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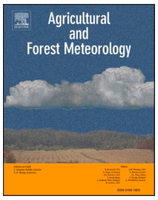

Canopy cover at the crown-scale best predicts spatial heterogeneity of soil moisture within a temperate Atlantic forest

Eva Meijers [a,*], Roos Groenewoud [a], Jorad de Vries [a], Jens van der Zee [b], Gert-Jan Nabuurs [a,c], Marleen Vos [a], Frank Sterck [a]

[a] *Forest Ecology and Forest Management, Wageningen University & Research, Droevendaalsesteeg 4, 6708PB, Wageningen, , the Netherlands*
[b] *Laboratory of Geo-information Science and Remote Sensing, Wageningen University & Research, Droevendaalsesteeg 4, 6708PB, Wageningen, the Netherlands*
[c] *Wageningen Environmental Research, Wageningen University and Research, 6708PB, Wageningen, the Netherlands*

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ABSTRACT

Managing forest openness can enhance drought resilience during dry, hot summer periods by reducing competition for soil moisture among trees. The purpose of our study was to better understand how different components of forest structure influence soil moisture variability. In our study, we utilized Terrestrial Laser Scanning to quantify the relationships between five forest structural attributes and the spatial distribution of soil moisture within experimental forest plots dominated by Douglas fir, Scots pine, and common beech in The Netherlands. In these plots the canopy openness ranged from 0, 20, 80 to 100 %. Observations were conducted during the hot and dry summer of 2022. Our findings revealed that all forest structural attributes related negatively with soil moisture and that the *crown features* canopy cover and plant area index predicted between 30 and 60 % of the spatial variability of soil moisture. In addition, these *crown features* consistently predicted 17 % more variation than the *trunk-centred* features basal area, stem density, and a density-dependent competition index. The *crown*-scale, corresponding to the crown radius of the dominant tree species, consistently explained most variation in soil moisture across species and time. We expect that tree water uptake is the primary factor influencing the spatial variability of soil moisture, rather than throughfall or interception, yet direct measurements of these processes are needed to substantiate this. This study suggests that forest management could benefit from information on forest structural attributes to guide tree harvest and improve soil moisture availability, contributing to developing a climate-smart forest management strategy.

1. Introduction

Heat and drought stress are prompting a re-evaluation of priorities for forest management, shifting the focus towards reducing tree water stress to maintain wood production and other ecosystem services provided by forests (del Campo et al., 2022; Grant et al., 2013). Tree water stress is driven by reduced soil moisture availability, which, on a larger scale, can undermine overall forest health and functioning (He et al., 2014; Trumbore et al., 2015). Understanding the factors that govern forest soil moisture dynamics is crucial for climate-smart forest management (Asbjornsen et al., 2011; Ma et al., 2014). Such management aims to preserve forest productivity, carbon storage, and resilience in the face of increasing drought and heat waves linked to global climate change. However, soil moisture exhibits great variability due to the complex heterogeneity of forest structure (Asbjornsen et al., 2011; He et al., 2014), and there remains a gap in identifying effective measures to improve soil water availability by means of forest structural heterogeneity. Recent advancements in terrestrial laser scanning (TLS) have revolutionized our ability to quantify forest structure, providing a promising pathway to better understand the link between soil moisture variability and forest structure under climate extremes (Ehbrecht et al., 2021; Lines et al., 2022).

Soil moisture in forested areas varies both temporally and spatially. Past research indicates that soil moisture fluctuates over time due to variations in water inflow (e.g., precipitation, throughfall, stemflow) and outflow (e.g., wet leaf evaporation, root water uptake, soil evaporation, lateral flows, deep drainage) (Bramer et al., 2018; Sterck et al., 2021). Spatial variability in soil moisture is influenced by variation in above-ground forest structure, soil properties, litter density, root distribution, and other landscape heterogeneities (Griffiths et al., 2009;

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* Corresponding author.
E-mail address: a.c.e.meijers93@gmail.com (E. Meijers).

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Gwak and Kim, 2017; He et al., 2014; Ma et al., 2014; Xu et al., 2013). While soil properties are the primary driver of spatial variability in soil moisture under wet conditions, forest structure is the primary driver under dry conditions (Baroni et al., 2013; Gwak and Kim, 2017). This is because trees influence the spatial variability in soil moisture through the spatial occupancy of their crown, stem, and root structures. The crown intercepts precipitation, buffers the microclimate, and provides shade; the stem directs water flow; and the roots extract moisture from the soil at varying depths (Chang, 2006). These processes create uneven patterns of soil moisture within forests, contributing to spatial variability across the landscape. While these processes are challenging to measure directly, the resulting soil moisture levels and the physical structure of above-ground trees are more accessible to quantify. Such structure measurements may serve as a crucial first step in understanding forest soil moisture dynamics, particularly under hot and dry conditions.

Forest structure is characterized by the degree of heterogeneity in biomass distribution in three-dimensional space (Ehbrecht et al., 2021). Historically, forest structure was quantified through visual classifications, measuring tapes, prisms, hypsometers, or photography. These approaches often resulted in small sample sizes with a limited spatial extent and a focus on smaller trees (Atkins et al., 2023). Typically, these methods provided two-dimensional metrics at the plot level, such as basal area, diameter at breast height, stem density, and tree height (Wei and Liang, 2021), with stem density often receiving the most attention due to its ease of management (Aldea et al., 2017; Bravo-Oviedo et al., 2018; McDowell et al., 2007; Sterck et al., 2021). However, these traditional *trunk-centred* forest structural attributes (FSA), though cheap and easy to assess, exclude and oversimplify the complex three-dimensional structure of the forest canopy (Montgomery and Chazdon, 2001), which is identified as a strong driver of soil moisture in forests (De Frenne et al., 2021; Schumacher and Christiansen, 2015; Zellweger et al., 2019). Recent technological advances, particularly TLS, have refined our view from the plot- to the tree-, and even to the leaf-level, allowing us to investigate the role of three-dimensional crown structures in soil moisture dynamics (Ehbrecht et al., 2021; Rieder and Kneisel, 2023; Santos et al., 2024). The ability to dynamically shift between spatial scales is crucial as water-related processes operate at varying scales—from plot-level precipitation to tree-level throughfall, shading, and water uptake, and down to leaf-level evaporation and transpiration (Atkins et al., 2023). TLS can help identify the dominant spatial scale at which forest attributes affect soil moisture variation, a largely unknown factor that complicates determining the optimal scale for interventions to mitigate tree water stress under hot, dry conditions.

Earlier studies have shown that soil moisture often correlates with *canopy* features in spatially explicit analyses of three-dimensional forest structures, while its relationship with *trunk* features tends to be less consistent (Belmonte et al., 2022; Breshears et al., 1997; Cai et al., 2021; Gray et al., 2002; Lenk et al., 2024; Lin et al., 1992; Ma et al., 2014; Rieder and Kneisel, 2023). These studies vary greatly in experimental design and methodology, ranging from the use of measuring tapes to TLS, from observational studies to experimental blocks. Furthermore, they differ greatly in the structural attributes they consider, which sometimes include leaf area index, crown area, tree number, diameter at breast height, throughfall, canopy openness, crown projection area, basal area, canopy cover, tree height, gap sizes, and gap orientations. Nonetheless, their findings underscore the strong link between soil moisture and structural attributes, particularly canopy attributes. In this study, we aim to elucidate (1) which forest structural attributes best describe spatial soil moisture patterns, and (2) what spatial scale (sub-crown, crown, plot) yields the highest correlations between forest structural attributes and soil moisture patterns.

To this end, we use spatially- and temporally coupled soil moisture measurements and TLS forest structural data, that we collected in a forest density experiment on well-drained sandy soils in The Netherlands. The density experiment includes closed forest (0 % harvest), thinned forest (∼20 % removal), shelterwood system (∼80 % removal) and clearcut (∼100 % removal), and thus covers a broad range of forest structure. We measured during the hot and dry summer months of 2022 in monoculture forest plots of common beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), and Douglas fir (*Pseudotsuga menziesii*).

2. Methods

2.1. Study sites, environmental conditions, and experimental design

This study makes use of a forest experiment initiated in 2019 (Sterck et al., 2021; van der Woude et al., 2024; Vos et al., 2023a,b), and was conducted on three 1-ha forest plots in the Veluwe area of The Netherlands (52°3′ N, 6°0′ E) during the growing season of 2022. The region has a temperate maritime climate characterized by mild winters, mild summers, and year-round precipitation. Over the past ∼30 years (1991–2023), the mean annual precipitation has been 900 mm, and the mean annual temperature has been 10.2 °C (KNMI, 2022). The year 2022 was, retrospectively, particularly suitable for this study due to its dry growing season, ranking among the driest 5 % since 1906, with a maximum precipitation deficit of ∼320 mm (KNMI, 2022). We used monospecific forest plots dominated by a single species: common beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*), or Scots pine (*Pinus sylvestris*), which are significant forestry species in Central Europe (ForestEurope, 2020). These plots are all located on dry sandy podzols with an average organic layer thickness of 10 cm, on predominantly flat terrain at altitudes between 30 and 70 m above sea level, and out of reach of groundwater tables (M.A.E. Vos et al., 2023) (Supplementary S2 for more details). The abundance of regeneration was typical for the species in the Scots pine and Douglas fir plots, while none was observed in the beech plot. In 2019, canopy openness treatments were established by harvesting, dividing each plot into four 0.25-ha treatments where 100 %, ∼80 %, ∼20 %, and 0 % of the total basal area was harvested (Fig. 1). All plot locations were no >35 km apart to ensure similar weather conditions.

2.2. Soil moisture transects and measurements

In each of the plots, we established permanent transects along which we repeatedly measured Volumetric Water Content (VWC, in %) using a portable Time Domain Reflectometry (TDR) sensor (‘6050×1 TRASE system 1′, Soilmoisture Equipment Corp., USA). Two 40-meter transects were set up within each of the four subplots (Fig. 1), with the start and end of each transect marked by reflective poles to facilitate integration with georeferenced terrestrial laser scanning data. Within the Scots pine 80 % harvest plot, a small third transect was created due to impenetrable soil due to rocks at the end of the second transect. The transect locations were chosen based on the following criteria: uniform orientation within the plot, a minimum distance of five meters from the plot border, and the presence of at least one tree on the transect (excluding the 100 % harvest treatments). Soil moisture levels along the transects were measured three times throughout the dry-down period for each species (Supplementary S1). The exact dates were: common beech: 28th June, 11th July, 18th July; Douglas fir: 27th June, 13th July, 20th July; Scots pine: 23rd June, 14th July, 22nd July, all in 2022.

To capture spatial variability, measurements were taken at two-meter intervals in the 0 %, ∼20 %, and ∼80 % openness systems, and at five-meter intervals in the 100 % openness system, where forest structural attribute variation was less pronounced. Each VWC measurement point on the transect was measured three times to ensure robustness. Measurements were taken after removing the litter layer, by pushing down the measurements rods to a depth of 30 cm in the mineral soil, which was the maximum depth possible due to soil stones. This depth aligns with the placement of permanent soil moisture sensors in the study area (Supplementary S7). Additionally, 50–55 % of fine roots biomass are typically located within the upper 30 cm of the mineral soil,

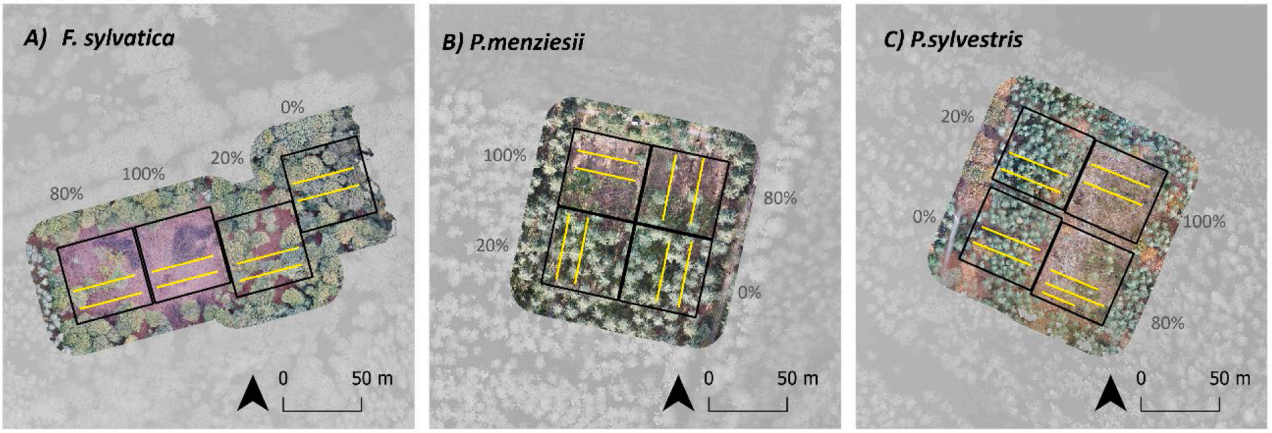

Fig. 1. Maps of the 1-ha experimental forest plots, each plot dominated by one tree species: Fagus sylvatica (common beech), Pseudotsuga menziesii (Douglas fir), Pinus sylvestris (Scots pine). Within the 1-ha plots four different canopy openness treatments were established in 2019; 100 %, ~80 %, ~20 %, and 0 % harvest. Yellow lines indicate location of 40 m long measurement transects.

as reported by Olsthoorn et al. (1991) and Weemstra et al. (2016) and (2018), whose studies were conducted on similar soils and species in close proximity (~50 km) to our research plots. While trees may also tap water from deeper layers, we consider this 30 cm depth as representative of an biologically active soil root-zone capturing variation in soil water availability for trees in our study. In total, 1296 measurements were taken per plot. Both permanent wilting point and field capacity were modelled using the Van Genuchten-Mualem equation and parameterization of local soil parameters (Supplementary S2).

2.3. *Terrestrial laser scanning (TLS)*

To capture forest structure, we created a three-dimensional scan of the forest plots using a RIEGL VZ-400 terrestrial laser scanner (RIEGL Laser Measurement Systems GmbH, Austria). Scans were conducted in June 2022 and represent the forest structure during the days of soil moisture measurements. Both horizontal and upright scans were taken at 25-meter intervals to ensure sufficient scan quality throughout the plot. Cylindrical reflectors (5 cm) were strategically placed and relocated to facilitate the co-registration of scans, following the protocol by Wilkes et al. (2017).

2.3.1. *Processing of the TLS data*

We pre-processed the TLS data using RiSCAN PRO software (version 2.12.1, RIEGL Horn, Austria) and CloudCompare (version v2.12.4). In RiSCAN, cylindrical reflectors were used as tiepoints for co-registration, and the Multi Station Adjustment 1 algorithm (RIEGL Laser Measurement Systems GmbH, 2019) was applied to improve the co-registration. The start and end coordinates of the transects, marked by reflective poles, were derived from the point clouds, and the coordinates of the measurement locations were calculated by linear interpolation.

For further scan cleaning, we removed ghost points with Riegl's "pulse shape deviation" value greater than 15 (-) as done by Liu et al. (2019). In CloudCompare, we filtered the point clouds by subsampling to maintain a minimum distance of 0.01 m between neighboring points, homogenizing point cloud density. Noise was removed using the built-in Statistical Outlier Removal filter with the 10 nearest Euclidean neighbors and a standard deviation multiplier of 1.00 (Rusu, 2008; Wilkes et al., 2017).

The processed point clouds were then analyzed using the Forest Structural Complexity Tool (FSCT) by Krisanski et al. (2021) in Python (version 3.9). We visually validated the FSCT output tables with the point cloud to ensure accurate identification of trees and corrected any misclassified objects. To accurately calculate forest structural parameters, we corrected the point clouds for ground surface height using the Digital Terrain Model (DTM) created by the FSCT. Due to occasional occlusion errors by the FSCT, we interpolated missing DTM points in CloudCompare. The improved DTM was used to normalize the height of the cleaned point clouds using the lidR package (Roussel et al., 2020) in R version 4.2.2 (R Core Team, 2022).

2.3.2. *Forest structural attributes*

For each location where we measured soil moisture, we derived the forest structural attributes from these processed TLS point clouds. Derived forest structural attributes were: basal area, canopy cover, competition, plant area index, and stem density (Table 1). The attributes were quantified at three horizontal spatial scales: 2 m, crown radius level (3 m for Scots pine, 5 m for Douglas fir, and 7.5 m for Beech), and plot level (10 m). The derivation of these spatial scales is detailed in the Supplementary (S7). This multi-scale approach allowed us to capture the influence of forest structure on soil moisture at different spatial resolutions, highlighting how finer-scale structural features (e.g., individual

Table 1
Forest structural attributes derivations and definitions.

Forest structural attribute	Abbreviation	Description
Basal area	BA	Sum of square meters of all basal areas in circular focal area of varying size^2
Canopy cover^1	CC	% of 5 cm horizontal square pixels that contained at least 1 point in circular focal area of varying size^2
Competition	COMP$_i$	$\sum \frac{DBH_j}{1+\ distance_{ij}}$, for all trees *j* within distance, as dependent on varying focal area size^2, from location *i*. DBH is the diameter breast height of tree *j* and distance is the distance from tree *j* to the measurement point *i*. We add one to the distance to maintain linear weighing of trees with a distance <1m.
Plant area index^1	PAI	Number of 5 cm cubic voxels with at least one point in circular focal area of varying size^2
Stem density	SD	Number of trees (excl. regeneration) in circular focal area of varying size^2

1 using the VoxR package (Lecigne, 2020). TLS points below a height of 0.5 m were removed to exclude points that belong to the soil surface rather than vegetation.

2 Focal area sizes: smallest focal area was 2 m, then a focal area that was as large as an average crown radius per species (beech= 7.5 m, Douglas fir= 5 m, and Scots pine= 3 m), and a largest focal dependent on the maximum attainable spatial scale of our experimental boundaries at 10 m.

tree crowns) and broader-scale features (e.g., overall plot characteristics) could both contribute in explaining soil moisture distribution (Atkins et al., 2023). All calculations were performed in R version 4.2.2. (R Core Team, 2022).

2.4. Statistical analyses

The final dataset consisted of soil moisture measurements taken on 408 measurement points on three different days for each of the three forests and tree species, along with FSA at three spatial scales at each of those measurement points. Our aim was to describe the link between soil moisture and FSA for each tree species and attribute separately (also mandated by the high levels of collinearity between FSA, Supplementary S4). We built Linear Models (LM) and Generalized Least Squares (GLS) models (R package 'nlme'), for every species, FSA, canopy openness treatment, and spatial scale separately, and incorporated spatial correlation structures in the GLS models to account for spatial autocorrelation (Supplementary S3). "Date" was included as a predictor to reduce noise and contribute to the normal distribution of the data. Residuals from the linear models were examined using bubble plots and variograms (R package 'gstat') (Supplementary S3). GLS models were evaluated based on spatial autocorrelation and AIC, followed in BIC and log-likelihood performance. Pseudo R-squared values (here the squared correlation between observed and fitted values) were calculated to assess the explanatory power of the GLS models (Nagelkerke, 1991). The final GLS models, particularly those with exponential correlation structures, were selected for their robust performance and variograms without spatial patterns.

3. Results

3.1. Soil moisture variability across canopy openness

Across all species, soil moisture (VWC, in %) was significantly higher by 2 % and 6 % in the 80 % and 100 % canopy openness plots, respectively, compared to the control plot ($p < 0.005$, GLS model, Fig. 2 and Supplementary S6). No significant differences in soil moisture were observed between the 0 % and 20 % openness plots across all species ($p > 0.05$, GLS model). Despite these plot-wide trends, a high level of intra-plot variability was observed across all canopy openness plots and species, generally covering the full range between permanent wilting point and field capacity. Beech exhibited a consistent and substantial increase in soil moisture in the 100 % openness plot, with levels rising by 11 % ($p < 0.001$, GLS model). In contrast, Douglas fir showed a more moderate increase of 4 % ($p < 0.005$, GLS model), while Scots pine exhibited no significant change, with only a 1 % increase ($p = 0.174$, GLS model), which may be attributed to species-specific variations in regeneration. On average, soil moisture was 6 % and 4 % higher in the beech plots relative to the Douglas fir and Scots pine plots, respectively ($p < 0.005$, GLS model), with minimal differences between the latter two. A decreasing trend in soil moisture was observed from measurement day 1 to day 3, indicating the soil's drying process over time. By measurement day 3, soil moisture values approached the wilting point, highlighting the rapid drying within this period (Supplementary S1 for full-year 2022 context).

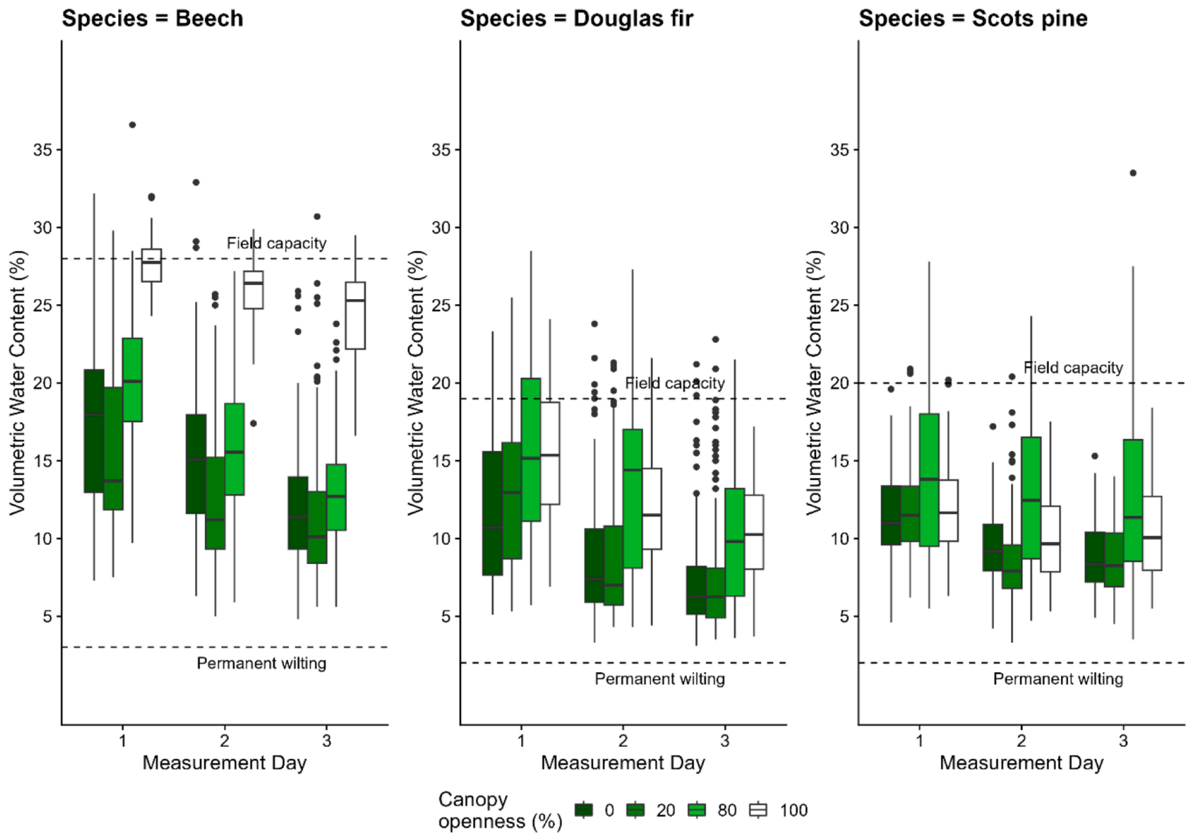

Fig. 2. Distribution of soil moisture (Volumetric Water Content, in %) measurements across four canopy openness plots (0 %, ~20 %, ~80 %, and 100 %) on the three drying-down measurement days (1–3), for the investigated species: beech (F.sylvatica) Douglas fir (P.menziesii), and Scots pine (P.sylvestris). Sample sizes were $n = 54$ for canopy openness=100, $n = 126$ for all others. The bottom dashed line indicates the calculated permanent wilting points at 3 %, 2 %, and 2 % soil moisture in the BE, DG, and SP plots, respectively. The top dashed line indicates the field capacity at 28 %, 19 %, and 20 % soil moisture in the BE, DG, and SP plots, respectively. Both permanent wilting and field capacity were modelled using the Van Genuchten-Mualem equation and parameterization of local soil parameters (Supplementary S2).

3.2. Spatial distribution of soil moisture

The spatial distribution of soil moisture and forest structural attributes (FSA) is illustrated for each species for a transect in ~20 % openness plot (Fig. 3). Soil moisture varied substantially within each transect and decreased over the three days during the four-week dry-down period. All FSA revealed great spatial heterogeneity. Some FSA (competition, basal area, stem density) varied more strongly (for adjacent grids) than others (PAI, canopy cover), and this effect was strongest at the 2 m-scale. Despite the quantitative differences in FSA distributions, all FSA inversely related with soil moisture. This illustrates that a denser forest structure comes with reduced soil moisture availability. The FSA were calculated at three spatial scales: 2 m, crown level (3 m for Scots pine, 5 m for Douglas fir, and 7.5 m for beech), and the plot level (10 m). At the 2-meter scale, the FSA captured dense pockets of localized variations in forest structure, revealing a weak alignment with soil moisture, particularly for basal area, competition, and stem density. At the crown level, a more consistent pattern emerged, demonstrating an improved (inverse) relationship between FSA and soil moisture across all species, with the effect being most pronounced in beech. At the plot level, the pattern became more diffuse, indicating that the relationship between forest structure and soil moisture may weaken as the spatial scale increases.

3.3. Predictive power of forest structural attributes at different scales

Soil moisture significantly decreased with all FSA across all three days and species ($p < 0.05$, GLS model) (Fig. 4a and 4b, with all scatterplots per GLS model in Supplementary S5). Crown-related features, such as canopy cover and plant area index, explained 17 % more variation in soil moisture compared to trunk-related features like basal area, competition, or stem density (Fig. 4a), with a species-specific difference of +30 % for beech, +14 % for Douglas fir, and +6 % for Scots pine. Generally, best predictions were found in beech (max pseudo $R^2 = 0.61$), followed by lower predictions in Douglas fir (max pseudo $R^2 = 0.48$) and Scots pine (max pseudo $R^2 = 0.35$).

Overall, the crown-scale FSAs were the most effective in predicting soil moisture patterns (Fig. 4a, Fig. 3). The varying crown sizes across species influenced how the crown scale compared to the 2-meter and plot scales. In beech trees, which have the widest crowns of the three species studied (Fig. 3), the crown and plot scales yielded similar results due to the large overlap. For Douglas fir, whose crown radius falls between the plot and 2-meter scales, the crown scale consistently provided the most accurate predictions. In Scots pine, with the smallest crown radius, the crown and 2-meter scales produced similar and more accurate predictions. This pattern highlights that the crown scale, adjusted for species-specific crown size, is most effective for predicting soil moisture. This notion was particularly true for crown-related features, while trunk-related features showed consistently lower predictive power at this scale across all species.

4. Discussion

The aim of this study was to answer (i) which forest structural attributes (FSA) best describe spatial soil moisture patterns, and (ii) to determine what spatial scale (sub-crown, crown, plot) yields the highest correlation between soil moisture and forest structure, particularly under hot-and dry conditions. We observed that crown-related FSA, such as canopy cover and plant area index resolved at the tree crown-scale, best explained the high level of spatial variability of soil moisture.

4.1. Influence of forest structural attributes on soil moisture

Our results demonstrate that canopy cover and plant area index best

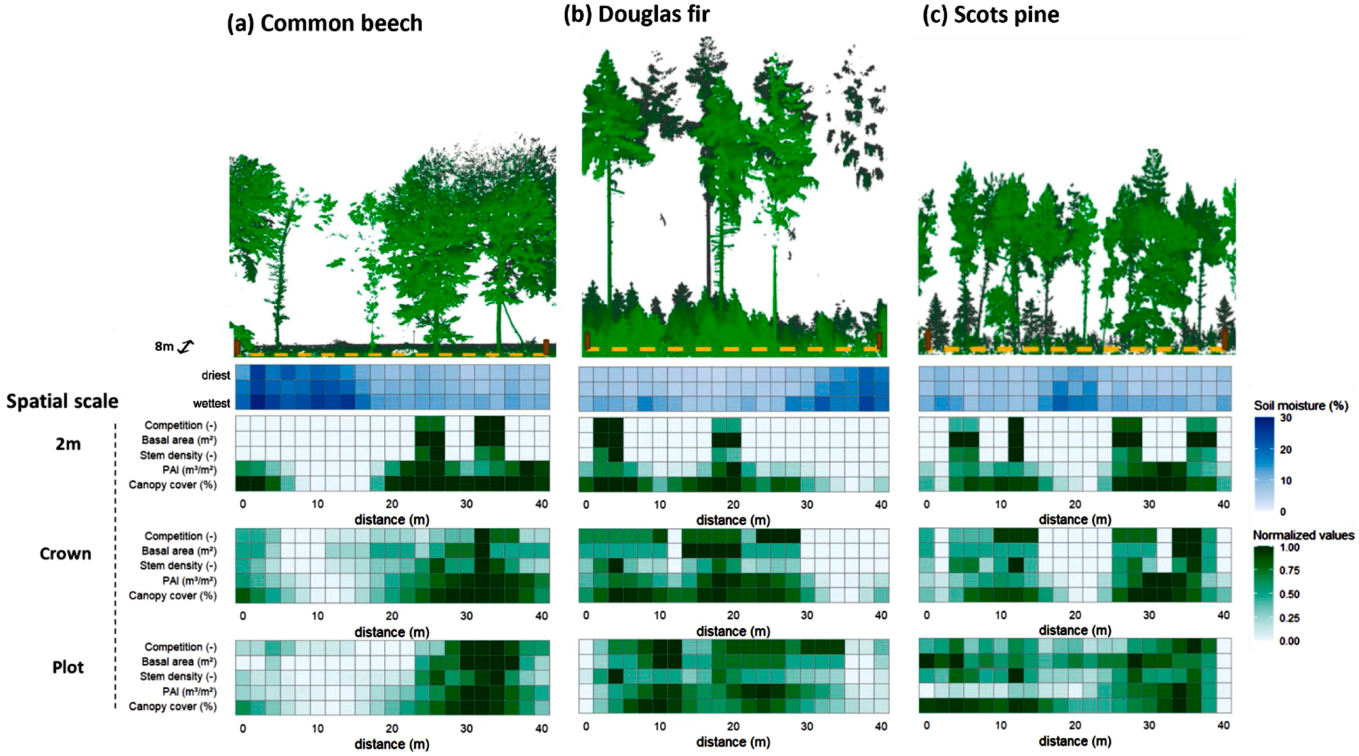

Fig. 3. Terrestrial Laser Scan cross-sections of ~20 % canopy openness plots for (A) Common beech (Fagus sylvatica), (B) Douglas fir (Pseudotsuga menziesii), and (C) Scots pine (Pinus sylvestris). Each cross-section spans a length of 40 m and a width of 8 m, with height scaled proportionally. The Volumetric Water Content (VWC, in %) of the soil is depicted in blue for three increasingly dry days along a dry-down for each species. Five Forest Structural Attributes – Competition, Basal Area (m^2), Stem Density, Plant Area Index (PAI, m^2/m^2), and Canopy Cover (%) – are calculated at three spatial scales (2m, crown [Scots pine = 3 m, Douglas fir = 5 m, Beech = 7.5 m], and plot) and shown in green. Darker shades indicate higher values for both VWC and FSA.

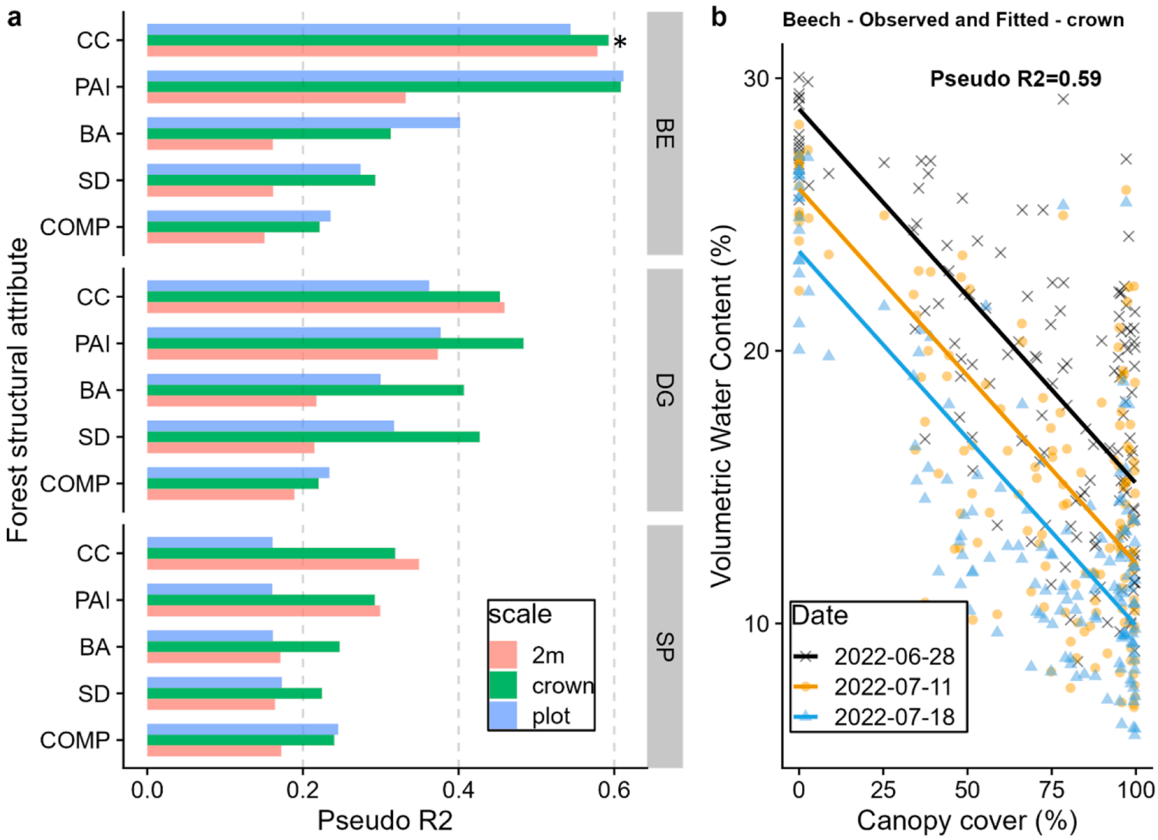

Fig. 4. Panel A) Pseudo R^2 values (here calculated as the squared negative correlation between observed and GLS fitted values) for the relationship between Volumetric Water Content (VWC, %) and various Forest Structural Attributes at different spatial scales for Scots pine (SP, Pinus sylvestris), Douglas fir (DG, Pseudotsuga menziesii), and common beech (BE, Fagus sylvatica). FSA include Canopy Cover (CC), Plant Area Index (PAI), Basal Area (BA), Stem Density (SD), and Competition (COMP). The spatial scales analyzed are 2 meter grid (pink), tree (3 m for Scots pine, 5 m for Douglas fir, and 7.5 m for Beech, green), and plot (10 m, blue). Higher pseudo R^2 values indicate a stronger predictive relationship between the FSA and VWC. Asterisk indicates highlighted FSA in panel B. Panel B) Scatterplot illustrating the relationship between Volumetric Water Content (VWC, %) and Canopy Cover (%). Negative correlation with pseudo R^2 value of 0.59 for common beech (Fagus sylvatica) across three measurement dates during the dry-down period at the crown-scale. Data points represent measurements taken on June 28, 2022 (black crosses), July 11, 2022 (orange circles), and July 18, 2022 (blue triangles). The fitted lines illustrate the trend for each date as modelled using a GLS approach with an autocorrelation structure fitted on the residuals.

explain soil moisture across the studied species, time, and spatial scales (Fig. 4A). These attributes consistently explained 17 % more variation than the other attributes, indicating their strong ecological relevance on soil moisture dynamics. This finding aligns with previous studies that emphasize the importance of crown-related attributes in regulating soil moisture (Belmonte et al., 2022; Breshears et al., 1997; Cai et al., 2021; Gray et al., 2002; Lenk et al., 2024; Ma et al., 2014; Rieder and Kneisel, 2023). The strong negative link of canopy cover and plant area index with soil moisture in our study likely stems from their effectiveness as proxies for key water-related processes under hot and dry conditions, such as interception, throughfall, stemflow, and water uptake by the roots. The latter follows from the general understanding that the physical occupancy of tree root systems mirrors that of the tree crowns (Gllman, 1988; Smith, 1964), granted that under scarce or unevenly distributed conditions roots may extend beyond the crown in search of nutrients (Montero et al., 2004). In addition, all FSA revealed a consistent *negative* relation with soil moisture, suggesting that a reduction of evaporation from the soil through canopy shading and microclimatic buffering did not balance the increase in transpiration and interception under a more dense crown.

We showed that crown-related attributes better explain soil moisture variation than trunk-related features such as basal area and stem numbers, which are commonly used in forestry (Castagneri et al., 2021; Sohn et al., 2016). While these conventional metrics are often utilized in forest ecology and management for other purposes such as tree growth under drought conditions, they appeared less insightful in explaining soil moisture variability in our study. This underscores the different roles that crowns and stems can have in ecological terms. The robustness of our findings is highlighted by the temporal consistency of the observed relationships between soil moisture and FSA over the different measurement dates (Fig. 4B, and more in Supplementary S5).

4.2. Spatial scaling

Our findings indicate that canopy cover, a two-dimensional forest attribute, explained soil moisture variability just as effectively as the three-dimensional plant area index (Fig. 4A). This similarity likely reflects the high collinearity between these attributes (Figure S4.1 and S4.3), as both are closely linked to processes influencing soil moisture, such as water uptake and interception. These processes reduce local soil moisture levels, as supported by prior studies (Goebes et al., 2015; Livesley et al., 2014; Maass et al., 1995; Morris et al., 2003; Nooraei Beidokhti and Moore, 2021; Song et al., 2018). In addition, our study underscores the importance of spatial scale, as FSA aggregated at the species-specific crown scale provided the best predictions of soil moisture variability (Fig. 4A). The more local scale (2m) and plot (10m) scales both did not provide additional insights into the relationship between forest structure and soil moisture over the crown scale (3–7.5 m, depending on species). Our findings imply that this species-specific crown-scale best aligns with the scale of the most important process that drive spatial variation in soil moisture (Atkins et al., 2023). From a practical standpoint, these finding suggests that assessing crown-scale canopy cover alone – whether through satellite data or visual assessment - will be sufficient for future studies and practices aimed at modifying local soil moisture status.

4.3. Differences across species

The relationship between soil moisture and forest structure attributes (FSA) varied considerably across species (Figs. 2–4). Common beech exhibited the most pronounced spatial contrasts in soil moisture, with the strongest correlations to canopy cover and plant area index. In contrast, Scots pine and Douglas fir showed more uniform soil moisture levels and weaker correlations with these FSA, with Scots pine exhibiting the weakest relationship overall. The relationship between soil moisture and canopy FSA is driven by two processes that impact soil moisture in opposing directions; precipitation throughfall and water uptake driven by transpiration. Conifers are known to have lower precipitation throughfall than broadleaf species due to their increased canopy storage capacity (Klamerus-Iwan and Błońska, 2018; Pflug et al., 2021), which reduces soil water content under a coniferous canopy compared to a broadleaf canopy. However, broadleaf species are known to transpire more during the growing season than coniferous species due to a higher leaf area index (Fig. 3), and less strict stomatal control (Peters 2023), which reduces soil water content under a broadleaf canopy compared to a coniferous one. Our results suggest that transpiration and subsequent water uptake plays a larger role than precipitation throughfall in determining the canopy cover – soil moisture relationship, as the soil water content under the canopy was equally low for all species. Furthermore, we observed abundant juvenile regeneration in the conifer plots but not in the beech plots, where regeneration was scarce. The presence of regeneration can dampen the correlation between the canopy cover of the canopy trees and soil water content (Balandier et al., 2022; Bodo et al., 2023; Wang et al., 2021). Our results suggest that this dampening effect is present in the conifer plots, where the soil water content in the canopy gaps was lower than in the beech plots. The scarce regeneration in the beech plots also explains the high soil water content in the 100 % removal treatment (Fig. 2) compared to the same treatment in the conifer plots. This can be explained by a rapid decline of the evaporation rate as the topmost soil layer (i.e. 1–2 cm) dries and creates a resistance to water transport from the saturated soil and the atmosphere. Conversely, a small vegetation of juvenile trees is well able to transpire water from the soil layers where we conducted our measurements (i.e. up to 30 cm below the organic layer). In summary, we propose that the observed species-specific differences in soil moisture variability can be primarily attributed to variation in transpiration and subsequent tree water uptake either by mature or juvenile regeneration trees.

Another factor influencing species-specific differences in soil moisture variability may be the spatial extent of lateral root systems. The differences in the crown profiles between the species likely correspond to variations in their extent of their root system, as crown profiles are often considered indicative of lateral root extent. While direct measurements on this relation are limited, several studies suggest a general correlation between aboveground and belowground architecture (Gllman, 1988; Hruska et al., 1999; Olsthoorn, 1991; Smith, 1964), granted that under scarce or unevenly distributed conditions roots may extend beyond the crown in search of nutrients (Montero et al., 2004). This alignment between crown size and root system helps to explain species-specific differences in water uptake and soil moisture depletion, with larger crowns supposedly supporting more extensive root systems that access a broader soil volume. This spatial extent of the root system may be further extended by symbiotic relationships with soil arbuscular (AM) and ectomycorrhizal (ECM) fungi (Moser et al., 2014; Phillips et al., 2016) that enhancing nutrient and water uptake. This could amplify the effects of crown size and root system extent on soil moisture variability. The extent and nature of these symbiotic relationships are complex and vary across species, thereby potentially contributing to the observed disparities in soil moisture variability.

4.4. Study implications for forest management: does thinning enhance tree water availability?

In concordance with our findings, thinning operations have been shown to generally enhance plot-wide soil moisture availability, especially at higher thinning intensities (Zhang et al., 2018). We showed that this increased moisture is accompanied by significant spatial variability in soil moisture within the managed areas, which can be largely attributed to factors such as local canopy cover. While this finding sheds light on the soil variability post-thinning, it remains uncertain whether the remaining trees can effectively capitalize on the elevated soil moisture. Research suggests that trees do capitalize on the newly available water after thinning, as evidence by increased growth and reduced mortality rates (Castagneri et al., 2021; Giuggiola et al., 2018). However, caution is warranted in interpreting these results, as growth and mortality are not direct indicators of tree water status alone. Growth responses, in particular, are likely confounded by increased light availability following thinning, which also boosts photosynthesis and productivity. Data on actual improvements in tree water status following thinning operations are still scarce (Gouveia and Freitas, 2008; Montero et al., 2004), but are promising. Furthermore, the timing, location, and extent to which trees are able to extend their roots through hydrotropism to access this newly available water pool are still unclear (even in model species *Arabidopsis)* (Cassab et al., 2013; Eapen et al., 2005). Mycorrhizal fungi may play a critical role in this process, as these symbiotic organisms potentially allow the tree to access water outside of the space occupied by its own root system (Lehto and Zwiazek, 2011). Some studies suggest that increased light exposure through thinning even might inadvertently increase a stand's drought sensitivity by reducing carbon allocation to roots and mycorrhizal fungi – thereby potentially leading to shallower root systems (Ibáñez and McCarthy-Neumann, 2016). Understanding these complex interactions and the true impact of thinning on tree water status requires a comprehensive approach across multiple temporal scales. This should involve root mapping, soil moisture monitoring, tree water status assessments, isotopic tracing, and measurements of plant hydraulic conductance. Conducting these measurements over short-term, seasonal, and long-term periods will provide a clearer picture of how various factors influence soil moisture variability and tree water status over time in response to thinning practices. Such insights will ultimately guide more effective, species-tailored forest management practices. Our findings suggest that strategic thinning enhances soil moisture, but whether this will translate into improved tree water status during future hot and dry conditions remains uncertain. Further investigation is needed to better understand the extent of these benefits and their implications for forest management.

5. Conclusion

Our study quantified how forest structures link with spatial patterns of soil moisture under hot and dry conditions. We observed that species-specific crown-scale FSA, such as canopy cover and plant area index best explained the high level of spatial variability of soil moisture. This implies that forest management aiming at climate resilient forests could use local crown radii as the measurement units for releasing soil water stress, for example, by harvesting trees with their stem and/or crown within a local crown-radius distance from a target trees' projection area. In addition, we suggest that the observed species-specific differences in soil moisture variability in our study were primarily attributed to variations in evapotranspiration and subsequent tree water uptake either by mature trees or regeneration. We hope that our insights provide a steppingstone for shifting towards climate-smart forestry practices that prioritise reducing forest water stress to maintain wood production and other ecosystem services.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT$_{4o}$ in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Data availability

The data and code that support the findings of this study are available at:

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CRediT authorship contribution statement

Eva Meijers: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Roos Groenewoud:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Jorad de Vries:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Jens van der Zee:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Gert-Jan Nabuurs:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition. **Marleen Vos:** Writing – review & editing, Writing – original draft, Conceptualization. **Frank Sterck:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110431.

Data availability

The data and code that support the findings of this study will be made available upon acceptance.

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