleaved trees were analysed separately from the coniferous trees, except for tree height, which was significant for the broadleaved species only. The traits branch length and branch surface area per *CPA* were positively related to I_{cum} (mm). The negative effect of the maximum crown width on I_{cum} (mm) was caused by the three coniferous trees, which had a small crown width and a high I_{cum} (mm).

4 | DISCUSSION

In this study we measured the seasonal interception ratios, the canopy storage capacity as well as the relationship between cumulative seasonal interception and tree traits of 10 temperate tree species common to NW Europe. While there appear to be differences between the different species with similar leaf habit, the largest difference is between the group of broadleaved deciduous species and the coniferous evergreen species.

In the following, the results are discussed in the context of previous publications and an attempt is made to explain the differences in the interception patterns between broadleaved and coniferous species.

4.1 | Interception ratios

The summer and winter interception ratios vary more within the broadleaved species than within the coniferous species, which are more similar to each other; with the caveat that only three evergreen conifers were available as common representatives of NW-European forests. As expected, the coniferous species intercept more rain in both summer and winter than the broadleaved species (Barbier et al., 2009; Horton, 1919). The three coniferous species studied here are well represented in the scientific literature. For all three species, quite a large range of interception ratios has been reported: for *Picea abies*, interception ratios can range from 0.17 to 0.54, for *Pinus sylvestris* from 0.20 to 0.32 and for *Pseudotsuga menziesii* from 0.21 to 0.49 (Table 6). With evergreen coniferous species, normally no distinction is made between summer and winter period, that is, reported ratios often span several seasons. This is noteworthy mentioning since we have found slightly higher winter interception ratios than summer

TABLE 3 Correlation matrix of tree traits

	DBH	*H*	*CH*	*CPA*	CW_{max}	*CPM:CPA*	*BA*	*BD*	*BC*	BL_{tot}	BL_{max}	*BSA*	DW_B	DW_{tot}	BC_{CPA}	BL_{CPA}	BSA_{CPA}
H	0.89																
CH	0.80	**0.94**															
CPA	0.68		0.44														
CW_{max}	0.35	0.30	0.48	0.76													
CPM:CPA																	
BA																	
BD	0.76	0.85	0.67	0.21	0.07		−0.45										
BC							0.81	−**0.66**									
BL_{tot}			0.88														
BL_{max}	0.92	**0.89**	0.78	0.52	0.27			**0.92**									
BSA	0.91	0.87	0.87	0.73						0.70	0.92						
DW_B	0.92		0.73	0.78				0.77			0.92	**0.97**					
DW_{tot}	**0.99**	0.87	0.78	0.72	0.42			0.76			**0.92**	0.92	0.95				
BC_{CPA}	−0.52	−0.36		−0.48	−0.29			−0.65	0.79		−0.59			−0.60			
BL_{CPA}									0.38	0.84					0.46		
BSA_{CPA}										0.76						0.66	
DW_{CPA}												0.86	0.86				0.89

Note: Pearson correlation coefficients are presented. $P > 0.05$ n.s., blank; $p < 0.05$ in plain text; $p < 0.01$ underlined; $p < 0.001$ in bold and underlined.

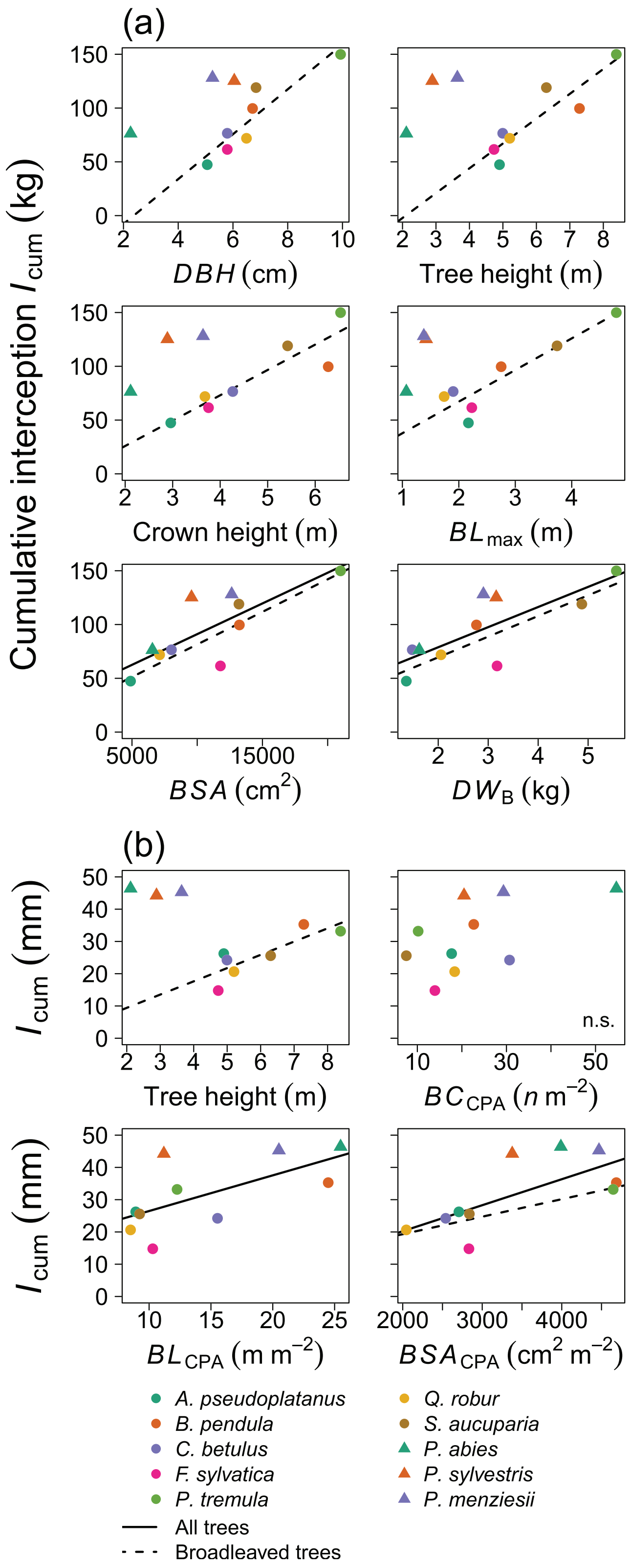

FIGURE 6 Relationship between the cumulative interception in the summer and tree traits. (a) Cumulative interception in kg; (b) cumulative interception in mm. Regression line for significant effects only (continuous: all trees, dashed: broadleaved trees only). For regression parameters, R^2 and p values, see Tables 4(a) and 5(b)

interception ratios for the conifers. An explanation for this is that rain intensity was higher in summer than in winter (average rain per rain day was 6.5 and 4.5 mm respectively), which means that during summer a lower fraction of the rain was intercepted by the canopy. A more even rainfall distribution in winter than in summer is a common phenomenon in temperate climates. Summer and winter interception ratios have been studied less well for the investigated seven broadleaved species, with the exception of *Fagus sylvatica* (Table 6). For most reported interception ratios, the winter interception is about half of the summer interception when leaf shedding occurred in autumn. This is also the case in our study. Two broadleaved species had winter interception ratios comparable to summer interception ratios, that is, *F. sylvatica* and *Carpinus betulus*. Both trees retained most of their dead leaves during the winter period where they continued to contribute to rainfall interception. The dead, dried up leaves may even absorb intercepted water.

The interception ratios measured in this study are consistently lower or at the lower range of the published interception ratios. This holds true for all species. There could be several reasons for this effect. First, there is a natural variation in interception ratios of the same tree or stand over the years. In a *Populus* stand in the Netherlands, for example, the yearly interception ratio ranged from 0.14 to 0.22 over a period of 4 years (Dolman et al., 2000). In the same time period, the yearly interception ratio of *Pinus sylvestris* ranged from 0.22 to 0.31. These variations can be caused by both biotic and abiotic factors, such as changes in canopy cover and precipitation patterns. The *LAI* changes drastically in the course of a year for deciduous species, and to a lesser extent also for the evergreen species. The timing of bud breaking and leaf development as well as leaf senescence and shedding is species dependent and also partly determined by the prevailing meteorological conditions. In this study, the canopy traits were only measured at the end of the growing season, which means that we cannot exclude the possibility that the traits that affect interception had changed through the growing season. A smaller crown projected area at the beginning compared to the end of the season could have led to an overall lower seasonal interception ratio than what was actually the case. Summer temperatures and precipitation amounts can also influence *LAI* interannually in evergreen species (Sumida et al., 2018). Interception ratios can also change in the course of the vegetative season due to changes in wettability of the leaves. *Quercus robur*, for instance, has a high seasonal variability in leaf wettability, starting with highly hydrophobic leaves in spring and becoming increasingly hydrophilic towards the end of the season (Klamerus-Iwan & Błonska, 2017; Neinhuis & Barthlott, 1998). Furthermore, crown development and health are influenced by pests and drought periods, among others. This means that interception ratios do not only vary in the course of a year, but that they can also vary substantially within seasons (Rowe, 1983). While our interception ratios seem low for most species, they may have just been at the lower end of possible values for these trees. A second reason for the low interception ratios is the size of the studied trees. While the trees had a

TABLE 4 Regression coefficients, R^2 and *p* value for the linear regression I_{cum} (kg) = a + b × T, with T being a trait

Trait	All trees				Broadleaved trees only			
	a	b	R^2	*p* value	a	b	R^2	*p* value
DBH	34.42	10.17	0.24	n.s.	−49.53	20.87	0.81	0.0035
Tree height, *H*	67.98	5.48	−0.02	n.s.	−48.39	23.09	0.79	0.0044
Crown height, *CH*	46.34	11.87	0.18	n.s.	−21.23	23.57	0.80	0.0040
CPA	49.30	14.53	0.10	n.s.	7.04	23.46	0.34	n.s.
Max. crown width, CW_{max}	66.41	10.29	−0.09	n.s.	−35.09	40.37	0.07	n.s.
Mean distance between branches, *BD*	71.80	309.31	0.06	n.s.	29.28	644.85	0.50	0.0460
Total branch count, *BC*	104.24	−0.14	−0.12	n.s.	106.10	−0.29	−0.16	n.s.
Total branch length, BL_{tot}	45.21	1.15	0.19	n.s.	32.80	1.30	0.27	n.s.
Max. branch length, BL_{max}	63.44	13.89	0.13	n.s.	8.34	29.41	0.81	0.0034
Total branch surface area, *BSA*	33.98	0.01	0.58	0.0067	20.96	0.01	0.78	0.0052
Total branch dry weight, DW_B	41.47	18.70	0.56	0.0075	31.12	19.20	0.73	0.0091
Total aboveground wood dry weight, DW_{tot}	53.10	5.37	0.31	n.s.	11.98	8.47	0.86	0.0017

Note: The regression was done for all 10 trees and the seven broadleaved trees only.

TABLE 5 Regression coefficients, R^2 and *p* value for the linear regression I_{cum} (mm) = a + b × T, with T being a trait

Trait	All trees				Broadleaved trees only			
	a	b	R^2	*p* value	a	b	R^2	*p* value
DBH	42.10	−1.74	−0.02	n.s.	9.68	2.41	0.15	n.s.
Tree height, *H*	43.66	−2.39	0.07	n.s.	1.20	4.11	0.62	0.0222
Crown height, *CH*	38.33	−1.62	−0.07	n.s.	7.81	3.81	0.48	n.s.
Max. crown width, CW_{max}	69.78	−13.44	0.38	0.0346	32.21	−2.10	−0.18	n.s.
Ratio crown perimeter: *CPA*, *CPM:CPA*	53.79	−3.60	−0.02	n.s.	16.72	1.41	−0.17	n.s.
Mean branch angle, *BA*	24.50	0.11	−0.10	n.s.	34.82	−0.15	−0.06	n.s.
Mean distance between branches, *BD*	37.39	−74.94	−0.03	n.s.	17.30	90.29	0.16	n.s.
Branch count per m², BC_{CPA}	21.04	0.47	0.24	n.s.	25.22	0.03	−0.20	n.s.
Branch length per m², BL_{CPA}	15.42	1.11	0.36	0.0404	15.93	0.77	0.27	n.s.
Branch surface area per m², BSA_{CPA}	4.12	0.01	0.43	0.0236	8.46	0.01	0.59	0.0273
Branch dry weight per m², DW_{CPA}	5.79	28.81	0.32	n.s.	12.48	15.90	0.24	n.s.

Note: The regression was done for all 10 trees and the seven broadleaved trees only.

fully developed crown, they may not be comparable to adult specimens which are usually chosen for field studies. This especially concerns the *LAI*, which can increase with higher age (Jagodziński & Kałucka, 2008). A higher *LAI* is in turn positively related to rainfall interception (Fathizadeh et al., 2017; Llorens & Domingo, 2007). Third, the interception process is an interaction between tree structural traits and meteorological conditions. This means that the effect of the meteorological conditions on rainfall interception can change in the course of the season. For instance, Staelens et al. (2008) detected a positive effect of wind speed on interception only in the foliated season and Zabret et al. (2018) showed that for both *Pinus nigra* and *Betula pendula*, the relative influence of different meteorological parameters differed between the two trees and also between the foliated and the leafless season. Shifts in seasonal precipitation patterns can therefore also change patterns in the seasonal interception ratios. Additionally, there are likely to be differences in interception processes between single trees and a closed stand due to different exposures to, for example, wind and radiation. Given the small size of the trees (compared to trees usually investigated) and the distance between our trees, they were certainly more exposed to wind during and after the rainfall than adult trees in a dense stand. In our case, interception storage may have been lower and evaporation from the wet canopy after the event may have been higher compared to trees in a dense stand under the same meteorological conditions.

Next to the effect of environmental conditions on rainfall interception, differences in interception ratios can also be explained by the differences in methods used to measure interception. In most of the studies cited here, rainfall interception was measured indirectly through measurements of gross rainfall (G_P), throughfall (*TF*) and stemflow (*SF*). Interception *I* is then calculated with $I = G_P - TF - SF$.

TABLE 6 Comparison of interception ratios and canopy storage capacities with literature values for the different species

	Interception ratio (mm mm^{-1})				
Species	Summer	Winter	Multiple seasons	Canopy storage capacity (mm)	References
Acer pseudoplatanus	0.12	0.09	0.11	1.5	This study
Acer platanoides				1.9	Klimenko et al., 2019
	0.35		0.39	2.4–2.5	Smets et al., 2019
Betula pendula	0.16	0.11	0.14	1.4	This study
			0.24	2.8	Zabret & Šrai, 2019; Klimenko et al., 2019
Carpinus betulus	0.11	0.12	0.12	1.3	This study
			0.17[a]	1.9	Aussenac, 1968
Fagus sylvatica	0.07	0.07	0.07	0.8	This study
	0.21	0.06	0.15	1.7	Aussenac & Boulangeat, 1980
	0.31	0.10	0.21	0.9 summer, 0.4 winter	Staelens et al., 2008; Gerrits, 2010
			0.37	1.3 summer, 0.8 winter	Rötzer et al., 2010; Herbst et al., 1999
Populus tremula	0.15	0.09	0.13	1.5	This study
				0.5	Klimenko et al., 2019
Populus sp.	0.22	0.14			Dolman et al., 2000
	0.31	0.14	0.26		Verry & Timmons, 1977
Quercus robur	0.10	0.04	0.08	0.8	This study
				0.8 summer, 0.3 winter	Dolman, 1987
Quercus rubra	0.20	0.12	0.16		Hendriks, 1990
Quercus sp.	0.34	0.16			Dolman et al., 2000
Sorbus aucuparia	0.12	0.04	0.09	1.2	This study
Picea abies	0.22	0.24	0.23	3.1	This study
			0.17	4.6	Cape et al., 1991; Klimenko et al., 2020
			0.34	3.1	Aussenac, 1968
			0.44	0.8–0.9	Holko et al., 2009
				0.8 young, 1.2 mature[b]	Ringgaard et al., 2014
			0.49	2.2	Rötzer et al., 2010
			0.54		Gebhardt et al., 2014
Pinus sylvestris	0.21	0.25	0.22	2.4	This study
			0.20		Aydin et al., 2018
			0.24	2.4	Llorens et al., 1997; Klimenko et al., 2020
			0.31	3	Aussenac, 1968
			0.32	1.4–1.8	Rutter, 1963
Pseudotsuga menziesii	0.21	0.25	0.23	2.6	This study
			0.21	1.4	Pypker et al., 2005
			0.39	2.4	Robins, 1969; Klaassen et al., 1998
			0.49	3.3	Asadian & Weiler, 2009; Link et al., 2004

Note: When no data for the investigated species was found, a similar species was taken. The canopy storage capacity refers to the foliated season, unless specified otherwise.

[a] Mixed stand with *Fagus sylvatica*.

[b] Young: 20 years old, mature: 40 years old.

Throughfall is typically measured with a set of rain gauges below the canopy. The representativeness of the placement of the rain gauges regarding the (heterogeneity of the) canopy openness (Frischbier et al., 2019) largely determines the accuracy of the interception measurement (Fathizadeh et al., 2021). While our measurements were not affected by the heterogeneity of the canopy cover, since we measured interception directly by placing the trees on balances, we also measured interception by the plant container and rain cape. We assumed these amounts to be the same for all trees and did therefore not correct for them in the analysis. Field measurements of rainfall interception as described above can also lead to higher interception amounts compared to our data, as there can be difference in the amounts actually held by the leaves and branches (assessed by weighing) and the amounts that remain when the volumes reaching the ground as throughfall, drips, splashes or stemflow are subtracted from the gross precipitation. In fact, evaporation can occur during heavy rain events in the form of splash droplet evaporation (splash droplets small enough to evaporate even under high humidity conditions, Murakami, 2006). In our case, splash droplet evaporation is not part of the measured interception, while it is in the case of throughfall measurements. In an outdoor experiment using artificial trees, Murakami (2021) suggested that splash droplet evaporation can be 52%–58% of the total interception.

4.2 | Canopy storage capacity

To determine the canopy storage capacity *S*, the largest cumulative interception of the distinct rain events was taken. Cumulative reference evapotranspiration during these events was ≤0.05 mm. The average *S* of the broadleaved species was 1.2 mm (±0.3 *SD*), the average of the coniferous species 2.7 mm (±0.4 *SD*). As with the interception ratios discussed above, *S* of the coniferous species falls within the range of other published values (Table 6). As for the deciduous species, only a few or no studies were found for most of the specific species we studied which makes a comparison more difficult (Table 6). The general relatively low values for *S* of *F. sylvatica* and *Q. robur* ($S < 1$ mm) may have been caused by their very low leaf wettability at least at the beginning of the season (Klamerus-Iwan & Błonska, 2017; Neinhuis & Barthlott, 1998) which may also be related to the overall low summer interception ratio of these two species.

The environmental factors influencing interception ratios, which were discussed in Section 4.1, also apply to the canopy storage capacity. Similarly, also the measurement methods for determining the canopy storage capacity differ largely. Here the canopy storage capacity *S* was measured directly as a property of the entire tree and at a single large rain event in an otherwise unusually dry season. In most other studies different methods were used to obtain *S*, of which some are summarized here (for more methods on measuring *S* and rainfall interception, see Friesen et al., 2015). Under natural, uncontrolled conditions, *S* is commonly determined with interception models (e.g., Rutter et al., 1971; Gash, 1979 and their derivations) by using gross precipitation, throughfall and stemflow measurements as inputs. *S* is then presented as a seasonal average of rain events large enough to saturate the canopy (e.g., Herbst et al., 1999; Link et al., 2004; Tallaksen et al., 1996). In a study by Li et al. (2016), *S* of the different tree parts stem, branches and foliage had been determined from the weight differences of the fully immersed and saturated tree parts compared to the dry parts. Comparable to this study, Li et al. (2015) also directly measured the canopy storage capacity of entire trees on weighing balances, but then in a laboratory set up with artificial rain of varying intensities. Similarly, individual branches had been continuously weighed and wetted by artificial sprinkling until the weight stabilized to determine *S* (e.g., Keim et al., 2006; Klimenko et al., 2019; Xiao & McPherson, 2016). While measuring individual tree parts with artificial rain provides more experimental control, artificial rain is unlikely to be representative for the natural variation in rain regarding droplet size and velocity (Ries et al., 2013) which has been shown to have an effect on interception processes (Calder, 2001; Zabret et al., 2017). In summary, accurate determination of rainfall interception and storage capacity is not straightforward and the differences in methods and plant densities used in different studies make direct comparisons of interception properties difficult.

4.3 | Relationship with tree traits

The analysis of the relationship between the cumulative (summer) interception and the tree traits showed that for the broadleaved trees, the cumulative interception (in kg) is directly related to tree size characteristics such as tree and canopy height, *DBH* and maximum branch length. This is not surprising since a tree with a large vertical and horizontal extension can also hold more rain water than a smaller tree. This effect does not apply to the coniferous species since, even though they were relatively small trees compared to the broadleaved trees, *P. sylvestris* and *P. menziesii* had cumulative interception values similar to the much larger broadleaved trees *S. aucuparia*, *B. pendula*, and *P. tremula*. Traits related to the (woody) surface area available for interception (branch surface areas and branch dry weights), are significant predictors of cumulative interception for both coniferous and broadleaved trees. Given the smaller size of the three coniferous species, this means that they actually had denser canopies (less distance between the branches) than the broadleaved species.

Once cumulative interception is corrected for the horizontal crown extension (I_{cum} in mm), branch length and branch surface area per *CPA* were significantly positively related to cumulative interception by both broadleaved and coniferous species. These traits represent a denser canopy independently of tree height (see Table 3). We expect that the branch surface area per unit crown projected area is directly positively related to the *LAI* (and therefore plant area index) since at least in smaller trees, larger/more branches can also support a larger leaf area. For the broadleaved trees only, there was a positive relationship between I_{cum} (mm) and tree height. This indicated that, across the broadleaved species, larger trees also had a denser canopy which would logically translate to a higher branch surface area and a higher *LAI*. Our broadleaved trees in fact had, with increasing tree height, less branches, a higher total branch surface area and a higher branch dry weight per *CPA*; individual branches were thus thicker (Table 2). Fathizadeh et al. (2017) made a similar observation in a field study on adult *Quercus brantii* trees. They found positive linear relationships between tree height, *DBH* and the interception ratio. The denser canopy was represented by a positive relationship between tree height and *LAI*. Baptista et al. (2018) also reported a positive relationship between (plant) surface area per *CPA* and canopy storage capacity.

Higher interception ratios and storage capacities of the coniferous compared to the broadleaved trees are not a surprising result (Barbier et al., 2009; Horton, 1919). The question arises what the underlying structural differences between these two groups are.

A major difference is logically the seasonality of the canopy cover of the studied species: the coniferous (evergreen) species also intercept rainfall in winter, when most broadleaved deciduous species have lost their leaves. In this study, winter interception by the broadleaved trees that shed their leaves was still about 56% of the summer interception, so interception by the broadleaved trees plays an important part also in the leafless season.

A high *LAI* relates to a larger number of branch and leaf layers within the vertical extension of the canopy. In our study, this is represented by the variables branch count, branch length and branch surface area per *CPA*. But then, for those traits, the values of the three coniferous species are in a similar range as the broadleaved species and yet they have a higher cumulative interception. Even though some of the measured tree traits clearly explain cumulative interception, our observations do not completely explain the differences between broadleaved and coniferous trees. Another crucial trait apparently has not been measured. Possibly the branch density has not been assessed accurately enough since only the primary branch was counted and measured. However, for the branch dry weight, all other parts of the primary branch (secondary and lower order branches) were included. Possibly the coniferous trees had a larger number of these lower order branches and with that a larger surface area and dry weight. The effect of an increased dry weight may not have been discovered since the measured coniferous trees had a lower wood density than the broadleaved trees. That leaves the needles: rain drops can cling to the individual needles and can accumulate in needle clusters (e.g., *Pinus* sp.). Needles can therefore potentially hold more water than leaves which are aligned vertically (Crockford & Richardson, 2000). In addition, evergreen needles may be stiffer due to their longevity than leaves which are shed at the end of the vegetative season, and stiffer needles (and leaves) are less prone to bending under the impact of rain drops, which leads to lower dripping and more rain water retention.

5 | CONCLUSIONS

In this study, seasonal interception and canopy storage capacities were determined for 10 temperate tree species and the explanatory effect of tree architectural traits analysed. We found that the difference between the broadleaved and the coniferous species is larger than the variation within these two leaf habit groups. Coniferous species have both higher canopy storage capacities and seasonal interception ratios than the broadleaved species. Tree traits related to branch surface area explain the differences in interception among all trees well. However, the trait(s) responsible for the difference in interception volumes between broadleaved and coniferous trees could not be explained comprehensively by the current suite of traits and therefore requires further research. Our results will be useful for improving estimates of interception capacity and related interception parameters from plant traits and to simulate interception by trees in a more reliable manner. In a world where drought periods are becoming more frequent and severe in many regions and where precipitation patterns change, our findings will also help to better model and predict effects of climatic changes on the hydrological cycle via trees. Moreover, our novel and accurate approach of measuring rainfall interception by rather large trees directly on weighing balances bears promise for future experiments not only in the temperate regions, but in forested climate zones worldwide.

ACKNOWLEDGEMENTS

We would like to thank Rien Aerts for his input at the designing phase of the experiment, Sidney Meijering and Harry van Wegen for their help in setting up the experiment, and Richard van Logtestijn and Bastiaan Clement for their support during the plant harvest. We also thank two anonymous reviewers for their constructive comments. This research was funded by the European Union's Horizon 2020 research and innovation programme under grant agreement no. 641739.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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How to cite this article: Pflug, S., Voortman, B. R., Cornelissen, J. H. C., & Witte, J.-P. M. (2021). The effect of plant size and branch traits on rainfall interception of 10 temperate tree species. *Ecohydrology*, e2349. https://doi.org/10.1002/eco.2349