RESEARCH PAPER



Sapwood biomass carbon in northern boreal and temperate forests

Martin Thurner^{1,2} | Christian Beer^{1,2} | Thomas Crowther³ | Daniel Falster⁴ | Stefano Manzoni^{5,2} | Anatoly Prokushkin⁶ | Ernst-Detlef Schulze⁷

¹Department of Environmental Science and Analytical Chemistry (ACES), Stockholm University, Stockholm, Sweden

²Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

³Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zurich, Zurich, Switzerland

⁴Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

⁵Department of Physical Geography, Stockholm University, Stockholm, Sweden

⁶V.N. Sukachev Institute of Forest SB RAS, Krasnoyarsk, Russia

⁷Max Planck Institute for Biogeochemistry, Jena, Germany

Correspondence

Martin Thurner, Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

Email: martin.thurner@senckenberg.de

Funding information

Svenska Forskningsrådet Formas, Grant/Award Number: 2016-00998; Vetenskapsrådet, Grant/Award Number: 621-2014-4266; Russian Foundation for Basic Research (RFBR), Grant/Award Number: # 18-05-60203-Arktika

Editor: Thomas Gillespie

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.

© 2019 The Authors Global Ecology and Biogeography Published by John Wiley & Sons Ltd

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

KEYWORDS

biomass allometry, boreal forest, heartwood biomass, sapwood biomass, sapwood crosssectional area, stand density, stem biomass, temperate forest, tree species distribution

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:

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

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

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

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

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

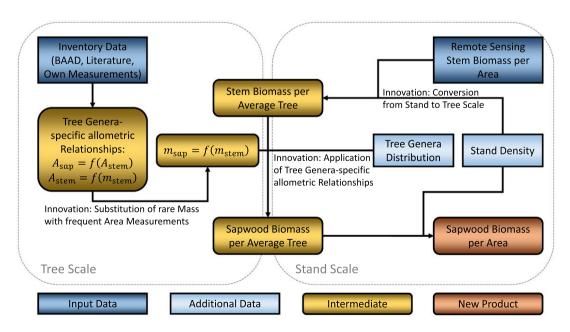


FIGURE 1 Methodical approach (A_{sap} = sapwood cross-sectional area; A_{stem} = stem cross-sectional area; m_{sap} = sapwood biomass; m_{stem} = stem biomass) [Colour figure can be viewed at wileyonlinelibrary.com]

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 $A_{\rm sap}$ and $A_{\rm stem}$ 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 $A_{\rm sap}$ and $A_{\rm stem}$ throughout the height of the tree with the relationship between $A_{\rm sap}$ and $A_{\rm stem}$ derived from measurements of trees of different age (Equation 1). Under this assumption, sapwood volume $(V_{\rm sap})$ can now be expressed as a function of $A_{\rm sap}$. In addition, $V_{\rm sap}$ 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:

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

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

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

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

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

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

$$m_{\text{sap}} = \frac{n}{(n-1)b+1} \cdot a \cdot c^{b-1} \cdot m_{\text{stem}}^{(b-1)d+1}$$
 (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 $A_{\rm sap}$ and $A_{\rm stem}$ 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 $A_{\rm sap}$ and $A_{\rm stem}$ 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 $A_{\rm stem}$ and $m_{\rm stem}$ 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 $A_{\rm sap}$ and $A_{\rm stem}$ 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 $A_{\rm stem}$ and $m_{\rm stem}$ 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 $0.01^{\circ} \times 0.01^{\circ}$ 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 ($m_{\text{stemCarea}}$ 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:

$$m_{\text{stemC}} = \frac{m_{\text{stemCarea}}}{\bar{D}} \tag{9}$$

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):

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

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

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

After deriving $m_{\rm sap}$ from $m_{\rm stem}$ by applying Equation (8), the obtained $m_{\rm sap}$ 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 $m_{\rm sap}$ instead of $m_{\rm stem}$). 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 $m_{\rm stemCarea}$, 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

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 $A_{\rm sap}$ and $A_{\rm stem}$ for different tree genera are partly attributable to species-specific differences, as is the case for *Larix* species (Supporting

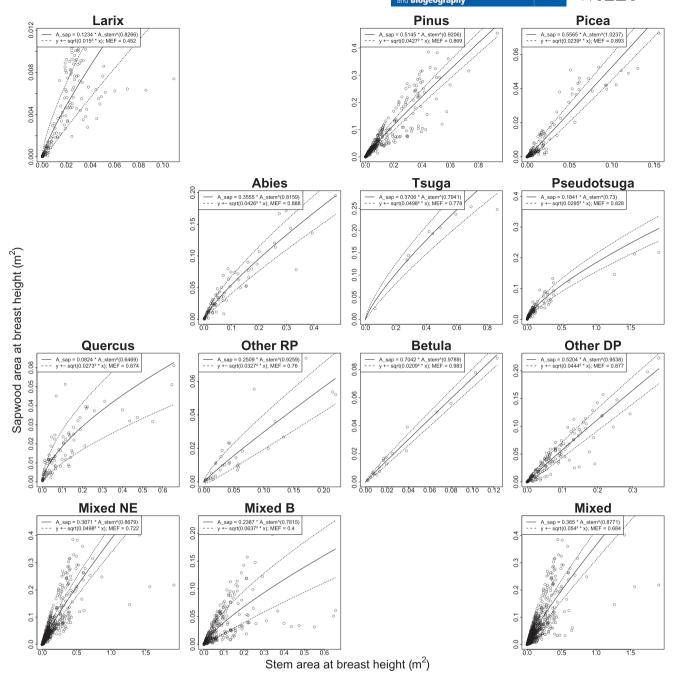


FIGURE 2 Sapwood area at breast height as a function of stem area at breast height for different tree genera [mixed = all tree genera together; mixed B = all broadleaf tree genera together; mixed NE = all needleleaf evergreen tree genera together; other DP = other (than *Betula*) diffuse-porous tree 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 $A_{\rm sap}$ and $A_{\rm stem}$ (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 $A_{\rm sap}$ from $A_{\rm stem}$ 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 $m_{\rm sap}$ from $m_{\rm stem}$ at each grid cell according to the present tree genera class (Supporting Information Appendix S9). The spatial patterns in $m_{\rm sap}$ are thus influenced

nonlinearly by differences in $m_{\rm stem}$ and by the tree genera distribution, and also by the applied stand density product. As a result, $m_{\rm sap}$ 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 $m_{\rm sap}$ (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., southerncentral 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 \pm 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 $(0.46 \pm 0.21 \text{ kgC m}^{-2} \text{ in Russian boreal for-}$ ests). Needleleaf evergreen forests exhibit higher carbon densities in temperate (2.23 \pm 1.14 kgC m⁻²) than in boreal (1.43 \pm 0.71 kgC m⁻²) forests, with higher values in Pinus than Picea forests in boreal $(1.94 \pm 0.96 \text{ vs. } 1.07 \pm 0.51 \text{ kgC m}^{-2})$, but not in temperate forests $(2.20 \pm 1.17 \text{ vs. } 2.14 \pm 1.10 \text{ kgC m}^{-2})$. Forests composed of DP trees have higher mean sapwood carbon densities (2.36 ± 1.17 kgC m⁻² in boreal forests and $2.39 \pm 1.42 \text{ kgC m}^{-2}$ in temperate forests) than forests dominated by RP trees (1.47 \pm 1.04 kgC m⁻² in boreal forests and $1.14 \pm 0.80 \text{ kgC m}^{-2}$ 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 $2.33 \pm 1.16 \text{ kgC m}^{-2}$ in boreal broadleaf forests.

3.4 Uncertainty in the estimated sapwood biomass

The uncertainty in $m_{\rm sap}$ is, in general, between 30 and 40% in central and eastern Siberia, south-western Canada and the north-western

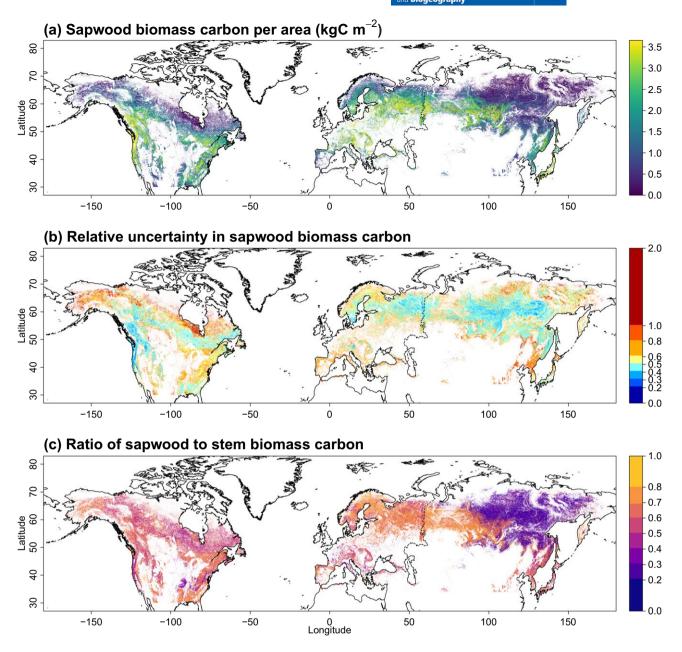


FIGURE 3 (a) Sapwood biomass carbon per area (in kilograms of carbon per square metre). (b) Relative uncertainty in sapwood biomass carbon. (c) Ratio of sapwood to stem biomass carbon. Non-forest areas have been masked out using GLC2000 (Bartholomé & Belward, 2005) [Colour figure can be viewed at wileyonlinelibrary.com]

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 $A_{\rm sap}$ and $A_{\rm stem}$ (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 nonforest biomes in parts of southern Siberia.

An important contribution to the overall uncertainty of $m_{\rm sap}$ 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 $A_{\rm sap}$ to $A_{\rm stem}$. The contribution of the uncertainty in the relationship of $A_{\rm stem}$ to $m_{\rm stem}$ 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 (<i>Larix</i>)	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

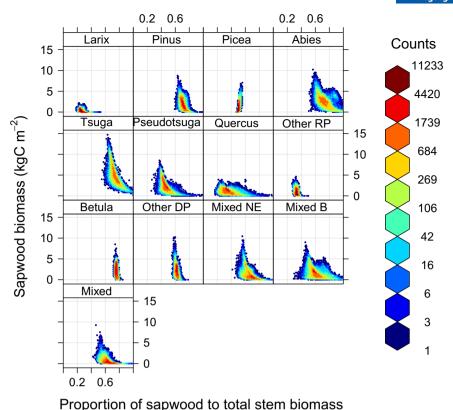


FIGURE 4 Frequency of the estimated sapwood biomass carbon per area (in kilograms of carbon per square metre) with different proportions of sapwood to total stem biomass for the tree genera classes distinguished [mixed = all tree genera together; mixed B = all broadleaf tree genera together; mixed NE = 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:

- 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.
- 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).

ACKNOWLEDGMENTS

We are very grateful to Barry Tyler Wilson (United States Department of Agriculture Forest Service), Dmitry Schepaschenko (International Institute for Applied Systems Analysis), Dick Brus (Wageningen University and Research Centre) and André Beaudoin (Natural Resources Canada) for providing tree species distribution maps for the USA, Russia, Europe and Canada. We want to thank Takuya Kajimoto (Forestry and Forest Products Research Institute, Tsukuba, Japan) and Akio Koizumi (Graduate School of Agriculture, Hokkaido University, Sapporo, Japan) for providing the original measurements underlying their studies of sapwood contents in Siberian Larix species. Martin Thurner and Christian Beer acknowledge funding from the Vetenskapsrådet grant 621-2014-4266 of the Swedish Research Council. Stefano Manzoni acknowledges partial support from the Swedish Research Council Formas (2016-00998). Anatoly Prokushkin acknowledges funding from the RFBR (Russian Foundation for Basic Research) # 18-05-60203-Arktika.

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

ORCID

Martin Thurner https://orcid.org/0000-0003-2362-5161

REFERENCES

- Akaike, H. (1974). A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19, 716-723. https://doi. org/10.1109/TAC.1974.1100705
- Bartholomé, E., & Belward, A. S. (2005). GLC2000: A new approach to global land cover mapping from Earth observation data. International Journal of Remote Sensing, 26, 1959-1977. https://doi.org/10.1080/0 1431160412331291297
- Beaudoin, A., Bernier, P. Y., Villemaire, P., Guindon, L., & Guo, X. J. (2017). Species composition, forest properties and land cover types across Canada's forests at 250m resolution for 2001 and 2011. Quebec, Canada: Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre. Retrieved from https://doi. org/10.23687/ec9e2659-1c29-4ddb-87a2-6aced147a990
- Beaudoin, A., Bernier, P. Y., Villemaire, P., Guindon, L., & Guo, X. J. (2018). Tracking forest attributes across Canada between 2001 and 2011 using a kNN mapping approach applied to MODIS imagery. Canadian Journal of Forest Research, 48, 85-93.
- Beer, C., Lucht, W., Schmullius, C., & Shvidenko, A. (2006). Small net carbon dioxide uptake by Russian forests during 1981-1999. Geophysical Research Letters, 33, 1981-1999, https://doi. org/10.1029/2006GL026919
- Björklund, L. (1999). Identifying heartwood-rich stands or stems of Pinus sylvestris by using inventory data. Silva Fennica, 33, 119-129. https:// doi.org/10.14214/sf.662
- Bond-Lamberty, B., Wang, C., & Gower, S. T. (2002). Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Canadian Journal of Forest Research, 32, 1441-1450. https://doi.org/10.1139/x02-063
- Brus, D. J., Hengeveld, G. M., Walvoort, D. J. J., Goedhart, P. W., Heidema, A. H., Nabuurs, G. J., & Gunia, K. (2012). Statistical mapping of tree species over Europea. European Journal of Forest Research, 131, 145-157. https://doi.org/10.1007/s10342-011-0513-5
- Carslaw, D. C., & Ropkins, K. (2012). Openair-An R package for air quality data analysis. Environmental Modelling & Software, 27-28, 52-61. https://doi.org/10.1016/j.envsoft.2011.09.008
- Cermak, J., Kucera, J., Bauerle, W. L., Phillips, N., & Hinckley, T. M. (2007). Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. Tree Physiology, 27, 181-198. https://doi.org/10.1093/treephys/27.2.181
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. Ecology Letters, 12, 351-366. https://doi. org/10.1111/j.1461-0248.2009.01285.x
- Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., Thomas, S. M., ... Bradford, M. A. (2015). Mapping tree density at a global scale. Nature, 525, 201-205. https://doi.org/10.1038/ nature14967
- DeLucia, E. H., Maherali, H., & Carey, E. V. (2000). Climate-driven changes in biomass allocation in pines. Global Change Biology, 6, 587-593. https://doi.org/10.1046/j.1365-2486.2000.00338.x
- Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions? Global Change Biology, 24, 1150-1163. https://doi. org/10.1111/gcb.13925
- Falster, D. S., Duursma, R., & FitzJohn, R. G. (2018). How functional traits influence plant growth and shade tolerance across the lifecycle. Proceedings of the National Academy of Sciences USA, 115, E6789-E6798. https://doi.org/10.1101/083451
- Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., ... York, R. A. (2015). BAAD: A biomass and allometry database for woody plants. Ecology, 96, 1445. https://doi. org/10.1890/14-1889.1

- Gartner, B. L. (2002). Sapwood and inner bark quantities in relation to leaf area and wood density in Douglas-fir. *IAWA Journal*, *23*, 267–285. https://doi.org/10.1163/22941932-90000303
- Gjerdrum, P. (2003). Heartwood in relation to age and growth rate in Pinus sylvestris L. in Scandinavia. Forestry: An International Journal of Forest Research, 76, 413–424. https://doi.org/10.1093/forestry/76.4.413
- Gominho, J., Lourenço, A., Miranda, I., & Pereira, H. (2015). Radial and axial variation of heartwood properties and extractives in mature trees of *Eucalyptus globulus*. *BioResources*, 10, 721–731.
- Hunt, A., & Manzoni, S. (2015). Chapter 6—Allometric scaling and metabolism. In A. Hunt & S. Manzoni (Eds.), Networks on networks: The physics of geobiology and geochemistry (pp. 6.1-6.21). San Rafael, CA: Morgan & Claypool/IOP Concise Physics. https://doi.org/10.1088/978-1-6817-4159-8
- Kärenlampi, P. P., & Riekkinen, M. (2003). Prediction of the heartwood content of pine logs. *Wood and Fiber Science*, 35, 83–89.
- Knapic, S., & Pereira, H. (2005). Within-tree variation of heart-wood and ring width in maritime pine (*Pinus pinaster Ait.*). Forest Ecology and Management, 210, 81–89. https://doi.org/10.1016/j.foreco.2005.02.017
- Köstner, B. M. M., Schulze, E.-D., Kelliher, F. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., ... Weir, P. L. (1992). Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: An analysis of xylem sap flow and eddy correlation measurements. *Oecologia*, 91, 350–359. https://doi.org/10.1007/bf00317623
- Kozlowski, J., & Konarzewski, M. (2004). Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? Functional Ecology, 18, 283–289. https://doi. org/10.1111/j.0269-8463.2004.00830.x
- Kramer, R. D., Sillett, S. C., & Carroll, A. L. (2014). Structural development of redwood branches and its effects on wood growth. *Tree Physiology*, 34, 314–330. https://doi.org/10.1093/treephys/tpu011
- Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., ... Prentice, I. C. (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles, 19, GB1015. https://doi.org/10.1029/2003gb002199
- Larjavaara, M., Berninger, F., Palviainen, M., Prokushkin, A., & Wallenius, T. (2017). Post-fire carbon and nitrogen accumulation and succession in Central Siberia. Scientific Reports, 7, 12776. https://doi.org/10.1038/s41598-017-13039-2
- Longuetaud, F., Mothe, F., Leban, J.-M., & Mäkelä, A. (2006). *Picea abies* sapwood width: Variations within and between trees. *Scandinavian Journal of Forest Research*, 21, 41–53. https://doi.org/10.1080/02827580500518632
- Mäkelä, A., & Valentine, H. T. (2006). Crown ratio influences allometric scaling in trees. *Ecology*, 87, 2967–2972. https://doi.org/10.1890/0012-9658(2006) 87[2967:CRIASI]2.0.CO;2
- Manzoni, S., Vico, G., Porporato, A., & Katul, G. (2013). Biological constraints on water transport in the soil-plant-atmosphere system. Advances in Water Resources, 51, 292–304. https://doi.org/10.1016/j.advwatres.2012.03.016
- McDowell, N., Barnard, H., Bond, B., Hinckley, T., Hubbard, R., Ishii, H., ... Whitehead, D. (2002). The relationship between tree height and leaf area: Sapwood area ratio. *Oecologia*, 132, 12–20. https://doi.org/10.1007/s00442-002-0904-x
- Mencuccini, M., & Grace, J. (1994). Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology*, 15, 1–10.
- Mörling, T., & Valinger, E. (1999). Effects of fertilization and thinning on heartwood area, sapwood area and growth in Scots pine. Scandinavian Journal of Forest Research, 14, 462–469. https://doi.org/10.1080/02827589950154168
- Nash, J. E., & Sutcliffe, J. V. (1970). River flow forecasting through conceptual models part I—A discussion of principles. *Journal of Hydrology*, 10, 282–290. https://doi.org/10.1016/0022-1694(70)90255-6

- Novick, K., Oren, R., Stoy, P., Juang, J.-Y., Siqueira, M., & Katul, G. (2009). The relationship between reference canopy conductance and simplified hydraulic architecture. *Advances in Water Resources*, 32, 809–819. https://doi.org/10.1016/j.advwatres.2009.02.004
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., ... Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2
- Pinto, I., Pereira, H., & Usenius, A. (2004). Heartwood and sapwood development within maritime pine (*Pinus pinaster Ait.*) stems. *Trees* - *Structure and Function*, 18, 284–294. https://doi.org/10.1007/ s00468-003-0305-8
- Pruyn, M. L., Gartner, B. L., & Harmon, M. E. (2002). Within-stem variation of respiration in *Pseudotsuga menziesii* (Douglasfir) trees. *New Phytologist*, 154, 359–372. https://doi.org/10.1046/j.1469-8137.2002.00380.x
- Ryan, M. G. (1990). Growth and maintenance respiration in stems of Pinuscontorta and Piceaengelmannii. Canadian Journal of Forest Research, 20, 48–57. https://doi.org/10.1139/x90-008
- Santoro, M., Beaudoin, A., Beer, C., Cartus, O., Fransson, J. E. S., Hall, R. J., ... Wegmüller, U. (2015). Forest growing stock volume of the northern hemisphere: Spatially explicit estimates for 2010 derived from Envisat ASAR. Remote Sensing of Environment, 168, 316–334. https://doi.org/10.1016/j.rse.2015.07.005
- Schepaschenko, D., McCallum, I., Shvidenko, A., Fritz, S., Kraxner, F., & Obersteiner, M. (2011). A new hybrid land cover dataset for Russia: A methodology for integrating statistics, remote sensing and in situ information. *Journal of Land Use Science*, 6, 245–259. https://doi.org/10.1080/1747423x.2010.511681
- Sellin, A. (1994). Sapwood-heartwood proportion related to tree diameter, age, and growth rate in *Picea abies. Canadian Journal of Forest Research*, 24, 1022–1028. https://doi.org/10.1139/x94-133
- Shinozaki, K., Yoda, K., Hozumi, K., & Kira, T. (1964a). A quantitative analysis of plant form—The pipe model theory. I. Basic analyses. *Japanese Journal of Ecology*, 14, 97–105.
- Shinozaki, K., Yoda, K., Hozumi, K., & Kira, T. (1964b). A quantitative analysis of plant form—The pipe model theory. II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology*, 14, 133–139.
- Shuman, J. K., Shugart, H. H., & O'Halloran, T. L. (2011). Sensitivity of Siberian larch forests to climate change. *Global Change Biology*, 17, 2370–2384. https://doi.org/10.1111/j.1365-2486.2011.02417.x
- Sillett, S. C., Van Pelt, R., Carroll, A. L., Kramer, R. D., Ambrose, A. R., & Trask, D. A. (2015). How do tree structure and old age affect growth potential of California redwoods? *Ecological Monographs*, 85, 181–212. https://doi.org/10.1890/14-1016.1
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., ... Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*, 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x
- Sprugel, D. G. (1990). Components of woody-tissue respiration in young Abies amabilis (Dougl.) Forbes trees. Trees, 4(2), 88-98. https://doi. org/10.1007/bf00226071
- Thomas, S. C., & Martin, A. R. (2012). Carbon content of tree tissues: A synthesis. *Forests*, 3, 332–352. https://doi.org/10.3390/f3020332
- Thurner, M., Beer, C., Ciais, P., Friend, A. D., Ito, A., Kleidon, A., ... Carvalhais, N. (2017). Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. *Global Change Biology*, 23, 3076–3091. https://doi.org/10.1111/gcb.13660
- Thurner, M., Beer, C., Santoro, M., Carvalhais, N., Wutzler, T., Schepaschenko, D., ... Schmullius, C. (2014). Carbon stock and

- density of northern boreal and temperate forests. *Global Ecology and Biogeography*, 23, 297–310. https://doi.org/10.1111/geb.12125
- Vanninen, P., Ylitalo, H., Sievänen, R., & Mäkelä, A. (1996). Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees, 10, 231–238. https://doi.org/10.1007/BF02185674
- Vertessy, R. A., Benyon, R. G., O'Sullivan, S. K., & Gribben, P. R. (1995). Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, 15, 559–567. https://doi.org/10.1093/treephys/15.9.559
- Waring, R. H., Schroeder, P. E., & Oren, R. (1982). Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research*, 12, 556–560. https://doi.org/10.1139/x82-086
- West, G. B., Brown, J. H., & Enquist, B. J. (1999). A general model for the structure and allometry of plant vascular systems. *Nature*, 400, 664–667. https://doi.org/10.1038/23251
- Wilson, B. T., Lister, A. J., & Riemann, R. I. (2012). A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. Forest Ecology and Management, 271, 182–198. https://doi.org/10.1016/j. foreco.2012.02.002
- Wilson, B. T., Lister, A. J., Riemann, R. I., & Griffith, D. M. (2013). Live tree species basal area of the contiguous United States (2000–2009). Newtown Square, PA: USDA Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RDS-2013-0013
- Yang, C.-E., Mao, J., Hoffman, F. M., Ricciuto, D. M., Fu, J. S., Jones, C. D., & Thurner, M. (2018). Uncertainty quantification of extratropical forest biomass in CMIP5 models over the Northern Hemisphere. *Scientific Reports*, 8, 10962. https://doi.org/10.1038/s41598-018-29227-7
- Zimmermann, R., Schulze, E.-D., Wirth, C., Schulze, E.-E., McDonald, K. C., Vygodskaya, N. N., & Ziegler, W. (2000). Canopy transpiration in a chronosequence of Central Siberian pine forests. *Global Change Biology*, 6, 25–37. https://doi.org/10.1046/j.1365-2486.2000.00289.x

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.

How to cite this article: Thurner M, Beer C, Crowther T, et al. Sapwood biomass carbon in northern boreal and temperate forests. *Global Ecol Biogeogr.* 2019;28:640–660. https://doi.org/10.1111/geb.12883

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.
- Abe, N. (1981). Studies on the management of Abies sachalinensis Mast. planted forest (III) On biomass estimation of 53-year-old stand. Bulletin of the Hokkaido Forest Experiment Station, 19, 115–127.
- Addington, R. N., Donovan, L. A., Mitchell, R. J., Vose, J. M., Pecot, S. D., Jack, S. B., ... Oren, R. (2006). Adjustments in hydraulic architecture of Pinus palustris maintain similar stomatal conductance in xeric and mesic habitats. Plant, Cell and Environment, 29(4), 535–545. https://doi.org/10.1111/j.1365-3040.2005.01430.x
- Albrektson, A. (1984). Sapwood basal area and needle mass of Scots pine (Pinus sylvestris L.) trees in central Sweden. Forestry, 57(1), 35–43.
- Alsheimer, M., Köstner, B., Falge, E., & Tenhunen, J. D. (1998). Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany. Annals of Forest Science, 55, 103–123.
- Ando, T., Sakaguchi, K., Narita, T., & Satoo, S. (1962). Growth analysis on the natural stands of Japanese red pine (Pinus densiflora Sieb. et Zucc.) I. Effects of improvement cutting and relative growth. Bulletin of the Forestry and Forest Products Research Institute, 144, 1–30.
- Arneth, A., Kelliher, F. M., Bauer, G., Hollinger, D. Y., Byers, J. N., Hunt, J. E., ... Schulze, E.-D. (1996). Environmental regulation of xylem sap flow and total conductance of Larix gmelinii trees in eastern Siberia. Tree Physiology, 16, 247–255.
- Asbjornsen, H., Tomer, M. D., Gomez-Cardenas, M., Brudvig, L. A., Greenan, C. M., & Schilling, K. (2007). Tree and stand transpiration in a Midwestern bur oak savanna after elm encroachment and restoration thinning. Forest Ecology and Management, 247(1–3), 209–219. https://doi.org/10.1016/j. foreco.2007.04.043
- Aspinwall, M. J., King, J. S., & McKeand, S. E. (2013). Productivity differences among loblolly pine genotypes are independent of individual-tree biomass partitioning and growth efficiency. Trees, 27(3), 533–545. https://doi.org/10.1007/s00468-012-0806-4
- Baral, S. K., Berninger, F., Schneider, R., & Pothier, D. (2017). Effects of heartwood formation on sugar maple (Acer saccharum Marshall) discoloured wood proportion. Trees, 31(1), 105–114. https://doi.org/10.1007/s00468-016-1459-5
- Barnard, D. M., Meinzer, F. C., Lachenbruch, B., McCulloh, K. A., Johnson, D. M., & Woodruff, D. R. (2011). Climate-related trends

- in sapwood biophysical properties in two conifers: avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance. Plant Cell Environ, 34(4), 643–654. https://doi.org/10.1111/j.1365-3040.2010.02269.x
- Beauchamp, K., Mencuccini, M., Perks, M., & Gardiner, B. (2013). The regulation of sapwood area, water transport and heartwood formation in Sitka spruce. Plant Ecology & Diversity, 6(1), 45–56. https://doi.org/10.1080/17550874.2012.702359
- Berner, L. T., & Law, B. E. (2015). Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon. Biogeosciences, 12(22), 6617-6635. https://doi.org/10.5194/bg-12-6617-2015
- Berthier, S., Kokutse, A. D., Stokes, A., & Fourcaud, T. (2001). Irregular Heartwood Formation in Maritime Pine (Pinus pinaster Ait): Consequences for Biomechanical and Hydraulic Tree Functioning. Annals of Botany, 87, 19–25.
- Best, C., & Schulze, E.-D. Sapwood measurements for Abies sibirica, Betula pubescens, Picea obovata, Sorbus aucuparia, and Pinus sibirica trees close to the Zotino Tall Tower Observation Facility. Unpublished.
- Boggs, J., Sun, G., Domec, J.-C., McNulty, S., & Treasure, E. (2015). Clearcutting upland forest alters transpiration of residual trees in the riparian buffer zone. Hydrological Processes, 29(24), 4979– 4992. https://doi.org/10.1002/hyp.10474
- Bond-Lamberty, B., Wang, C., & Gower, S. T. (2002). Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Canadian Journal of Forest Research, 32(8), 1441–1450. https://doi.org/10.1139/x02-063
- Cerny, M. (1990). Biomass ofpicea abies(L.) Karst. in midwestern bohemia. Scandinavian Journal of Forest Research, 5(1–4), 83–95. https://doi.org/10.1080/02827589009382595
- Chang, X., Zhao, W., Zhang, Z., & Su, Y. (2006). Sap flow and tree conductance of shelter-belt in arid region of China. Agricultural and Forest Meteorology, 138(1-4), 132-141. https://doi.org/10.1016/j.agrformet.2006.04.003
- Chen, L., Zhang, Z., Zeppel, M., Liu, C., Guo, J., Zhu, J., ... Zha, T. (2014). Response of transpiration to rain pulses for two tree species in a semiarid plantation. Int J Biometeorol, 58(7), 1569–1581. https://doi.org/10.1007/s00484-013-0761-9
- Chiu, C.-W., Komatsu, H., Katayama, A., & Otsuki, K. (2016). Scalingup from tree to stand transpiration for a warm-temperate multispecific broadleaved forest with a wide variation in stem diameter. Journal of Forest Research, 21(4), 161–169. https://doi. org/10.1007/s10310-016-0532-7
- DeBell, J. D., & Lachenbruch, B. (2009). Heartwood/sapwood variation of western redcedar as influenced by cultural treatments and position in tree. Forest Ecology and Management, 258(9), 2026–2032. https://doi.org/10.1016/j.foreco.2009.07.054
- Delzon, S., Sartore, M., Burlett, R., Dewar, R., & Loustau, D. (2004). Hydraulic responses to height growth in maritime pine trees. Plant, Cell and Environment, 27, 1077–1087.

- Domec, J.-C., Lachenbruch, B., Pruyn, M. L., & Spicer, R. (2012). Effects of age-related increases in sapwood area, leaf area, and xylem conductivity on height-related hydraulic costs in two contrasting coniferous species. Annals of Forest Science, 69(1), 17–27. https://doi.org/10.1007/s13595-011-0154-3
- Domec, J.-C., Pruyn, M. L., & Gartner, B. L. (2005). Axial and radial profiles in conductivities, water storage and native embolism in trunks of young and old-growth ponderosa pine trees. Plant, Cell and Environment, 28, 1103–1113.
- Engel, V. C., Stieglitz, M., Williams, M., & Griffin, K. L. (2002). Forest canopy hydraulic properties and catchment water balance: observations and modeling. Ecological Modelling, 154, 263–288.
- Espinosa Bancalari, M. A., Perry, D. A., & Marshall, J. D. (1987). Leaf area sapwood area relationships in adjacent young Douglasfir stands with different early growth rates. Canadian Journal of Forest Research, 17(2), 174–180. https://doi.org/10.1139/x87-030
- Ewers, B. E., Mackay, D. S., Gower, S. T., Ahl, D. E., Burrows, S. N., & Samanta, S. S. (2002). Tree species effects on stand transpiration in northern Wisconsin. Water Resources Research, 38(7), 8-1-8-11. https://doi.org/10.1029/2001wr000830
- Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., ... York, R. A. (2015). BAAD: a biomass and allometry database for woody plants. Ecology, 96(5), 1445. https://doi.org/10.1890/14-1889.1
- Fischer, D. G., Kolb, T. E., & DeWald, L. E. (2002). Changes in wholetree water relations during ontogeny of Pinus flexilis and Pinus ponderosa in a high-elevation meadow. Tree Physiology, 22, 675–685.
- FLFU. (1963). Forest production data from the perspective of material cycle 1. Forestry Laboratories of Kyoto University, Tokyo University, Niigata University and Shinshu University.
- FLFU. (1965). Forest production data from the perspective of material cycle 2. Forestry Laboratories of Kyoto University, Tokyo University, Niigata University and Shinshu University.
- Ford, C. R., Hubbard, R. M., Kloeppel, B. D., & Vose, J. M. (2007). A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance. Agricultural and Forest Meteorology, 145(3-4), 176-185. https://doi.org/10.1016/j.agrformet.2007.04.010
- Fukatsu, E., Fukuda, Y., Takahashi, M., & Nakada, R. (2008). Clonal variation of carbon content in wood of Larix kaempferi (Japanese larch). Journal of Wood Science, 54(3), 247–251. https://doi.org/10.1007/s10086-007-0939-z
- Furuno, T., & Kawanabe, S. (1967). Investigations on the productivity of Japanese fir (Abies firma Sieb. et Zucc.) and hemlock (Tsuga sieboldii Carr.) stands in Kyoto University Forest of Wakayama (I) On the growth of Japanese fir stands. Bulletin of the Kyoto University Forests, 39, 9–26.
- Galvan, J. D., Camarero, J. J., Gutierrez, E., & Zuidema, P. (2014). Seeing the trees for the forest: drivers of individual growth responses to climate in Pinus uncinatamountain forests. Journal of

- Ecology, 102(5), 1244-1257. https://doi.org/10.1111/1365-2745.12268
- Garber, S. M., & Maguire, D. A. (2005). The response of vertical foliage distribution to spacing and species composition in mixed conifer stands in central Oregon. Forest Ecology and Management, 211(3), 341–355. https://doi.org/10.1016/j.foreco.2005.02.053
- Gartner, B. L. (2002). Sapwood and inner bark quantities in relation to leaf area and wood density in Douglas-fir. IAWA Journal, 23(3), 267–285.
- Gartner, B. L., Baker, D. C., & Spicer, R. (2000). Distribution and vitality of xylem rays in relation to tree leaf area in Douglas-fir. IAWA Journal, 21(4), 389–401.
- Gazal, R. M., Scott, R. L., Goodrich, D. C., & Williams, D. G. (2006). Controls on transpiration in a semiarid riparian cottonwood forest. Agricultural and Forest Meteorology, 137(1-2), 56-67. https://doi.org/10.1016/j.agrformet.2006.03.002
- Gebauer, T., Horna, V., & Leuschner, C. (2008). Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species. Tree Physiology, 28, 1821–1830.
- Gilmore, D. W., & Seymour, R. S. (1996). Alternative measures of stem growth efficiency applied to Abies balsamea from four canopy positions in central Maine, USA. Forest Ecology and Management, 84, 209–218.
- Goto, Y., Kominami, Y., Miyama, T., Tamai, K., & Kanazawa, Y. (2003). Aboveground biomass and net primary production of a broadleaved secondary forest in the southern part of Kyoto prefecture, central Japan. Bulletin of the Forestry and Forest Products Research Institute, 2, 115–147.
- Granier, A., Biron, P., Köstner, B., Gay, L. W., & Najjar, G. (1996). Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. Theoretical and Applied Climatology, 53, 115–122.
- Granier, A., Bobay, V., Gash, J. H. C., Gelpe, J., Saugier, B., & Shuttleworth, W. J. (1990). Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (Pinus pinaster Ait.) in Les Landes forest. Agricultural and Forest Meteorology, 51, 309–319.
- Guiterman, C. H., Seymour, R. S., & Weiskittel, A. R. (2012). Long-Term Thinning Effects on the Leaf Area of <I>Pinus strobus</I>
 L. as Estimated from Litterfall and Individual-Tree Allometric Models. Forest Science, 58(1), 85–93. https://doi.org/10.5849/forsci.10-002
- Hagihara, A., Yokota, T., & Ogawa, K. (1993). Allometric relations in hinoki (Chamaecyparis obtusa (Sieb. et Zucc.) Endl.) trees. Bulletin of the Nagoya University Forests, 12, 11–29.
- Harada, H., Satoo, H., Hotta, I., Hatiya, K., & Tadaki, Y. (1972). Study on the nutrient contents of mature Cryptomeria forest. Bulletin of the Government Forest Experiment Station, 249, 17–74.
- Haruki, M. (1979). Studies on the material biomass of Abies sachalinensis artificial forest. Research bulletin of the Hokkaido University Forests, 36, 147–247.

- Hashizume, H. (1985). Studies on the improvement of the secondary forest of broad-leaved trees (II) The effect of improvement cutting and manuring on the growth of the secondary forest of Kunugi (Quercus acutissima Carruth.). Bulletin of the Faculty of Agriculture, Tottori University, 38, 60–67.
- Hashizume, H., & Onishi, Y. (1980). On the production structure and productivity of beech forests in the Hiruzen district. Hardwood Research. 1, 73–84.
- Hein, S., Weiskittel, A. R., & Kohnle, U. (2008). Effect of wide spacing on tree growth, branch and sapwood properties of young Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] in southwestern Germany. European Journal of Forest Research, 127(6), 481–493. https://doi.org/10.1007/s10342-008-0231-9
- Hernandez-Santana, V., Asbjornsen, H., Sauer, T., Isenhart, T., Schilling, K., & Schultz, R. (2011). Enhanced transpiration by riparian buffer trees in response to advection in a humid temperate agricultural landscape. Forest Ecology and Management, 261(8), 1415–1427. https://doi.org/10.1016/j.foreco.2011.01.027
- lida, S., Tanaka, T., & Sugita, M. (2006). Change of evapotranspiration components due to the succession from Japanese red pine to evergreen oak. Journal of Hydrology, 326(1–4), 166–180. https://doi.org/10.1016/j.jhydrol.2005.11.002
- lijima, K. (1991). Growth of the stem volume of hinoki trees. (Master), Faculty of Agriculture, Nagoya University, Japan.
- Ilomäki, S., Nikinmaa, E., & Mäkelä, A. (2003). Crown rise due to competition drives biomass allocation in silver birch. Canadian Journal of Forest Research, 33(12), 2395–2404. https://doi.org/10.1139/x03-164
- Infante, J. M., Mauchamp, A., Fernandez-Ales, R., Joffre, R., & Rambal, S. (2001). Within-tree variation in transpiration in isolated evergreen oak trees: evidence in support of the pipe model theory. Tree Physiology, 21, 409–414.
- Irvine, J., Perks, M. P., Magnani, F., & Grace, J. (1998). The response of Pinus sylvestris to drought: stomatal control of transpiration and hydraulic conductance. Tree Physiology, 18, 393–402.
- Ishii, H., & Tadaki, Y. (2000). Structure and biomass of a secondary broad-leaved forest growing in the campus of Nagoya University. Nagoya University forest science, 19, 197–206.
- Jiao, L., Lu, N., Fu, B., Gao, G., Wang, S., Jin, T., ... Zhang, D. (2016). Comparison of transpiration between different aged black locust (Robinia pseudoacacia) trees on the semi-arid Loess Plateau, China. Journal of Arid Land, 8(4), 604–617.
- Jung, E.-Y., Otieno, D., Lee, B., Lim, J. H., Kang, S. K., Schmidt, M. W. T., & Tenhunen, J. (2011). Up-scaling to stand transpiration of an Asian temperate mixed-deciduous forest from single tree sapflow measurements. Plant Ecology, 212, 383–395. https://doi.org/10.1007/sl
- Kabaya, H. (1981). Causal analyses of poor growth observed at the inner part of the pine plantations on costal sand dune. Bulletin of the Tokyo University Forests, 70, 11–80.
- Kabaya, H., & Sato, T. (1968). Estimation of the biomass, growth and nitrogen biomass in Pinus thunbergii forest. Bulletin of the Japanese Forestry Society, 79, 93–94.

- Kajimoto, T., Matsuura, Y., Osawa, A., Abaimov, A. P., Zyryanova, O. A., Isaev, A. P., ... Koike, T. (2006). Size-mass allometry and biomass allocation of two larch species growing on the continuous permafrost region in Siberia. Forest Ecology and Management, 222(1), 314–325. https://doi.org/10.1016/j.foreco.2005.10.031
- Karizumi, N., & Terada, M. (1984). Root structure in a Chamaecyparis obtusa forest. Bulletin of the Japanese Forestry Society, 95, 337–338.
- Katagiri, S., Ishii, H., Miyake, N., & Ando, Y. (1984). Studies on mineral cycling in a deciduous broad-leaved forest at Sanbe Forest of Shimane University (XII): Difference of above ground biomass in a deciduous broad-leaved forest along a slope. Bulletin of the Faculty of Agriculture, Shimane University, 18, 53–60.
- Katakura, M., Yamauchi, M., & Koyama, Y. (2007). Biomass and carbon stock in Larix, Pinus, and Quercus forests and the changes in soil carbon after clear cut of a Pinus forest. Bulletin of the Nagano Prefecture Forestry Research Center, 22, 33–55.
- Kato, R., & Segawa, K. (1973). Growth and primary productivity of Kobanoyamahannoki (Alnus Inokumai Murai et Kusaka) stand at Mamurogawa experimental plot. Bulletin of the Forestry and Forest Products Research Institute. 252, 135–147.
- Kawanabe, S., & Ando, M. (1988). Studies on the regeneration of natural forest on lower limit of cool temperate deciduous broadleaved forest V. Biomass and growth in natural forest of Cryptomeria japonica [in Japanese with English abstract]. Bulletin of the Kyoto University Forests, 60, 67–76.
- Kenefic, L. S., & Seymour, R. S. (1999). Leaf area prediction models for Tsuga canadensis in Maine. Canadian Journal of Forest Research, 29, 1574–1582.
- Kline, J. R., Reed, K. L., Waring, R. H., & Stewart, M. L. (1976). Field measurement of transpiration in Douglas-fir. Journal of Applied Ecology, 13(1), 273–283.
- Köcher, P., Horna, V., & Leuschner, C. (2013). Stem water storage in five coexisting temperate broad-leaved tree species: significance, temporal dynamics and dependence on tree functional traits. Tree Physiology, 33, 817–832.
- Koizumi, A., Takata, K., Yamashita, K., & Nakada, R. (2003). Anatomical characteristics and mechanical properties of Larix sibirica grown in south-central Siberia. IAWA Journal, 24(4), 355– 370. https://doi.org/10.1163/22941932-90000341
- Komatsu, H., Shinohara, Y., Kumagai, T. o., Kume, T., Tsuruta, K., Xiang, Y., ... Otsuki, K. (2014). A model relating transpiration for Japanese cedar and cypress plantations with stand structure. Forest Ecology and Management, 334, 301–312. https://doi. org/10.1016/j.foreco.2014.08.041
- Komiyama, A., Kato, S., & Ninomiya, I. (2002). Allometric Relationships for Deciduous Broad-leaved Forests in Hida District, Gifu Prefecture, Japan. JOURNAL OF THE JAPANESE FORESTRY SOCIETY, 84(2), 130–134. https://doi.org/10.11519/jjfs1953.84.2_130
- Köstner, B., Falge, E. M., Alsheimer, M., Geyer, R., & Tenhunen, J. D. (1998). Estimating tree canopy water use via xylem sapflow in an old Norway spruce forest and a comparison with

- simulation-based canopy transpiration estimates. Annals of Forest Science, 55, 125–139.
- Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., ... Otsuki, K. (2005). Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. Agricultural and Forest Meteorology, 135(1–4), 110–116. https://doi.org/10.1016/j.agrformet.2005.11.007
- Kumagai, T., Tateishi, M., Miyazawa, Y., Kobayashi, M., Yoshifuji, N., Komatsu, H., & Shimizu, T. (2014). Estimation of annual forest evapotranspiration from a coniferous plantation watershed in Japan (1): Water use components in Japanese cedar stands. Journal of Hydrology, 508, 66–76. https://doi.org/10.1016/j.jhydrol. 2013.10.047
- Kume, T., Tsuruta, K., Komatsu, H., Kumagai, T., Higashi, N., Shinohara, Y., & Otsuki, K. (2010). Effects of sample size on sap flux-based stand-scale transpiration estimates. Tree Physiol, 30(1), 129–138. https://doi.org/10.1093/treephys/tpp074
- Larjavaara, M., Berninger, F., Palviainen, M., Prokushkin, A., & Wallenius, T. (2017). Post-fire carbon and nitrogen accumulation and succession in Central Siberia. Scientific Reports, 7(12776). https://doi.org/10.1038/s41598-017-13039-2
- Law, B. E., Van Tuyl, S., Cescatti, A., & Baldocchi, D. D. (2001).
 Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. Agricultural and Forest Meteorology, 108, 1–14.
- Litvak, E., McCarthy, H. R., & Pataki, D. E. (2017). A method for estimating transpiration of irrigated urban trees in California. Landscape and Urban Planning, 158, 48–61. https://doi.org/10.1016/j.landurbplan.2016.09.021
- Liu, X., Silins, U., Lieffers, V. J., & Man, R. (2003). Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Canadian Journal of Forest Research, 33, 1295–1303.
- Lohmann, J., & Becker, G. (1993). Die Xylemleitquerschnitte von Fichten (Picea abies (L.) Karst.) unterschiedlicher Vitalitätsgrade und Altersklassen. Holz als Roh- und Werkstoff, 51, 93–100.
- Loustau, D., Berbigier, P., Roumagnac, P., Arruda-Pacheco, C., David, J. S., Ferreira, M. I., ... Tavares, R. (1996). Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. Oecologia, 107, 33–42.
- Maier, C. A., Albaugh, T. J., Cook, R. I., Hall, K., McInnis, D., Johnsen, K. H., ... Vose, J. M. (2017). Comparative water use in short-rotation Eucalyptus benthamii and Pinus taeda trees in the Southern United States. Forest Ecology and Management, 397, 126–138. https://doi.org/10.1016/j.foreco.2017.04.038
- Martin, J. G., Kloeppel, B. D., Schaefer, T. L., Kimbler, D. L., & McNulty, S. G. (1998). Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. Canadian Journal of Forest Research, 28, 1648–1659.
- Martin-StPaul, N. K., Limousin, J. M., Vogt-Schilb, H., Rodriguez-Calcerrada, J., Rambal, S., Longepierre, D., & Misson, L. (2013). The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a

- throughfall exclusion experiment. Glob Chang Biol, 19(8), 2413–2426. https://doi.org/10.1111/gcb.12215
- Meinzer, F. C., Woodruff, D. R., & Shaw, D. C. (2004). Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. Plant, Cell and Environment. 27, 937–946.
- Mencuccini, M., & Grace, J. (1994). Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiology, 15(1–10).
- Monserud, R. A., & Marshall, J. D. (1999). Allometric crown relations in three northern Idaho conifer species. Canadian Journal of Forest Research, 29, 521–535.
- Moore, G. W., Bond, B. J., & Jones, J. A. (2011). A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands. Forest Ecology and Management, 262(12), 2263–2270. https://doi.org/10.1016/j.foreco.2011.08.018
- Moore, G. W., Bond, B. J., Jones, J. A., Phillips, N., & Meinzer, F. C. (2004). Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. Tree Physiology, 24, 481–491.
- Mori, S., & Hagihara, A. (1991). Crown profile of foliage area characterized with the Weibull distribution in a hinoki (Chamaecyparis obtusa) stand. Trees, 5(3), 149–152. https://doi.org/10.1007/bf00204336
- Mörling, T., & Valinger, E. (1999). Effects of fertilization and thinning on heartwood area, sapwood area and growth in Scots pine. Scandinavian Journal of Forest Research, 14(5), 462–469. https://doi.org/10.1080/02827589950154168
- Nagano, M., & Kira, T. (1978). Aboveground biomass. JIBP synthesis Vol. 18 Biological production in a warm-temperate evergreen oak forest of Japan. University of Tokyo Press, 69–82.
- Naidu, S. L., DeLucia, E. H., & Thomas, R. B. (1998). Contrasting patterns of biomass allocation in dominate and suppressed loblolly pine. Canadian Journal of Forest Research, 28, 1116–1124.
- Nakagaki, K. (1983). Biomass of attached dead branches and their CO2 release in hinoki cypress and Japanese red cedar plantations. (Master), Faculty of Agriculture, Nagoya University, Japan.
- Nishioka, M., Umehara, T., & Nagano, M. (1982). Leaf, branch and stem biomass of composing tree species of forests near the Japanese macaque habitat on Mt. Minoh (in Japanese with title translated by Masae Ishihara). Reports on Japanese macaque on Mt. Minoh, 117–139.
- O'Hara, K. L., & Valappil, N. I. (1995). Sapwood leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Canadian Journal of Forest Research, 25, 1553–1557.
- Ohtsuka, T., Akiyama, T., Hashimoto, Y., Inatomi, M., Sakai, T., Jia, S., ... Koizumi, H. (2005). Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. Agricultural and Forest Meteorology, 134(1), 27–38. https://doi.org/10.1016/j.agrformet.2005.11.005
- Ojansuu, R., & Maltamo, M. (1995). Sapwood and heartwood taper in Scots pine stems. Canadian Journal of Forest Research, 25, 1928–1943.

- Parviainen, T. (1999). Investigating the biomass and crown structure of mixed stand birch trees for process-based models [In Finnish]. (Master), University of Helsinki, Finland.
- Phillips, N., Bond, B. J., McDowell, N. G., & Ryan, M. G. (2002). Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiology, 22, 205–211.
- Phillips, N., Bond, B. J., McDowell, N. G., Ryan, M. G., & Schauer, A. (2003). Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees. Ecology, 17, 832–840.
- Poyatos, R., Llorens, P., & Gallart, F. (2005). Transpiration of montane Pinus sylvestris L. and Quercus pubescens Willd. forest stands measured with sap flow sensors in NE Spain. Hydrology and Earth System Sciences, 9, 493–505.
- Prokushkin, A. Sapwood measurements for Larix gmelinii trees in the central part of Nizhnyaya Tunguska River basin in Central Siberia. Unpublished.
- Reid, D. B., Lieffers, V., & Silins, U. (2004). Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient? Trees, 18(4). https://doi.org/10.1007/s00468-003-0317-4
- Reid, D. E. B., Silins, U., & Lieffers, V. J. (2006). Sapwood hydraulic recovery following thinning in lodgepole pine. Annals of Forest Science, 63(4), 329–338. https://doi.org/10.1051/forest:2006013
- Roberts, S. D., Dean, T. J., & Evans, D. L. (2003). Family influences on leaf area estimates derived from crown and tree dimensions in Pinus taeda. Forest Ecology and Management, 172(2), 261–270. https://doi.org/10.1016/S0378-1127(01)00796-4
- Roberts, S. D., Friend, A. L., & Gerard, P. D. (2004). The effect of large applications of nutrients from organic waste on biomass allocation and allometric relations in loblolly pine. Proc. 12th Biennial South. Silvicultural Res. Conf. Gen Tech. Rep. SRS-48.
 US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 398-402.
- Roeh, R. L., & Maguire, D. A. (1997). Crown profile models based on branch attributes in coastal Douglas-fir. Forest Ecology and Management, 96, 77–100.
- Roth, B. E., Jokela, E. J., Martin, T. A., Huber, D. A., & White, T. L. (2007). Genotype × environment interactions in selected loblolly and slash pine plantations in the Southeastern United States. Forest Ecology and Management, 238(1), 175–188. https://doi.org/10.1016/j.foreco.2006.10.010
- Rust, S., Lüttschwager, D., & Hüttl, R. F. (1995). Transpiration and hydraulic conductivity in three Scots pine (Pinus sylvestris L.) stands with different air pollution histories. Water, Air and Soil Pollution, 85, 1677–1682.
- Saito, M. (1981). Estimation of biomass of natural Cryptomeria stand in the Sado experimental forest. Bulletin of Niigata University Forest, 14, 107–114.
- Saito, T., Kumagai, T. o., Tateishi, M., Kobayashi, N., Otsuki, K., & Giambelluca, T. W. (2017). Differences in seasonality and temperature dependency of stand transpiration and canopy conductance between Japanese cypress (Hinoki) and Japanese

- cedar (Sugi) in a plantation. Hydrological Processes, 31(10), 1952–1965. https://doi.org/10.1002/hyp.11162
- Salazar, S., Sanchez, L., Galindo, P., & Santa-Regina, I. (2010). Above-ground tree biomass equations and nutrient pools for a paraclimax chestnut stand and for a climax oak stand in the Sierra de Francia Mountains, Salamanca, Spain. Scientific Research and Essays, 5(11), 1294–1301.
- Santa-Regina, I. Biomass measurements for Castanea sativa and Quercus pyrenaica trees in Spain. Unpublished.
- Santa-Regina, I., & Tarazona, T. (1999). Organic matter dynamics in beech and pine stands of mountainous Mediterranean climate area. Annals of Forest Science, 56(8), 667–677.
- Sato, A., Kato, R., & Mori, M. (1971). Growth analysis on the old-growth natural stands of Pinus densiflora. Bulletin of the Japan Forest Society, 82, 180–182.
- Satoo, T. (1974a). Primary production relations in a natural forest of Betula maximowicziana in Hokkaido: Materials for the studies of growth in forest stands. Bulletin of the Tokyo University Forests, 66, 109–117.
- Satoo, T. (1974b). Primary production relations in a plantation of Larix leptolepis in Hokkaido: Materials for the studies of growth in forest stands. Bulletin of the Tokyo University Forests, 66, 119–126.
- Satoo, T. (1974c). Primary production relations in a young plantation of Abies sachalinensis in Hokkaido: Materials for the studies of growth in forest stands 11. Bulletin of the Tokyo University Forests, 66, 127–137.
- Schulze, E.-D., Schulze, W., Kelliher, F. M., Vygodskaya, N. N., Ziegler, W., Kobak, K. I., ... Hollinger, D. Y. (1995). Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian Larix stands in eastern Siberia. Canadian Journal of Forest Research, 25, 943–960.
- Segawa, K., & Kato, R. (1969). Growth of Quercus serrata coppice forest in Koma Experimental Forest. Technical Report 11, Touhoku Research Center, Forestry and Forest Products Research Institute.
- Segawa, K., Kato, R., & Yoshimura, K. (1973). Populus plantation at mountainous area. Growth and biomass at Terada Experimental stand. Touhoku Research Center, Forestry and Forest Products Research Institute.
- Shinohara, Y., Tsuruta, K., Ogura, A., Noto, F., Komatsu, H., Otsuki, K., & Maruyama, T. (2013). Azimuthal and radial variations in sap flux density and effects on stand-scale transpiration estimates in a Japanese cedar forest. Tree Physiol, 33(5), 550–558. https://doi.org/10.1093/treephys/tpt029
- Simpson, D. G. (2000). Water use of interior Douglas-fir. Canadian Journal of Forest Research, 30, 534–547.
- Sturm, N., Köstner, B., Hartung, W., & Tenhunen, J. D. (1998). Environmental and endogenous controls on leaf- and stand-level water conductance in a Scots pine plantation. Annals of Forest Science, 55, 237–253.
- Sun, X., Onda, Y., Otsuki, K., Kato, H., Hirata, A., & Gomi, T. (2014).

 The effect of strip thinning on tree transpiration in a Japanese cypress (Chamaecyparis obtusa Endl.) plantation. Agricultural

- and Forest Meteorology, 197, 123–135. https://doi.org/10.1016/j.agrformet.2014.06.011
- Suzuki, H. (2012). Estimation of aboveground and belowground carbon stock in a forest of Northern Hokkaido. (Master), Hokkaido University, Japan.
- Sweda, T., & Shimokawa, G. (2003). Estimation of biomass of secondary deciduous broadleaved forest in the Experimental Forest of Ehime University. Estimation of bioproductivity and carbon fix ability on broadleaved secondary forests. Report of Grant-in-Aid for Scientific Research.
- Tadaki, Y., Takeuchi, I., Kawahara, T., Sato, A., & Hatiya, K. (1979).
 Growth analysis on the natural stands of Japanese red pine (Pinus densiflora Sieb. et Zucc.) III. Results of experiment (Research note). Bulletin of the Forestry and Forest Products Research Institute, 305, 125–144.
- Takagi, K., Kotsuka, C., Fukuzawa, K., Kayama, M., Makoto, K., Watanabe, T., ... Akibayashi, Y. (2010). Allometric relationships and carbon and nitrogen contents for three major tree species (Quercus crispula, Betula ermanii, and Abies sachalinensis) in Northern Hokkaido, Japan. Eurasian Journal of Forest Research, 13, 1-7.
- Takahashi, K., Yoshida, K., Suzuki, M., Seino, T., Tani, T., Tashiro, N., ... Kohyama, T. (1999). Stand biomass, net production and canopy structure in a secondary deciduous broad-leaved forest, northern Japan. Research bulletin of the Hokkaido University Forests, 56, 70–85.
- Tanao, T. (1982). Biomass and its increment in a hinoki plantation. (Master), Faculty of Agriculture, Nagoya University, Japan.
- Tange, T. (1995). Ecophysiological study on the growth of Cryptomeria japonica planted trees. Bulletin of the Tokyo University Forests, 93, 65–145.
- Tange, T., & Kojima, K. (2010). Aboveground biomass data of Anno growth monitoring stands of Cryptomeria japonica in the University Forest in Chiba, The University of Tokyo. Technical Report 49, Miscellaneous information, the Tokyo University Forests.
- Telander, A. C., Slesak, R. A., D'Amato, A. W., Palik, B. J., Brooks, K. N., & Lenhart, C. F. (2015). Sap flow of black ash in wetland forests of northern Minnesota, USA: Hydrologic implications of tree mortality due to emerald ash borer. Agricultural and Forest Meteorology, 206, 4–11. https://doi.org/10.1016/j.agrformet.2015.02.019
- Tognetti, R., Longobucco, A., Miglietta, F., & Raschi, A. (1998).
 Transpiration and stomatal behaviour of Quercus ilex plants during the summer in a Mediterranean carbon dioxide spring. Plant, Cell and Environment, 21, 613–622.
- Tognetti, R., Longobucco, A., Miglietta, F., & Raschi, A. (1999). Water relations, stomatal response and transpiration of Quercus pubescens trees during summer in a Mediterranean carbon dioxide spring. Tree Physiology, 19, 261–270.
- Traver, E., Ewers, B. E., Mackay, D. S., & Loranty, M. M. (2010). Tree transpiration varies spatially in response to atmospheric but not edaphic conditions. Functional Ecology, 24, 273–282.
- Utsugi, H., Abe, S., Iida, S., Tobita, H., Tanouchi, H., & Sato, M. (2004). The above ground biomass components of boreal deciduous

- forest in Northen Japan 1: The above ground biomass estimation and vertical distribution of foliage area. The Bulletin of Hokkaido Branch of the Japanese Forestry Society, 52, 99–101.
- Utsugi, H., & Tanouchi, H. Biomass measurements for Larix kaempferi trees in Japan. Unpublished.
- van Hees, A. F. M., & Bartelink, H. H. (1993). Needle area relationships of Scots pine in the Netherlands. Forest Ecology and Management, 58, 19–31.
- Vanderklein, D. W., Schäfer, K. V. R., & Martinez-Vilalta, J. (2012). Crown conductance in dwarf, medium, and tall pitch pines in the Long Island Pine Plains. Trees, 26(5), 1617–1625. https://doi. org/10.1007/s00468-012-0736-1
- Vanninen, P., & Mäkelä, A. (2005). Carbon budget for Scots pine trees: effects of size, competition and site fertility on growth allocation and production. Tree Physiology, 25(1), 17–30. https://doi.org/10.1093/treephys/25.1.17
- Verbeeck, H., Steppe, K., Nadezhdina, N., op de Beeck, M., Deckmyn, G., Meiresonne, L., ... Janssens, I. A. (2007). Stored water use and transpiration in Scots pine: a modeling analysis with ANAFORE. Tree Physiology, 27, 1671–1685.
- Wang, J. R., Letchford, T., Comeau, P., & Kimmins, J. P. (2000). Above- and below-ground biomass and nutrient distribution of a paper birch and subalpine fir mixed-species stand in the Sub-Boreal Spruce zone of British Columbia. Forest Ecology and Management, 130(1), 17–26. https://doi.org/10.1016/ S0378-1127(99)00193-0
- Wang, J. R., Zhong, A. L., Comeau, P., Tsze, M., & Kimmins, J. P. (1995). Aboveground biomass and nutrient accumulation in an age sequence of aspen (Populus tremuloides) stands in the Boreal White and Black Spruce Zone, British Columbia. Forest Ecology and Management, 78(1), 127–138. https://doi.org/10.1016/0378-1127(95)03590-0
- Wang, J. R., Zhong, A. L., Simard, S. W., & Kimmins, J. P. (1996).

 Aboveground biomass and nutrient accumulation in an age sequence of paper birch (Betula papyrifera) in the Interior Cedar Hemlock zone, British Columbia. Forest Ecology and Management, 83(1), 27–38. https://doi.org/10.1016/0378-1127(96)03703-6
- Wang, X., Wang, C., Zhang, Q., & Quan, X. (2010). Heartwood and sapwood allometry of seven Chinese temperate tree species. Annals of Forest Science, 67(4), 410–410. https://doi. org/10.1051/forest/2009131
- Watanabe, T., & Yagi, K. (1984). Above-ground biomass and its vertical distribution in a plantation of Quercus myrsinaefolia.

 Technical Report 23, Miscellaneous information, the Tokyo University Forests.
- Watanabe, T., & Yagi, K. (1985). Above-ground biomass and its vertical distribution of a young Quercus serrata plantation. Bulletin of the Tokyo University Forests, 74, 165–174.
- Whitehead, D., Edwards, W. R. N., & Jarvis, P. G. (1984). Conducting sapwood area, foliage area, and permeability in mature trees of Picea sitchensis and Picea contorta. Canadian Journal of Forest Research, 14, 940–947.

- Whittaker, R. H., Bormann, F. H., Likens, G. E., & Siccama, T. G. (1974). The Hubbard Brook Ecosystem Study: Forest Biomass and Production. Ecological Monographs, 44(2), 233–254. https:// doi.org/10.2307/1942313
- Wullschleger, S. D., Hanson, P. J., & Todd, D. E. (2001). Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. Forest Ecology and Management, 143, 205–213.
- Wullschleger, S. D., & King, A. W. (2000). Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. Tree Physiology, 20, 511–518.
- Wullschleger, S. D., Wilson, K. B., & Hanson, P. J. (2000). Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. Agricultural and Forest Meteorology, 104, 157-168.
- Xiao, C.-W., & Ceulemans, R. (2004). Allometric relationships for needle area of different needle age classes in young Scots pines: needles, branches and trees. Forestry, 77(5), 369–382.
- Yamaba, A. (2007). Estimation of underground biomass of major tree species in forests, Hiroshima prefecture. Bulletin of the Hiroshima Prefectural Forestry Research Center, 39, 23–30.
- Yamada, S., Maruyama, K., & Miyazawa, S. (1957). Biomass of Pinus densiflora mature trees along topographic gradient. Bulletin of the Japan Forest Society, 67, 218–222.
- Yamaji, K. (1991). On the estimation of radiation interception by woody organs in a hinoki plantation. (Master), Faculty of Agriculture, Nagoya University, Japan.
- Yamakura, T., Saito, H., & Shidei, T. (1972). Production and structure of under-ground part of Hinoki (Chamaecyparis obtusa) stand (I). Estimation of root production by means of root analysis. JOURNAL OF THE JAPANESE FORESTRY SOCIETY, 54(4), 118–125. https://doi.org/10.11519/jjfs1953.54.4.118
- Yasui, H., & Fujie, I. (1970). Studies on the productive structure of Shirakashi (Cyclobalanopsis myrsinaefolia Oerst.) coppice-forest managed by selection method. 7. On the growth of third circulation-period at the Shimoyamasa permanent plot. Bulletin of the Faculty of Agriculture, Shimane University, 4, 85–92.
- Yasui, H., & Fujie, I. (1971). Studies on the productive structure of Shirakashi (Cyclobalanopsis myrsinaefolia Oerst.) coppice-forest managed by selection method. 8. On the growth and the biomass at Shirakashi sprout forest by clearing system. Bulletin of the Faculty of Agriculture, Shimane University, 5, 49–55.
- Yasui, H., Fujie, I., & Yamamoto, M. (1983). Studies on the productive structure of Shirakashi (Cyclobalanopsis myrsinaefolia Oerst.) coppice-forest managed by selection method. 10. On the biomass in fifth circulation-period at the Shimoyamasa permanent plot. Bulletin of the Faculty of Agriculture, Shimane University, 17, 29–33.
- Yi, M., Suzaki, T., & Yahata, H. (1989). Nutrient cycling of Pinus thunbergii forests on sand soil in coast (IV) Above ground biomass and nutrient contents of stands. Bulletin of Kyushu Branch of the Japanese Forestry Society, 42, 201–202.

- Younger, N. L., Temesgen, H., & Garber, S. M. (2008). Taper and volume responses of Douglas-fir to sulfur treatments for control of Swiss needle cast in the Coast Range of Oregon. Western Journal of Applied Forestry, 23(3), 142–148.
- Yu, T., Feng, Q., Si, J., Zhang, X., Alec, D., & Zhao, C. (2016). Evidences and magnitude of nighttime transpiration derived from Populus euphratica in the extreme arid region of China. Journal of Plant Biology, 59(6), 648–657. https://doi.org/10.1007/s12374-015-0536-4
- Zhang, J.-G., He, Q.-Y., Shi, W.-Y., Otsuki, K., Yamanaka, N., & Du, S. (2015). Radial variations in xylem sap flow and their effect on whole-tree water use estimates. Hydrological Processes, 29(24), 4993–5002. https://doi.org/10.1002/hyp.10465
- Zimmermann, R., Schulze, E.-D., Wirth, C., Schulze, E.-E., McDonald, K. C., Vygodskaya, N. N., & Ziegler, W. (2000). Canopy transpiration in a chronosequence of Central Siberian pine forests. Global Change Biology, 6, 25–37.