

RESEARCH ARTICLE

Internal stem decay is not a major source of error for carbon stock estimates in managed temperate forests of Central Europe

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Handling Editor: Giovanna Battipaglia**Abstract**

1. Forest biomass and carbon stock estimates are critically important for the understanding of the global carbon cycle and the mitigation potential of forest ecosystems with respect to climate change. Forest biomass is routinely assessed using allometric biomass functions, which rely on stem diameter and tree height data and thus on the outer shape of the trees. Internal stem decay and tree cavities are neglected in these calculations.
2. In a global survey, it has been postulated that the 1% largest trees contain 50% of the above-ground tree biomass of a forest stand. This postulate assigns the largest trees a prominent role in the biomass of the entire stand. This also means that estimation errors in determining the biomass of these individual trees would have a significant effect on stand biomass. At the same time, the largest and oldest trees have an increased risk of internal wood decay, which in turn increases the probability of overestimating the stand biomass using allometric biomass functions.
3. We studied above-ground tree biomass and carbon stocks in temperate forests of *Fagus sylvatica*, *Abies alba*, *Picea abies* and *Pinus sylvestris* in SW Germany and selected 168 plots with 2359 trees with a disproportionally high proportion of large old trees. We calculated biomass based on allometric regression functions and corrected the results with data of internal stem decay obtained with sonic tomography.
4. In the studied tree species, 18%–25% of the largest trees constituted 50% of the above-ground biomass and thus far more than the 1% largest trees.
5. Overestimation of above-ground stand biomass and carbon stock density due to internal stem decay amounted to only 0.2%–0.3% on stand level and was thus negligible compared to other potential sources of error linked with biomass and carbon stock estimates.
6. Allometric biomass functions can be used for biomass and carbon stock estimates in managed temperate forests of Central Europe, even in stands with high shares

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of large old trees. It should be tested whether this conclusion is transferable to forests with less or no intensive management in other regions and biomes.

KEYWORDS

above-ground biomass, allometric regression, internal stem decay, sonic tomography, tree biomass, tree cavities

1 | INTRODUCTION

Forest biomass estimates generally rely on stem diameter and tree height data and thus on the outer shape of trees using allometric regression functions (Romero et al., 2022; Sileshi, 2014). This widely used methodology neglects potential error due to internal stem decay, even though case studies from temperate hardwood forests (Marra et al., 2018) and savanna trees (Calvert et al., 2024) substantiated stem-internal biomass losses of up to 30%–35% in individual trees. Yet, much more important than estimation errors on tree level are biases at larger scales, for example, on stand or biome levels, because they have the potential to influence C stock balances significantly.

Normally, one would assume that the effects are already limited at stand level, as experiences from timber harvest and wood-core sampling for dendrochronological analyses often suggest that a high percentage of trees is not affected by severe internal wood decay, at least in managed temperate forests. However, this assumption conflicts with Lutz et al. (2018), who found in a global analysis that the 1% largest trees of a forest stand usually represent 50% of the stand's above-ground biomass. If a very small proportion of trees has such a strong influence on stand biomass, precise biomass estimates on tree level matter. In a stand of 100 trees, overestimating the biomass of the largest tree by 30% due to a cavity would mean overestimating the stand biomass by no less than 15%.

Large old trees are naturally subject to a particularly high risk of wood decay inside the trunk and the formation of cavities (Brazee & Burcham, 2023; Frank et al., 2018). Therefore, the assumption that the oldest and largest trees in a stand are the overriding predictors of the biomass of the entire stand is a cause for concern for the quality of the existing forest biomass estimates, as long as these biomass estimates are based only on the outer shape of the trees. It is, therefore, necessary to quantify the error due to internal stem decay and tree cavities in these estimates.

Stand surveys that attempt to quantify the influence of internal stem decay on stand biomass and C stock densities are scarce. Hauck et al. (2023) surveyed the above-ground biomass of *Quercus robur* forests in southwestern Germany and corrected estimates that were based on allometric regression for biomass losses due to internal wood decay based on sonic tomograms. Although stands with a high share of large old trees were selected, stand above-ground biomass and C stock density were only overestimated by <1%, if not corrected for internal stem decay.

Flores-Moreno et al. (2024) conducted stand surveys in savannas and tropical forests of northeastern Australia and found ca. 30% of the stand biomass in dry savannas and ca. 3% in rainforests to be affected by stem decay recorded with resistography. The high internal stem decay in the dry savanna was primarily due to wood-feeding termites (Flores-Moreno et al., 2024; Yatsko et al., 2025).

Since the knowledge of the influence of internal stem decay on forest biomass and C stock densities is limited to few studies, we analysed the bias by internal stem decay for allometric biomass estimates in managed temperate forests in Central Europe, including stands of four major tree species that represent more than 60% of the forested area in Germany in the core of Central Europe's temperate forest region (BMEL, 2024). Together with oak, which was already studied by Hauck et al. (2023), these tree species (i.e. *Abies alba*, *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*) cover 75% of Germany's forests.

In addition to the quantification of the bias in stand biomass and C stock estimates that is due to relying merely on the outer shape of the trees when using allometric regression functions, our study covered another more applied aspect related to this methodological question. Large old trees are often discussed in the context of biodiversity conservation, because many organisms depend on the microhabitats and the longevity of such trees (Lindenmayer, 2017; Lindenmayer & Laurence, 2017). Therefore, different forms of retention forestry have been developed to support species with a preference for large old trees even in managed forests (Fedrowitz et al., 2014; Gustafsson et al., 2012; Mölder et al., 2020). The dominant role of large old trees in determining forest biomass and C stocks at stand level that has been suggested by Lutz et al. (2018) assigns such trees not only a key function for biodiversity conservation, but also in the protection of the global climate. For this reason, it is important to know what proportion of the total C in the biomass of forest stands can be protected by sparing the largest and oldest trees from logging. This kind of information is of high practical relevance for Central European forestry, because the retention of large old trees plays a major role in certification and governmental funding schemes (Asbeck et al., 2021) and there is therefore a demand for information on the effectiveness of such measures for both biodiversity conservation and carbon storage (Emrich et al., 2025).

The universal validity of the postulation of the 1% largest trees representing 50% of forest biomass (Lutz et al., 2012, 2018) has been challenged by other recent studies. Based on data from 120 forest stands, Slik et al. (2013) reported the 2%–4% largest trees

to contain less than 50% of the above-ground biomass in tropical lowland forests of South America (25%), Southeast Asia (39%) and Africa (45%). Mildrexler et al. (2020) found the 3% largest trees to contain 42% of the above-ground C stock in dry temperate conifer forests of the northwestern United States. Hauck et al. (2023) found the ca. 10% largest trees to represent 50% of the above-ground biomass in *Quercus robur* forests of Germany. This wide variation in the percentage of trees that make up half of the stand biomass has implications for the role that these large old trees can play in climate protection, especially as Lutz et al. (2012, 2018), Slik et al. (2013) and Mildrexler et al. (2020) did not take internal wood decay into account.

Therefore, we examined two research questions in our study: First, we aimed at quantifying the estimation error for above-ground stand biomass and C stock density by not considering internal stem decay. Second, we wanted to check the validity of the postulate by Lutz et al. (2018) that the ca. 1% largest trees would contain 50% of the above-ground stand biomass. Referring to these research questions, we tested the hypotheses that (1) neglecting internal stem decay leads to a significant overestimation of above-ground forest biomass and C stock densities and (2) clearly more than 1% of the largest trees are needed to represent half of the above-ground forest biomass and C stock in managed temperate forests of Germany.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

Fieldwork for the study was conducted in southwestern Germany, which is located in the core of the temperate forest biome of Central Europe. We targeted on sampling ca. 40 forest stands of our four study species *Fagus sylvatica* L. ($N=47$ stands), *Abies alba* Mill. ($N=41$), *Picea abies* (L.) H. Karst. ($N=41$) and *Pinus sylvestris* L. ($N=39$) and selected sample plots of ca. 350 m² with a high share of large old trees. Stands of *F. sylvatica*, *A. alba* and *P. abies* were located in the southern Black Forest at 500–1100 m a.s.l., whereas *P. sylvestris* stands were sampled in the Palatinate Forest SE Kaiserslautern and in the upper Rhine valley (Hardtwald, St. Leon-Rot SE Speyer) at elevations of 100–350 m a.s.l. The selection of forest sites was based on local knowledge and on selecting suitable plots with the dominance of our study species from a database of 135 existing

1-ha stands that are used by us in the scope of a larger research project that deals with the effects of large old trees on biodiversity (Research Training Group 'Conservation of Forest Biodiversity in Multiple-Use Landscapes of Central Europe (ConFoBi)'; Storch et al., 2020). Within these forests, we selected patches of ca. 350 m² with the largest trees. Sample plots included on average 14 ± 1 trees or 402 ± 13 trees ha⁻¹ with a diameter at breast height (dbh) ≥ 7 cm. Basic stand characteristics are compiled in Table 1. Overall, we investigated 2359 trees on 168 plots. Tree age was not recorded, because we applied noninvasive sampling in our study and because the tree biomass directly depends on tree size and not tree age. Fieldwork was non-destructive and conducted on unprotected public forest land and thus did not require formal permission by authorities, but was permitted by the forest owners. Work conducted in the framework of the ConFoBi project in the Black Forest was covered by the general permit of ForstBW (Tübingen-Bebenhausen, Germany) to the Faculty of Environment and Natural Resources, University of Freiburg, to use the field sites. In the upper Rhine valley, fieldwork was approved orally by Landesforsten Rheinland-Pfalz, Forest District Waldleiningen, Germany.

2.2 | Stand surveys and sonic tomography

Biomass calculations were based on measurements of the dbh and tree height of all trees on the sample plots with a dbh ≥ 7 cm. Tree height measurements were conducted with a Vertex IV ultrasonic clinometer and T3 transponder (Haglöf, Långsele, Sweden). Of the average of 14 ± 1 trees per sample plot, the five trees with the highest dbh (minimum dbh >30 cm), which were considered to have the highest risk of internal trunk rot, were selected for sonic tomographic examination in order to search non-destructively for cavities inside the trunk. These trees had a mean dbh ($\pm$ SD) of 58.5 ± 9.6 cm (1%-confidence intervals 57.9–59.2 cm) and a mean tree height of 32.0 ± 4.1 m (1%-confidence intervals 31.7–32.3 m). Sonic tomograms were recorded with a Picus 3 sonic tomograph (IML, Rostock, Germany) equipped with 12 sensors that were evenly distributed along the stem circumference at ca. 60 cm and 160 cm height. Percentages of solid wood area in the stem cross section were calculated with the Picus Q74.2 software using the tomogram version SoT2, which produces fewer artefacts (and thus less cavity overestimation) than the alternative option SoT1 for marginal areas in the stem cross section (Göcke, 2017).

TABLE 1 Stand density and tree sizes (mean $\pm$ SD) of the studied forests dominated by *Fagus sylvatica* ($N=47$), *Abies alba* ($N=41$), *Picea abies* ($N=41$), or *Pinus sylvestris* ($N=39$).

	<i>Fagus sylvatica</i>	<i>Abies alba</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>
Stand density (trees ha ⁻¹)	423 $\pm$ 174	449 $\pm$ 142	428 $\pm$ 174	372 $\pm$ 179
Mean dbh (cm)	36.9 $\pm$ 9.2	43.2 $\pm$ 9.8	44.3 $\pm$ 10.7	36.4 $\pm$ 7.2
Max. dbh (cm)	66.6 $\pm$ 11.6	70.4 $\pm$ 12.7	66.3 $\pm$ 7.8	63.2 $\pm$ 8.5
Mean tree height (m)	22.9 $\pm$ 5.4	27.8 $\pm$ 5.0	27.2 $\pm$ 5.2	21.8 $\pm$ 2.9
Max. tree height (m)	35.1 $\pm$ 4.9	35.6 $\pm$ 2.8	35.4 $\pm$ 2.9	32.6 $\pm$ 2.1

2.3 | Allometric biomass and carbon stock estimates

We selected several allometric biomass functions from the literature to derive above-ground biomass and stem biomass separately from our dbh and tree height data. These biomass functions are compiled in [Table S1](#) for our main target species (*Fagus sylvatica*, *Abies alba*, *Picea abies* and *Pinus sylvestris*) and in [Table S2](#) for accessory tree species that occurred on our sample plots. The equations were checked to see whether the range of the tree sizes used to build the allometric functions fell within the range of the trees we measured. Equations with strongly deviating results were not taken into account when calculating the mean values for above-ground and stem biomass. Biomass values were converted to C stock densities based on C concentrations of 48.8% for temperate and boreal broadleaves and 50.8% for temperate and boreal conifers (Thomas & Martin, 2012).

2.4 | Correction of biomass estimates for internal stem decay

Since wood decay inside the trunk and cavity formation often spread from below (Gilbert et al., 2016; Gilmartin, 2020; Yatsko et al., 2025), it was assumed that the entire trunk had no decay if solid wood was found at both measurement heights. If wood decay was only detected at the lower measuring height, the damage was assumed to be present in a stem segment of 0–1 m height above the ground. If wood decay was detected at a height of 160 cm, it was assumed that it had spread further up the trunk. Therefore, in such cases, the percentage of solid wood in the trunk cross section determined at a height of 160 cm was assumed for a trunk segment from 1 m height up to half the tree height. Above this, solid wood was assumed because internal stem decay usually decreases with tree height (Calvert et al., 2024; Yatsko et al., 2025).

The sonic diagrams provide areas of intact and damaged wood and of cavities that are void of wood as area percentages in the stem cross section. These values were used to calculate losses of wood volume in the stem segments. Afterwards, these volumetric data were converted to biomass-related values, using wood density. Tree species-specific wood densities were extracted from the literature ([Table S3](#)).

2.5 | Statistical analysis

Arithmetic mean $\pm$ standard deviation (SD) are given for data describing stand and tree properties that refer to the setting of general stand characteristics, whereas mean $\pm$ standard error (SE) are presented for all values that refer to our measurements and biomass or C stock estimates. Statistical analyses were computed in R 4.4.1 (R core team, Vienna, Austria). Effects of the dominant tree species on C stock density were analysed with linear models using the `lm` function in R, because no relevant random factor could be

identified in the dataset. The significance of reductions in biomass and C stock densities by internal stem decay was tested with one-sided paired *t*-tests.

3 | RESULTS

3.1 | Extent of internal stem decay

In the complete dataset of 2359 sample trees, the mean percentage of solid wood in the stem cross-section was $>99\%$ ([Table 2](#)). This value was always greater at 160 cm height than at 60 cm. In only 3% of all trees, we detected internal stem decay ([Table 2](#)). In these trees with damage, the mean percentage of solid wood amounted to 79% at 60 cm and 83% at 160 cm ([Table 2](#)). Mean solid wood percentages in damaged trees ranged from 74% to 75% in *Picea abies* and *Abies alba* stands via 80% in *Pinus sylvestris* stands to 84% in *Fagus sylvatica* stands at 60 cm height ([Table 2](#)). At 160 cm, on average 79%–86% of the stem cross sections of damaged trees contained solid wood.

3.2 | Above-ground biomass based on allometric regression

Based on allometry, the above-ground tree biomass was highest in stands dominated by *Fagus sylvatica* (535 Mg ha^{-1}) or *Abies alba* (539 Mg ha^{-1}). It was lower in *Picea abies* (442 Mg ha^{-1}) and *Pinus sylvestris* (298 Mg ha^{-1}) stands ([Table 3](#)). These differences between tree species were significant, as evidenced by linear modelling ([Table 4](#)). Around 70% of the above-ground biomass was allocated in the stem, with $68.2 \pm 0.4\%$ (mean $\pm$ SE) in *Abies alba*, $70.3 \pm 0.3\%$ in *Fagus sylvatica*, $73.8 \pm 0.3\%$ in *Picea abies*, except for *Pinus sylvestris*, where this ratio amounted to $80.0 \pm 0.5\%$ ([Figure S1](#)).

C stock densities in the tree above-ground biomass were derived from the allometric biomass data as 262 Mg C ha^{-1} in *Fagus sylvatica*, 273 Mg C ha^{-1} in *Abies alba*, 224 Mg C ha^{-1} in *Picea abies*, and 150 Mg C ha^{-1} in *Pinus sylvestris* stands ([Table 3](#)).

3.3 | Above-ground biomass after correction for internal stem decay

On stand level, biomass and C stock densities were generally significantly lower after correction for internal stem decay ([Table 3](#)). However, subtracting the biomass lost by wood decay from the values calculated according to dbh and tree height data with allometric biomass functions only led to a minor reduction of the original values ([Table 3](#)). The corrected biomass and C stock values amounted to 99.7%–99.8% of the uncorrected values.

When either beech, fir or spruce were dominant, they were associated with smaller amounts of the other two species, which accordingly contributed to the stand biomass and C stocks ([Figure 1](#)). In pine stands, beech and spruce also contributed to stand biomass.

TABLE 2 Percentage of solid wood (with lower and upper 5% confidence intervals, CI) in the stem cross-sectional area of forests dominated by *Fagus sylvatica* (N=47), *Abies alba* (N=41), *Picea abies* (N=41) or *Pinus sylvestris* (N=39) based on sonic tomography at ca. 60 and 160 cm height.

Height		All trees		Trees with internal stem decay only	
		60 cm	160 cm	60 cm	160 cm
All forest types	Mean ± SE	99.2 ± 0.2	99.6 ± 1.4	78.7 ± 2.2	82.7 ± 2.5
	CI	(98.9–99.5)	(99.4–99.8)	(74.4–83.1)	(77.7–87.7)
	N	2359	2359	73 (3.1%)	43 (1.8%)
<i>Fagus sylvatica</i>	Mean ± SE	99.5 ± 0.2	99.6 ± 0.2	84.1 ± 3.4	83.4 ± 5.4
	CI	(99.2–99.9)	(99.2–100.0)	(77.4–91.0)	(72.9–93.9)
	N	706	706	20	15
<i>Abies alba</i>	Mean ± SE	99.1 ± 0.4	99.5 ± 0.3	75.0 ± 7.2	85.9 ± 3.2
	CI	(98.4–99.9)	(98.9–100.0)	(60.9–89.1)	(79.6–92.1)
	N	569	569	15	13
<i>Picea abies</i>	Mean ± SE	99.0 ± 0.4	99.6 ± 0.2	73.9 ± 4.4	79.6 ± 4.3
	CI	(98.2–99.8)	(99.2–100.0)	(65.3–82.5)	(71.2–87.9)
	N	545	545	15	9
<i>Pinus sylvestris</i>	Mean ± SE	99.1 ± 0.2	99.8 ± 0.1	79.7 ± 3.3	78.8 ± 8.9
	CI	(98.7–99.6)	(99.5–100.0)	(73.2–86.1)	(61.3–96.4)
	N	539	539	23	6

3.4 | Proportion of trees accounting for 50% of the stand biomass

Since trees contain discrete amounts of biomass and organic C, the share of the largest trees needed to form a certain percentage of stand biomass can only be determined approximately using the original data (Figure 2). Medians of tree percentages ranged from 25% to 33% of the stand's trees that was needed to account for approximately 50% of the C stock in the tree above-ground biomass (Figure 2a). This corresponded to mean values ($\pm$ SE) of $23.6 \pm 1.4\%$ (*Fagus sylvatica*), $25.8 \pm 1.2\%$ (*Pinus sylvestris*), $28.4 \pm 1.5\%$ (*Abies alba*) and $31.7 \pm 1.6\%$ (*Picea abies*). The means of the exact C stock densities in the above-ground biomass amounted to 52%–53% (Figure 2b).

If the tree percentage/C stock data were fitted with polynomial functions, the 50%-line for above-ground C was crossed at 18%–25% of the largest trees (Figure 3). The 18% largest trees in beech forests and the 22%–25% in fir, pine and spruce forest represented 50% of the C stock in the above-ground biomass (Figure 3).

4 | DISCUSSION

Because the overestimation of above-ground stand biomass and C stocks therein due to internal stem decay only amounted to 0.2%–0.3%, we have to reject our first hypothesis that wood decay in the interior of living trees is a significant source of error in forest biomass and C estimates, which are based on allometric regression functions with dbh and tree height as input variables. This result is in favour of the reliability of countless forest biomass and C stock estimates that have been developed in the recent past (Brown, 2002; Ciais et al., 2008; Thurner et al., 2014).

There are few studies that have addressed the influence of internal stem decay on stand level biomass and C stock estimates systematically so far. The results of the present study come close to a 0.6%–0.7% reduction of tree above-ground biomass by internal stem decay in *Quercus robur* forests of southwestern Germany (Hauck et al., 2023). Since the risk for internal stem decay increases with tree age and stem diameter (Frank et al., 2018), the data of the present study and of Hauck et al. (2023) probably even overestimate the significance of internal stem decay for the average temperate forest of Germany or Central Europe. As we specifically selected stands with particularly high shares of large old trees, our above-ground biomass stock densities are considerably higher than the average forest of Germany (BMEL, 2024) or temperate Europe (Ciais et al., 2008; Thurner et al., 2014). Nevertheless, the influence of internal wood decomposition on the biomass was well below 1%. It is likely to assume that this effect is even smaller in stands with smaller and younger trees and thus negligible in such forests on a stand level. Our biomass estimates even exceed above-ground biomass values that have been published from unmanaged old-growth stands of *Fagus sylvatica* (Glatthorn et al., 2018; Meyer et al., 2021) and *Picea abies* (Jacob et al., 2013) because those studies did not deliberately select the largest and oldest trees but included different stages of the forest development cycle.

The low significance of internal stem decay for forest biomass estimates raises the question of how generally valid this result is for forests globally. Temperate forests in Central Europe have been managed since centuries, regionally since millennia (Kaplan et al., 2009), which still has an effect on the age and stem diameter structure if compared to forests in North America (Besnard et al., 2021). It therefore remains an open question whether stands in forests that have not been managed at all or have been managed less intensively and for a shorter period of time also exhibit such a low effect of

TABLE 3 Above-ground biomass and C stock density ($\pm$ SE) of trees with dbh ≥ 7 cm in forests dominated by *Fagus sylvatica* ($N=47$), *Abies alba* ($N=41$), *Picea abies* ($N=41$) or *Pinus sylvestris* ($N=39$) based on allometric regression functions without or with correction for internal stem decay.

		Stock density		<i>p</i> ^a	Corrected to uncorrected ratio
		Allometry	Corrected		
<i>Fagus sylvatica</i>					
Biomass					
Total above-ground (Mg ha ⁻¹)		534.9±26.5	531.8±26.2	0.01	99.8±0.1%
Stem (Mg ha ⁻¹)		394.4±20.6	391.9±20.3	0.01	99.7±0.1%
Organic C					
Total above-ground (Mg C ha ⁻¹)		261.9±12.9	260.4±12.8	0.01	99.8±0.1%
Stem (Mg C ha ⁻¹)		193.1±10.1	191.9±9.9	0.01	99.7±0.1%
<i>Abies alba</i>					
Biomass					
Total above-ground (Mg ha ⁻¹)		538.5±32.9	533.8±31.4	0.03	99.7±0.2%
Stem (Mg ha ⁻¹)		389.0±25.6	385.1±24.3	0.03	99.7±0.2%
Organic C					
Total above-ground (Mg C ha ⁻¹)		272.6±16.7	270.2±16.0	0.03	99.7±0.2%
Stem (Mg C ha ⁻¹)		197.0±13.0	194.9±12.4	0.03	99.7±0.2%
<i>Picea abies</i>					
Biomass					
Total above-ground (Mg ha ⁻¹)		442.4±18.9	440.6±18.8	0.005	99.7±0.1%
Stem (Mg ha ⁻¹)		333.9±14.3	332.4±14.2	0.004	99.7±0.3%
Organic C					
Total above-ground (Mg C ha ⁻¹)		224.3±12.9	223.4±9.5	0.005	99.7±0.1%
Stem (Mg C ha ⁻¹)		169.3±7.3	168.9±7.2	0.004	99.7±0.3%
<i>Pinus sylvestris</i>					
Biomass					
Total above-ground (Mg ha ⁻¹)		297.8±12.5	296.8±12.5	0.01	99.8±0.1%
Stem (Mg ha ⁻¹)		259.9±11.1	258.9±11.2	0.01	99.8±0.1%
Organic C					
Total above-ground (Mg C ha ⁻¹)		150.1±6.3	149.5±6.3	0.01	99.8±0.1%
Stem (Mg C ha ⁻¹)		131.1±5.7	130.6±5.7	0.01	99.8±0.1%

^aOne-sided paired *t*-test.

	Above-ground		Stem	
	Estimate $\pm$ SE	p	Estimate $\pm$ SE	p
Biomass, uncorrected				
(Intercept) ^a	1254.54 ± 41.19	<0.001	923.36 ± 32.13	<0.001
<i>Abies alba</i>	-142.16 ± 61.63	0.02	-113.39 ± 48.08	0.02
<i>Picea abies</i>	-285.13 ± 62.38	<0.001	-191.32 ± 48.66	<0.001
<i>Pinus sylvestris</i>	-415.73 ± 62.64	<0.001	-194.73 ± 48.8	<0.001
C stock density, corrected for internal stem decay				
(Intercept) ^a	610.38 ± 20.15	<0.001	449.13 ± 15.76	<0.001
<i>Abies alba</i>	-52.18 ± 30.16	0.08	-43.14 ± 23.58	0.07
<i>Picea abies</i>	-121.11 ± 30.52	<0.001	-79.75 ± 23.86	<0.001
<i>Pinus sylvestris</i>	-189.63 ± 30.65	<0.001	-83.16 ± 23.96	<0.001

^aBaseline reference is *Fagus sylvatica*.

TABLE 4 Linear models analysing the effect of the dominant tree species on above-ground tree and stem biomass (not corrected for internal stem decay) and on C stock densities in the above-ground tree and stem biomass (after correction for internal stem decay).

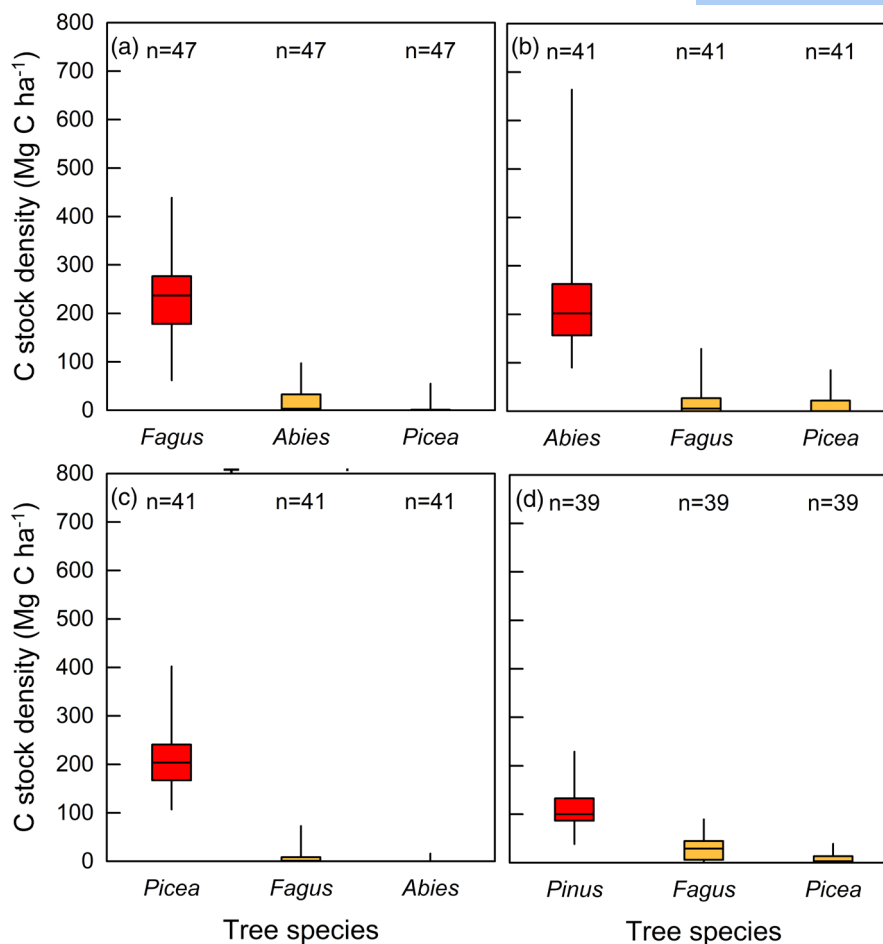


FIGURE 1 C stock density in tree above-ground biomass of forest stands dominated by (a) *Fagus sylvatica*, (b) *Abies alba*, (c) *Picea abies*, and (d) *Pinus sylvestris* by tree species. Carbon stock densities are corrected for internal stem decay. Only 3 tree species per forest type with the highest share in stand C stock density are included.

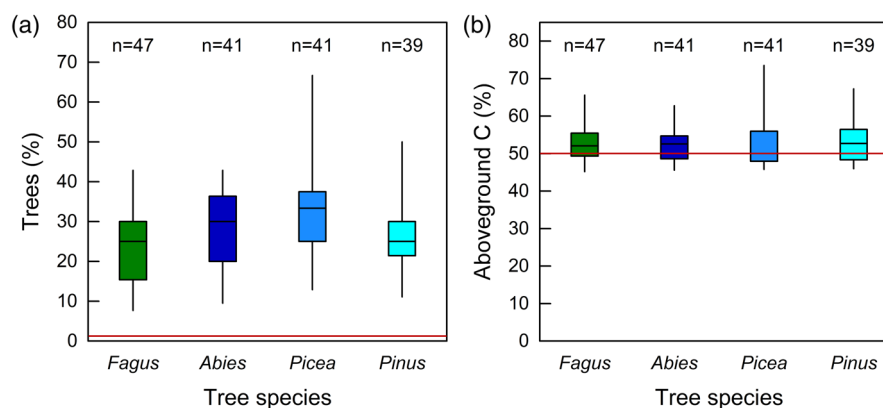


FIGURE 2 Proportion of trees accounting for ca. 50% of above-ground C density in the stand biomass in forests dominated by *Fagus sylvatica*, *Abies alba*, *Picea abies*, or *Pinus sylvestris* considering all trees with dbh ≥ 7 cm. Boxplots showing (a) the percentage of trees representing 50% of the biomass C stock and (b) the actual values of the biomass C stock estimate around 50%. Data are corrected for internal stem decay. Red lines display the hypothetical percent values according to the 1% trees-50% biomass postulate by Lutz et al. (2018).

internal stem decay for stand biomass. It has already been demonstrated that internal stem decay is much more relevant for stand biomass in dry savannas, but this was due to the special case of termite infestation (Flores-Moreno et al., 2024; Yatsko et al., 2025), which

are of subordinate importance outside savannas and tropical forests (Jones & Eggleton, 2011).

Despite the selection of forest stands in which large old trees were strongly overrepresented, our analyses do not support the global

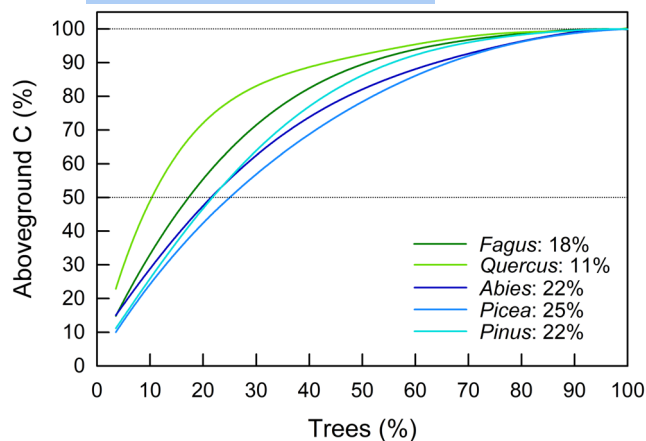


FIGURE 3 Increase in the relative contribution of above-ground C density in the stand biomass with increasing tree number shown as cumulative values for stands dominated by *Fagus sylvatica*, *Abies alba*, *Picea abies*, *Pinus sylvestris* (this study) and *Quercus robur* (data from Hauck et al., 2023). Percentages specify the proportions of the largest trees accounting for 50% of the total C density in the stand above-ground biomass.

TABLE 5 Share of the 5% or 10% largest trees in the above-ground organic C stock of forest stands dominated by *Fagus sylvatica*, *Quercus robur*, *Abies alba*, *Picea abies* or *Pinus sylvestris*.

	5% largest trees	10% largest trees
<i>Fagus sylvatica</i>	19%	33%
<i>Quercus robur</i> ^a	30%	49%
<i>Abies alba</i>	18%	29%
<i>Picea abies</i>	14%	24%
<i>Pinus sylvestris</i>	15%	26%

^aData refer to Hauck et al. (2023).

postulate of Lutz et al. (2018) that the ca. 1% largest trees would contain 50% of above-ground stand biomass. Rather, our present data and the results of Hauck et al. (2023) suggest that, depending on the tree species, ca. 10%–25% of the largest trees in managed temperate forests of Germany are needed for 50% stand biomass. This result, which confirms our second hypothesis, may be influenced by forest structure, but is, as Hauck et al. (2023) already pointed out, also the result of the lower size limit from which we accepted young growth as a tree. We selected a dbh ≥ 7 cm in our calculations, which is a traditional threshold in German forestry for the definition of our tree populations. Lutz et al. (2018) defined tree regeneration with a stem diameter as low as 1 cm as trees in their calculation, which increases the denominator and leads to lower values when the percentage of large old trees that represent 50% of the stand biomass is calculated. We prefer a higher threshold, like the dbh of 7 cm, because the contribution of smaller trees to stand biomass and C stocks is minor (Dulamsuren et al., 2016; Jacob et al., 2013; Nascimento & Laurence, 2004).

Although we did not confirm the postulate of the 1% largest trees containing half of the forest above-ground biomass and C stock (Lutz et al., 2018), we can confirm that large old trees are

important reservoirs of organic carbon with long residence times. These trees can, therefore, make a disproportionately large contribution to climate protection as part of natural climate solutions (Griscom et al., 2017). Yet, at least in the managed temperate forests of Central Europe, much higher shares than the 1% largest trees should be retained in the forest to secure a significant proportion of the forest biomass C pool (Table 5). Our results that internal stem decay in the largest trees does not lead to a significant reduction of the above-ground biomass and C stock on stand level corroborates that sparing the largest and oldest trees of managed trees from logging does not only conserve biodiversity (Emrich et al., 2025; Hendel et al., 2023; Rappa et al., 2023) but at the same time contributes to the protection of the global climate by the long-term storage of C on a centenary scale.

5 | CONCLUSIONS

We could show for the first time with a larger dataset that internal stem decay is not a significant source of error in forest biomass and C stock estimates in managed forests of temperate Central Europe. The overestimation by ignoring tree cavities in stand surveys, where biomass stocks are inferred on allometric biomass functions and thus on the outer shape of the tree, is therefore negligible compared to other sources of error, like dbh biases and small sample sizes during the establishment of allometric functions or influences of volatile C.

Specifying percentages of the largest trees in a stand that contribute to a certain proportion of stand biomass and C stock density is strongly dependent on the denominator in the calculation, which is the number of trees in a stand. The more small trees are included in the calculation, the lower the percentage of trees that represents, for example, 50% of forest biomass. To ensure that such values are meaningful and reproducible, plants that are too small and do not yet make a significant contribution to stand biomass should be excluded from the calculations. Otherwise, if the stand biomass is approximately the same, these percentage values can vary within wide limits depending on whether stands with strong or weak regeneration are selected, which would make such specifications less informative.

AUTHOR CONTRIBUTIONS

Markus Hauck: Conceptualization, methodology, formal analysis, writing—original draft, writing—review and editing, funding acquisition. Germar Csapek: Methodology, investigation, data curation, writing—original draft, writing—review and editing. Choimaa Dulamsuren: Conceptualization, methodology, formal analysis, writing—original draft, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Zenodo. <https://doi.org/10.5281/zenodo.15814018> (Hauck et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Allometric biomass functions for the target tree species *Fagus sylvatica*, *Abies alba*, *Picea abies*, and *Pinus sylvestris*.

Table S2. Allometric biomass functions for the accessory tree species.

Table S3. Mean wood densities used for biomass calculations.

Figure S1. Share of stem biomass in total tree aboveground biomass in stands dominated by (a) *Fagus sylvatica*, (b) *Abies alba*, (c) *Picea abies*, and (d) *Pinus sylvestris* based on estimates obtained with allometric biomass functions (without correction for internal stem decay).

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