

Beyond cloud cover: Low- and high-altitude clouds have distinct impacts on tree sap flow and transpiration

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ABSTRACT

Transpiration drives up to 40 % of terrestrial precipitation, with forests playing a critical role. This study combines long-term sap flow measurements and surface-based cloud observations to examine how different clouds affect tree transpiration across boreal and temperate European forests. Under specific cloudy conditions, sap flow can exceed clear-sky levels, reflecting distinct radiation effects of various cloud types. However, overall cloudiness reduces maximum sap flow by up to 40 %. A key finding is the contrasting influence of low- and high-altitude clouds: low-altitude clouds suppress transpiration by limiting incoming radiation, while high-altitude clouds have negligible impact even when overcast. Structural equation modelling further indicates a pathway linking transpiration to cloudiness when other meteorological and site factors are accounted for. Satellite data show a decline in low-altitude cloud fraction over boreal forests, and a highly simplified model-based order-of-magnitude estimate suggests a potential associated increase in transpiration equivalent to ~0.6–1.2 mm of precipitation annually. These results emphasize how climate change driven changes in cloud cover and type may alter the moisture flux to the atmosphere, impacting regional and global water cycles.

1. Introduction

Forests cover ~30 % of land area (FAO and UNEP, 2020) and contribute ~40–60 % of atmospheric water vapor through transpiration, accounting for 39 % of terrestrial precipitation globally (Ellison et al.,

2017; Schlesinger and Jasechko, 2014). Thus, forest transpiration is a major driver of the hydrological cycle. To understand the biosphere-atmosphere interactions in a changing climate, it is essential to explore the relationship between transpiration and its environmental drivers.

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In our work we investigate the role of forests in the climate system, specifically through the lens of tree transpiration, which is often inferred from sap flow (Čermák et al., 2004; Steppe et al., 2015). Tree sap flow is strongly influenced by atmospheric factors such as solar radiation, and atmospheric water demand (Katul et al., 2009; Oogathoo et al., 2020). Solar radiation triggers stomatal opening (Araújo et al., 2011; Kimura et al., 2020), allowing water release into the atmosphere. Soil water availability is another crucial regulator: plants protect themselves from extreme conditions (such as drought) by stomatal closure leading to reduced gas exchange and transpiration (Fu et al., 2024; Green, 2024). The relative importance of these drivers varies by ecosystem and species. Overall, atmospheric dryness (vapor pressure deficit, VPD) is the dominant driver of transpiration, modulated by soil moisture (Novick et al., 2016). Its role is critical as future projections indicate increasing VPD (Nagavciuc et al., 2024) due to declining near-surface relative humidity (RH) over land (Gulev et al., 2023). Higher VPD can stress plants, reducing stomatal conductance, transpiration, and CO₂ uptake (Grossiord et al., 2017; Shekhar et al., 2023), leading to unforeseen effects for both hydrological and carbon cycles. Changes in transpiration and VPD also directly affect the amount of water vapour in planetary boundary layer available for cloud formation, linking plant physiological responses to atmospheric processes.

Clouds are a vital component of the hydrological cycle, efficiently redistributing moisture through the troposphere and influencing regional and global climate. Consistent with this, VPD and its reciprocal RH are closely linked to cloudiness as water vapor supersaturation is required for cloud formation (Lohmann et al., 2016; Seinfeld and Pandis, 2016). VPD impacts cloudiness by: 1) altering forest transpiration, 2) by modulating the relative importance of turbulent fluxes of sensible and latent heat, 3) impacting volatile organic compound emissions from trees and thus formation and number of aerosol particles eventually acting as cloud condensation nuclei and 4) changing the canopy productivity which can further impact both 1) and 3) (Ellison et al., 2024; Heerwaarden and Arellano, 2008; Kanniah et al., 2013; Luo et al., 2024; Teuling et al., 2017; Vilà-Guerau de Arellano et al., 2014). Cloudiness itself has an indirect impact on ecosystem processes by changing local meteorological drivers (such as temperature, via impact on radiation, and humidity, via impact on precipitation) further affecting tree physiology. Clouds and aerosol particles also increase the proportion of diffuse over direct radiation, thus influencing photosynthesis rates. Diffuse radiation better penetrates the shaded parts of the canopy enhancing photosynthesis and gross primary production (Chakraborty et al., 2022; Deng et al., 2022; Ezhova et al., 2018; Rap et al., 2018). The processes from points 1–4 above form a feedback mechanism, whereby the atmosphere (clouds, temperature, humidity) impacts the biosphere (transpiration, emission of cloud nuclei precursors), which in turn impacts the atmosphere (cloud formation).

Clouds form when water vapor condenses around aerosols, with formation mechanisms differing for low- and high-altitude clouds (Lohmann et al., 2016; Seinfeld and Pandis, 2016). Low clouds typically form in the lower troposphere when air reaches its dew point (Seinfeld and Pandis, 2016), whereas high clouds form in the upper troposphere through large-scale lifting (e.g., jet streams, fronts) and are often ice-dominated. Long-term changes in cloud cover have been reported from satellite measurements, global climate models and reanalyses (Devasthale et al., 2025, 2022; Liu et al., 2023; Xu et al., 2022; Zhang et al., 2024), but trends are spatially heterogeneous. Globally, on average, cloud cover has decreased over continents and increased over tropical and subtropical oceans, mainly due to changes in low- and mid-altitude clouds (Devasthale et al., 2022; Liu et al., 2023). In parallel, evidence is accumulating that land cover change can modify clouds and precipitation: deforestation can reduce tropical precipitation, while boreal forests can enhance rainfall (Räty et al., 2023; Smith et al., 2023). At the global scale, Luo et al. (2024) showed that deforestation-driven decreases in cloud cover exert a warming effect that partially offsets the cooling from increased surface albedo. Forests can also enhance

convective cloud formation relative to nearby grassland (Teuling et al., 2017), and afforestation tends to increase low cloud cover, with particularly strong effects in needleleaf forests in Europe (Caporaso et al., 2024; Duveiller et al., 2021; Ellison et al., 2024; Zhang et al., 2024).

To our knowledge, all previous ecohydrological studies, with focus on forests and transpiration, have treated cloud cover as a binary or undifferentiated variable (i.e., “cloudy” vs. “clear” or 0–100 % cloudiness) by utilizing cloud proxies or satellite measurements (Carbone et al., 2013; Goldsmith et al., 2013; Liu et al., 2024; Sumargo and Cayan, 2018; Xu et al., 2018). A major limitation in such analyses is the lack of differentiation between cloud types. This is ecologically important for understanding future climate transpiration feedbacks, as low- and high-altitude clouds have different radiative and microclimatic effects. For instance, during daytime, low-altitude cumulus clouds can reflect incoming solar radiation and cool the surface, while at night, high-altitude cirrus clouds can trap outgoing longwave radiation and cause warming (Forster et al., 2021). More crucially, these different cloud types also have divergent trends as highlighted above. In addition, surface-based cloud measurements, coincident with sap flow data, are becoming available, and essential for capturing the actual atmospheric conditions experienced by the forest. This allows for a more precise assessment of cloud impacts on transpiration at the forest stand level, improving our understanding of fine-scale atmosphere-biosphere interactions.

In our work we focus on how different cloud types affect forests’ water release (Fig. 1A). We do this by investigating long-term measurements of tree sap flow from different boreal and temperate forests in Europe (Fig. 1B) together with surface-based remote sensing measurements of clouds, resolving both cloud fraction and altitude. Specifically, we aimed at

1. resolving the impact of clouds on sap flow relative to the impacts of VPD and soil moisture,
2. investigating whether low- and high-altitude clouds have different impacts on sap flow and its drivers, and
3. estimating the magnitude of the potential changes in transpiration due to current trends in different cloud types.

Our results highlight the differing impacts of low- and high-altitude clouds on tree sap flow, with low-altitude clouds reducing sap flow and high-altitude clouds showing little to no effect. These distinct responses, combined with the observed long-term decline in summertime low-altitude cloud cover, suggest a potential reinforcement of positive climate feedbacks through enhanced transpiration. Together, these findings underscore the importance of separating cloud types when evaluating biosphere-atmosphere interactions under changing climate conditions.

2. Results

2.1. Impact of atmospheric dryness and soil moisture on sap flow: comparison across forest types and tree species

As a necessary foundation for the subsequent analysis of cloud effects, we first examined the controlling roles of the well-known drivers of sap flow—vapor pressure deficit (VPD) and soil moisture—across all sites and species. Sap flow increased with rising VPD once a site-specific threshold was exceeded, indicating a strong and consistent response across forest types. However, when soil moisture was low, sap flow was clearly limited at several sites, highlighting the combined influence of both VPD and soil moisture on tree water use.

At very low VPD (0–20th percentiles), little to no sap flow occurred (Fig. 2), but above this threshold (0.3–0.6 kPa), normalized sap flow increased. Thresholds were lowest at CZ-BK1 and SE-Svb, and highest at CZ-RAJ, reflecting site-level average summertime VPDs (Table S1).

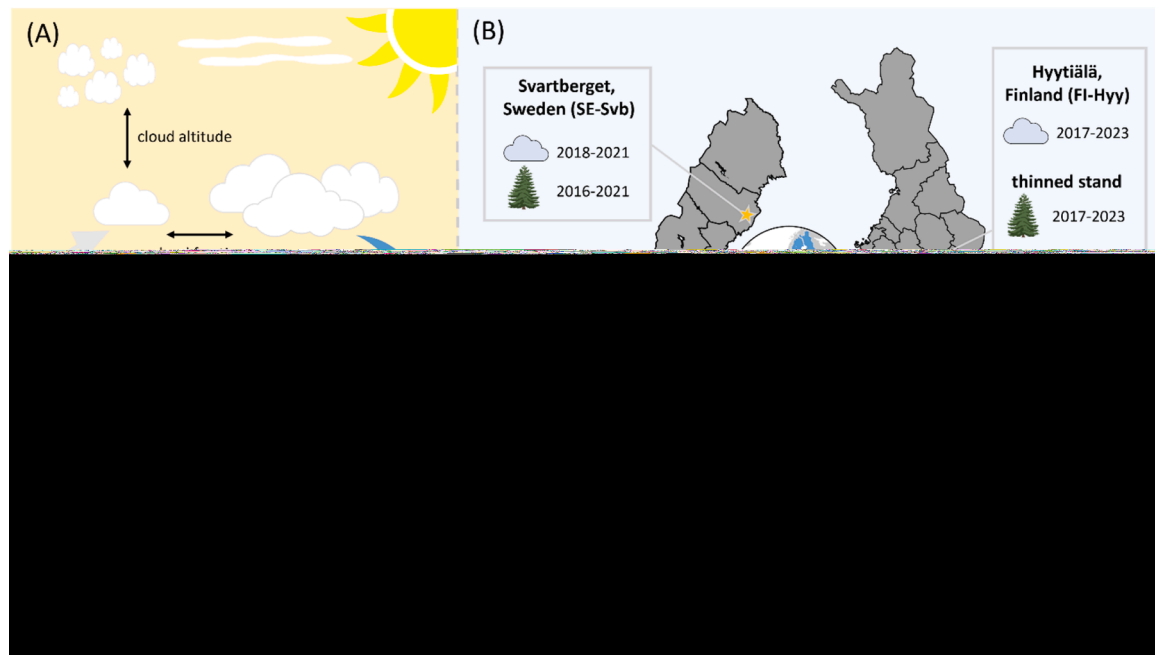


Fig. 1. Schematic overview of the investigated processes and key data. (A) Conceptual illustration of the cloud–tree pathway and associated meteorological variables. (B) Locations and key data coverage of the study sites. Cloud icons indicate surface-based remote sensing observations, and tree icons represent sap flow measurements from coniferous and broadleaf species. Country sizes are not shown to scale.

Below 0.6 kPa, sap flow generally remained below 0.12 (or 0.25 in SE-Nor and CZ-RAJ). When soil moisture was above the 20th percentile, sap flow increased with VPD across all sites and species (Fig. 2A–H). However, in SE-Nor, FI-Hyy (control), and CZ-RAJ, low soil moisture limited sap flow even under high VPD, with values not exceeding 0.6. The respective soil moisture thresholds (8.6 %, 14.9 %, 16.6 %) align with previous studies (Clausnitzer et al., 2011; Fu et al., 2024).

At constant VPD, sap flow responses to soil moisture varied by site and species. In thinned FI-Hyy, sap flow remained high at VPD > 0.8 kPa regardless of soil moisture in both pines and birches (Fig. 2B and Fig. 2I), while in the control forest (Fig. 2C), sap flow increased with soil moisture. In SE-Svb, soil moisture had little effect on pine sap flow (Fig. 2D), but did affect spruces (Fig. 2H). For spruces in SE-Nor and CZ-RAJ, highest sap flow occurred under combined high VPD and soil moisture. In contrast, for pines in SE-Nor and spruces in CZ-BK1, peak sap flow occurred before either VPD or soil moisture reached their maximum, and no clear response pattern was observed.

2.2. Overall impacts of cloudiness on tree sap flow

2.2.1. Cloudiness via proxy

The overall impact of cloudiness was inspected via diel sap flow during clear skies and cloudy days (see S1.2 for definitions). Sap flow was lower during cloudy days compared to clear skies (Fig. 3A), a pattern observed across sites and species (Fig. S4). The peak sap flow was, on average, 7 % (CZ-RAJ) to 40 % (SE-Svb) lower in the cloudy days compared to clear sky days. However, maximum sap flow during cloudy days occasionally exceeded that on clear sky days (Fig. 3A and Fig. S4). The main drivers of sap flow were also impacted by changes in cloudiness conditions (Fig. 3B), highlighting the importance of distinguishing the direct effect of cloudiness from its indirect effects via other drivers.

The Structural Equation Modelling (SEM) results (details in S3.1) revealed a direct path from clearness index to sap flow for all sites and tree species except for spruces in SE-Nor, where only indirect paths via direct and diffuse photosynthetic photon flux density (PPFD) were found. In CZ-RAJ, clearness index significantly predicted total PPFD,

which in turn predicted sap flow (Sect. S3.1.1). However, the total effect of clearness index considering the full SEM was not significant at this site. The direct effect sizes for clearness index varied from −0.15 to 0.37, and the indirect effect for SE-Nor (spruce) was 0.31. For SE-Svb (pines) and CZ-BK1 a significant indirect effect was also found. The total effects were always positive, i.e., clearer skies enhance sap flow. VPD consistently emerged as the most important variable across all sap flow sub-models, whereas the clearness index ranked between the 2nd and 4th positions in importance, thus sometimes positioning higher than soil moisture (Table S4). Variance partitioning also revealed that clearness index explained unique sap flow variability not captured by other variables.

The direct effects of VPD and soil moisture were between 0.08–0.38 and 0.19–0.44 (Table S5), respectively, and thus in some instances, the effect of clearness index was similar than the effects of these two well-known main drivers. For pines in SE-Nor, clearness index's direct effect was 0.37, greatly exceeding the direct effect of VPD and soil moisture (0.14 and 0.20, respectively). Across all the sites, explained variances for the sap flow sub-model were relatively high, between 62–83 % (Table S3). Comparison of sap flow sub-models with and without cloud parameters using ANOVA consistently favoured the more complex models that included cloud parameters ($p < 0.05$). Earlier observed differences in the limiting potential of soil moisture for sap flow between thinned and control stand in FI-Hyy (Fig. 2B versus Fig. 2C) were supported with our SEM results. The total effect of soil moisture was 0.20 and 0.44 for the thinned and control stands (pines), respectively, implying a larger role of soil moisture in the latter in limiting sap flow.

2.2.2. Cloudiness via surface-based cloud observations

Cloud properties influenced sap flow in distinct ways, with cloud fraction and cloud base height showing differing but consistent effects across species and sites. Behaviour of pine sap flow with cloud fraction and cloud base height for boreal stations is shown in Fig. 4 (other tree species, and the control stand in FI-Hyy are shown in Fig. S5). Longest sap flow data overlapping with the cloud measurements were available from the thinned forest at FI-Hyy (Fig. 4A and D, see also Fig. 1B), thus

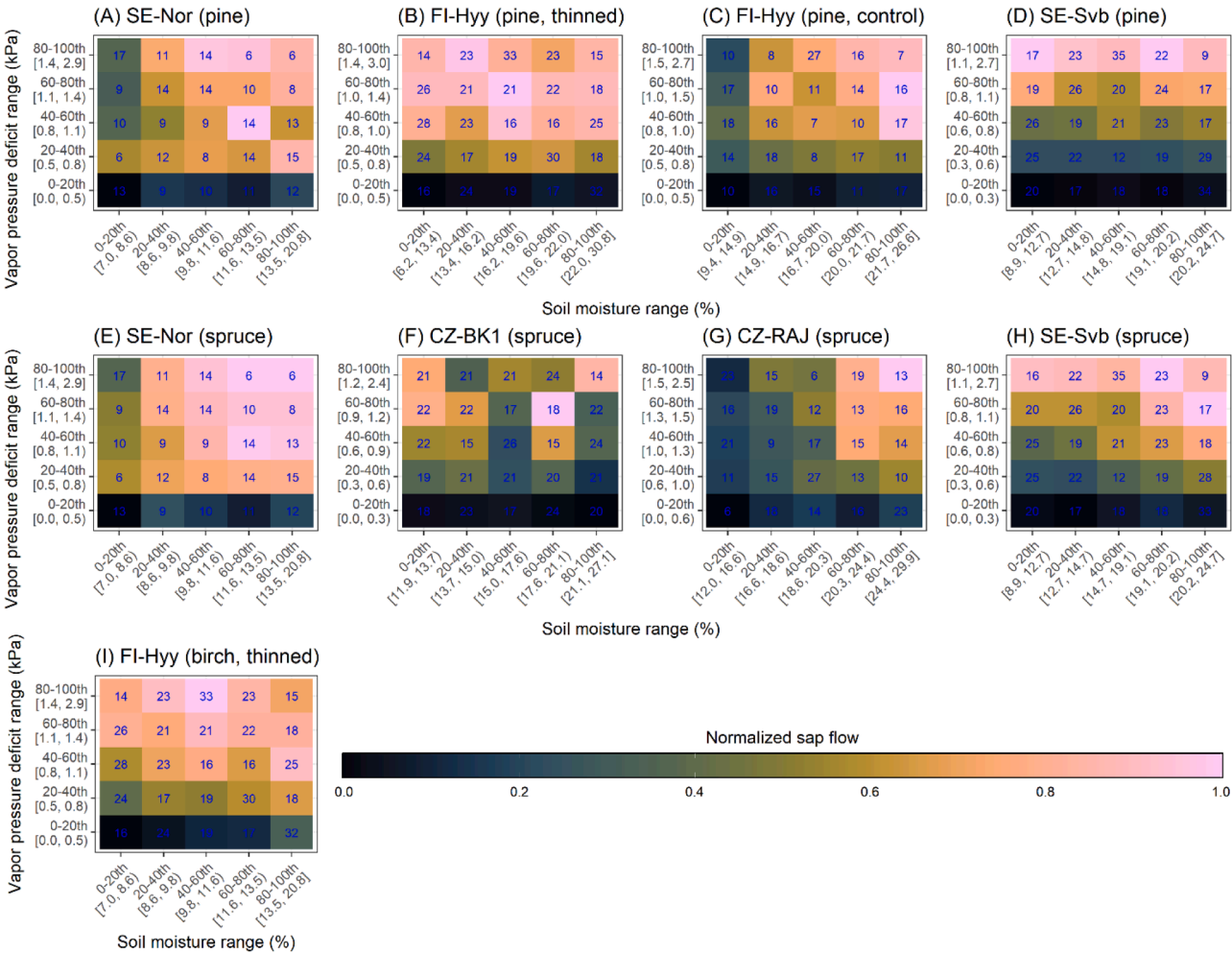


Fig. 2. Normalized sap flow across all sites, stands and species investigated in this work. Sap flow values were normalized separately for each site and tree species to range from 0 to 1, enabling comparison of patterns across different sap flow measurement techniques, varying climatic conditions and species. Sap flow is depicted with the colour bar for 2D percentile bins of vapor pressure deficit (y-axis) and soil moisture (x-axis). The number overlay indicates the number of days for each bin.

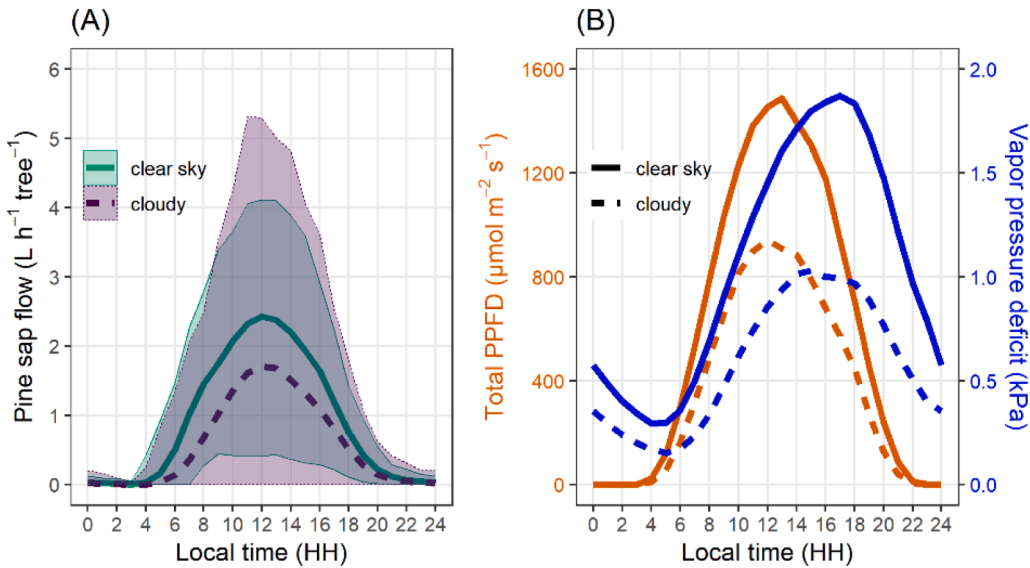


Fig. 3. Average behaviors of sap flow (A) and its drivers (B) during clear sky and cloudy days. The example is shown for SE-Nor, solid lines displaying the clear skies and dashed lines noting the cloudy days. The shaded areas in (A) extend from the minimum up to the maximum sap flow for each condition. Photosynthetic photon flux density (PPFD, orange) and vapor pressure deficit (blue) are presented in (B).

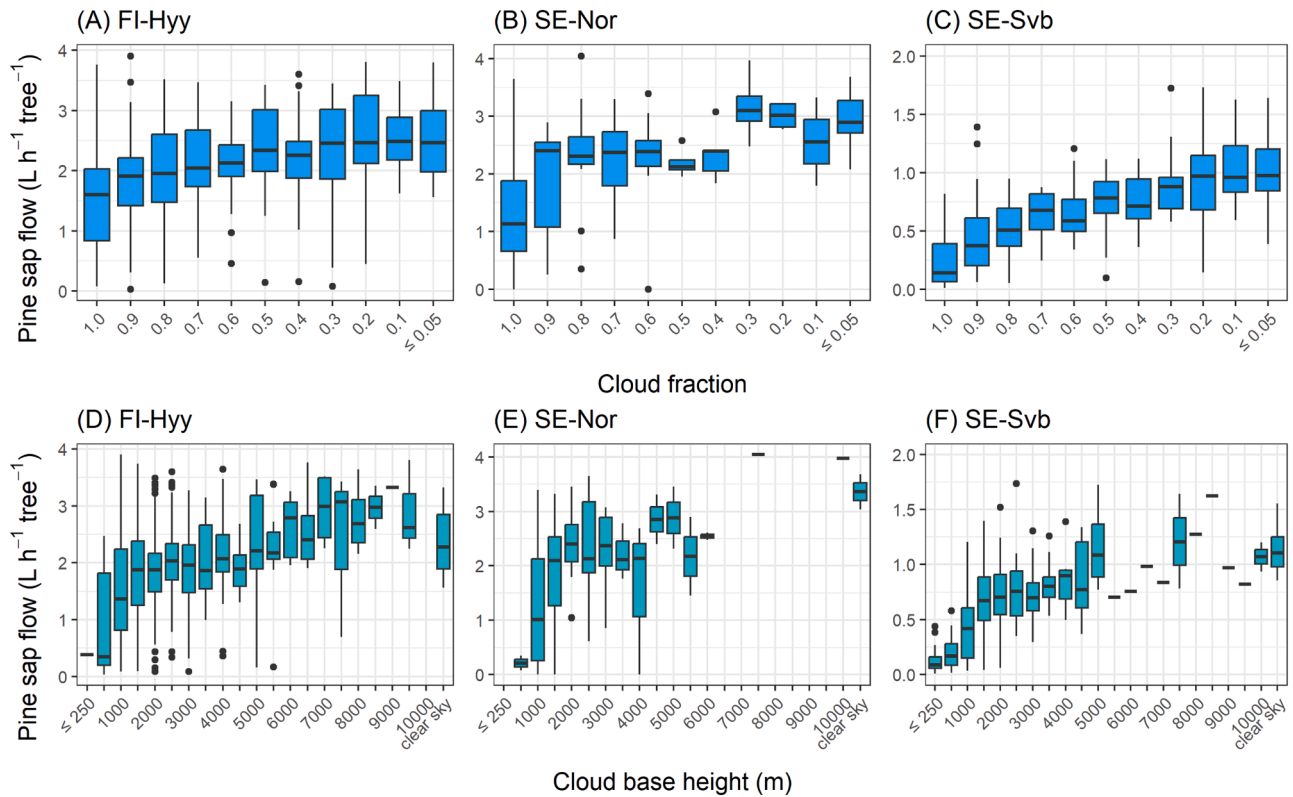


Fig. 4. Pine sap flow in boreal sites as a function of binned cloud fraction and cloud base height. Other trees for these sites are shown in Fig. S5. For cloud fractions, bin width of 0.1 is used, and for cloud base height the bin width is 500 m. In the bottom row, cloud fraction is zero for clear skies. The boxplot extends from the 25th to the 75th percentile, with the thick horizontal line being the median. The whiskers indicate the 1.5*IQR, individual black points denote outliers.

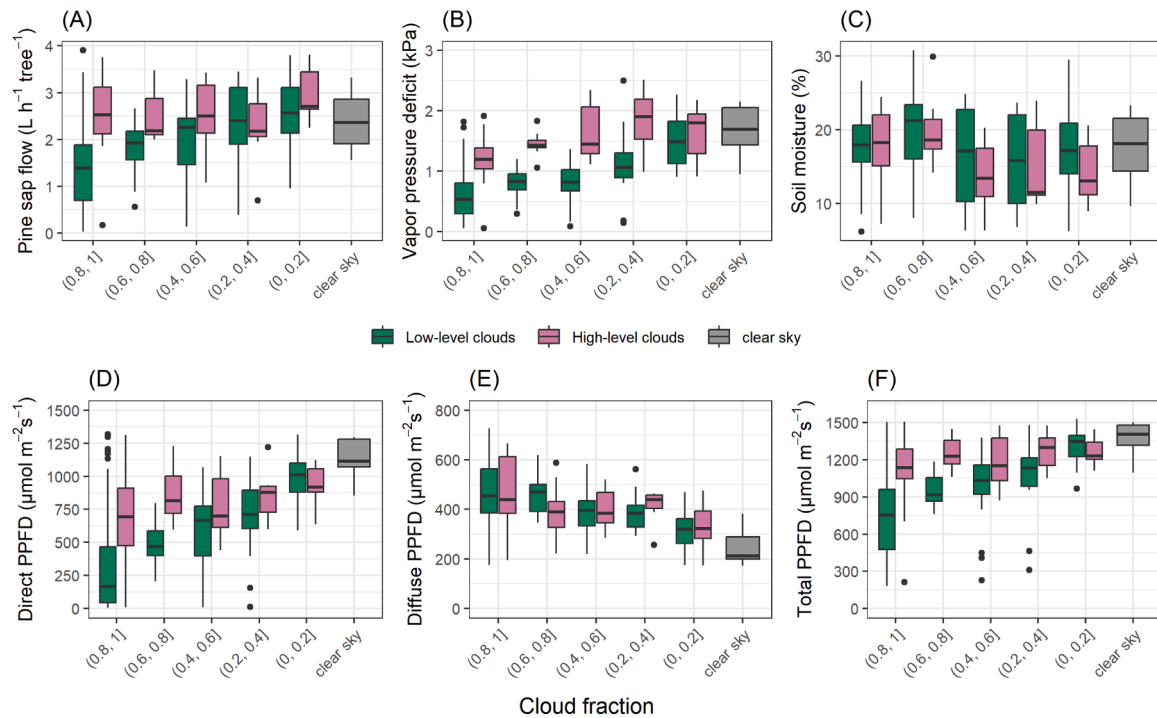


Fig. 5. Pine sap flow and environmental drivers as a function of binned cloud fractions for low- and high-altitude clouds. The figure shows data for the thinned stand in FI-Hyy, other boreal sites and tree species being shown in Fig. S6-S11. Green colour denotes the low-altitude clouds, and pink high-altitude clouds. Days with clear skies (cloud fraction is zero) are shown with grey. The boxplot extends from the 25th to the 75th percentile with the median in between as thick horizontal line. The whiskers indicate the 1.5*IQR, individual black points denote outliers. PPFD denotes the photosynthetic photon flux density.

exhibiting the least scatter and clearer trends. However, overall, behaviour was somewhat similar in all of the sites, and no differences were observed between species. Sap flow increased as cloud fraction decreased (Fig. 4A–C) until the cloud fractions were relatively small (cloud fraction < 0.2–0.3) or the skies were clear. For fully overcast skies (cloud fraction = 1), small to moderate sap flow was observed. Sap flow increased with increasing cloud base height (Fig. 4C–D). This increase was very strong for low clouds, but less pronounced for higher cloud base heights. SEMs utilising the measured cloud data (details in S3.2) instead of the clearness index further supported the role of clouds, and a pathway from the cloud fraction to sap flow was found. Cloud fraction's total effect varied between -0.02 (pines in FI-Hyy, thinned stand) and -0.23 (spruces in SE-Svb) with a mean of -0.12 (Table S8), and the negative effects aligned with the observed relationships (Fig. 4A–C). Cloud base height influenced sap flow indirectly with a small, but significant, positive effect (~ 0.10 , Table S10), consistent with relationships shown in Fig. 4D–E (higher sap flow with higher cloud base height). Effects of cloud fraction, soil moisture and VPD did not change significantly when cloud base height was added to the model (Table S8 vs Table S10).

2.2.3. Sap flow and its drivers for low- and high-altitude cloud days

Pine sap flow (FI-Hyy, thinned stand) as a function of cloud fraction is presented in Fig. 5A separated into low- and high-altitude clouds (other stands and species shown in Fig. S6–S11). Sap flow clearly decreased with increasing cloud cover for low-altitude clouds for all boreal sites and species, but not for high-altitude clouds. Instead, in overcast situations with high-altitude clouds (cloud fraction > 0.8), the sap flow was similar ($p = 0.22$) to the clear sky conditions. The same applied to birches (Fig. S6A) at the same stand. In the FI-Hyy control stand (Fig. S7A), pine sap flow rose as low-altitude cloud fraction decreased from 1 to 0.4 but showed no clear trend below 0.4.

A decreasing cloud fraction related to increasing VPD (Fig. 5B) for both cloud types; under overcast skies, VPD was higher for high-altitude clouds ($p < 0.001$). Soil moisture (Fig. 5C) did not systematically relate to cloud fraction for either cloud type and remained similar under overcast skies ($p = 0.67$). Decreasing cloud fraction raised direct PPFD

(Fig. 5D) and lowered diffuse PPFD (Fig. 5E) for both high- and low-altitude clouds, but the changing balance of these components resulted in differing trends for total PPFD (Fig. 5F). Total PPFD had little to no change during high-altitude cloud days, but a clear increasing trend with decreasing cloud fraction for low-altitude cloud days. For the low-altitude clouds, in SE-Nor and SE-Svb (Figs. S8–S11), sap flow (both pines and spruces) and the drivers exhibited similar behaviour as the corresponding variables during the low-altitude cloud days at FI-Hyy. Overall, these patterns demonstrated that all boreal sites and species studied responded consistently, with sap flow increasing under decreasing low-altitude cloud cover but showing no systematic response under high-altitude clouds.

2.2.4. Cloud fraction driven changes in transpiration for low- and high-altitude cloud days

The univariate regression lines (fit details in Table S2) in Fig. 6A for the low-altitude clouds in FI-Hyy indicate a positive change in transpiration as cloud fraction decreases (when not considering other factors). This trend is supported by both TLS (total least squares) and OLS (ordinary least squares) fits, with slopes for pines ranging from 13.9 (OLS) to 28.7 (TLS) $\text{L day}^{-1} \text{ tree}^{-1}$ per unit of cloud fraction (i.e., from fully overcast to clear sky, Fig. 6A) for pines, and from 24.8 (OLS) to 43.9 (TLS) for birches (Fig. S12A). For high-altitude cloud days (Fig. 6B, Fig. S12B and Table S2), no statistically significant trend is observed for neither species. For the low-altitude cloud days in both SE-Nor and SE-Svb, a significant positive trend is found for both pines and spruces (Fig. 6C–D and Fig. S12C–D, respectively), with slopes ranging from 4.5 to 37.0 $\text{L day}^{-1} \text{ tree}^{-1}$ per unit of cloud fraction depending on fit, site and tree species.

To approximate above-mentioned changes at stand level—which is necessary for the subsequent estimates of transpiration under varying cloud cover—we employed coarse estimates of tree density and species distribution (see *Methods*). In FI-Hyy, a unit decrease of cloud fraction (from fully overcast to clear sky), for low-altitude clouds, the above-reported slope for pines corresponded to a transpiration increase of ~ 8.5 (OLS) to 17.6 (TLS) m^3 (of water) $\text{ha}^{-1} \text{ day}^{-1}$ during summertime. For SE-Nor, to the corresponding increases were 8.3 – 10.8 and 3.9 – 5.1

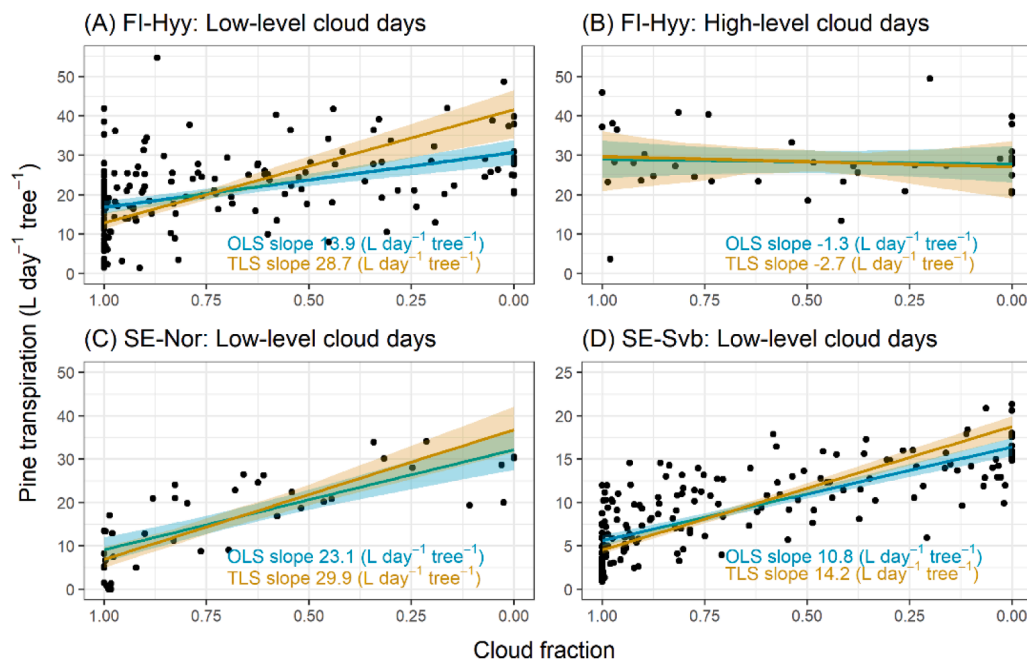


Fig. 6. Pine transpiration as a function of cloud fraction. The figure shows data for the thinned stand in FI-Hyy (A–B), SE-Nor (C) and SE-Svb (D). For FI-Hyy, both low-altitude and high-altitude cloud days are shown. Lines show univariate regression lines, orange for total least squares (TLS) and blue for ordinary least squares (OLS), shaded areas display the 95 % confidence intervals obtained via bootstrapping.

$\text{m}^3 \text{ha}^{-1} \text{day}^{-1}$ from pines and spruces, respectively, with a forest total (not accounting other tree species) of $12.2\text{--}15.9 \text{ m}^3 \text{ha}^{-1} \text{day}^{-1}$ (the lower and upper values from OLS and TLS fits, respectively). For SE-Svb, the slopes corresponded to increased transpiration of $5.8\text{--}7.6$ and $1.9\text{--}2.7 \text{ m}^3 \text{ha}^{-1} \text{day}^{-1}$ from pines and spruces, respectively, and a forest total of $7.7\text{--}10.3 \text{ m}^3 \text{ha}^{-1} \text{day}^{-1}$ (lower and upper limits for OLS and TLS, respectively).

2.2.5. Impacts of long-term cloudiness trends on stand transpiration

To roughly investigate potential stand-level changes in transpiration respective to the long-term trends in cloudiness, CLARA-A3 satellite derivatives of clouds (1982–2020) were utilized (details in S4). For FI-Hyy, the summertime low-altitude cloudiness decreased by about 0.66 % per decade (Fig. S17). This means $55.9\text{--}120.2 \text{ m}^3$ more water per hectare per decade was transpired during summer. This corresponds to an increase of $\sim 0.6\text{--}1.2 \text{ mm year}^{-1}$ being equivalent to an addition of about 3–7 trees of average size (age of 58 years, Table 1) ha^{-1} per decade to the already existing 614 trees in this forest stand (an average pine transpires $\sim 20 \text{ L day}^{-1}$, or 18.4 m^3 per summer decade).

For birches, the change was more pronounced (slopes of 24.8 and $44.9 \text{ L day}^{-1} \text{tree}^{-1}$ per unit of cloud fraction, Fig. S10A and Table S3) as birch sap flow rates are generally higher compared to pines. However, birch density was low in this stand, thus their contribution to stand-level transpiration is expected to be minimal.

In SE-Nor, the low-altitude cloudiness decreased 0.48 % per decade, implying an increase of $39.5\text{--}51.2$ and $18.7\text{--}24.3 \text{ m}^3 \text{ha}^{-1}$ (from pines and spruces, respectively) per decade in transpiration from this forest during summertime, corresponding to $\sim 0.6\text{--}0.8 \text{ mm year}^{-1}$. These numbers would be equivalent to the addition of 2–3 pines and one spruce (of average size) per hectare per decade to the already existing ~ 500 trees in this forest stand (in SE-Nor, pine and spruce transpire ~ 16 and 23 L day^{-1} i.e., 14.7 and 21.2 m^3 per decade over the summer months).

In SE-Svb, the trend in low-altitude cloudiness was significantly smaller (-0.06 % per decade), and the potential changes in transpiration due to clouds are negligible at this site.

3. Discussion

The results presented here, combining long-term sap flow data and surface-based cloud measurements for the first time, contribute to understanding atmosphere-biosphere interactions by unravelling how the combined effect of cloud cover and altitude interact with tree sap flow and transpiration.

Table 1

Summary of the sites including location, mean annual accumulated precipitation, mean annual temperature, mean annual incoming shortwave radiation, forest type, measured trees species, number and tree age.

Full site name and country	Coordinates	Abbreviation	Climate	Forest type	Measured tree species (N)	Average tree age (2020)
Norunda research station, Sweden	60° 05' N 17° 29' E 46 m.a.s.l	SE-Nor	565 mm 7.0 °C 113 W m^{-2} (1991–2020)	Boreal	Scots pine (4) Norway spruce (3)	$\sim 100\text{--}130$ years
Svartberget research station, Sweden	64° 15' N 19° 46' E 270 m.a.s.l	SE-Svb	614 mm 1.8 °C 93 W m^{-2} (1981–2010)	Boreal	Scots pine (8) Norway spruce (10)	>120 years
Hyytiälä forest station, Finland	61° 51' N 24° 17' E 181 m.a.s.l	FI-Hyy	711 mm 3.5 °C 100 W m^{-2} (1981–2010)	Boreal	Scots pine (8) Silver birch (4)	58 years
Bílý Kríž forest, Czech Republic	49° 30' N 18° 32' E 875 m.a.s.l	CZ-BK1	1246 mm 6.5 °C 145 W m^{-2} (1998–2016)	Temperate	Norway spruce (24)	39 years
Rájec, Czech Republic	49° 26' N 16° 41' E 625 m.a.s.l	CZ-RAJ	679 mm 7.8 °C (1975–2016) 134 W m^{-2} (2011–2024)	Temperate	Norway spruce (25)	117 years

On average, cloudiness reduced sap flow by reducing incoming radiation, as expected based on previous studies. However, maximum sap flow on cloudy days can also exceed that on clear sky days (Fig. 3A), implying from the different roles of different cloud types. A pathway between cloudiness and sap flow was found, even when controlling for tree water stress factors. On a daily scale, VPD and soil moisture were the strongest predictors for sap flow, consistent with previous studies (Ma et al., 2017; Oogathoo et al., 2020). However, models incorporating cloudiness-related parameters outperformed simpler models in both boreal and temperate sites. While cloudiness is often underrepresented in favour of simpler approaches in ecohydrological modelling (Spitters et al., 1986; Wang et al., 2018), our results show its effect can, in some cases, be comparable to those of VPD and soil moisture reflecting its role as an integrative indicator that inherently captures information from multiple environmental drivers.

Cloud fraction had a negative effect on sap flow (Fig. 4A–C), as higher cloud cover generally reduces radiation, temperature, and VPD. This negative effect was supported by the Structural Equation Model, which accounted for other environmental factors known to impact sap flow. With low cloud fractions, sap flow showed minimal differences, suggesting sufficient direct radiation and enhanced diffuse radiation at these levels create optimal conditions for sap flow and transpiration. The nonlinearity of sap flow with cloud base height (Fig. 4D–F and Fig. S5E–H), as shown for the boreal sites, implied cloud influence on sap flow is not only related to the fraction of sky covered by clouds, but also to the cloud optical properties. Low-altitude clouds, especially Stratus clouds, have often high optical thickness and are rather homogenous compared to clouds at higher altitudes (Aebi et al., 2020; Luo et al., 2023; Ylivinkka et al., 2020), thus blocking incoming solar radiation more effectively and being associated with lower VPD. Low-altitude clouds are also more likely associated with precipitation. Therefore, at cloud base heights below one kilometre, sap flow is expected to be small as also observed here. Patchy cumulus clouds allow more radiation to pass through them, and are associated with higher cloud bases (Ylivinkka et al., 2020). This aligns with our findings of a sharp increase in sap flow with up to two kilometres of cloud base height.

Sap flow clearly increased with decreasing cloud fraction for low-altitude cloud days (Fig. 5A, Figs. S6A–S11A), i.e., the behaviour was similar to when all clouds were considered (Fig. 4A–C and Fig. S5A–D). Mid-level clouds were excluded from the analysis as previous studies indicate that the general decline in cloud cover across the Nordic countries is mainly driven by low- and high-level clouds, and mid-level clouds show broadly similar patterns (see Fig. S13). With high-altitude cloud days sap flow showed little change with decreasing cloud

fraction, and with overcast high-altitude cloud days sap flow was similar to clear sky days. Clear differences in the relationships between sap flow drivers and cloud fraction were also observed (Fig. 5B-F, Figs. S6B-F-S11B-F). Our results could suggest sap flow being primarily driven by VPD on low-altitude cloud days, thus related to optically thicker clouds via their control over radiation and temperature. On high-altitude cloud days, VPD's role diminishes with no clear relationship to cloud fraction. Instead, larger total radiation could compensate to the missing effect of VPD by influencing stomatal opening (Durand et al., 2021) via photosynthesis, and causing higher leaf temperatures, thus indirectly enhancing transpiration and sap flow. Due to the differences in the cloudiness trends for low- and high-altitude clouds, the differences in the behaviour of sap flow and its drivers with cloud fraction between low- and high-altitude cloud days highlight the importance of their separation in future studies. Grouping these together hides both the different sap flow and its drivers' responses to cloud fraction. The importance of especially low-altitude clouds in relation to tree water stress has also been noted in earlier work (Carbone et al., 2013).

Decreasing cloudiness is interlinked with the observed increases in VPD (Grossiord et al., 2020, 2017; Yuan et al., 2019), which is further linked to enhanced transpiration and faster depletion of soil water leading to adverse ecosystem- and plant specific impacts (Grossiord et al., 2020). Decreases in low-altitude clouds also modulate planetary albedo, increasing temperatures (Goessling et al., 2025). Moreover, it has also been shown that decreasing cloudiness can lengthen the summers in Northern Europe (Post and Aun, 2024). These could lead to further enhancement of transpiration via higher temperatures and longer growing seasons, assuming sufficient water availability in the soil. This combined effect (increasing VPD and decreasing low-altitude clouds)—driven by climate-induced cloud regime changes—is a novel mechanism with implications for forest water cycling and feedbacks to regional climate.

In our boreal sites, a decrease in low-altitude cloud fraction enhanced transpiration (Fig. 6), but no trend was found for high-altitude clouds. Because climate change impacts cloudiness (Devasthale et al., 2022; Liu et al., 2023), we conducted a trend analysis using state-of-the-art satellite data and, consistent with previous work (Devasthale et al., 2022), found decreasing trends for total and low-altitude clouds (mid-altitude clouds were not investigated). We estimate that the resulting transpiration changes are equivalent to adding 3–7 trees ha⁻¹ per decade to the existing forest. Cumulatively over the decade, these changes correspond to about 1.1–1.7 % of the typical annual precipitation at the study sites under current cloudiness conditions. These values are back-of-the-envelope estimate which do not account for other factors, assume a relatively homogenous tree density, size and species distribution, and ignore potential feedbacks. Moreover, upscaling sap flow measurements from individual trees to forest level transpiration remains challenging (Dukat et al., 2023) and our simple methodology might not have let to full accuracy in upscaling. Therefore, the numbers provided are not precise estimates of the actual changes and instead serve as indicators of the potential magnitude of transpiration changes in response to changes in cloudiness. Still, similar relationships between sap flow and cloudiness across sites despite methodological variation (cloud observations, sap flow measurements, forest stand properties) support the robustness of our findings. Given that boreal forests account for 27 % of the total forest area—over one billion hectares (FAO and UNEP, 2020)—even small, but widespread cloudiness changes could substantially affect biosphere-atmosphere hydrological cycling.

Alternatively, this extra water released to the atmosphere, could also contribute to cloud formation, creating the feedback visualised in Fig. 1A. Therefore, it could be possible that this climate change driven cloudiness trend is also partly masked via the forest feedback presented here, highlighting the biosphere-atmosphere coupling. However, high VPD with low soil moisture can trigger protective responses in trees, reducing transpiration (Grossiord et al., 2020; Novick et al., 2016). This

can lead to less atmospheric moisture and fewer low-altitude clouds—similar impact to what has been observed for deforestation (Lawrence and Vandecar, 2015; Teuling et al., 2010), eventually leading to the reinforcement of the positive climate feedback loop. On the other hand, enhanced transpiration together with higher temperatures could influence biogenic volatile organic compound emissions (BVOCs). Previous studies have linked transpiration to the release of oxygenated water-soluble BVOCs (Cojocariu et al., 2004; Filella et al., 2007; Kreuzwieser et al., 2001; Rissanen et al., 2018). Combined with our findings, sap flow and transpiration, modulated by cloudiness, may therefore act as additional controls for soluble oxygenated BVOCs, potentially affecting their composition and role in cloud condensation nuclei formation. Moreover, increased direct radiation due to decreased low-altitude cloud cover increases leaf temperatures, with further potential enhancement of BVOC emissions. These eventually influence aerosol-cloud interactions and thus the global hydrological cycle (Pratap and Markonis, 2022; Sun et al., 2024; Yli-Juuti et al., 2021). Future impacts of climate change on cloudiness, such as temperature increases from declining anthropogenic aerosol concentrations (Quaas et al., 2022), may further modulate these effects, and create various feedbacks that should be investigated in future studies.

Overall, our findings highlight the modulating role of low- and high-altitude clouds for sap flow and its drivers, illustrating the different effects these cloud types have on tree sap flow and transpiration. By providing empirical evidence, our study complements modelling approaches in a field where atmospheric feedbacks and interactions remain an active area of research. Our results also indicate, that in the boreal region, transpiration may be enhanced in the future due to the decreasing low-altitude cloudiness, thus further strengthening the enhancement via increasing VPD. However, because cloud responses and biosphere-atmosphere feedbacks are highly coupled, the extent to which past decreases in low-altitude cloudiness will continue is uncertain; thus, its effect on transpiration warrants further investigation.

4. Methods

4.1. Field sites and sap flow data

We investigated data from three sites in the European boreal forest zone in Sweden and Finland, and from two sites in temperate forests in Czech Republic (Fig. 1B). Different tree species were investigated, leading to seven combinations of site x species. In addition, two different stands were available from one site. A summary of the sites is given in Table 1.

Norunda research station is an Integrated Carbon Observation System (ICOS) Sweden site (<https://www.icos-sweden.se/>, last access 29 September 2025) and thus part of the ICOS Research Infrastructure (Heiskanen et al., 2022), here abbreviated as SE-Nor following the ICOS Ecosystem code. SE-Nor also hosts facilities that are part of the European Aerosols, Clouds and Trace Gases Research Infrastructure ACTRIS (<https://www.actris.eu/>, last access: 13 January 2025). The forest consisted of Scots Pine (*Pinus sylvestris* L., ~ 67 %) and Norway Spruce (*Picea abies* L., ~ 26 %) and small fraction of broadleaf species (< 7 %) (Petersen et al., 2023) before it was clear cut in 2022. Sap flow data used in this work extends from 2017 to 2019 and includes measurements of a total of 12 trees. Sap flow was measured using the thermal heat balance method, similarly as described in previous work done at the site (Lagergren and Lindroth, 2004).

Svartberget research station (Laudon et al., 2013) (SE-SvB) is also an ICOS Sweden site. SE-SvB additionally belongs to the national Swedish Infrastructure for Ecosystem Science (SITES) network (<https://www.fieldsites.se/>, last access: 13 January 2025) and hosts facilities belonging to ACTRIS. The forest in SE-SvB is relatively even-aged mixed-forest of Scots pine (~ 56 %) and Norway spruce (~ 44 %). Sap flow data used in this work extends from 2016 to 2021, and in total, 18 trees were measured. Sap flow was measured using custom-made heat pulse

and thermal dissipation probes, and details of the measurements and raw data processing can be found from previous literature (Gutierrez Lopez, 2015; Gutierrez Lopez et al., 2021).

Hyttiälä forestry field station (Hari and Kulmala, 2005), FI-Hyy, is an ICOS Finland site. The station also belongs to the FLUXNET eddy covariance data initiative, and hosts facilities belonging to ACTRIS. The forest around the station is relatively even-aged, dominated by Scots pine. A large portion of the forest was thinned in 2019–2020 reducing the mean stand density from 954 to 614 trees ha⁻¹. A small portion of the forest was left intact to ensure sufficient number of control trees for various long-term measurements (Aalto et al., 2023; Aslan et al., 2024). The sap flow measurements at the site are based on thermal dissipation and measured using custom-built sensors. Details of the measurement system and raw data processing can be found from earlier work (Dukat et al., 2024; Lintunen et al., 2020; Vanhatalo et al., 2015). Sap flow measurements employed here extend from 2017 to 2023, and include a total of 12 trees, from which three are measured since 2017, and nine since 2020. From these, four pines (measured since 2020) reside in the control area, and four pines (two measured since 2017, another two added in 2020) and four birches (Silver Birch, *Betula pendula* Roth, one measured since 2017 and three added in 2020) in the thinned area.

Bílý Kríž forest site (McGloin et al., 2019, 2018), CZ-BK1, is an ICOS Czech Republic site since 2022. The station also belongs to the FLUXNET data initiative. The forest is situated on a planar mountain slope that is approximately 100 m below the crest (McGloin et al., 2018), consisting of a monoculture of even-aged Norway spruce (*Picea abies* L.). Sap flow was measured from 24 individual trees between 2017 and 2022.

Rájec site is a part of FLUXNET and located in the Drahaný Highlands. The site is abbreviated as CZ-RAJ, following the FLUXNET protocol. The forest consisted of a monoculture of even-aged spruces, but was clear cut during the winter 2021–2022 because of a series of heat waves leading to a bark beetle infestation. Sap flow data was obtained prior to the clear cut and was measured on 25 individual spruces (Norway spruce) between 2017 and 2021. In CZ-BK1 and CZ-RAJ, the sap flow as measured using the tissue heat balance method (Čermák et al., 2004). The measurement setup and raw data processing were identical for both CZ-BK1 and CZ-RAJ (Kyselova et al., 2021; Petřík et al., 2022; Zavadilová et al., 2023).

As noted above, sap flow measurements were obtained using different techniques across sites. These methods differ in their

assumptions, sensitivity to sapwood depth, and as a result, absolute sap flow rates (Flo et al., 2019). Previous intercomparisons (Lundblad et al., 2001; Poyatos et al., 2016) have shown that although absolute values can diverge, all methods reliably capture temporal dynamics and yield consistent relationships with ecosystem-scale evapotranspiration. Likewise, tree age and size varied across sites, but because our analyses are based on normalized sap flow responses and site-level averages, rather than absolute rates, such structural differences are not expected to confound the comparability of results. Because the focus of this study is on relative patterns rather than cross-site comparisons of absolute rates, we consider the different methodologies and stand structures to not affect our conclusions.

4.2. Other environmental data

The environmental variables were selected based on their known importance on sap flow (see *Introduction*) and were obtained above the tree canopy. These include relative humidity (RH, %), air temperature (T_{air} , °C), total incoming photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$), diffuse PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$), global incoming shortwave ($\lambda = 0.3\text{--}4.8 \mu\text{m}$ spectral range) radiation (SW, W m^{-2}) and precipitation (mm day^{-1}). Diffuse PPFD was not available from CZ-RAJ. Volumetric soil water content (at the depth of 20–30 cm in the mineral soil, referred as soil moisture) was also investigated. The instrumental details can be found in Table 2.

Direct PPFD was derived by subtracting the diffuse PPFD from the total PPFD. In addition to the measured radiation, theoretical radiation at the top of the atmosphere (R_{TOA}) was also inspected. Calculation of R_{TOA} was conducted by the R-package *sunttools* (Bivand et al., 2023), following the equations given by the National Oceanic & Atmospheric Administration (National Oceanic and Atmospheric Administration, 2024). Atmospheric vapor pressure deficit (VPD, kPa) was derived from the measured RH and T_{air} following previous literature (Monteith and Unsworth, 2013; Murray, 1967):

$$\text{If } T_{\text{air}} \geq 0^\circ\text{C} : \text{VPD} = \left(\frac{100 - \text{RH}}{100} \right) * 0.61078 \text{ hPa} * \exp \left(\frac{17.27 * T_{\text{air}}}{T_{\text{air}} + 273.3^\circ\text{C}} \right) \quad (1a)$$

Table 2

Instrumentation for the supporting environmental variables (measurement height denoted in brackets). The period included below each site refers to the sap flow (SF) data sets used in this work, and if the environmental variable was not available for the whole period, it is noted separately.

Variable	Measurement site				
	SE–Nor SF: 2017–2019	SE–Svb SF: 2016–2021	FI–Hyy SF: 2017–2023	CZ–RAJ SF: 2017–2021	CZ–BK1 SF: 2017–2022
RH	Rotronic MP102H (28 m)	Rotronic MP102H (32.5 m)	Rotronic MP102H RH sensor (35 m)	EMS Brno EMS33 Rotro and Vaisala HMP155 (120 % of canopy height)	EMS Brno EMS33 Rotro and Vaisala HMP155 (130–140 % of canopy height)
T_{air}	Rotronic MP102H (32.5 m)	Rotronic MP102H (32.5 m)	Pt100 inside custom shield (16.8 m)	EMS Brno EMS33 Rotro and Vaisala HMP155 (120 % of canopy height)	EMS Brno EMS33 Rotro and Vaisala HMP155 (130–140 % of canopy height)
Incoming PPFD	Delta-T BF5 sunshine sensor (50 m)	Delta-T BF5 sunshine sensor (50 m)	Li-Cor Li-190SZ quantum sensor (18 m until 08/2017, after 35 m)	EMS Brno EMS12 quantum sensor (40 m)	Li-Cor Li-190/R quantum sensor (36 m)
Diffuse PPFD	Delta-T BF5 sunshine sensor (50 m)	Delta-T BF5 sunshine sensor (50 m)	Delta-T BF3/BF5 sunshine sensor (18 m until 08/2017, after 35 m)	Not available	BF5 Sunshine Sensor, Delta-T (36 m)
SW radiation	Kipp&Zonen CNR4 (55 m)	Kipp&Zonen CNR4 (50 m)	Middleton SK08 and EQ08 pyranometer (18 m until 08/2017, after 35 m)	Kipp&Zonen CNR4 (40 m)	Kipp&Zonen CNR4 (36 m)
SM	Depth 30 cm Delta-T ML2x	Depth 30 cm Delta-T ML2x	Depth 30 cm Delta-T ML3	Depth 20 cm CS616L, Campbell scientific Inc.	Depth 22 cm CS616L, Campbell scientific Inc.
precipitation	Geonor T200BM	Geonor T200BM 2016–2020	Vaisala FD12P weather sensor (18 m) 2017–2018, 2020–2023	Thies Laser Precipitation Monitor (40 m)	MetOne 385C (20 m)

If $T_{\text{air}} < 0^{\circ}\text{C}$: VPD

$$= \left(\frac{100 - RH}{100} \right) * 0.61078 \text{ hPa} * \exp\left(\frac{21.875 * T_{\text{air}}}{T_{\text{air}} + 265.5^{\circ}\text{C}} \right) \quad (1b)$$

4.3. Cloud observations and proxies

Surface-based observations of cloud base height for FI-Hyy (2017–2023) and SE-Nor (2019) were obtained via ACTRIS Cloudnet data portal. In the data portal, cloud base heights reside in the classification-product, which is calculated automatically near real-time with the CloudnetPy-algorithms (Tukiainen et al., 2020), developed upon earlier work (Illingworth et al., 2007) to fulfil the strict requirements by ACTRIS (testing, documentation, user-friendliness). The classification-product in Cloudnet is calculated only if both cloud lidar (for water clouds) and radar (for ice clouds) data are available, thus ensuring high accuracy for both cloud types. Complete documentation for the CloudnetPy-algorithms, including the calculation of the classification product, can be found from <https://actris-cloudnet.github.io/cloudnetpy/index.html> (last access 29th of September 2025) and references therein. From SE-Svb, the measurements (2018–2021) directly obtained from the in-situ lidar ceilometer (Vaisala CL51) were used as the site is not part of Cloudnet. Therefore, for SE-Svb, the cloud base heights were obtained via a single instrument only, thus potentially introducing small differences to Cloudnet values if ice clouds are present. For our purposes, however, the cloud base height values obtained via Cloudnet (SE-Nor, FI-Hyy) and from ceilometer directly (SE-Svb) are comparable; we only employed summertime data from daytime and are not interested in small differences as we employ coarse grouping for low- and high-altitude clouds. Ground-based ceilometer data has been used in many studies to investigate cloud base height (Martucci et al., 2010; Maturilli and Ebell, 2018; Tian et al., 2024), and previous studies have indicated the ground-based systems generally provide consistent patterns despite instrumental differences (Kim et al., 2011; Liu et al., 2013; Ylivinkka et al., 2020). Raw ceilometer data from SE-Svb were processed into usable cloud base height values following the approach described in previous work (Kuma et al., 2021) and implemented in publicly available code (Kuma, 2024).

Cloud base heights were used to inspect the average cloud altitudes, and to calculate the cloud fractions (Sect. S1.1). Cloud base height was used to classify clouds into low- (cloud base below 2 km) and high-altitude (cloud base above 5 km) clouds. These definitions align with the general guidelines provided in the International Cloud Atlas by the World Meteorological Organization (<https://cloudatlas.wmo.int/en/home.html>, last access: 27 January 2025). Mid-level clouds were excluded to keep the analysis focused, as the general decline in cloud cover across the Nordic countries is primarily driven by low- and mid-level clouds (Devasthale et al., 2022), and preliminary analyses indicated that mid-level clouds showed similar trends and sap flow relationships as low-level clouds (see Figure S13). The surface-based cloud observations from FI-Hyy and SE-Nor were additionally employed to develop a simple, but robust methodology based on SW and R_{TOA} alone to determine clear sky dates for all the sites (see S1.2 for details). Long-term (1982–2020) trends of cloudiness at the boreal sites were analysed using satellite data (presented in *Supplementary Material*).

To investigate the effect of cloud fraction in all sites, including those sites that have no surface-based observations of clouds available, cloud proxy was employed in the statistical modelling. For this, we utilized the Clearness Index (Dada et al., 2017; Sogacheva et al., 2008) (CI). The CI is defined as a ratio between the measured radiation (SW) and theoretical radiation at the top of atmosphere (R_{TOA}):

$$CI = \frac{SW}{R_{\text{TOA}}} \quad (2)$$

Usually, a CI > 0.7 is associated with a clear sky and high-altitude cirrus clouds, whereas a CI < 0.3 indicates mostly optically thicker,

low-altitude stratocumulus and stratus clouds (Ylivinkka et al., 2020).

4.4. Data pre-processing

For all sites, the sap flow measurements are presented in this work as specific sap flow rate ($\text{L h}^{-1} \text{ tree}^{-1}$). For FI-Hyy, SE-Svb and SE-Nor sap flow rates per tree were calculated from the sap flux densities per unit sapwood area, with sapwood areas estimated based on the tree diameters at breast height (DBH). For CZ-BK1 and CZ-RAJ, raw sap flow data is expressed in $\text{kg h}^{-1} \text{ cm}^{-1}$ of DBH, from which they were converted into $\text{L h}^{-1} \text{ tree}^{-1}$ by the DBH values. Sap flow rates were then averaged over individual trees of the same species and condition (thinned vs. control in FI-Hyy) if more than one tree was available. The averaging was applied to ensure our sap flow rates are descriptive of the average tree of certain species at each stand. Only boreal summertime (June–August) measurements are used. Only summertime sap flow data was used, as sap flow is negligible in winter at our sites and shows large variability during early spring and late autumn due to phenological changes. Focusing on summer we remove the seasonality influence to study the actual effect of meteorological parameters, thus allowing us to more reliably analyse relationships between sap flow and cloud cover without confounding effects from periods with pronounced seasonality.

Daytime averages were calculated considering daytime from three hours prior to three hours after the local solar noon at each site, in order to harmonize solar radiation influence on investigated parameters across sites and to focus on the period of highest sap flow. This window was used to calculate daytime averages for sap flow as well as other environmental variables, including cloud observations, ensuring that all variables used are temporally synchronized and representative of peak transpiration activity. Precipitation was calculated as the accumulated value over the entire day. Total diel sap flow ($\text{L day}^{-1} \text{ tree}^{-1}$) was also calculated for the boreal sites by summing the hourly averages over the 24 h, providing average diel rates. These are used as estimates for transpiration, and further to estimate total per-day transpiration from trees at the stand level. These values provide intermediate estimates of transpiration, which are then used to calculate changes in per-hectare transpiration associated with different trends in cloud fraction. For the stand-level estimates, simplistic assumptions regarding tree size, density and species composition are used; therefore, these values should not be interpreted as precise measurements, but rather as approximate indicators of the magnitude of transpiration. The 24-hour calculation described above is applied only to sap flow, as for other environmental variables daily accumulation would be difficult to interpret. In analyses relating transpiration to cloud fraction, the cloud fraction is taken from the solar-noon-centred period, reflecting conditions when transpiration is highest. This approach allows us to quantify both relative dynamics of sap flow in response to environmental drivers and total daily water use, with solar-noon-centred averages used for main analyses of relative responses and 24-hour sums used solely to estimate stand-level transpiration.

For stand level estimates of transpiration, assumptions of tree density and species distribution are needed. In FI-Hyy, thinning favoured pines, reducing forest heterogeneity (see *Field sites and sap flow data*), with a mean post-thinning tree density of $614 \text{ trees ha}^{-1}$ (Aalto et al., 2023). For SE-Nor, the average tree density around continuous plot (CP) 01 was used as it resided close to the sap flow measurements. Before the clear cut, there were approximately 360 pines and 140 spruces ha^{-1} around this plot (SE-Nor ICOS Ecosystem Station Labelling Report, 2021). In SE-Svb, there are ~535 pines and 415 spruces ha^{-1} (<https://www.icos-sweden.se/Svartberget>, last access: 21 January 2025). Our assumptions regarding the forest density and species distribution are coarse, and we also assume similar behaviour among trees of the same species within a given stand, implying broadly comparable age and phenological state. These stand-level estimates of transpiration, however, are not intended to be interpreted as absolute estimates of forest water use but merely used as intermediate values to roughly estimate the

long-term impacts of changing cloud cover on forest transpiration.

4.5. Statistical analyses

Piecewise Structural Equation Modelling (Kline, 2016) (SEM) was applied to investigate the role of cloudiness on sap flow while accounting for the known drivers, such as vapor pressure deficit and soil moisture, which are also themselves influenced by cloudiness (e.g., Fig. 3B). The variables included sap flow, soil moisture and direct and diffuse photosynthetic photon flux density (PPFD) as endogenous (dependent) variables (four preliminary structural equations). Other variables included day of the year, observation year, precipitation (sum over the last 10 days), clearness index (Eq. (2)) or alternatively cloud fraction and cloud base height, and theoretical radiation. Both direct and diffuse PPFD were included, as their impacts to vegetation are, in general, different (Zhou et al., 2021). For CZ-RAJ, however, a model with total PPFD was explored instead due to the lack of diffuse PPFD measurements. To ensure the variables related to cloudiness were significant predictors for sap flow, analysis-of-variance (ANOVA) tables were also constructed to compare models with and without these parameters.

The models were applied to each site and tree species separately (total of nine site x species combinations). For the thinned forest in FI-Hyy, additional analysis was conducted to ensure the stand structure changes were not driving the sap flow-cloudiness relationships. The SEM and potential inclusion of any missing and/or unnecessary paths (Fig. 7) were evaluated by using Fisher's C statistic (Shipley, 2009). All relationships were modelled using linear mixed-effect models (Demidenko, 2013) where the observation year was considered as random intercept and other variables were estimated as fixed effects. Conditional R^2 were inspected to assess the reliability of each sub-model. The exogenous (independent) variables in each sub-model were assessed for (multi)collinearity by the variance inflation factors. Relative importance of the predictors for sap flow in the clearness index models was assessed by variance partitioning tests. Log-transformation was used for vapor pressure deficit, as often its' dependence with sap

flow is logarithmic (Liu et al., 2015). Analyses were conducted in R (R Core Team, 2024) (version 4.3.3), with SEMs fitted using the R-package *piecewiseSEM* (Lefcheck, 2016). Direct and indirect effects on sap flow across sites and tree species were calculated using *semEff* (Murphy, 2022) based on standardized path coefficients (scaled to mean of zero and unit standard deviation). Total effects were obtained by summing direct and all indirect effects. To ensure that potential autocorrelation does not inflict our path coefficients and derived effects, block bootstrap was used as an additional sensitivity test. The mixed-effect models were constructed with *lme4* (Bates et al., 2015). For transparency and reproducibility, complete analysis details and all site-/species-level figures/tables are compiled in *Supplementary Materials S3*.

To investigate sap flow and transpiration under low-and high-altitude clouds, univariate regression analysis (ordinary and total least squares) was additionally employed to examine if high- and low-altitude cloud fractions have different impacts on transpiration. This cloud-type-specific analysis was kept univariate because including additional covariates (e.g., VPD and soil moisture) would substantially reduce the matched sample size; their joint effects are instead assessed in the SEM analysis described above. Accordingly, the univariate regressions should be interpreted as an indicative estimate of cloud-type-specific associations rather than a complete attribution of multiple transpiration drivers.

For pairwise comparison of groups, the Mann-Whitney U test was used. All model details can be found from the *Supplementary Materials S4*.

Data availability

Pre-processed data can be found from [10.5281/zenodo.19124555](https://zenodo.org/record/19124555) and the R-scripts to reproduce the findings are available at [10.5281/zenodo.19125337](https://zenodo.org/record/19125337).

The environmental data (see also Table 2 for instrumental details) for SE-Nor and SE-Syb are also available from ICOS Carbon portal and originate from the Warm Winter 2020 ecosystem datasets (Mölder et al., 2022; Peichl et al., 2022). Raw data on meteorological variables from

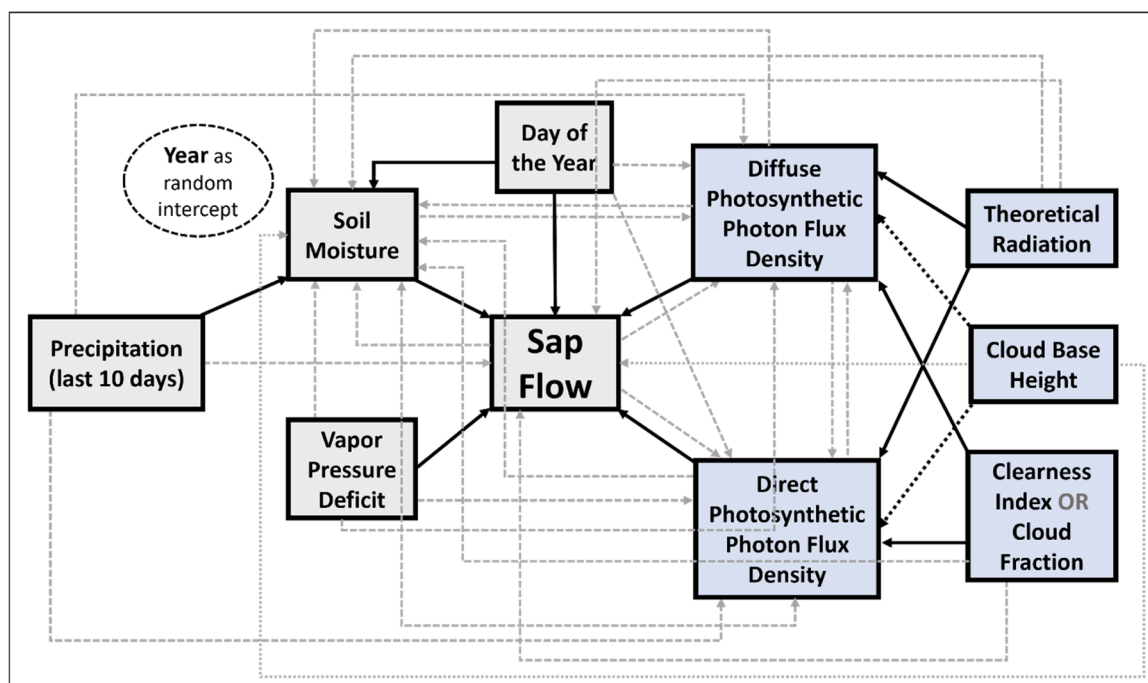


Fig. 7. Visualization of the investigated pathways in the structural equation models. Black solid arrows indicate the preliminary structural equations including either clearness index or cloud fraction in the model. Dotted arrows indicate additional investigated pathways when cloud base height was also included in the model (black arrows referring to the modified preliminary structural equations). Variables directly related to cloudiness are in blue colour.

FI-Hyy are freely available from AVAA-portal (<https://smear.avaa.csc.fi/download>, last access: 30 September 2024).

The Cloudnet (<https://cloudnet.fmi.fi/>, last access: 4 January 2025) classification data products providing the cloud base heights for FI-Hyy and SE-Nor can be found from the ACTRIS Data Centre along with the full data files for cloud radar (Eliasson, 2024; Moisseev et al., 2024) and lidar (Moisseev and Petäjä, 2024; Mölder, 2024). The ceilometer data files for SE-Svb utilized in this work can be found from (Larmanou and Talvinen, 2025).

Access to CLARA-A3 dataset and its documentation, used to determine the long-term trends in cloudiness over the boreal forests, can be found from sources given the Supplementary Material).

CRediT authorship contribution statement

Sini Talvinen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yann Salmon:** Writing – review & editing, Data curation. **Jose Gutierrez Lopez:** Writing – review & editing, Data curation. **Maj-Lena Finnander Linderson:** Writing – review & editing, Investigation, Data curation. **Štěpánka Řehorková:** Writing – review & editing, Data curation. **Ladislav Šigut:** Writing – review & editing, Investigation, Data curation. **Abhay Devasthale:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Ilona Ylivinkka:** Writing – review & editing. **Caroline Greiser:** Writing – review & editing, Visualization. **Ekaterina Ezhova:** Writing – review & editing, Investigation. **Johannes Quaas:** Writing – review & editing. **Natalia Kowalska:** Writing – review & editing. **Marian Pavelka:** Writing – review & editing. **Stanislav Jurán:** Writing – review & editing. **Eric Larmanou:** Writing – review & editing, Data curation. **Teemu Paljakka:** Writing – review & editing, Data curation. **Claudia Mohr:** Writing – review & editing, Funding acquisition, Conceptualization. **Ilona Riipinen:** Writing – review & editing, Supervision, Investigation, Funding acquisition. **Radovan Krejci:** Writing – review & editing, Supervision, Investigation, 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.2026.111182](https://doi.org/10.1016/j.agrformet.2026.111182).

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