Contribution of fine roots on carbon allocation patterns in Norwegian forests

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Abstract. Boreal forests play a key role in the global carbon (C) cycle, with fine root production and turnover contributing to belowground C fluxes and inputs to soil organic carbon (SOC) stocks. However, fine root biomass and production are difficult to quantify and introduce uncertainty in estimates of net primary production (NPP), limiting the assessment of C allocation patterns in boreal forests.

The objective of the present study was to assess how different fine root modelling approaches influence estimates of NPP, gross primary production (GPP), carbon use efficiency (CUE), and belowground C allocation to fine roots in Norwegian boreal and nemo-boreal forests. Using Norway's national forest resource map together with MODIS remote sensing data, we estimated fine root biomass and production using three approaches that differed in how foliage biomass was derived: two based on leaf area index (from MODIS or the forest resource map) and one based on allometric biomass equations. These approaches were combined with alternative fine-root turnover rates and foliage-to-fine-root biomass ratios.

Mean NPP derived from the forest resource map ranged from 318 to 243 $g\,C\,m^{-2}\,yr^{-1}$ across young to mature forests. In Norway spruce and Scots pine forests, NPP increased during early stand development, peaked between 50 and 80 years, and declined with increasing age. Comparison against European MODIS NPP revealed that tree growth alone accounted for 16 % of MODIS NPP, while including fine root and understory NPP contributions increased total NPP by roughly 3–5 times, depending on the fine root estimation method. CUE ranged from 0.63 to ~~0.30~~, showing age-related declines and species-level variation, ~~with the lowest values in mature Norway spruce forests~~.

Our analysis sheds light on the role of fine root biomass and production in forest C budgeting and their influence on NPP, CUE, and belowground C allocation. Excluding fine roots creates a major gap in forest C analyses and we conclude that the choice of method for fine root estimation has a strong impact on regional NPP and its component fluxes. Estimates of forest CUE may guide management by identifying areas with low efficiency, where interventions may enhance forest C uptake.

1 Introduction

Forest ecosystems play a pivotal role in carbon (C) storage globally, with boreal forests serving as one of the primary contributors to the global C sink (Pan et al., 2011). Boreal forests' soil organic carbon (SOC) stocks store 3–4 times more C than the above ground biomass (Batjes, 1996), reflecting the long-term balance between organic matter inputs and outputs through processes such as litter production, decomposition, leaching, and erosion. A major portion of this organic matter originates from belowground sources, primarily fine root litter and associated fungal mycelium. For instance, Clemmensen et al. (2013) estimated that root-derived inputs contribute 50 %–70 % of the organic matter in the upper 20 cm of boreal forest soils. Similarly, Kyaschenko et al. (2019) reported that root inputs accounted for 73 %–81 % of total accumulated SOC in the mor (raw humus) layer, rather than from aboveground leaf litter. Plant allocation of C to belowground is supported by photosynthesis, with gross primary production (GPP) representing the total amount of C fixed from the atmosphere through photosynthesis, providing energy for plant metabolism and growth. In boreal forests,

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Table 1. Summary of fine root and foliage parameters.

Variable	Norway spruce	Scots pine	Deciduous	Source
Ratio of fine root biomass to foliage biomass (CT)	0.54	0.70	2.50	Härkönen et al. (2011)
Ratio of fine root biomass to foliage biomass (MT)	0.30	0.36	1.50	Härkönen et al. (2011)
Ratio of fine root biomass to foliage biomass (VT)	0.42	0.51	2.00	Härkönen et al. (2011)
Ratio of fine root biomass to foliage biomass (OMT)	0.18	0.20	1.00	Härkönen et al. (2011)
Ratio of fine root biomass to foliage biomass (MODIS)	1.20	1.20	1.10	MOD17 Collection 6 User's Guide (2019) TS4
Specific leaf area ($m^2\,kg^{-1}$ biomass)	4.95	6.2	13.55	Lintunen et al. (2011); Palmroth and Hari (2001); Stenberg et al. (1999)
Fine root biomass turnover (times yr^{-1})	0.81	0.87	1.00	Härkönen et al. (2011)
Foliage biomass turnover (times yr^{-1})	0.14	0.33	1.00	Norwegian NFI; Dalsgaard et al. (2016)

biomass values by turnover rates specific to each understory component (Table S2; Dalsgaard et al., 2016). Production was converted to units of C by assuming a biomass C fraction of 0.5. After conversions, the final expressed understory NPP in $g\,C\,m^{-2}\,yr^{-1}$.

2.5 Net primary production and gross primary production

The estimated tree NPP, fine root NPP and understory NPP, were summed to represent total NPP ($g\,C\,m^{-2}\,yr^{-1}$), hereafter referred to as SR16-based NPP. Both SR16-based NPP and MODIS Euro NPP were used in the calculation of GPP ($g\,C\,m^{-2}\,yr^{-1}$), to assess sensitivity to the choice of NPP source. We employed a C balance framework conceptually consistent with the MOD17 algorithm, but with modifications. The MOD17 algorithm estimates GPP using a light-use efficiency model and subsequently derives NPP by subtracting autotrophic respiration (R_a). R_a is estimated using a combination of biome-specific parameters from the Biome Property Look-Up Tables (BPLUT) and temperature- and biomass-dependent functions. In contrast, our approach reconstructs GPP from independently estimated NPP and R_a components. The C balance relationship is expressed as:

$$\mathrm{GPP} = \mathrm{NPP} + R_a \quad (1)$$

where GPP represents the total C captured via photosynthesis and is equal to the sum of NPP and autotrophic respiration (R_a). Autotrophic respiration consists of growth respiration (R_g TS5) and maintenance respiration (R_m TS6), defined as:

$$R_a = R_g + R_m \quad (2)$$

Growth respiration (R_g) represents the energy required to synthesize organic compounds during photosynthesis. In the MODIS algorithm, R_g is empirically parameterized as 25 % of NPP (Cannell and Thornley, 2000; Ryan, 1991). We applied this parameterization by setting R_g to 25 % of tree NPP, understory NPP, and fine root NPP, thereby yielding R_g values for each respective component. Maintenance respiration (R_m) represents the energy required to sustain basic cellular functions, such as cell integrity, tissue repair, and essential processes like ion transport, and is calculated as:

$$R_m = \text{foliage-}R_m + \text{f.root-}R_m + \text{wood-}R_m \quad (3)$$

where foliage-R_m, f.root-R_m, and wood-R_m represent the maintenance respiration of foliage biomass, fine roots, and living wood, respectively. Each R_m component is calculated as the product of biomass, a base respiration rate per unit biomass (reflecting C maintenance costs), and a Q_{10} TS7 parameter, which adjusts respiration according to temperature (°C). For instance, foliage-R_m can be expressed as: TS8

$$\text{foliage-}R_m = \text{foliage-biomass} \times \text{foliage-}R_{base} \times Q_{10}{}^{(T_{avg}-20.0)/10.0}R_m \quad (4)$$

Maintenance respiration is calculated similarly for foliage, fine roots, and living wood. For living wood, biomass is estimated indirectly based on foliage biomass by applying livewood-to-foliage ratios. For evergreen needleleaf forests (ENF), this ratio is 1.2; for deciduous broadleaf forests (DBF), it is 1.1. Since the equations from Eid et al. (2016) provide estimates of total wood volume rather than living wood, we applied the same ENF and DBF foliage-to-wood ratios to estimate living wood biomass in needle-leaved (spruce and pine) forest and deciduous (birch) forests accordingly. Q_{10} is set to 2.0 for both living wood and fine roots (adopting Q_{10} values from BPLUT), while for foliage biomass it is calculated using a temperature-dependent Q_{10} equation from Tjoelker et al. (2001 TS9):

$$Q_{10} = 3.22 - 0.046 \times T_{avg} \quad (5)$$

After estimating NPP and R_m, GPP was calculated for the three fine-root NPP estimation methods (foliage-based, scaled SR16 LAI, and MODIS LAI) as:

$$\mathrm{GPP} = 1.25 \times (\text{tree NPP} + \text{understory NPP} + \text{fine root NPP}) + R_m \quad (6)$$

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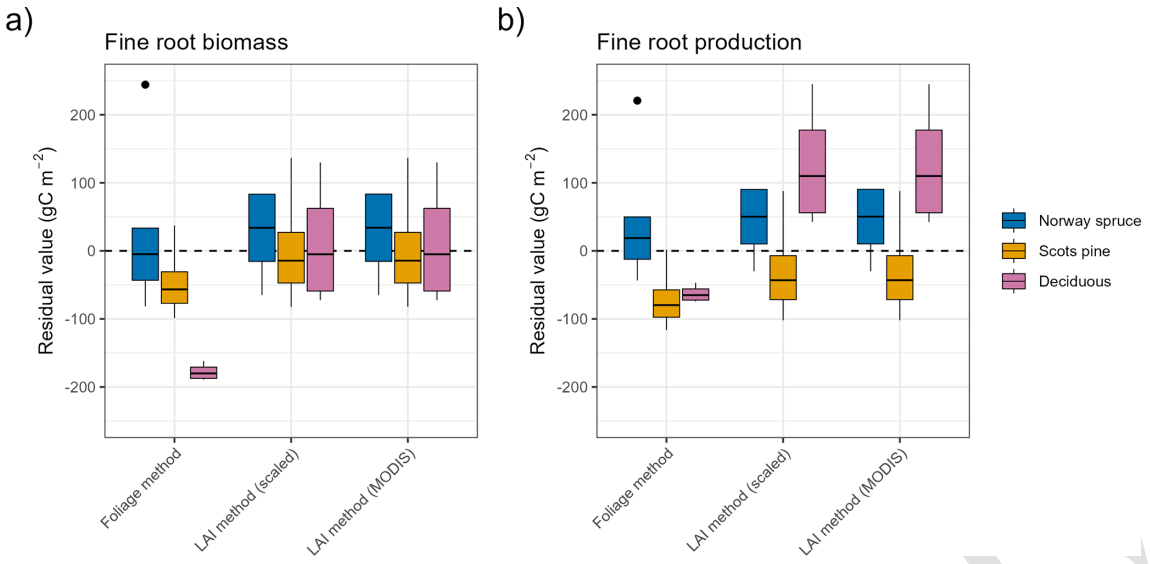

Figure 2. Residuals for fine root biomass **(a)** and fine root production **(b)** across tree species and methods for estimating foliage biomass and related fine root biomass and production. For each species, five foliage-to-fine-root biomass ratios were assumed (Table 1). The foliage-based method used allometric foliage biomass, while the two LAI-based methods estimate foliage biomass from LAU and specific leaf area. LAI data were obtained from MODIS (MODIS LAI) or from optically scaled SR16 values (SR16 LAI). Each boxplot shows the interquartile range (Q1–Q3), with whiskers extending to the smallest and largest values within 1.5 × IQR from Q1 and Q3.

method estimating an average NPP of 87 g C m^{-2} yr^{-1}, while the two LAI-based methods produced an average NPP of 332 g C m^{-2} yr^{-1} (Fig. 4).

GPP ranged from ~~149–1845~~ g C m^{-2} yr^{-1} for Norway spruce, ~~225–1326~~ g C m^{-2} yr^{-1} for Scots pine, and ~~60–1081~~ g C m^{-2} yr^{-1} for deciduous forests, with means of ~~750~~, ~~671~~, and ~~378~~ g C m^{-2} yr^{-1}, respectively (Fig. S2). Similar to NPP, GPP increased with forest age until mid-succession peak (Fig. S2) and then declined (Norway spruce) or stabilised (Scots pine). No clear age-related variation in GPP was observed for deciduous (birch) forests.

3.4 Forest carbon use efficiency

The ratio of NPP to GPP (CUE) decreased with increasing forest age in both Norway spruce and Scots pine forests. According to the power-law fit, CUE declined from a maximum of ~~0.56~~ to a minimum of ~~0.30~~ in Norway spruce forests, and from a maximum of ~~0.58~~ to a minimum of ~~0.40~~ in Scots pine forests (Fig. 5). The corresponding CUE values, derived from the ~~mode~~ of the density distribution, ranged from ~~0.32–0.40~~ for Norway spruce and from ~~0.43–0.44~~ for Scots pine, depending on the fine root production estimation method and whether MODIS data were used (Fig. 6). In contrast, the power-law fit for deciduous forests did not indicate an age-related decline in CUE (Fig. 5). However, the variability in CUE estimates for deciduous forests was similar to that observed in Norway spruce and Scots pine forests (Fig. 6). According to the power law fit, CUE in deciduous forests ranged from ~~0.47–0.63~~ across various forest ages, generally higher than values estimated for Norway spruce and Scots pine (Figs. 5, 6).

3.5 Allocation of carbon to fine roots

The estimated fraction of GPP allocated to fine roots varied across forests dominated by Norway spruce, Scots pine, and deciduous trees, and was influenced by the method used to assess fine root production (Fig. S3). For Norway spruce, median allocation ranged from ~~0.20–0.25~~, for Scots pine from ~~0.22–0.30~~, and for deciduous forests from ~~0.20–0.50~~. Deciduous forests showed the largest variability and generally higher allocation to fine roots, reflecting their greater estimated fine root production (Figs. 1b, 2b).

4 Discussion

Quantifying the contribution of fine roots to the ecosystem C cycle remains a major challenge and a key source of uncertainty in forest C modelling. This study provides a quantitative assessment of how uncertainty in fine root representation propagates into estimates of NPP and CUE by comparing multiple modelling approaches across Norwegian boreal and nemo-boreal forests. When considering only tree growth (annual increment in tree biomass + foliage production), SR16-derived tree NPP represented on average 16 % of MODIS NPP. Including the production of understory vegetation and fine roots increased SR16 total NPP to an average of 52 %–86 % of MODIS NPP, depending on the method used to estimate fine root production, with the two LAI-based ap-

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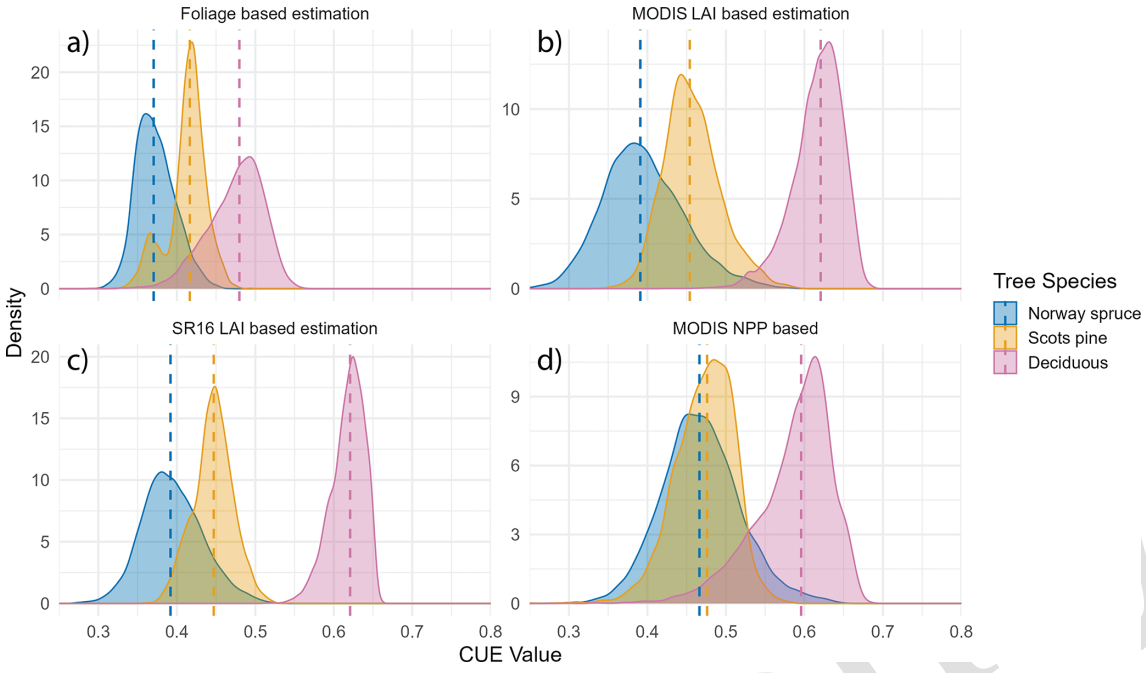

Figure 6. Density distribution of the ratio of net primary production (NPP) to gross primary production (GPP), estimated using different methods for determining fine root production. Panel **(a)** shows CUE based on the foliage-based method using allometric estimates of foliage biomass. Panels **(b)** and **(c)** show CUE derived from LAI-based methods, either using LAI from MODIS **(b)** or SR16 **(c)** scaled from allometric to optical LAI. Panel **(d)** represent the CUE distribution adopting European MODIS data but SR16 data for estimating ecosystem respiration in the GPP calculations.

timating fine root production appears to align with this observation, in contrast to the foliage-based approach, which yielded lower estimates of fine root production.

4.2 SR16-based NPP relative to external sources

Global estimates of NPP from the ForC database show that young (< 100 years) boreal forests have an average NPP of 372 g C m^{-2} yr^{-1}, while mature (> 100 years) forests have a lower values averaging 270 g C m^{-2} yr^{-1} (Anderson-Teixeira et al., 2021). In comparison, SR16-derived NPP for young forests averaged 285, 318, and 248 g C m^{-2} yr^{-1} for Norway spruce, Scots pine, and deciduous forests, respectively. For mature forests, the corresponding SR16-based NPP values were 243, 306, and 249 g C m^{-2} yr^{-1}.

Overall, SR16-based NPP followed the same general pattern as the ForC database, with higher NPP in young forests compared to mature forests. However, absolute values were generally lower than the global averages, with the exception of mature Scots pine forests, which exhibited higher average NPP than reported in the ForC dataset.

A similar pattern was observed for GPP. Global ForC estimates indicate average GPP values of 835 g C m^{-2} yr^{-1} for young boreal forests and 758 g C m^{-2} yr^{-1} for mature forests (Anderson-Teixeira et al., 2021). In comparison, SR16-based GPP estimates for young forests averaged ~~731, 680, and 423~~ g C m^{-2} yr^{-1} for Norway spruce, Scots pine, and deciduous forests, respectively. For mature forests, mean GPP values were ~~697, 687, and 416~~ g C m^{-2} yr^{-1}. Thus, SR16-based GPP estimates exhibit similar age-related trends but are consistently lower than the global averages.

Moreover, large discrepancies in NPP and GPP estimates for deciduous forests were observed between the foliage-based and LAI-based approaches. The foliage-based method produced NPP estimates that were, on average, only 26 % of those derived from the LAI-based methods, primarily due to lower estimates of foliage biomass and fine root production. This highlights the sensitivity of NPP estimates to assumptions regarding foliage and fine root allocation in deciduous forests. It is also important to note that NPP values in Nordic forests tend to be at the lower end of the range for global boreal forests (Gower et al., 2001), and that external NPP observations are relatively limited for Nordic forests compared with other boreal and temperate regions (Anderson-Teixeira et al., 2021). However, the lack of a direct 1 : 1 correlation between MODIS Euro NPP and our SR16-based NPP estimates likely stem from model uncertainties and underestimation of certain NPP component, both yielding prediction biases.

MODIS Euro NPP is derived from the global MODIS NPP product but incorporates downscaled European climate data, providing more realistic NPP estimates that align closely with European NFI data (Neumann et al., 2016), including Norwegian NFI data. Nevertheless, MODIS Euro

may overestimate NPP in areas with inherently low NPP ($\sim 400\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), which could partly explain the generally lower SR16-based NPP values.

Despite the generally lower NPP and GPP values in our analysis, the SR16-based NPP and GPP estimates remain of the same order of magnitude as those reported in external datasets (Anderson-Teixeira et al., 2021; Gower et al., 2001). Yet, discrepancies between the SR16-based NPP estimates and global NPP datasets may arise from variations in climate, forest structure (e.g., differences in stand age distributions), and forest management practices. For example, areas with a high frequency of logging or clearcutting could still be present and may potentially contribute to lower SR16-derived NPP estimates compared to MODIS Euro. Finally, while the Eid et al. (2016) model was developed to estimate stand-level biomass of Norwegian forests, it has some predictive biases, particularly in forested areas of western and northern Norway, where it tends to underestimate biomass. This bias may also contribute to explaining the overall low estimated NPP.

4.3 Carbon use efficiency of Norwegian forests

According to the power-law fits, the NPP/GPP ratio (CUE) in Norwegian forests ranged from a maximum of 0.63 to a minimum of ~~0.32~~, consistent with our hypothesis that CUE falls within the theoretical limits of 0.2–0.75 proposed by Amthor (2000), based on calculations of growth- and maintenance respiration costs. Moreover, CUE declined with increasing forest age, consistent with observations by De Lucia et al. (2007) and Piao et al. (2010), and reflecting that early-succession forests fix more atmospheric CO_2 relative to their uptake than late-succession forests. ~~In addition to forest age, CUE variation according to tree species was observed. Scots pine-dominated forests displayed higher CUE (0.58–0.42) than Norway spruce forests (0.56–0.30). The highest CUE was observed in deciduous forests (0.63–0.47), although this result is confounded by large uncertainties related to fine root production predictions. Value of CUE were generally lowest in Norway spruce forests, due to exhibiting the strongest age-related CUE decline, with a minimum CUE of 0.30, compared to a minimum CUE of 0.40 in Scots pine forests.~~ Additionally, ~~our CUE~~ the estimates were consistent with the empirical CUE range of 0.22 to 0.54 derived from boreal forests (Malhi et al., 1999; Ryan et al., 1997b; Turner et al., 2003) and summarized by De Lucia et al. (2007), with an average CUE of 0.32.

Global MODIS-based estimates from Zhang et al. (2014) reported mean CUE values of 0.59 for evergreen needle-leaf forests and 0.47 for deciduous broadleaf forests in the Northern Hemisphere. Expanding beyond MODIS data, Jin et al. (2025) used FLUXNET eddy-covariance measurements and reported a CUE range of 0.46–0.67 for continental evergreen needle-leaf forests across Canada, Finland, and Russia, with an average of 0.57. In comparison, the ~~mode~~ of our CUE estimates ranged from ~~0.32–0.40~~ for Norway spruce forests, ~~0.43–0.44~~ for Scots pine forests, and from ~~0.47 to 0.63~~ for deciduous (birch) forests. When compared with the CUE ranges reported by Zhang et al. (2014) and Jin et al. (2025), our CUE estimates are generally lower, especially for Norway spruce and Scots pine forests.

Norwegian forests span a wide range of ecological conditions, extending from the temperate zone in the south to the Arctic zone in the north, and includes strong gradients in both temperature and precipitation. Previous work highlights large spatial variation on CUE globally and concluded that CUE is largely driven by variations in vegetation type (Bradford and Crowther, 2013; Zhang et al., 2009), soil fertility (Vicca et al., 2012; Zhang et al., 2019), temperature (Piao et al., 2010) and as well as precipitation and hydrology (Chen and Yu, 2019), with Zhang et al. (2009) reporting declining vegetation CUE with increasing annual precipitation until it reaches a threshold of 2000–2500 mm, after which it remains stable.

Global studies have documented a parabolic relationship between precipitation, temperature, and CUE (Chen and Yu, 2019; Jin et al., 2025; Piao et al., 2010). Specifically, CUE increases with air temperature between 5 and 25 °C but declines when precipitation exceeds about 500 mm, possibly attributed to increased cloudiness that leads to reduced solar radiation (Zhang et al., 2009). In this study, the SR16 dataset showed an average annual precipitation of 1092 mm (range: 326–4434 mm, median 983 mm) and a mean temperature of 2.8 °C (range: −2.0 to 8.4 °C, median 2.8 °C), as shown in the precipitation and temperature density distribution plots of the resampled SR16 data (Fig. S4). Potentially, variation in temperature combined with both extreme high and low precipitation contribute to the generally lower CUE estimates observed in this study. However, disentangling these effects is difficult due to the multiple interacting factors influencing CUE (Jin et al., 2025). Additionally, climatic factors also strongly influenced tree species distributions in our analysis. Scots pine and deciduous forests were most prevalent under the driest and wettest conditions, while Norway spruce dominated areas with intermediate precipitation ($\sim$ 1000 mm). At temperatures below 0 °C, deciduous forests, primarily birch, were most common, followed by Scots pine. As temperatures increased, Norway spruce became more prevalent, while the warmest conditions again favoured deciduous forests and Scots pine and potential confounding factors, such as tree species-specific variations in NPP, makes it challenging to establish the precise drivers of CUE in our study.

4.4 Methodological limitations

Estimates of CUE are often contentious due to the propagation of uncertainties associated with methods for calculating NPP and GPP (De Lucia et al., 2007; Jin et al., 2025; Vicca et al., 2012). GPP, NPP, and autotrophic respiration (R_a) are linked through C balance relationships and are there-

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fore not independent. Consequently, uncertainties or parameter choices affecting one component propagate to the others, influencing derived CUE estimates. This is particularly relevant for satellite-based GPP products, which are typically derived using light-use efficiency approaches driven by fAPAR and meteorological data (Justice et al., 2002; Running et al., 2004).

Alternative GPP products also exist, including GOSIF-GPP derived from Orbiting Carbon Observatory-2 observations of solar-induced chlorophyll fluorescence (Li and Xiao, 2019), NIRv-GPP based on near-infrared reflectance of vegetation (Badgley et al., 2019), and more recently GPP-net, which is a predictive deep-learning model trained on Sentinel-2 data (Wang et al., 2026). These approaches are less dependent on C-balance closure assumptions and may therefore provide more independent estimates of GPP. Combining such GPP products with MODIS Euro NPP could consequently enable more independent calculations of CUE. However, uncertainty related to transferability and model performance in northern ecosystems remains an important consideration for remote-sensing-based GPP products (Li and Xiao, 2019; Marsh and Zhang, 2022). In the present study, we instead retained a MOD17-consistent framework to enable comparison of respiration and belowground C allocation across the different fine root modelling approaches.

To reduce the interdependence between MODIS-derived NPP and GPP, we incorporated external SR16 forest data into the NPP analyses. However, our GPP estimates still rely on the MOD17 framework, which applies generalized parameterizations to estimate autotrophic respiration from biomass, introducing uncertainty into the estimated GPP and CUE. In addition, the biomass models used in this study exhibit known predictive uncertainties, including underestimation biases in western and northern Norway (Eid et al., 2016), further contributing to uncertainty in the estimated NPP.

Another limitation of our approach is the use of fixed turnover rates for fine roots across forest ages. Fine root turnover, along with mycorrhizal mycelial turnover, decreases with forest age (Hagenbo et al., 2017; Yuan and Chen, 2012), but this dynamic was not accounted for in our approach. Instead, we used fixed turnover rates across forest ages, which constrained our estimates of belowground C allocation. As a result, our model predicted lower CUE under conditions of high fertility, as indicated by site index which is likely incorrect.

Forest CUE generally increases with soil nutrient availability (Zhang et al., 2019), with the effect that trees allocate proportionally more C to aboveground parts in nutrient-rich soil (Vicca et al., 2012) because constraints on belowground nutrient acquisition are alleviated. However, assuming fixed turnover rates creates a linear relationship between foliage biomass and fine root biomass. High foliage biomass directly increases fine root biomass, thereby elevating maintenance respiration. This approach implicitly assumes that variation in fine root dynamics is driven solely by foliage biomass, neglecting shifts in nutrient-mediated belowground C allocation (Vicca et al., 2012). Consequently, the use of fixed turnover rates restricts the modelled variability in belowground allocation and likely explains the relatively narrow range of fine root allocation estimated in this study. Specifically, the interquartile range of the estimated fraction of GPP allocated to fine roots was ~~0.13–0.32~~ for Norway spruce, ~~0.13–0.42~~ for Scots pine, and ~~0.04–0.74~~ for deciduous forests. Likely this natural variability in C allocation is greater. Nevertheless, considering that about 60 % of GPP is allocated belowground in boreal forests (Gill and Finzi, 2016; Litton et al., 2007), our estimates of fine root allocation align with this value when considering additional C allocation to mycorrhizal fungi.

Variation in fine-root-to-foliage biomass ratios across vegetation types can be used to represent fertility-related differences in fine root biomass, with vegetation type serving as a proxy for site fertility. However, as vegetation type is not currently available in the SR16 dataset, we were unable to fully integrate site index and fertility into the analyses, and we therefore treat site index as a descriptive variable. As a result, incomplete representation of fertility means that some of the observed forest age-related patterns may also partly reflect variation in site index, which is linked to both site fertility and likely management-driven differences in stand age structure.

A further limitation is that the datasets used in this study are not temporally aligned. The MODIS Euro NPP data used in this study cover the period 2003–2012 and are therefore temporally aligned with the MODIS LAI (MCD15A2H) data, which were derived from observations over 2003–2013 and averaged to produce a single representative estimate. However, the SR16 forest structure data and associated LAI are based on airborne laser scanning campaigns initiated from 2009 onwards, resulting in a temporal discrepancy between the remote sensing and forest inventory datasets. Consequently, the analysis combines information from different time periods and should be interpreted as a structural comparison among alternative approaches to estimating forest C fluxes, rather than as a temporally explicit C budget for a specific year. Despite this temporal mismatch, the similarity between results derived from the two LAI-based approaches (MODIS and SR16) suggests that its influence is limited relative to the differences between the LAI modelling approaches, likely stemming from the quantile mapping applied to align the SR16 LAI distribution with that of MODIS.

While our analyses integrate data from different time periods, they also do not explicitly represent longer-term temporal responses in respiration. Maintenance respiration was calculated using fixed temperature sensitivities (Q_{10}), consistent with the MOD17 framework. However, experimental evidence suggests that plant respiration can acclimate to sustained warming, reducing its temperature sensitivity over time and thereby dampening the temperature-driven increase in respiration (Reich et al., 2016). Accounting for such accli-

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mation could influence estimates of GPP and CUE and may provide insight into potential responses of forest C cycling to climate warming. However, further empirical work on respiration acclimation across boreal tree species, and its scaling from individual trees to stand and regional levels, is needed to better constrain and evaluate such approaches.

5 Conclusion

Here we evaluated how three approaches for estimating fine root production affect NPP and CUE estimates in Norwegian forests. The results show that the choice of method has a strong impact on both total NPP and its component fluxes. Excluding fine roots creates a major gap and underestimates total NPP. For example, tree growth alone accounted for just 16 % of MODIS NPP, while including understory and fine root production increased NPP to 52 %–86 % of MODIS values, depending on the method used, with LAI-based approaches contributing the most. These findings highlight that estimates of regional C fluxes are sensitive to assumptions about fine root dynamics, underscoring the importance of evaluation of fine root contributions into forest C analyses, such as national C accounting methods.

Mean NPP across young to mature forests ranged from 318–243 $g\,C\,m^{-2}\,yr^{-1}$, which are generally lower than NPP values reported in global analyses of boreal forests (typically 372–270 $g\,C\,m^{-2}\,yr^{-1}$ for comparable age classes). Nevertheless, NPP patterns for Norway spruce and Scots pine followed expected age-related dynamics, with productivity increasing in young stands, peaking at mid-succession, and declining with advancing age. Forest CUE, derived from estimated NPP and GPP, also decreased with age, ranging from 0.63 in younger stands to 0.32 in older stands, consistent with theoretical CUE limits between 0.6 and 0.2.

Regional estimates of forest CUE may guide management by identifying areas with low efficiency where interventions may enhance C sequestration. The effectiveness of forest-based climate mitigation strategies – such as afforestation, deforestation reduction, and forest restoration – partly depends on site-level CUE. Prioritizing areas with low but improvable CUE could increase C uptake and strengthen the impact of these mitigation efforts. However, strategies targeting improved CUE should also account for broader ecosystem services, including biodiversity and resilience to climate extremes, to ensure that gains in C sequestration do not compromise other key forest functions. Prioritizing areas with low but potentially improvable CUE could increase C uptake and strengthen forest-based climate mitigation outcomes. However, this should be interpreted with caution, as total ecosystem C sequestration is not fully captured here; in particular, soil C sequestration is not considered in this study, although it is a critical component of forest C dynamics. Finally, strategies targeting improved CUE should also account for broader ecosystem services, including biodiversity and resilience to climate extremes, to ensure that gains in C sequestration do not compromise other key forest functions.

Data availability. Data are available from the corresponding author upon reasonable request.

Supplement. The supplement related to this article is available online at [the link will be implemented upon publication].

Author contributions. AH: conceptualization, data curation, formal analysis, methodology, visualization, writing–original draft, project administration. RMB: data curation, formal analysis, methodology, investigation. CWM: investigation, methodology. MH: data curation, investigation. SW: investigation. LD: conceptualization, formal analysis, methodology, investigation. All authors: writing–review & editing.

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