WILEY **Global Ecology and Biogeography** A Journal of Macroecology

Sapwood biomass carbon in northern boreal and temperate forests

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Abstract

Aim: Information on the amount of carbon stored in the living tissue of tree stems (sapwood) is crucial for carbon and water cycle applications. Here, we aim to investigate sapwood-to-stem proportions and differences therein between tree genera and derive a sapwood biomass map.

Location: Northern Hemisphere boreal and temperate forests.

Time period: 2010.

Major taxa studied: Twenty-five common tree genera.

Methods: First, we develop a theoretical framework to estimate sapwood biomass for a given stem biomass by applying relationships between sapwood cross-sectional area (CSA) and stem CSA and between stem CSA and stem biomass. These measurements are extracted from a biomass and allometry database (BAAD), an extensive literature review and our own studies. The established allometric relationships are applied to a remote sensing-based stem biomass product in order to derive a spatially continuous sapwood biomass map. The application of new products on the distribution of stand density and tree genera facilitates the synergy of satellite and forest inventory data.

Results: Sapwood-to-stem CSA relationships can be modelled with moderate to very high modelling efficiency for different genera. The total estimated sapwood biomass equals 12.87 ± 6.56 petagrams of carbon (PgC) in boreal (mean carbon density: 1.13 ± 0.58 kgC m^{-2}) and 15.80 ± 9.10 PgC in temperate (2.03 ± 1.17 kgC m^{-2}) forests. Spatial patterns of sapwood-to-stem biomass proportions are crucially driven by the distribution of genera (spanning from 20–30% in *Larix* to > 70% in *Pinus* and *Betula* forests).

Main conclusions: The presented sapwood biomass map will be the basis for large-scale estimates of plant respiration and transpiration. The enormous spatial differences in sapwood biomass proportions reveal the need to consider the functionally more important sapwood instead of the entire stem biomass in global carbon and water cycle studies. Alterations in tree species distribution, induced by forest management or climate change, can strongly affect the available sapwood biomass even if stem biomass remains unchanged.

1 | INTRODUCTION

In addition to the pith, cambium, phloem and bark, tree stems consist most importantly of heartwood and sapwood. Sapwood is the youngest formed wood and has the function of transportation of water and nutrients between tree compartments. Thus, sapwood cross-sectional area (CSA) is related to foliage area and transpiration (Köstner et al., 1992; Vertessy, Benyon, O'Sullivan, & Gribben, 1995). Later in the life of a tree, the inner sapwood is transformed to heartwood, which is no longer involved in water and nutrient transport but is more decay resistant and fulfils the function of giving the tree support. As a living tissue, sapwood contributes to autotrophic respiration, unlike heartwood (Pruyn, Gartner, & Harmon, 2002). The maintenance respiration of tree stems is mainly determined by the magnitude of sapwood biomass (Ryan, 1990; Sprugel, 1990). Therefore, prognostic biogeochemical models, such as dynamic global vegetation models, explicitly simulate sapwood mass density as a state variable (Krinner et al., 2005; Sitch et al., 2003). Although total forest biomass has been used for model evaluation (Beer, Lucht, Schmullius, & Shvidenko, 2006; Thurner et al., 2017; Yang et al., 2018), an assessment of sapwood mass per ground area at large spatial scales is still lacking. In addition to their biogeochemical importance regarding the carbon, water and nutrient cycles, sapwood-to-heartwood ratios are relevant variables in wood industry, owing to the different chemical composition, mechanical properties and often colour of heartwood compared with sapwood.

The relationship between leaf area and sapwood CSA has been studied extensively, but its patterns of variation with tree height are not well understood. According to the pipe model theory (Shinozaki, Yoda, Hozumi, & Kira, 1964a, 1964b), the conversion of sapwood to heartwood can be considered as the effect of branch death, because lowered water requirements when leaves on dead branches are lost allow reduction of sapwood in favour of heartwood (Mäkelä & Valentine, 2006). Following this theory, the leaf area of a tree is supported by, and thus directly related in a linear manner to, a certain sapwood CSA. This relationship was found to hold across measurements of sapwood CSA taken at different heights within individual trees (e.g., Waring, Schroeder, & Oren, 1982) and across species in a large dataset of individual-level leaf area and sapwood CSA measurements (Falster, Duursma, & FitzJohn, 2018). However, the ratio of sapwood area to leaf area (Huber value) varies with tree size, exhibiting both increasing and decreasing trends (McDowell et al., 2002; Novick et al., 2009). The Huber value differs substantially among species and environmental conditions, increasing with factors favouring fast-growing species with high hydraulic conductivity but low resistance to desiccation. For instance, a higher sapwood area per unit leaf area has been observed in drier climatic conditions

for some species (DeLucia, Maherali, & Carey, 2000; Mencuccini & Grace, 1994). Owing to its role in setting the supply limits to transpiration rates, quantification of sapwood areas across climatic and edaphic gradients is key, both for our conceptual understanding of tree responses to drought and for parameterizing vegetation models that explicitly account for hydraulic traits (for a review, see Manzoni, Vico, Porporato, & Katul, 2013).

Less is known about relationships between sapwood and heartwood CSA, volume or mass and other traits (e.g., stem CSA, volume or mass). There is contrasting evidence regarding heartwood formation, showing either continuous accumulation after a certain age and irrespective of environmental influences (Gjerdrum, 2003) or variable accumulation depending on age and light availability (Sellin, 1994), and differing between fast- and slow-growing species (Bond-Lamberty, Wang, & Gower, 2002; Longuetaud, Mothe, Leban, & Mäkelä, 2006). Trees growing in more fertile and dominant conditions have been observed to develop comparably more sapwood CSA, whereas heartwood CSA did not increase significantly (Mörling & Valinger, 1999). Conversion of growth rings to heartwood is usually reported to increase with age (Knapic & Pereira, 2005; Pinto, Pereira, & Usenius, 2004). Moreover, in older trees, absolute heartwood production per year was found to be of similar size to total volume growth. Relative heartwood volume (as a fraction of total wood volume) thus increases with tree age, levelling off in very old trees (Sillett et al., 2015). Relative heartwood CSA relates to age or diameter in a similar way (Kärenlampi & Riekkinen, 2003). However, even within stands in similar growing conditions, heartwood proportions exhibit considerable intraspecific variation (Björklund, 1999).

By applying radar remote sensing observations gathered by the Advanced Synthetic Aperture Radar (ASAR) instrument aboard the Envisat satellite, stem volume (or growing stock volume) has recently been mapped for northern boreal and temperate forests (Santoro et al., 2015). This spatially extensive information at a spatial resolution of 0.01°, in combination with databases on wood density and biomass allometry, has allowed the estimation of stem biomass and, finally, total biomass and carbon stocks in these forest ecosystems (Thurner et al., 2014). Despite its relevance, information on the large-scale spatial distribution of sapwood biomass and on sapwood biomass as a proportion of total stem biomass is currently lacking. Here, we investigate the variability in sapwood proportions among boreal and temperate tree genera and demonstrate how to infer sapwood biomass from available remote sensing-based stem biomass maps (Thurner et al., 2014). We focus on boreal and temperate forests because these ecosystems are well covered by ground-sourced measurements and because they are characterized by distinct spatial patterns in tree species distribution and by important differences in sapwood proportions between tree genera. We analyse how sapwood proportions at tree level vary by

genera and how they are influenced by average climatic conditions. The inferred sapwood biomass product at the stand scale allows us to investigate the resulting spatial patterns in sapwood biomass proportions compared with total stem biomass and to quantify the overall amount of sapwood biomass in northern boreal and temperate forests. Understanding the spatial relationships between sapwood proportions and the present tree species is also important with regard to changes in the distribution of tree species as a result of forest management or climate change (Dyderski, Paź, Frelich, & Jagodziński, 2018; Shuman, Shugart, & O'Halloran, 2011).

2 | MATERIALS AND METHODS

Given that direct measurements of sapwood biomass are rare, we instead derive it indirectly from relationships between sapwood CSA and stem CSA and between stem CSA and stem biomass. For this task, we explore a biomass and allometry database (BAAD; Falster et al., 2015) and other studies and analyse whether there are allometric differences among tree genera and leaf types and habits. In addition, we examine the influence of average climatic conditions on these relationships. Finally, we quantify the amount and distribution of sapwood biomass and its proportion of stem biomass in northern boreal and temperate forests. In order to address the above-mentioned research objectives, here we: (a) develop a theoretical framework to estimate sapwood biomass for a given stem biomass; (b) collect measurements of sapwood proportions from the BAAD, an additional extensive literature review and our own studies; and (c) derive a sapwood biomass map based on remote sensing products (accompanied by an uncertainty estimate), inferred allometric relationships and new products on the distribution of stand density and tree genera (Figure 1). A global stand density

product (Crowther et al., 2015) allows scaling from measurements at tree level to areal estimates, and this is supplemented with information on tree species distribution (Beaudoin, Bernier, Villemaire, Guindon, & Guo, 2017, 2018; Brus et al., 2012; Schepaschenko et al., 2011; Wilson, Lister, & Riemann, 2012; Wilson, Lister, Riemann, & Griffith, 2013) that enable the application of allometric relationships for tree genera in addition to the leaf type level.

2.1 | Theoretical considerations

Sapwood biomass is derived from stem biomass based on the following assumptions and equations. For more detailed theoretical considerations, the reader is referred to Supporting Information Appendix S1, and in the Discussion section these equations and the respective parameters are compared with existing theories and other studies.

The tree-level sapwood CSA (A_{sap}) can be estimated from the stem CSA (A_{stem}) and the allometric parameters a and b which are fitted using measurements taken at breast height contained in the BAAD, other literature sources and our own measurements:

$$A_{sap} = a \cdot A_{stem}^b \tag{1}$$

The A_{stem} can be expressed as a function of stem biomass (m_{stem}) and the allometric parameters c and d using measurements contained in the BAAD:

$$A_{stem} = c \cdot m_{stem}^d \tag{2}$$

The volume of a tree stem (V_{stem}) can be calculated as follows:

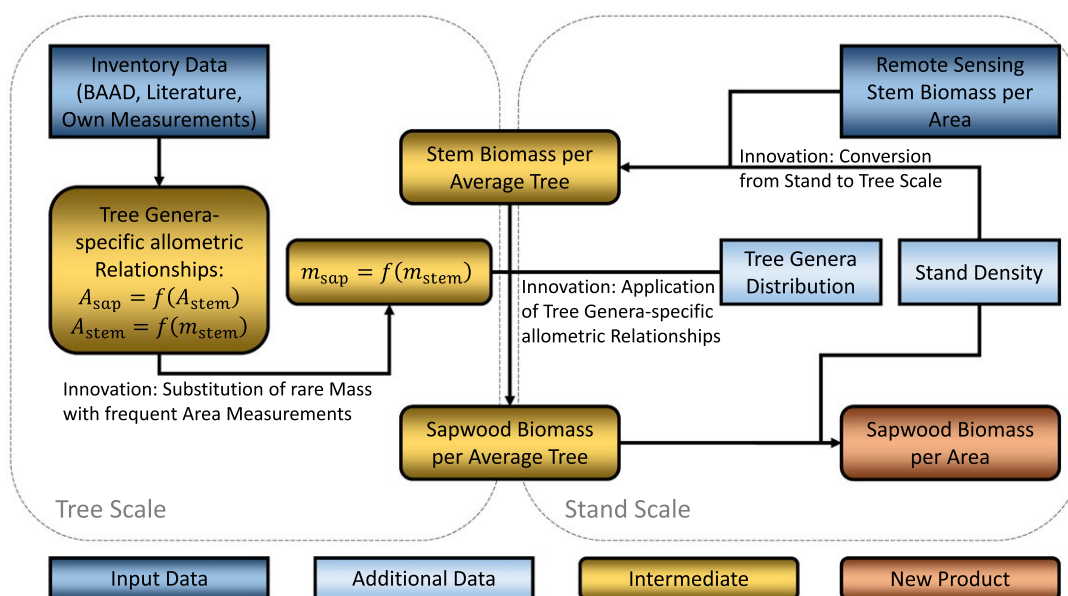$$V_{stem} = \frac{1}{n} \cdot A_{stem} \cdot h \tag{3}$$

FIGURE 1 Methodical approach (A_{sap} = sapwood cross-sectional area; A_{stem} = stem cross-sectional area; m_{sap} = sapwood biomass; m_{stem} = stem biomass) [Colour figure can be viewed at wileyonlinelibrary.com]

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with n describing the shape of the tree stem (e.g., cylinder, $n = 1$; paraboloid, $n = 2$; cone, $n = 3$; neiloid, $n = 4$) and h being the height of the tree stem (Supporting Information Appendix S1).

We account for a change in the relationship between A_{sap} and A_{stem} throughout the height of the tree. Tree stems vary in their shape, but always taper towards their top. The shape of the heartwood core in general follows the shape of the tree stem, and its volume per height increment decreases towards the top (Cermak, Kucera, Bauerle, Phillips, & Hinckley, 2007; Gominho, Lourenço, Miranda, & Pereira, 2015). Sapwood width has been observed to remain approximately constant within trees, independent of the measurement height (Knapic & Pereira, 2005); however, this implies a decrease in absolute sapwood CSA, but an increase in relative sapwood CSA per total stem CSA towards the top of the tree (Gartner, 2002; Longuetaud et al., 2006).

Given that tree stem tissues are younger towards the top of the stem, we substitute the relationship between A_{sap} and A_{stem} throughout the height of the tree with the relationship between A_{sap} and A_{stem} derived from measurements of trees of different age (Equation 1). Under this assumption, sapwood volume (V_{sap}) can now be expressed as a function of A_{sap}. In addition, V_{sap} depends on the factor n defining the shape of the tree stem, stem height (h) and the allometric exponent b (cf. Equation 1):

$$V_{sap} = \frac{1}{(n-1)\,b+1} \cdot A_{sap} \cdot h \tag{4}$$

By dividing V_{sap} by V_{stem}, we can eliminate the dependence on h, as follows:

$$\frac{V_{sap}}{V_{stem}} = \frac{n}{(n-1)\,b+1} \cdot \frac{A_{sap}}{A_{stem}} \tag{5}$$

Assuming equal wood densities (see Discussion section) in sapwood and overall stem wood ($\varrho_{sap} = \varrho_{stem}$), we can likewise express the ratio of sapwood biomass m_{sap} to m_{stem}:

$$\frac{m_{sap}}{m_{stem}} = \frac{n}{(n-1)\,b+1} \cdot \frac{A_{sap}}{A_{stem}} \tag{6}$$

Accordingly, we can derive m_{sap} as a function of m_{stem}:

$$m_{sap} = \frac{n}{(n-1)\,b+1} \cdot \frac{A_{sap}}{A_{stem}} \cdot m_{stem} \tag{7}$$

Finally, by expressing A_{sap} and A_{stem} in dependence of m_{stem} (Equations 1 and 2), we obtain:

$$m_{sap} = \frac{n}{(n-1)\,b+1} \cdot a \cdot c^{b-1} \cdot m_{stem}^{(b-1)d+1} \tag{8}$$

We can now express m_{sap} as a direct function of m_{stem}, the allometric parameters a, b, c and d, and the factor n, which defines the overall shape of the tree stem.

2.2 | Inventory data

We use the BAAD (Falster et al., 2015) to establish the relationships in Equations (1) and (2) for common Northern Hemisphere boreal and temperate tree genera. Given that the relationship between sapwood area and stem area varies considerably among tree genera, we collect additional data from the literature to cover the most common tree genera over the largest possible range of values. We also collected additional measurements of A_{sap} and A_{stem} to establish the allometric relationship between these properties for *Larix gmelinii* (central part of Nizhnyaya Tunguska River basin in Central Siberia, 64° N 100° E; Larjavaara, Berninger, Palviainen, Prokushkin, & Wallenius, 2017) and for *Abies sibirica*, *Betula pubescens*, *Picea obovata*, *Pinus sibirica* and *Sorbus aucuparia* trees (close to the Zotino Tall Tower Observation Facility, 61° N 90° E) in data-sparse regions (see Supporting Information Appendix S2.1). A list of all data sources is found in Appendix 1.

In total, we use 1920 simultaneous measurements of A_{sap} and A_{stem} for 25 tree genera (*Abies*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, *Chamaecyparis*, *Cornus*, *Cryptomeria*, *Fagus*, *Fraxinus*, *Larix*, *Liriodendron*, *Oxydendrum*, *Picea*, *Pinus*, *Populus*, *Pseudotsuga*, *Quercus*, *Robinia*, *Sorbus*, *Thuja*, *Tilia*, *Tsuga* and *Ulmus*; Supporting Information Appendix S2.2, Table S2.2), in addition to 2,194 simultaneous measurements of A_{stem} and m_{stem} for 23 tree genera (*Abies*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, *Castanea*, *Chamaecyparis*, *Cornus*, *Cryptomeria*, *Fagus*, *Fraxinus*, *Larix*, *Liriodendron*, *Magnolia*, *Oxydendrum*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Quercus*, *Sorbus* and *Tsuga*; Supporting Information Appendix S2.3, Table S2.3).

Measurements of A_{sap} and A_{stem} are aggregated into classes at the genus level (*Betula*, other broadleaf diffuse-porous, *Quercus*, other broadleaf ring-porous, *Larix*, *Abies*, *Picea*, *Pinus*, *Pseudotsuga* and *Tsuga*) in order to account for the variation in their relationship. A corresponding map of the dominant tree genera in northern boreal and temperate forests is derived at 0.01° resolution from available upscaled forest inventory data on tree species distribution for Canada (Beaudoin et al., 2017, 2018), the USA (Wilson et al., 2012, 2013), Europe (Brus et al., 2012) and Russia (Schepaschenko et al., 2011). The original tree species distribution maps are reclassified based on the tree genera classes identified above, adding other needleleaf evergreen and other (unidentified) and resampled or reprojected (nearest neighbour) to 0.01° resolution and geographical coordinates.

In addition, the measurements of A_{sap} and A_{stem} are classified according to leaf types (broadleaf, needleleaf deciduous, needleleaf evergreen and mixed forest) to be applied in areas where no information on tree genera is available. In these study areas (outside Canada, the USA, Europe and Russia), we apply the leaf type and leaf habit classification extracted from the GLC2000 land-use/land-cover map (Bartholomé & Belward, 2005; Supporting Information Appendix S3, Table S3). Measurements of A_{stem} and m_{stem} are solely aggregated by leaf type, because differences in their allometric relationship are relatively small between tree genera and thus neglected. Here, the dominant leaf type is identified by GLC2000 for each 0.01° × 0.01° pixel in the entire study area. GLC2000 is resampled using nearest

neighbour resampling from its original 1 km resolution to 0.01° in order to match the resolution of the stem biomass map.

2.3 | Application to a remote sensing-based stem biomass product

Stem volume (or growing stock volume; GSV) of northern boreal and temperate forests (30–80° N) for the year 2010 has been estimated from radar remote sensing at a spatial resolution of 0.01° (Santoro et al., 2015). This product has already been converted to stem biomass carbon density (Thurner et al., 2014), by making use of a global database on wood density (Chave et al., 2009). Here, we apply the above theoretical considerations, supported by evidence from the BAAD, to derive sapwood biomass from stem biomass. For this purpose, the allometric parameters a, b (Equation 1), c and d (Equation 2) are fitted for different tree genera and leaf types using observations from the BAAD and generalized nonlinear least square (GNLS) regression. For the tree stem shape factor n, a mean value of 2.5 is assumed, reflecting the mean value of the most common shapes of a paraboloid (n = 2) and a cone (n = 3; see Discussion section).

While the data contained in the BAAD are inventory measurements at the tree level, the original remote sensing stem biomass carbon density map (Thurner et al., 2014) reports biomass carbon per square metre ($m_{stemCarea}$, representing values at the stand scale. To apply tree-level parameters derived from the BAAD (Equation 8) to the stand-level remote sensing-based stem biomass product, the latter is first converted to tree-level stem biomass carbon (m_{stemC}). For this task, we apply a global stand density map, which is available at the original resolution of 1 km (Crowther et al., 2015). Based on forest inventory data and regression models taking into account the influence of climate, topography, vegetation characteristics and land use, this stand density map provides the spatial distribution of the number of trees per area (D). The implicit assumption in this calculation is that a representative tree can be defined for each 0.01° × 0.01° grid cell. The stand density map is first resampled to the spatial resolution of the stem biomass product (0.01°), and afterwards, the mean stand density value ($\bar{D}$) of an 11 × 11 moving window (0.11° × 0.11°) is used in order to dampen the effect of spatial variations in stand density:

$$m_{stemC} = \frac{m_{stemCarea}}{\bar{D}} \quad (9)$$

Subsequently, we convert the resulting stem biomass carbon into stem dry weight. This conversion accounts for the variation in wood carbon concentration among leaf types (Thomas & Martin, 2012):

$$m_{stem} = \frac{m_{stemC}}{0.488} \text{ for broadleaf tree species} \quad (10)$$

$$m_{stem} = \frac{m_{stemC}}{0.508} \text{ for needleleaf tree species} \quad (11)$$

$$m_{stem} = \frac{m_{stemC}}{0.498} \text{ for mixed tree species} \quad (12)$$

After deriving m_{sap} from m_{stem} by applying Equation (8), the obtained m_{sap} at tree level is converted back to sapwood biomass carbon and finally to sapwood biomass carbon density (per square metre) by reverse application of the above Equations (9–12; to m_{sap} instead of m_{stem}). Total and mean sapwood biomass values are then calculated for different tree genera according to the dominant genus distribution map in boreal and temperate forests [separation between boreal and temperate regions according to Olson et al. (2001)] over North America and Eurasia.

The uncertainty in sapwood biomass carbon density is estimated by means of propagation of the uncertainties of the independent variables $m_{stemCarea}$, D and n, and the uncertainties in the functional relationships (Equations 1 and 2) fitted to the measurements. For a detailed description of the implemented uncertainty analysis, see the Supporting Information (Appendix S4). In an additional analysis, we estimate the importance of tree genera, temperature and precipitation on these relationships by applying generalized additive models (GAMs; see Supporting Information Appendix S5).

3 | RESULTS

3.1 | Empirical evidence from databases

The value of A_{sap} increases as a power function (in general, with exponents $0 < b < 1$) of A_{stem} (at breast height; Equation 1). When distinguishing among different tree genera [*Larix*, *Pinus*, *Picea*, *Abies*, *Tsuga*, *Pseudotsuga*, *Quercus*, other broadleaf ring-porous (RP) trees, *Betula* and other broadleaf diffuse-porous (DP) trees], we find that these relationships can be approximated with moderate to very high modelling efficiencies (MEF; Nash & Sutcliffe, 1970). In particular, *Betula* (MEF = 0.983), other DP trees (MEF = 0.877) and needleleaf evergreen tree genera (*Pinus*: MEF = 0.869; *Picea*: MEF = 0.893; *Abies*: MEF = 0.888; *Tsuga*: MEF = 0.778; *Pseudotsuga*: MEF = 0.828) exhibit very well-defined relationships (Figure 2). The MEFs are a bit lower for *Quercus* (MEF = 0.674), other RP trees (MEF = 0.760) and, in particular, for *Larix* (MEF = 0.452). When grouping all needleleaf evergreen (mixed NE; MEF = 0.722), all broadleaf (mixed B; MEF = 0.400) or all explored tree genera (mixed; MEF = 0.684), the MEFs decrease considerably. The values of the parameters in Equation (1) differ strongly among tree genera, with *Larix*, *Pseudotsuga*, *Quercus* and other RP exhibiting comparably lower A_{sap} for a given A_{stem} than the other genera. Uncertainties increase with increasing stem CSA according to Equation S4.VII in the Supporting Information (Appendix S4).

An even finer separation among tree genera (instead of aggregating genera into the above-mentioned classes) reveals further differences (Supporting Information Appendix S6, Figure S6.2), but in some cases these differences are evaluated based on a limited number of data points. The remaining variation in the relationships between A_{sap} and A_{stem} for different tree genera are partly attributable to species-specific differences, as is the case for *Larix* species (Supporting
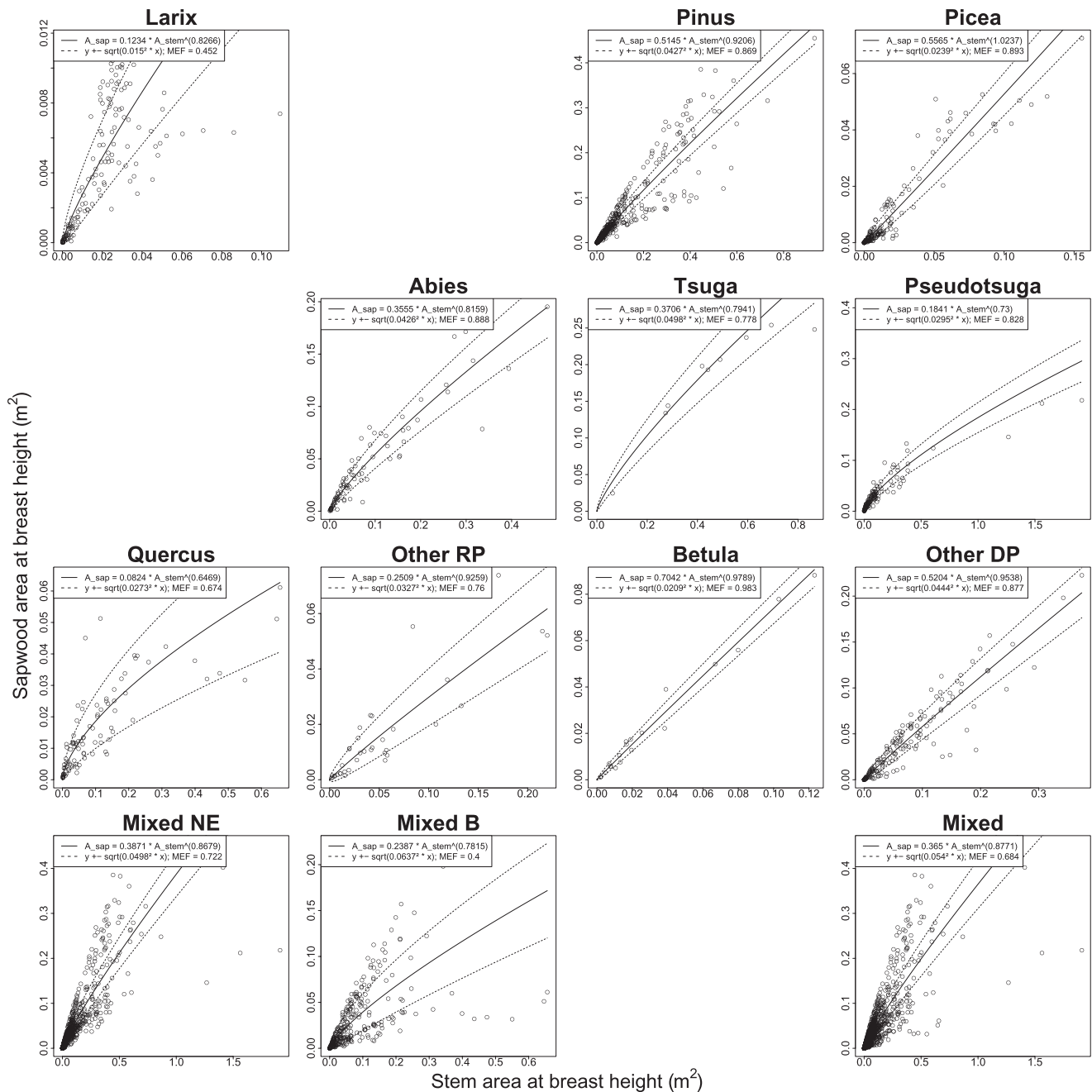
FIGURE 2 Sapwood area at breast height as a function of stem area at breast height for different tree genera [mixed = all tree genera together; mixed B = all broadleaf tree genera together; mixed NE = all needleleaf evergreen tree genera together; other DP = other (than *Betula*) diffuse-porous tree genera; other RP = other (than *Quercus*) ring-porous tree genera]. The continuous lines show the fitted relationship between sapwood area and stem area (Equation 1), and the dashed lines show the fitted relationships ± the estimated uncertainty in these relationships (Supporting Information Appendix S4, Equation S4.VII). See the Supporting Information (Appendix S6, Figure S6.1) for a visualization of the fitted functions for all tree genera in one plot

Information Appendix S6, Figure S6.3). However, their separation is not feasible for our purpose because reliable information on the spatial distribution of these *Larix* species is lacking. Overall, the applied classification of tree genera (as in Figure 2) leads to significant improvements, in terms of adjusted R^2, root mean square error (RMSE) and Akaike's information criterion (AIC; Akaike, 1974), in the derivation of A_{sap} from A_{stem} in comparison to aggregation by leaf type, also when GAMs are applied (Supporting Information Appendix S5,

Figure S5a). Accounting for both mean annual temperature and mean annual precipitation sum in addition can improve these models further, but only to a relatively small extent, and cannot explain the majority of the remaining variation in the relationship between A_{sap} and A_{stem} (with regard to adjusted R^2 and RMSE).

Likewise, A_{stem} (at breast height) is found to increase as a power function (with exponents $0 < d < 1$) of m_{stem} (Equation 2; Supporting Information Appendix S6, Figures S6.4 and S6.5). Given that these

relationships show very high MEFs on a leaf type level [MEF = 0.948 for broadleaf trees; MEF = 0.966 for needleleaf deciduous (*Larix*) trees; MEF = 0.933 for needleleaf evergreen trees], we do not further subdivide the dataset in tree genera.

3.2 | Evaluation

An evaluation of the estimated sapwood biomass at tree level (by applying Equation 8 to measurements of stem biomass contained in the BAAD; Supporting Information Appendix S7) against independent measurements reveals that our models have good predictive power for *Pinus* (normalized root mean square error: nRMSE = 0.38) and *Betula* (nRMSE = 0.26), and a relatively good agreement (but slight underestimation for very high biomass) for other DP (nRMSE = 0.54) trees (Supporting Information Appendix S7, Figure S7.1). In contrast, the sapwood biomass for *Quercus* (nRMSE = 0.71) and other RP (nRMSE = 0.76) trees is severely underestimated by *ca.* 50%, but only for trees with a sapwood biomass of > 200 kg. In addition, the two modelled relationships (Equations 1 and 2) are evaluated individually on test samples not used for model training. Based on this approach, the models perform well in estimating A_{sap} from A_{stem} for many of the distinguished tree genera classes, both in terms of bias (no strong under- or overestimation) and random error (nRMSE ≤ 0.4 for *Abies*, *Tsuga*, *Pseudotsuga* and *Betula*; Supporting Information Appendix S7, Figure S7.2). When no information on tree genera is available and the relationships have to be applied at leaf type level, the model performance decreases considerably (needleleaf evergreen trees: nRMSE = 1.23; broadleaf trees: nRMSE = 0.95; all trees together: nRMSE = 1.14). Concerning the estimation of A_{stem} from m_{stem}, the model performance evaluated on the test sample is very good for all leaf types, with no detectable bias and relatively small random errors (nRMSE = 0.42 for broadleaf trees, nRMSE = 0.2 for needleleaf deciduous trees, nRMSE = 0.38 for needleleaf evergreen trees; Supporting Information Appendix S7, Figure S7.3).

3.3 | Spatially continuous sapwood biomass carbon density estimates

A stand density (trees per area) map (Crowther et al., 2015; Supporting Information Appendix S8) based on 0.4 million plot data allows for scaling between inventory data at tree level and remote sensing data at stand scale. In general, stand density is highest in southern boreal forests of Canada and Eurasia with an average of > 0.07 trees m^{-2} (or > 700 trees ha^{-1}). The standard deviation in a spatial 11 × 11 moving window at 0.01° resolution, which has been used as a surrogate for uncertainty here, is highest in fragmented forest landscapes, such as those in central Europe, and transition regions between forest and non-forest biomes.

The parameters derived from the relationships shown in Figure 2 and Figure S6.4 in the Supporting Information (Appendix S6) are applied in Equation (8) to calculate m_{sap} from m_{stem} at each grid cell according to the present tree genera class (Supporting Information Appendix S9). The spatial patterns in m_{sap} are thus influenced

nonlinearly by differences in m_{stem} and by the tree genera distribution, and also by the applied stand density product. As a result, m_{sap} can reach values > 3 kgC m^{-2} in temperate forests in the western and eastern USA and western Canada, in central Europe and Japan, but also in temperate and even boreal forests in European Russia and western and central Siberia (Figure 3a). The lowest values of m_{sap} (values < 1 kgC m^{-2}) occur in *Larix* forests of central and eastern Siberia, the northern boreal forests in Alaska, Canada and Scandinavia, and in temperate forests in dry regions (e.g., southern-central USA, Spain, parts of northeast China).

In total, we estimate a sapwood biomass of 12.87 ± 6.56 petagrams of carbon (PgC) in boreal forests (Table 1) and 15.80 ± 9.10 PgC in temperate forests (Table 2) of the Northern Hemisphere. In the boreal zone, needleleaf evergreen forests account for 7.37 ± 3.63 PgC, in North America dominated by *Picea* forests, whereas in Eurasia *Pinus* forests contribute the largest amount. Broadleaf forests store 3.35 ± 1.68 PgC in their stem sapwood in the boreal zone, with Russian *Betula* forests being responsible for the bulk of this number. Interestingly, *Larix* forests account for only 1.53 ± 0.73 PgC of sapwood biomass in boreal forests, although they cover extensive areas. This is a result of their very low proportion of sapwood to stem biomass (Figure 3c) and, to a lesser extent, also owing to their comparably low stem biomass (Thurner et al., 2014).

In the temperate zone, needleleaf evergreen forests store 8.27 ± 4.23 PgC in their sapwood, with *Pinus* and *Picea* forests being responsible for the majority, but also important contributions of forests dominated by *Abies*, *Pseudotsuga* and *Tsuga*, mostly in North America. For temperate broadleaf forests, we estimate a sapwood biomass of 7.05 ± 4.57 PgC, with the largest part in DP trees. *Larix* forests account for only 0.28 ± 0.15 PgC in the temperate zone.

With regard to the mean sapwood biomass, boreal forests have a sapwood carbon density on average of 1.13 ± 0.58 kgC m^{-2} (Supporting Information Appendix S10, Table S10.1) and temperate forests of 2.03 ± 1.17 kgC m^{-2} (Supporting Information Appendix S10, Table S10.2). The lowest mean sapwood carbon densities by far occur in *Larix* forests (0.46 ± 0.21 kgC m^{-2} in Russian boreal forests). Needleleaf evergreen forests exhibit higher carbon densities in temperate (2.23 ± 1.14 kgC m^{-2}) than in boreal (1.43 ± 0.71 kgC m^{-2}) forests, with higher values in *Pinus* than *Picea* forests in boreal (1.94 ± 0.96 vs. 1.07 ± 0.51 kgC m^{-2}), but not in temperate forests (2.20 ± 1.17 vs. 2.14 ± 1.10 kgC m^{-2}). Forests composed of DP trees have higher mean sapwood carbon densities (2.36 ± 1.17 kgC m^{-2} in boreal forests and 2.39 ± 1.42 kgC m^{-2} in temperate forests) than forests dominated by RP trees (1.47 ± 1.04 kgC m^{-2} in boreal forests and 1.14 ± 0.80 kgC m^{-2} in temperate forests). The larger contribution of RP trees leads to lower mean sapwood carbon densities of 2.02 ± 1.31 kgC m^{-2} in temperate forests compared with 2.33 ± 1.16 kgC m^{-2} in boreal broadleaf forests.

3.4 | Uncertainty in the estimated sapwood biomass

The uncertainty in m_{sap} is, in general, between 30 and 40% in central and eastern Siberia, south-western Canada and the north-western
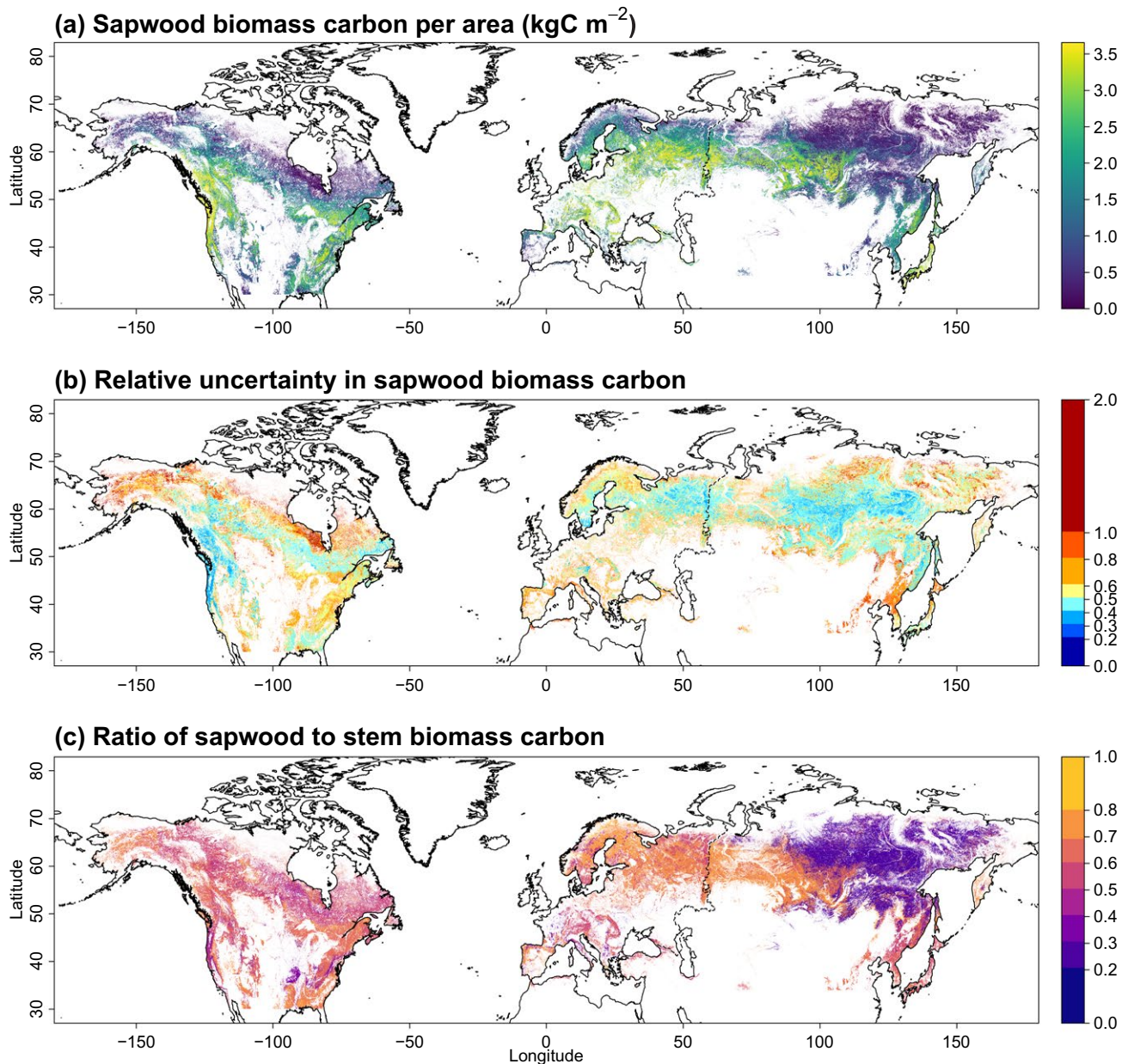
(a) Sapwood biomass carbon per area (kgC m^{-2})

(b) Relative uncertainty in sapwood biomass carbon

(c) Ratio of sapwood to stem biomass carbon

FIGURE 3 (a) Sapwood biomass carbon per area (in kilograms of carbon per square metre). (b) Relative uncertainty in sapwood biomass carbon. (c) Ratio of sapwood to stem biomass carbon. Non-forest areas have been masked out using GLC2000 (Bartholomé & Belward, 2005) [Colour figure can be viewed at wileyonlinelibrary.com]

USA and between 40 and 50% in European Russia, western Siberia, Canadian boreal forests and the south-western USA, among others (Figure 3b). These areas coincide with the predominance of specific needleleaf evergreen tree genera that exhibit the lowest uncertainties in their relationship between A_{sap} and A_{stem} (cf. Figure 2) and in their previously estimated stem biomass (Thurner et al., 2014). Uncertainties are higher in areas where broadleaf tree genera are prevalent (50–80% in the eastern USA and Mediterranean Europe) and highest in regions where only information on leaf type level is available or mixed forests are present (often > 80% in Alaska, the northern edge of boreal forests in Canada, in China, Korea and northern Japan) or where stand density has a high local

spatial variation (e.g., in the transition regions from forest to non-forest biomes in parts of southern Siberia.

An important contribution to the overall uncertainty of m_{sap} is already contained in the underlying stem biomass product (Supporting Information Appendix S11), which shows the highest uncertainties in the same regions, where biomass is very low or where broadleaf and mixed forests are situated (Thurner et al., 2014). In most of the study area, a higher contribution to the overall uncertainty originates from the relationships of A_{sap} to A_{stem}. The contribution of the uncertainty in the relationship of A_{stem} to m_{stem} is relatively small, and the one from the uncertainty in the parameter describing the shape of the tree stem (n) is negligible compared with the others.

TABLE 1 Total sapwood biomass and its corresponding uncertainty [in petagrams of carbon (PgC)] in Northern Hemisphere boreal forests, divided into regions and dominant tree genera

	Eurasia	Europe	Russia	North America	Canada	Contiguous USA
All	9.685 ± 4.737	0.850 ± 0.450	8.547 ± 4.077	3.188 ± 1.821	2.923 ± 1.619	<0.001 ± 0.001
Broadleaf	3.024 ± 1.475	0.054 ± 0.032	2.949 ± 1.423	0.328 ± 0.203	0.319 ± 0.194	–
Diffuse-porous	2.995 ± 1.449	0.054 ± 0.032	2.941 ± 1.417	0.316 ± 0.192	0.316 ± 0.192	–
Betula	2.384 ± 1.068	0.054 ± 0.032	2.330 ± 1.035	0.037 ± 0.016	0.037 ± 0.016	–
Ring-porous	0.008 ± 0.006	–	0.008 ± 0.006	–	–	–
Quercus	0.007 ± 0.004	–	0.007 ± 0.004	–	–	–
Needleleaf	6.569 ± 3.184	0.796 ± 0.418	5.598 ± 2.654	2.332 ± 1.176	2.234 ± 1.116	<0.001 ± 0.001
Needleleaf evergreen	5.040 ± 2.458	0.796 ± 0.418	4.148 ± 1.974	2.328 ± 1.174	2.230 ± 1.113	<0.001 ± 0.001
Abies	0.243 ± 0.117	0.022 ± 0.015	0.220 ± 0.102	0.167 ± 0.092	0.167 ± 0.092	<0.001 ± 0.001
Picea	1.082 ± 0.493	0.218 ± 0.106	0.863 ± 0.387	1.812 ± 0.886	1.812 ± 0.886	<0.001 ± 0.001
Pinus	3.620 ± 1.783	0.555 ± 0.297	3.064 ± 1.486	0.200 ± 0.103	0.200 ± 0.103	–
Pseudotsuga	–	–	–	<0.001 ± 0.001	<0.001 ± 0.001	–
Tsuga	–	–	–	0.010 ± 0.005	0.010 ± 0.005	–
Needleleaf deciduous (*Larix*)	1.529 ± 0.726	–	1.450 ± 0.680	0.004 ± 0.002	0.004 ± 0.002	–

TABLE 2 Total sapwood biomass and its corresponding uncertainty [in petagrams of carbon (PgC)] in Northern Hemisphere temperate forests, divided into regions and dominant tree genera

	Eurasia	Europe	Russia	North America	Canada	Contiguous USA
All	7.619 ± 4.831	2.931 ± 1.869	2.614 ± 1.464	8.181 ± 4.270	2.773 ± 1.403	5.264 ± 2.783
Broadleaf	3.897 ± 2.663	1.186 ± 0.819	1.507 ± 0.855	3.151 ± 1.905	0.827 ± 0.506	2.321 ± 1.396
Diffuse-porous	2.254 ± 1.338	0.815 ± 0.531	1.438 ± 0.808	2.715 ± 1.612	0.826 ± 0.505	1.889 ± 1.107
Betula	1.066 ± 0.572	0.119 ± 0.078	0.947 ± 0.494	0.147 ± 0.064	0.139 ± 0.061	0.008 ± 0.003
Ring-porous	0.341 ± 0.250	0.272 ± 0.203	0.069 ± 0.047	0.432 ± 0.289	<0.001 ± 0.001	0.432 ± 0.289
Quercus	0.290 ± 0.209	0.234 ± 0.171	0.056 ± 0.038	0.386 ± 0.252	<0.001 ± 0.001	0.386 ± 0.252
Needleleaf	3.638 ± 2.103	1.745 ± 1.050	1.106 ± 0.609	4.910 ± 2.275	1.838 ± 0.816	2.943 ± 1.386
Needleleaf evergreen	3.365 ± 1.955	1.742 ± 1.048	0.963 ± 0.530	4.904 ± 2.273	1.836 ± 0.816	2.939 ± 1.384
Abies	0.273 ± 0.146	0.116 ± 0.066	0.157 ± 0.079	0.583 ± 0.256	0.231 ± 0.108	0.352 ± 0.148
Picea	0.814 ± 0.456	0.649 ± 0.375	0.165 ± 0.081	0.638 ± 0.287	0.526 ± 0.239	0.112 ± 0.049
Pinus	1.611 ± 0.971	0.969 ± 0.602	0.642 ± 0.369	2.100 ± 1.001	0.613 ± 0.264	1.487 ± 0.736
Pseudotsuga	0.004 ± 0.002	0.004 ± 0.002	–	0.721 ± 0.296	0.115 ± 0.048	0.606 ± 0.247
Tsuga	–	–	–	0.406 ± 0.170	0.268 ± 0.116	0.137 ± 0.053
Needleleaf deciduous (*Larix*)	0.273 ± 0.148	0.003 ± 0.002	0.143 ± 0.080	0.006 ± 0.003	0.001 ± 0.001	0.004 ± 0.002

3.5 | The proportion of sapwood to total stem biomass

The proportion of sapwood to stem biomass is lowest in central and eastern Siberian *Larix* forests (20–30%) and also low in forests where *Quercus* and other RP trees are prevalent (30–40%; Figure 3c; and Supporting Information Appendix S12, Tables S12.1 and S12.2). Values of *ca.* 50% are common in needleleaf forests in Canada and central Europe, where *Picea* is the dominant tree genera. Sapwood proportions of 60–70% are characteristic mainly for other DP forests, which are distributed over large parts of the eastern USA. The highest proportions are estimated in forests dominated by *Betula* and *Pinus*, mainly in Scandinavia, European Russia and western Siberia (70–80%).

The spatial distribution of the derived sapwood biomass product differs strongly from the distribution of the entire stem biomass. This difference is driven importantly by the distribution of tree genera, but also by the sapwood biomass density itself
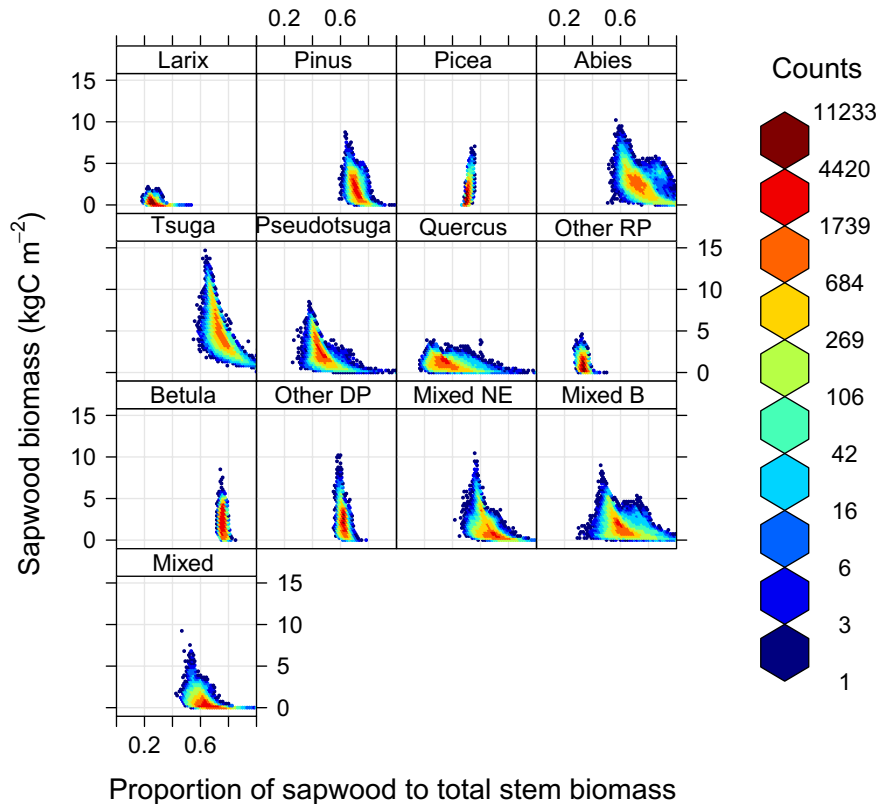
FIGURE 4 Frequency of the estimated sapwood biomass carbon per area (in kilograms of carbon per square metre) with different proportions of sapwood to total stem biomass for the tree genera classes distinguished [mixed = all tree genera together; mixed B = all broadleaf tree genera together; mixed NE = all needleleaf evergreen tree genera together; other DP = other (than *Betula*) diffuse-porous tree genera; other RP = other (than *Quercus*) ring-porous tree genera]. One hundred thousand representative 0.01° × 0.01° grid cells have been selected for each tree genera class randomly without replacement. The density of points in the scatterplot is visualized by means of hexagonal binning (Carslaw & Ropkins, 2012) [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 4). The proportion of sapwood to total stem biomass varies from generally 20–30% for *Larix*, 30–40% for other RP forests, *ca*. 50% for *Picea* and *ca*. 60% for other DP forests, to 60–80% for *Pinus*, *Tsuga* and *Betula* forests. *Abies* (usually 60–90%), *Pseudotsuga* (30–70%) and, especially, *Quercus* (20–70%) forests show the highest variation in sapwood to total stem biomass proportions. Taking into account the differences in abundance of the separate tree genera, the proportion of sapwood is most often between 50 and 80% when integrating over all genera (class 'mixed'). Owing to the increase of heartwood with age (and thus with increasing biomass), forests with the highest (sapwood and stem) biomass density exhibit the lowest proportion of sapwood and vice versa.

4 | DISCUSSION

4.1 | Allometric relationships among sapwood area, stem area and stem mass

The allometric relationships in Equations (1) and (2) and the stem diameter–height relationship (Supporting Information Appendix S1, Equation S1.III) have been proposed both as empirically motivated functions and as fundamental theoretical predictions arising from optimal structure of plants (see details in Supporting Information Appendix S13). Metabolic theory (Hunt & Manzoni, 2015; West, Brown, & Enquist, 1999) predicts that the exponent b of the sapwood area versus stem area relationship (Equation 1) should range between seven-sixths and one, and that the exponent d of the stem area versus stem mass relationship (Equation 2) should be equal to

three-quarters. Our estimates of b (range: 0.65–1.02) are generally lower than these predictions, whereas those of d (0.70–0.79) are in line with them. The exponent of Equation S1.III in Supporting Information Appendix S1 is $(n-1)/2$, with $n = 2.5$ (consistent with recommendations of the Food and Agriculture Organization), whereas theoretical predictions for n range between three and five.

There are at least two possible explanations for the discrepancy of observed b from the predicted values. First, fitting a reduced major axis regression (used to characterize the scaling relationship between two variables) instead of GNLS regression (used here to predict one variable from another) to the data would yield higher estimates of b, closer to the theoretical expectations (Supporting Information Appendix S13). However, given that slopes estimated with these different methods converge as $r^2 \rightarrow 1$ and the observed relationships are relatively strong, the values from our data would still be less than predicted for some of the investigated tree genera. Second and more fundamentally, allometric theory tends to underestimate the degree to which sapwood area tapers as trees grow larger. With $b = 7/6$, the metabolic model predicts that as plants grow, the fraction of the trunk that is sapwood increases until it reaches a maximum of one (West et al., 1999). Clearly, this pattern is unrealistic, as also noted on theoretical grounds by Kozlowski and Konarzewski (2004), and is not supported by our data (Figure 2).

4.2 | Uncertainties in the sapwood biomass product

The Northern Hemisphere sapwood biomass product is the first of its kind, and it is therefore challenging to evaluate it at its spatial

scale (0.01° × 0.01°). Few studies (e.g., Zimmermann et al., 2000) present areal estimates of sapwood biomass, and they are usually covering relatively small plots that do not match the square kilometre scale required for an appropriate evaluation of our product. In addition to this mismatch of the spatial scale, very precise coordinates of the inventory data are needed but often not available. In the absence of a direct evaluation of the sapwood biomass product at the stand scale, we make extensive efforts to evaluate the underlying allometric relationships at the tree level, revealing differences in their performance dependent on the applied tree genus class. Although there was strong agreement between estimated and measured sapwood mass at the tree level for most of the genus classes, *Quercus* and other RP trees showed considerable underestimation, but only for trees with a sapwood biomass of > 200 kg. However, these tree genera account for only 0.06% of the total estimated sapwood biomass in boreal forests and for 4.9% in temperate forests and, most importantly, only 0.95% (in the case of *Quercus*) and 3.27% (in the case of other RP) of the grid cells where these tree genera are prevalent exhibit an estimated average tree sapwood biomass of > 200 kg. Even when a stem mass distribution at sub-grid scale is assumed (see below), the mean probability that *Quercus* and other RP trees exceed a sapwood biomass of > 200 kg is still < 5 and < 8%, respectively (see Supporting Information Appendix S14). Moreover, the evaluation results emphasize the importance of distinguishing tree genera instead of leaf types when deriving sapwood CSA from stem CSA, because the scatter increases and thus the model performance decreases considerably in the latter case. The application of these relationships aggregated by leaf type is necessary only in very limited areas (outside Canada, the USA, Europe and Russia). The modelled relationship between stem CSA and stem biomass, in contrast, produced good results when applied to a test sample, although aggregated by leaf type. We conclude that the applied allometric relationships are robust in the greatest part of the study area.

Uncertainties of the estimated sapwood biomass densities are relatively high, especially in broadleaf and mixed forests. However, in many of the regions with the highest uncertainties, the biomass values are small. In areas with high biomass density, the uncertainty is usually within 50%, except for temperate broadleaf forests. The uncertainty could be reduced most importantly by more extensive field measurement campaigns, collecting both sapwood area and stem area (or diameter at breast height), including the most common tree species across their distributional range and thus covering possible adaptation to climatic or other environmental conditions. Alternatively, a greater number of field estimates of sapwood proportions of stem volume or biomass would be even more beneficial, because they would allow to circumvent generalized assumptions on the shape of the tree stem or, in the case of stem biomass estimates, on sapwood and heartwood densities. However, such measurements are complicated in practice, making the more widely available measurements of sapwood area a convenient surrogate. Most importantly, the dissemination of the original measurement data or, ideally, their contribution to biomass allometry databases, such as the BAAD (Falster et al., 2015), could greatly increase the amount of data available.

It is noted that our estimate of sapwood biomass only accounts for sapwood in tree stems, but not in branches or roots. Unfortunately, measurements on sapwood proportions in branches are comparably scarce. Heartwood production also affects branches after a certain age has been reached; however, young branches primarily consist of sapwood (Kramer, Sillett, & Carroll, 2014). In comparison to tree stems, the proportion of heartwood in branches increases more slowly with age and is thus of relatively minor importance except in old trees. For instance, in *Pinus sylvestris* trees in southern Finland, branch heartwood accounts for < 2% of total tree biomass and < 20% of branch biomass for trees < 100 years of age (Vanninen, Ylitalo, Sievänen, & Mäkelä, 1996). Given that sapwood content depends on the availability of light (Sellin, 1994), the branch sapwood content is related to the position of the branch in the tree crown, with branches that receive the most sunlight exhibiting the highest proportion of sapwood.

Other uncertainties that we do not account for (see a detailed discussion in Supporting Information Appendix S14) include measurement errors of sapwood area or thickness (especially for species that do not form a coloured heartwood), the accuracy of the applied tree genera distribution and stand density products, the implications of our assumptions of equal wood density and carbon content in sapwood and heartwood, and the biomass distribution among trees in each grid cell (0.01° × 0.01°). By applying a single mean stand density value per grid cell, here we assume that we can derive sapwood from stem biomass for an 'average tree' in each grid cell. When accounting for the distribution of stem mass within forest stands at the sub-grid scale, the impact on the estimated total sapwood biomass is very small (for a distribution typical for young forests, −2.3% in boreal and −3.9% in temperate forests; for a distribution typical for old forests, −1.1% in boreal and −1.8% in temperate forests) and negligible compared with other uncertainties (Supporting Information Appendix S14).

4.3 | Innovations in the synergy of satellite and forest inventory data for estimation of sapwood biomass

Notwithstanding the remaining uncertainties, which are unavoidable with the currently available data, the present study involves several innovations that go far beyond state of the art in the synergy of satellite and forest inventory data for biomass estimation:

1. Theoretical considerations on the sapwood distribution in the tree stem make it possible to apply relatively more frequent measurements of sapwood area for estimation of sapwood biomass.
2. The application of a global stand density product (Crowther et al., 2015) enables the gap to be bridged between inventory measurements at the tree level and satellite observations at the forest stand scale.
3. The application of a dominant tree genera map covering the boreal and temperate forests in Canada (Beaudoin et al., 2017,

2018), the USA (Wilson et al., 2012, 2013), Europe (Brus et al., 2012) and Russia (Schepaschenko et al., 2011) allows genera-specific differences in biomass allometry to be taken into account.

The presented sapwood biomass map shows important differences in its spatial distribution compared with the total stem biomass, strongly related to the distribution of tree genera. If the tree species distribution changes as a result of forest management or climate change, the available sapwood biomass may be altered significantly, even if the total stem biomass remains the same. For instance, a less harsh climate in Siberia that would lead to a retreat of *Larix* forests (Shuman et al., 2011) could imply a much higher sapwood biomass density (e.g., in the replacing *Pinus* forests) and, consequently, not only increased gross productivity, but also increased maintenance respiration levels. Thus, it is of crucial importance to use the functionally more important sapwood instead of the entire stem biomass in large-scale carbon and water cycle studies. For instance, the presented sapwood biomass density product can be the basis for new spatial estimates of plant respiration and transpiration. In addition, it can be used for comparison with and calibration of models that consider sapwood biomass, for instance LPJ (Sitch et al., 2003) or ORCHIDEE (Krinner et al., 2005).

DATA ACCESSIBILITY

The sapwood biomass product is available from the database of the Bolin Centre for Climate Research at https://bolin.su.se/data/Thurner-2019

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BIOSKETCH

MARTIN THURNER has led this work as a postdoctoral researcher at Stockholm University and the Bolin Centre for Climate Research and recently moved to the Senckenberg Biodiversity and Climate Research Centre (BiK-F). He is most interested in the vegetation carbon cycle in forest ecosystems and its response and feedback to climate change. He is integrating large-scale remote sensing products and forest inventory data in order to improve global vegetation models.

SUPPORTING INFORMATION

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

APPENDIX 1

Data sources

Forest inventory data from the following sources have been used to establish the allometric relationships between sapwood area and stem area and between stem area and stem mass. A detailed overview on these data is provided in Appendix S2 of the Supporting Information.

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