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Allometries for Widely Spaced *Populus ssp.* and *Betula ssp.* in Nurse Crop Systems

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Abstract: Nurse crops of widely spaced pioneer trees are a silvicultural approach to protect the regeneration of frost sensitive target tree species. If overstorey nurse crops are harvested, they can provide additional short-term benefits through increased biomass production, e.g., for bioenergy. However, the intensification of biomass exports from forests might impact negatively on ecosystem nutrient pools. Thus, precise allometric biomass equations are required to quantify biomass and nutrient removals. Since an analysis of published allometric equations developed for typical, dense aspen or birch forests showed that the tree height-to-diameter ratio correlated positively and the proportion of branch biomass negatively with stand density, we developed new allometric biomass equations for widely spaced aspen and birch growing at 4 × 4 m spacing. These equations yielded a root mean squared error of 13% when predicting total aboveground woody biomass for our sample trees. In contrast, the corresponding root mean squared error produced by allometric biomass equations from the literature ranged between 17% to 106% of actual dry biomass. Our results show that specific allometric biomass equations are needed for widely spaced pioneer trees both for accurate estimates of biomass and the nutrients contained within.

Keywords: allometric biomass equation; nurse crop; *Populus ssp.*; *Betula ssp.*; wide tree spacing; h/d ratio; branch biomass allocation

1. Introduction

European and national policies promote the production and use of renewable energies to support climate change mitigation. Energy from woody biomass is considered a crucial component within the set of possible renewable energies [1]. Expansion of short rotation coppice plantations (SRC) on agricultural land was proposed as one approach to increase biomass production [1,2], but for a number of reasons, this production system is currently not attractive to farmers in central Europe [3], and the competition with food production is in many situations not desirable [4,5]. Therefore, it has been suggested to intensify the provision of woody biomass from forests [5]. This may take place in conventional forest stands through increased removals or on areas specifically dedicated to increased biomass production.

Fast growing tree species suitable for rapid biomass production require large open areas, which are typically avoided in close-to-nature oriented forest management of central Europe [6]. However, storms, droughts, or pest insect outbreaks increasingly often result in large scale forest disturbance [7,8]. Large open areas created by these disturbances require restoration with site adapted tree species [9] and at the same time might be used to cultivate a crop of fast growing tree species to produce additional biomass [10,11].

Nurse crop (NC) systems can be one way to combine these restoration and production goals. They comprise a temporal nurse crop overstorey of fast growing, early successional tree species, as well as an understory of shade-tolerant target tree species, which is typically established after the sheltering canopy of the nurse crop has developed [11–13]. Nurse crops are particularly useful in places, where large forest gaps are prone to extreme temperature and moisture regimes [14] to moderate micro-climatic conditions and thus facilitate the establishment and growth of more sensitive target tree species [15–17]. Once the nurse crop understory trees have successfully established the biomass of the overstorey nurse crop trees may be harvested to release the target tree species from the competition of the overstorey.

Nurse crop management, biomass utilisation, and especially carbon sequestration estimates and nutrient sustainability considerations in forests require reliable information on the biomass storage and its distribution across various biomass compartments in trees [18–20]. For this purpose numerous yield tables and allometric biomass equations have been developed for commercially important tree species [21–26].

However, yield tables and biomass allometries of early successional tree species such as *Populus ssp.* or *Betula ssp.*, typical overstorey species in nurse crop stands, are few for Central Europe. Most of the studies dealing with *Populus ssp.* or *Betula ssp.* have been conducted in Canada, Finland, Sweden, or the USA owing to their commercial importance in these countries. The use and extrapolation of such allometric biomass equations from these situations to nurse crop systems in central Europe was questionable owing to differences in silvicultural treatments, genetics, or site conditions [27–29]. In addition, these studies from other regions focussed mostly on young forest stands aged between 3 to 10 years, with diameters at breast height between 1 to 10 cm, and stand densities around 10,000 stems per hectare. In contrast, the nurse crops assessed in this study were 19 years old, their diameters at breast height ranged between 10 and 30 cm, and the stand density was about 500 to 600 trees per hectare.

Trees in dense forests are exposed to intensive competition for light and other resources and thus typically allocate a high proportion of carbon to height growth to reach the top of the canopy [30]. In contrast and regardless of their height, trees in widely spaced forests have nearly unrestricted access to solar radiation, and thus allocate a larger proportion of carbon to the lateral development of branches and to radial stem growth [31,32]. Thus, allometric relationships reflect the adaptation of tree individuals to their environment [19]. As a consequence, one might expect the single tree stem biomass to be overestimated but branch biomass to be underestimated in widely spaced trees when applying allometric biomass equations developed for forests of higher stand density. Because branch biomass is usually rich in nutrients, its underestimation directly results in the underestimation of nutrient losses per unit exported biomass [33]. Hence, it is unclear how accurate existing allometric biomass equations from high density forests can estimate tree biomass in low density forests such as nurse crops.

Therefore, the objective of this study was to assess whether prediction of biomass for widely spaced trees typically found in nurse crops requires different allometric biomass equations from those provided in the literature.

We used a wide range of data from the literature to study this density effect in particular on the height-to-diameter ratio (h/d ratio) [27,34] and the proportion of branch biomass [32] of *Betula ssp.* (birch) and *Populus ssp.* (aspen) trees, which often dominate young forests following disturbance [35] or abandoning of agricultural land management [36]. We then developed allometric biomass equations for aspen and birch trees growing in widely spaced nurse crops. We fitted different equations to the four biomass compartments total aboveground woody biomass, stem wood, stem bark, and branches. We also developed allometric biomass equations for young *Quercus ssp.* trees growing in the understory of nurse crops. Eventually, we tested the precision of allometric biomass equations from the literature when applied to our sample trees from widely spaced nurse crops. Hence, this paper is the first of its kind to provide the required information for future biomass production and sustainability assessment in low density nurse crops.

2. Materials and Methods

2.1. Study Area and Forests

The nurse crop systems analysed in this study were established in 1991 following large scale wind-throw of pure stands of Norway spruce (*Picea abies* (L.) Karst.) [13]. Originally, the trial intended to examine the effects of nurse crops on the establishment, survival, and quality of target tree species at frost-prone sites. To allow for the comparison between nurse crop systems and traditional restoration methods, control plots were established and directly replanted with pure stands of the target tree species, in this case *Quercus ssp.*

The present study focussed on the two sites Kirchberg (K) and Sobernheim (S). The sites were located approximately 50 kilometres apart from each other at 450 and 420 m a.s.l., respectively, within the Hunsrück mountain region in the German federal state of Rhineland-Palatinate.

Mean annual air temperatures (1988 until 2011) were 8.1 °C in Kirchberg and 9.0 °C in Sobernheim with a mean air temperature during the vegetation season (daily average temperature >5 °C) of 12.4 and 13.0 °C in Kirchberg and Sobernheim, respectively. Mean annual precipitation (2002 until 2011) was 836.5 mm in Kirchberg and 613.8 mm in Sobernheim, with 66% and 69% of the annual precipitation occurring during the vegetation season, respectively [37] (data unpublished).

Both sites were characterised by periodically water logged soils identified as Pseudogley in Kirchberg and Cambisol-Pseudogley in Sobernheim. Mean soil acidity (pH) was 3.8 and 3.6, mean cation exchange capacity (CEC) was 71.4 and 68.2 $\mu\text{mol-c/g}$, and mean base cation saturation was 14.3% and 17.0% in Kirchberg and Sobernheim, respectively.

The nurse crop experiments comprised in the overstorey pure plots of hybrid aspen (*Populus tremula* L. \times *Populus tremuloides* Michx. “Austria”) and hybrid birch (*Betula pendula* Roth \times *Betula pubescens* Ehrh.) in Kirchberg and pure plots of hybrid aspen and common birch (*Betula pendula* Roth) in Sobernheim. These treatments will be referred to in the following simply as aspen and birch regardless of the specific species or hybrid. The understoreys of nurse crop plots as well as the control plots were established with *Quercus robur* L. in Kirchberg and *Quercus petraea* (Mattuschka) Liebl. on better drained soils in Sobernheim [38]. If necessary, possible effects that hybridization may have on tree height or diameter at breast height were analysed and accounted for within the modelling process. Any trees from the *Quercus ssp.* sections were called “oak”; if necessary, we differentiated between “oak mono” representing the control plots and ‘oak under nurse crops’ representing oak planted under a nurse crop shelter.

At each of the two study sites, two plots of aspen and two sample plots of birch nurse crop system, as well as four plots of oak monoculture were installed; a total of 16 plots. Aspen and birch nurse crops were underplanted with oak in 1996. Plots were of quadratic shape with a side length of 25 m for aspen and 50 m for birch nurse crop systems and 25 or 50 m for oak monocultures.

At establishment, seedlings of aspen and birch were 2 years old and planted at a spacing of 4 \times 4 m. Understorey oak seedlings were 5 and 3 years old and planted at 4 \times 1.5 m and 4 \times 1 m spacing in Sobernheim and Kirchberg, respectively; planting rows were parallel to nurse crop rows and offset by 2 m. Monoculture oak stands were planted in two ways: five out of eight stands were established using 2 year old standard seedlings with a plant spacing of 1.5 \times 0.7 m, and three stands were established using larger seedlings with a 2 \times 1 m spacing (Kirchberg 3 years; Sobernheim 5 years). However, we found (results not shown) that these two different spacings had no significant effect on yield and allocation of biomass at the time of sampling.

Hence, we compared only oak monocultures with 10,000 seedlings per hectare with plantings of oak (2500 seedlings per ha) beneath a nurse crop of 650 trees per hectare.

2.2. Biomass Sampling

Diameter at breast height (dbh) was measured for all aspen and birch trees as well as for all oak trees growing on a diagonal plot transect of 2 m width. At each plot, five aspen, birch, or oak trees were destructively sampled. In addition to recording diameter at breast height and height of those trees, stem discs were extracted at 2 m intervals for aspen and birch. The length of oak stems with a diameter larger than 4 cm was divided by six and stem discs were extracted at these relative intervals. Three branches were sampled from the lower, middle, and upper crown sections, respectively.

For each sample tree, the fresh weight was recorded for all branches, stem sections, and discs. For stem discs, fresh weight was recorded separately for wood and bark. Stem bark and sample branches were then chipped for further treatment. Finally, all samples were oven dried at 40 °C until weight constancy.

We used the mean stem wood-to-stem bark ratio, which was calculated from our fresh sample discs, to calculate the wood and bark biomass of the respective tree section. We then used a mean dry-to-fresh weight ratio to calculate the dry weight of all tree components.

For oaks growing in the understorey of nurse crops, only the total aboveground woody biomass was measured.

2.3. Supportive Information from the Literature

To test for the effect of stand density on allometric relationships in aspen and birch, we studied the effect of stand density on the tree height-to-diameter ratio and the allocation of branch biomass. Additionally, we studied the performance of published allometric biomass equations developed for stands of higher density (>650 N/ha) when applied to our sample trees.

For that purpose we compiled stand level data and allometric biomass equations from the literature. We searched the internet for publications using the key words “*Populus ssp.*”, “*Betula ssp.*”, “*Quercus ssp.*”, “aspen”, “birch”, “oak”, “tree height”, “dbh”, “stand density”, “tree allometry”, “dry weight”, “biomass equation”, “biomass”, “aboveground”, “biomass compartments”, “biomass production”, and various combinations of several words, respectively.

From each publication we collected information on stand age, mean tree height, mean diameter at breast height, stand density, study location, allometric biomass equations, respective parameters, and correction factors.

Some publications report detailed information for each replicate stand analysed, whereas only summary results can be found in others. In total, 58 allometric biomass equations developed for trees in Canada, China, Estonia, Finland, Germany, USA, and Sweden were consulted (Table 1). This literature review may not be complete, but we obtained a sufficient number of studies to analyse general trends related to our research question in a global context.

Table 1. Allometric biomass equations and parameters (a, b, c) compiled from the literature as used in this study.

Publication	Compartment	Species	Allometric equation	a	b	c
André (2010) <i>et al.</i> [39]	TotalAboveground	<i>Q. petraea</i>	$a \times (\pi \times dbh)^b$	0.009	2.428	n.a.
Fatemi (2011) <i>et al.</i> [40]	TotalAboveground	<i>B. papyrifera</i>	$10^{(a+b \times \log_{10}(dbh))}$	1.99	2.538	n.a.
Fatemi (2011) <i>et al.</i> [40]	StemWood	<i>B. papyrifera</i>	$10^{(a+b \times \log_{10}(dbh))}$	1.739	2.638	n.a.
Fatemi (2011) <i>et al.</i> [40]	StemBark	<i>B. papyrifera</i>	$10^{(a+b \times \log_{10}(dbh))}$	0.823	2.711	n.a.
Fatemi (2011) <i>et al.</i> [40]	Branch	<i>B. papyrifera</i>	$10^{(a+b \times \log_{10}(dbh))}$	1.476	2.195	n.a.
Fatemi (2011) <i>et al.</i> [40]	Leaves	<i>B. papyrifera</i>	$10^{(a+b \times \log_{10}(dbh))}$	0.622	2.485	n.a.
Grote (2003) <i>et al.</i> [22]	TotalAboveground	<i>Q. petraea</i>	$a \times ((\pi/4) \times (dbh^2))^b$	0.131	1.316	n.a.
Johansson (1999) [41]	TotalAboveground	<i>P. tremula</i>	$a \times dbh^b$	0.000146	2.604	n.a.
Johansson (1999) [41]	Stem	<i>P. tremula</i>	$a \times dbh^b$	0.000065	2.74	n.a.
Johansson (1999) [41]	Branch	<i>P. tremula</i>	$a \times dbh^b$	0.000515	1.873	n.a.
Johansson (1999) [41]	Leaves	<i>P. tremula</i>	$a \times dbh^b$	0.000847	1.416	n.a.
Johansson & Karačić (2011) [42]	TotalAboveground	<i>P. nigra</i> × <i>P. deltoides</i>	$a \times dbh^b$	0.00028	2.459	n.a.
Johansson & Karačić (2011) [42]	Stem	<i>P. nigra</i> × <i>P. deltoides</i>	$a \times dbh^b$	0.00021	2.462	n.a.
Johansson & Karačić (2011) [42]	Branch	<i>P. nigra</i> × <i>P. deltoides</i>	$a \times dbh^b$	0.00001	2.709	n.a.
Johansson & Karačić (2011) [42]	Leaves	<i>P. nigra</i> × <i>P. deltoides</i>	$a \times dbh^b$	0.00042	1.926	n.a.
Johansson (1999) [43]	TotalAboveground	<i>B. pendula</i>	$a \times dbh^b$	0.00087	2.286	n.a.
Johansson (1999) [43]	Stem	<i>B. pendula</i>	$a \times dbh^b$	0.0008	2.282	n.a.
Johansson (1999) [43]	Branch	<i>B. pendula</i>	$a \times dbh^b$	0.00002	2.63	n.a.
Johansson (1999) [43]	Leaves	<i>B. pendula</i>	$a \times dbh^b$	0.004	1.12	n.a.
Johansson (1999) [43]	TotalAboveground	<i>B. pubescens</i>	$a \times dbh^b$	0.00004	2.5	n.a.
Johansson (1999) [43]	Branch	<i>B. pubescens</i>	$a \times dbh^b$	0.00029	2.53	n.a.
Johansson (1999) [43]	Leaves	<i>B. pubescens</i>	$a \times dbh^b$	0.0009	1.477	n.a.
Johansson (1999) [43]	Stem	<i>B. pubescens</i>	$a \times dbh^b$	0.0002	2.543	n.a.
Muukkonen (2007) [44]	TotalAboveground	<i>Q. spp.</i>	$\exp(a + ((b \times dbh)/(dbh + c)))$	−0.604	10.677	15.9
Pastor <i>et al.</i> (1984) [45]	TotalAboveground	<i>P. tremuloides</i>	$a \times dbh^b$	0.086	2.449	n.a.
Pastor <i>et al.</i> (1984) [45]	Stem	<i>P. tremuloides</i>	$a \times dbh^b$	0.07	2.423	n.a.
Pastor <i>et al.</i> (1984) [45]	Branch	<i>P. tremuloides</i>	$a \times dbh^b$	0.012	2.349	n.a.
Rock (2007) [34]	Stem	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	0.0197	2.764	n.a.
Rock (2007) [34]	Branch	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	0.064	2.001	n.a.
Rock (2007) [34]	TotalAboveground	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	0.052	2.545	n.a.
Ruark & Bockheim (1988) [46]	StemWood	<i>P. tremuloides</i>	$\exp(a + b \times \log(dbh))$	−3.202	2.606	n.a.
Ruark & Bockheim (1988) [46]	StemBark	<i>P. tremuloides</i>	$\exp(a + b \times \log(dbh))$	−4.532	2.552	n.a.
Ruark & Bockheim (1988) [46]	Branch	<i>P. tremuloides</i>	$\exp(a + b \times \log(dbh))$	−5.04	2.695	n.a.
Ruark & Bockheim (1988) [46]	Twig	<i>P. tremuloides</i>	$\exp(a + b \times \log(dbh))$	−5.701	1.73	n.a.
this study	TotalAboveground	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b \times h^c$	0.021	2.084	0.936
this study	StemWood	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b \times h^c$	0.006	1.557	1.743
this study	StemBark	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b \times h^c$	0.007	1.763	0.818
this study	Branch	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b \times h^c$	0.015	3.301	−0.684
this study	TotalAboveground	<i>B. pendula</i> × <i>B. pubscenes</i>	$a \times dbh^b \times h^c$	0.019	1.944	1.154
this study	StemWood	<i>B. pendula</i> × <i>B. pubscenes</i>	$a \times dbh^b \times h^c$	0.012	1.432	1.708
this study	StemBark	<i>B. pendula</i> × <i>B. pubscenes</i>	$a \times dbh^b \times h^c$	0.098	2.088	−0.486
this study	Branch	<i>B. pendula</i> × <i>B. pubscenes</i>	$a \times dbh^b \times h^c$	0.001	2.862	0.779
this study	TotalAboveground	<i>Q. spp.</i>	$a \times dbh^b \times h^c$	0.161	2.122	0.21
Suchomel <i>et al.</i> (2012) [28]	TotalAboveground	<i>Q. petraea</i>	$a \times dbh^b$	0.093	2.51	n.a.
Telenius (1999) [47]	TotalAboveground	<i>P. tremula</i> × <i>P. tremuloides</i>	$a + b \times dbh^c$	−718.281	3.565	1.738
Telenius (1999) [47]	TotalAboveground	<i>B. pendula</i>	$a + b \times dbh^c$	32.317	0.329	2.328
Tullus <i>et al.</i> (2009) [48]	TotalAboveground	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	107.719	2.237	n.a.
Tullus <i>et al.</i> (2009) [48]	Stem	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	61.208	2.386	n.a.
Tullus <i>et al.</i> (2009) [48]	Branch	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	23.374	2.161	n.a.
Tullus <i>et al.</i> (2009) [48]	BranchNew	<i>P. tremula</i> × <i>P. tremuloides</i>	$a \times dbh^b$	18.819	1.651	n.a.
Uri <i>et al.</i> (2007) [36]	TotalAboveground	<i>B. pendula</i>	$a \times dbh^b$	142.19	2.25	n.a.
Uri <i>et al.</i> (2007) [36]	Stem	<i>B. pendula</i>	$a \times dbh^b$	118.74	2.19	n.a.
Uri <i>et al.</i> (2007) [36]	BranchOld	<i>B. pendula</i>	$a \times dbh^b$	12.68	2.33	n.a.
Uri <i>et al.</i> (2007) [36]	BranchNew	<i>B. pendula</i>	$a \times dbh^b$	0.93	3.25	n.a.
Uri <i>et al.</i> (2007) [36]	Leaves	<i>B. pendula</i>	$a \times dbh^b$	7.54	2.58	n.a.
Wang <i>et al.</i> (2002) [29]	StemWood	<i>P. tremuloides</i>	$a \times dbh^b$	0.042	2.64	n.a.
Wang <i>et al.</i> (2002) [29]	StemBark	<i>P. tremuloides</i>	$a \times dbh^b$	0.003	3.033	n.a.
Wang <i>et al.</i> (2002) [29]	Branch	<i>P. tremuloides</i>	$a \times dbh^b$	0.001	3.161	n.a.
Wang (2006) [49]	Stem	<i>P. davidiana</i>	$10^{(a+b \times \log_{10}(dbh))}$	1.836	2.471	n.a.
Wang (2006) [49]	Branch	<i>P. davidiana</i>	$10^{(a+b \times \log_{10}(dbh))}$	0.129	3.224	n.a.
Wang <i>et al.</i> (1996) [50]	StemWood	<i>B. papyrifera</i>	$a \times dbh^b$	0.028	2.64	n.a.
Wang <i>et al.</i> (1996) [50]	StemBark	<i>B. papyrifera</i>	$a \times dbh^b$	0.037	2.164	n.a.
Wang <i>et al.</i> (1996) [50]	Branch	<i>B. papyrifera</i>	$a \times dbh^b$	0.002	2.913	n.a.
Wang (2006) [49]	Stem	<i>B. platyphylla</i>	$10^{(a+b \times \log_{10}(dbh))}$	2.141	2.278	n.a.
Wang (2006) [49]	Branch	<i>B. platyphylla</i>	$10^{(a+b \times \log_{10}(dbh))}$	0.952	2.783	n.a.
Zabek & Prescott (2006) [51]	Stem	<i>P. trichocarpa</i> × <i>P. deltoides</i>	$a \times dbh^b \times h^c$	0.008	1.247	1.827
Zabek & Prescott (2006) [51]	Branch	<i>P. trichocarpa</i> × <i>P. deltoides</i>	$a \times dbh^b \times h^c$	0.01	1.492	1.023
Zell (2008) [52]	TotalAboveground	<i>Q. spp.</i>	$a \times dbh^b$	0.121	2.435	n.a.

2.4. Stand Density Effects on Tree Height-to-Diameter Ratio in Aspen and Birch Stands

All information on mean tree height, diameter at breast height, age, and stand density of aspen and birch forests collected from the literature were compiled using a linear mixed-effects model to study the general effect of stand density on the height-to-diameter (h/d) ratio. Since data on stand density and age were skewed to the right, a log-transformation was applied. The defined two-level mixed-effects model was:

$$r_{ijk} = \beta_0^{(1)} + \beta_1^{(1)} \times \log(\text{density}) + \beta_2^{(1)} \times \log(\text{age}) + b_i + b_{ij} + \epsilon_{ijk} \quad (1)$$

with $b_i \sim N(0, \delta^2)$, $b_{ij} \sim N(0, \kappa^2)$, and $\epsilon_{ijk} \sim N(0, \lambda^2)$. r_{ijk} was the mean tree height-to-diameter ratio for trees from sample stand k from species j from study i at given *age* and *density*. $\beta_0^{(1)}$ denoted the intercept, $\beta_1^{(1)}$ was the parameter for density, and $\beta_2^{(1)}$ the parameter for tree age. b_i was a random effect for tree species i , b_{ij} represented a random effect for study j nested within species b_i , and ϵ_{ijk} denoted the residual error.

During the model fitting process no significant fixed effect of the tree genus (aspen, birch) on the height-to-diameter ratio was found and thus it was not included in the model. The tree species effect could not be analysed, because there were too many different species or hybrids of *Betula* ssp. and *Populus* ssp. with only few replicates included in the literature based data set.

2.5. Stand Density Effects on Allocation of Branch Biomass in Aspen and Birch Stands

The proportion of branch biomass in relation to aboveground woody biomass was provided in some publications. For all other publications, we estimated branch biomass using the provided allometric biomass equations, respectively. For this, 100 values of diameter at breast height were randomly simulated from uniform distributions for each of 16 publications within their range of diameters, respectively.

For each simulated diameter at breast height, biomass of branches and of all other compartments were predicted. Compartment-wise biomass predictions were used to calculate the corresponding aboveground woody biomass for each simulated diameter at breast height. The biomass of leaves was not considered. One allometric biomass equation from the literature used tree height as an additional explanatory variable. In this case, height was predicted according to the mean height-to-diameter ratio given in the publications.

For each prediction, we added a residuum simulated from variance estimates provided. The variance indication was first related to the mean biomass predicted for all trees in a study. The produced relative variance was then used to simulate one residuum from a uniform distribution for each tree of each study. For publications that did not specify any variance, we assumed a compartment-specific global relative variance generalised from all other publications that indicated variance. Hence, the assumed relative variance was 30%, 19%, 18%, and 25% of dry mass for branches, stems, stem wood, and stem bark, respectively. The proportion of branch biomass was calculated as the ratio between branch and total aboveground woody biomass.

We then fitted the mixed-effects logistic regression model:

$$\Pi_{ij} = \frac{\exp(\eta_{ij})}{1 + \exp(\eta_{ij})}, \quad (2)$$

where Π_{ij} was the proportion of branch biomass presented for the stand $j = 1, \dots, n_i$ in publication $i = 1, \dots, n$. The linear predictor was:

$$\begin{aligned} \eta_{ij} = & \beta_0^{(2)} + \beta_1^{(2)} \times dbh + \beta_2^{(2)} \times density + \beta_3^{(2)} \times age + \beta_4^{(2)} \times density \times age \\ & + \beta_5^{(2)} \times density \times dbh + \beta_6^{(2)} \times dbh \times density \times age + b_i + \epsilon_{ij} \end{aligned} \quad (3)$$

and contained fixed effects parameters (β), a random parameter $b_i \sim N(0, \tau^2)$ for the study, and $\epsilon_{ij} \sim N(0, \nu^2)$ as residual error.

2.6. Allometric Biomass Equations

Compartment-specific dry mass data were used to fit new allometric biomass equations. Separate models were built for each tree species, individual biomass compartment, and total aboveground woody biomass. The allometric biomass equations were fitted using a non-linear regression least squares approach.

Two types of equations were fitted. In the first type, we used the diameter at breast height as sole explanatory variable (power function):

$$BM = \beta_1^{(3)} \times dbh^{\beta_2^{(3)} + \beta_3^{(3)} \times I\{site=K\}}, \quad (4)$$

with BM being the compartment specific single tree biomass in kilogram dependent on diameter at breast height (dbh) in centimetres. $\beta_3^{(3)}$ was an offset parameter for the study site Kirchberg and was only included when significant at the 5% level. We used residual standard errors (ResSE) as well as the coefficient of determination (R^2 , calculated as one minus residual sum of squares divided by total sum of squares) as a measure of fit.

In the second type of allometric biomass equations tree height was used as an additional explanatory variable:

$$BM = \beta_1^{(4)} \times dbh^{\beta_2^{(4)}} \times height^{\beta_3^{(4)}}. \quad (5)$$

Allometric biomass equations were also used to examine patterns of biomass allocation in relation to diameter at breast height. Compartment-specific biomass predictions were made for several classes of diameter at breast height, and the proportion of biomass of each compartment relative to the total aboveground woody biomass was calculated cumulatively.

2.7. Performance of Allometric Models and Comparison with Literature Allometries

To show how much the biomass estimates of the allometric biomass equation would change if the set of sample trees was a different one, the performance of the fitted allometric models was assessed by means of jackknife resampling in the form of leave-one-out [53,54]. Thus, the model was fitted as many times as observations were available and in each model run a different tree was removed from the sample

population. The prediction error was then recorded for each specific model run and all errors from all runs were finally used to calculate the root mean squared error. The root mean squared error divided by the mean sample tree biomass yielded the relative root mean squared error.

Additionally, bootstrap resampling was applied in form of 199 random samplings with replacement [53]. Pointwise 95% credibility intervals were constructed from the empirical distributions resulting from predictions with the 199 curves for a closely spaced grid of diameters at breast height.

Equations obtained from the literature were used to estimate the aboveground woody biomass and the biomass of branches for our sample tree data. If no allometric biomass equations existed for the prediction of aboveground woody biomass, it was calculated as the sum of compartment specific predictions.

Additionally, stand level aboveground woody biomass and branch biomass were estimated. For this, 650 trees were randomly sub-sampled with replacement from our original sample tree data set, and the probability of each tree to be selected into the sub-sample was weighted by the density probability of stand level tree diameters. The biomass of each tree in the sub-sample was then estimated and the total of all trees was regarded stand level biomass. This process was repeated 199 times for each biomass equation from this study and from the literature, respectively.

Eventually, the performance of the allometric biomass equations from the literature was assessed in terms of bias and root mean squared error and was compared with the performance of our new allometric equations for both single tree and stand level estimates.

2.8. Statistical Analysis

All data handling, calculations, and statistics were performed using the programming language and statistics package R, version 2.12.0 [55], MASS package [56], nlme package [57] and RODBC package for communication with Microsoft Access database [58].

3. Results

3.1. Study Forests

Mean tree height varied between 10.9 and 15.5 m in nurse crops and between 7.7 and 9.0 m in oak monocultures; the mean height of oaks growing in the understorey of nurse crops was 3.6 m. Accordingly, the mean diameter at breast height varied between 16.9 and 19.4 cm in nurse crops and between 5.8 and 7.5 cm in monoculture oaks; the mean diameter at breast height of oaks growing in the understorey of nurse crops was 2.5 cm (Table 2).

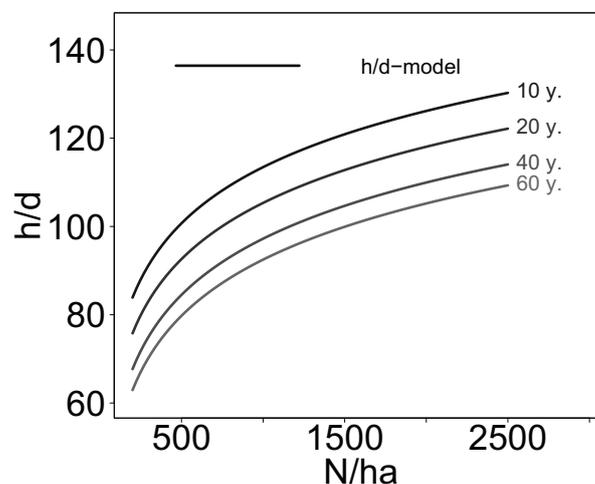
Table 2. Summary description of stand characteristics; K = Kirchberg, S = Sobernheim.

Site	Species	Basal Area m ² /ha	Stand Density N/ha	dbh			Height		
				Mean cm	Min. cm	Max. cm	Mean m	Min. m	Max. m
K	Aspen	17.9	541.0	19.4	4.0	30.5	15.5	12.0	18.8
	Birch	13.3	481.3	17.9	2.5	31.0	12.9	9.7	15.7
	Oak mono	22.1	4219.3	7.5	3.0	16.0	9.0	7.1	10.3
	Oak under Aspen	1.5	2497.0	2.5	0.4	6.2	3.9	1.5	6.4
	Oak under Birch	1.5	2499.2	2.5	0.4	7.9	3.6	1.3	7.9
S	Aspen	10.6	445.9	16.9	7.3	23.2	13.8	10.4	16.4
	Birch	12.8	499.8	17.4	6.0	28.0	10.9	9.2	13.0
	Oak mono	11.8	3841.6	5.8	2.0	13.8	7.7	6.1	8.7
	Oak under Aspen	0.9	1664.7	2.4	0.8	5.4	n.a.	n.a.	n.a.
	Oak under Birch	0.9	1665.0	2.5	0.6	5.5	n.a.	n.a.	n.a.

3.2. Stand Density Effects

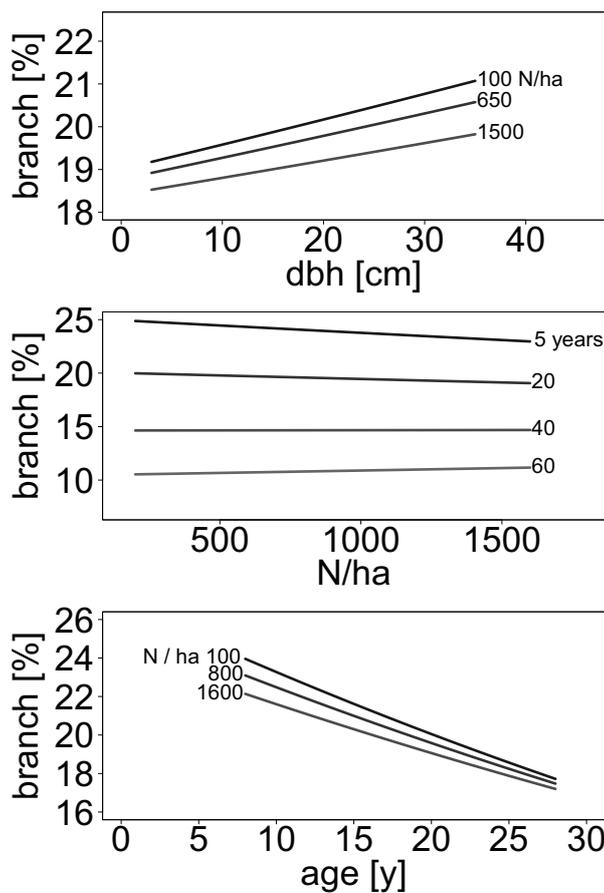
A linear mixed-effects model [Equation (1)] revealed significant effects of stand density and age on the height-to-diameter ratio. The parameter estimate for $\beta_1^{(1)}$ for the log of stand density was 18.366 ($p < 0.001$), for $\beta_2^{(1)}$ for the log of tree age was -12.342 ($p < 0.05$), and for $\beta_0^{(1)}$ for the intercept was 15.027 (n.s.). The model included random effects at the tree species level (0.004) and at the study level nested within the tree species level (9.693). Hence, the height-to-diameter ratio was positively correlated with stand density but negatively with tree age (Figure 1).

Figure 1. Relationship between height-to-diameter (h/d) ratio and stand density (N/ha) for a selection of stand ages according to data compiled from the literature [Equation (1)].



Model 2 and 3 identified *dbh*, *density*, *age*, and interactions of *density* with *age* as well as *density* with *dbh* to significantly affect the allocation of biomass into branches ($p < 0.001$). Parameter estimates were $\beta_0^{(2)} = -1.0666$, $\beta_1^{(2)} = 0.0049$, $\beta_2^{(2)} = 0.000033$, $\beta_3^{(2)} = -0.01967$, $\beta_4^{(2)} = -0.0000031$, $\beta_5^{(2)} = -0.0000067$, and $\beta_6^{(2)} = 0.0000003$. The standard deviation of the random effect at study level was 0.389 and the overall residual standard error was 0.129 (Figure 2).

Figure 2. Relationship between allocation of biomass and diameter at breast height (dbh, top), stand density (N/ha, middle), or tree age (bottom) [Equation (2)].



3.3. Allometric Biomass Equations and Analysis of Model Performance

The residual standard errors produced by allometric biomass equations using diameter at breast height as explanatory variable ranged between 1 and 13 kg (Table 3, Figure 3). Models including tree height as an additional explanatory variable reduced residual standard errors especially for stem wood but also for aboveground woody biomass (Table 4, Figure 4).

Table 3. Parameter estimates, p -values, residual standard errors (ResSE), and R^2 (calculated as one minus residual sum of squares divided by total sum of squares) for allometric biomass equations using diameter at breast height as explanatory variable [Equation (4)].

Species	Compartment	$\beta_1^{(3)}$			$\beta_2^{(3)}$			$\beta_3^{(3)}$			n	ResSE	ps. R^2
		Est.	St.Err.	p -value	Est.	St.Err.	p -value	Est.	St.Err.	p -value			
Aspen	stem wood	0.197	0.102	0.070	2.032	0.173	0.0	n.a.	n.a.	n.a.	19	9.638	0.94
	stem bark	0.035	0.011	0.005	1.985	0.103	0.0	0.031	0.014	0.046	19	0.938	0.96
	branch	0.004	0.004	0.352	3.182	0.342	0.0	-0.081	0.033	0.026	19	6.843	0.87
	aboveground woody	0.132	0.059	0.040	2.339	0.149	0.0	n.a.	n.a.	n.a.	19	12.527	0.97
Birch	stem wood	0.138	0.061	0.036	2.029	0.144	0.0	0.104	0.020	0.0	20	7.841	0.86
	stem bark	0.053	0.022	0.025	1.872	0.133	0.0	n.a.	n.a.	n.a.	20	1.578	0.96
	branch	0.002	0.002	0.159	3.282	0.215	0.0	n.a.	n.a.	n.a.	20	5.840	0.97
	aboveground woody	0.093	0.041	0.037	2.385	0.144	0.0	0.061	0.017	0.003	20	13.097	0.94
Oak mono	stem wood	0.097	0.023	0.0	2.236	0.099	0.0	0.060	0.022	0.011	35	2.622	0.95
	stem bark	0.052	0.012	0.0	1.874	0.091	0.0	n.a.	n.a.	n.a.	35	0.581	0.93
	branch	0.102	0.031	0.002	2.135	0.129	0.0	-0.117	0.027	0.0	40	2.275	0.84
	aboveground woody	0.23	0.034	0.0	2.169	0.058	0.0	n.a.	n.a.	n.a.	40	3.334	0.98
Oak under nurse crops	aboveground woody	0.138	0.025	0.0	2.341	0.092	0.0	n.a.	n.a.	n.a.	16	0.655	0.98
Oak overall	aboveground woody	0.212	0.026	0.0	2.199	0.048	0.0	n.a.	n.a.	n.a.	56	2.9	0.98

Figure 3. Allometric biomass equations for aspen, birch, and monoculture oak using diameter at breast height as explanatory variable; models with site effect (K & S) [Equation (4)] were plotted separately. Pointwise 95% credibility intervals (ci) were calculated from bootstrap resampling.

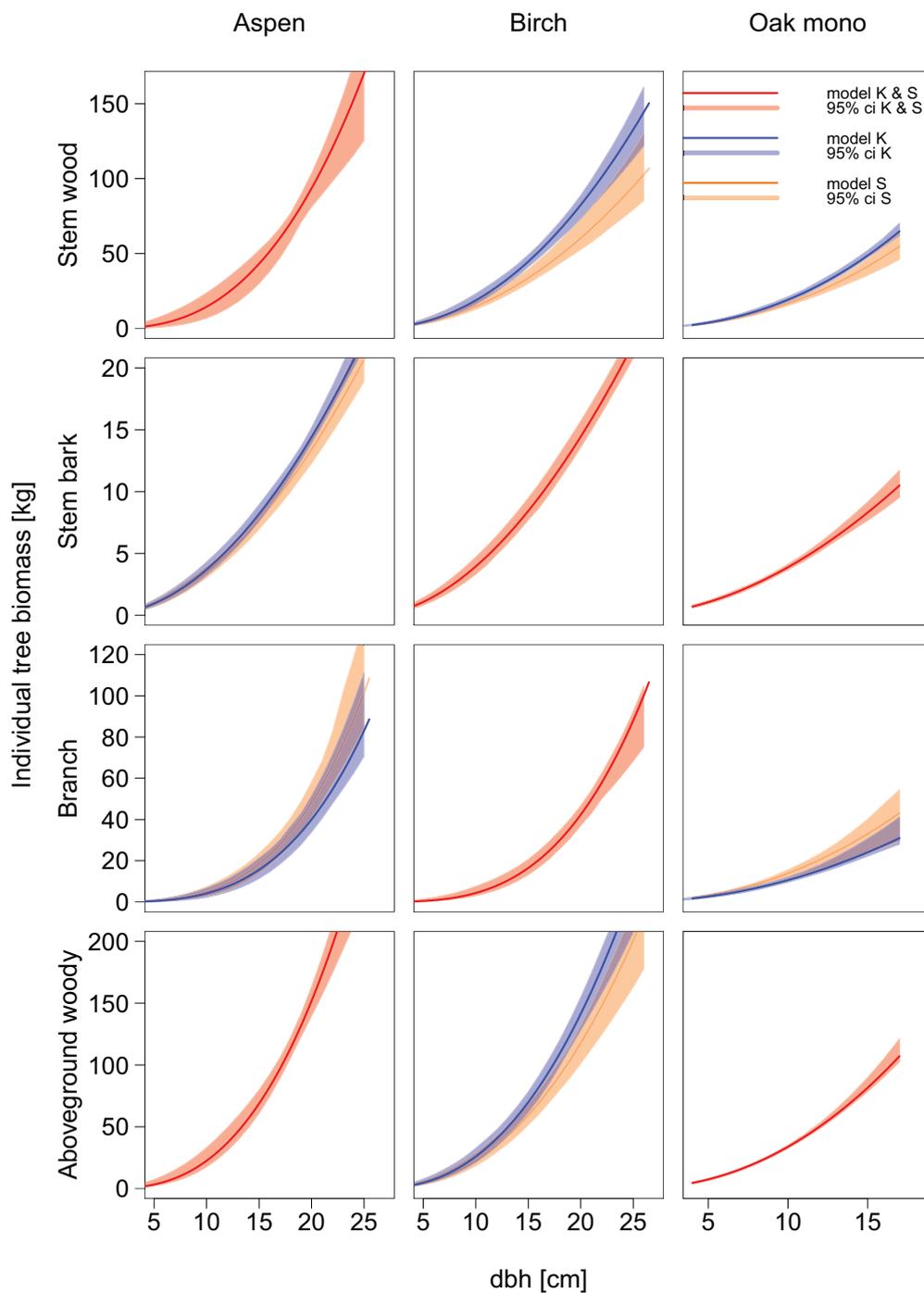
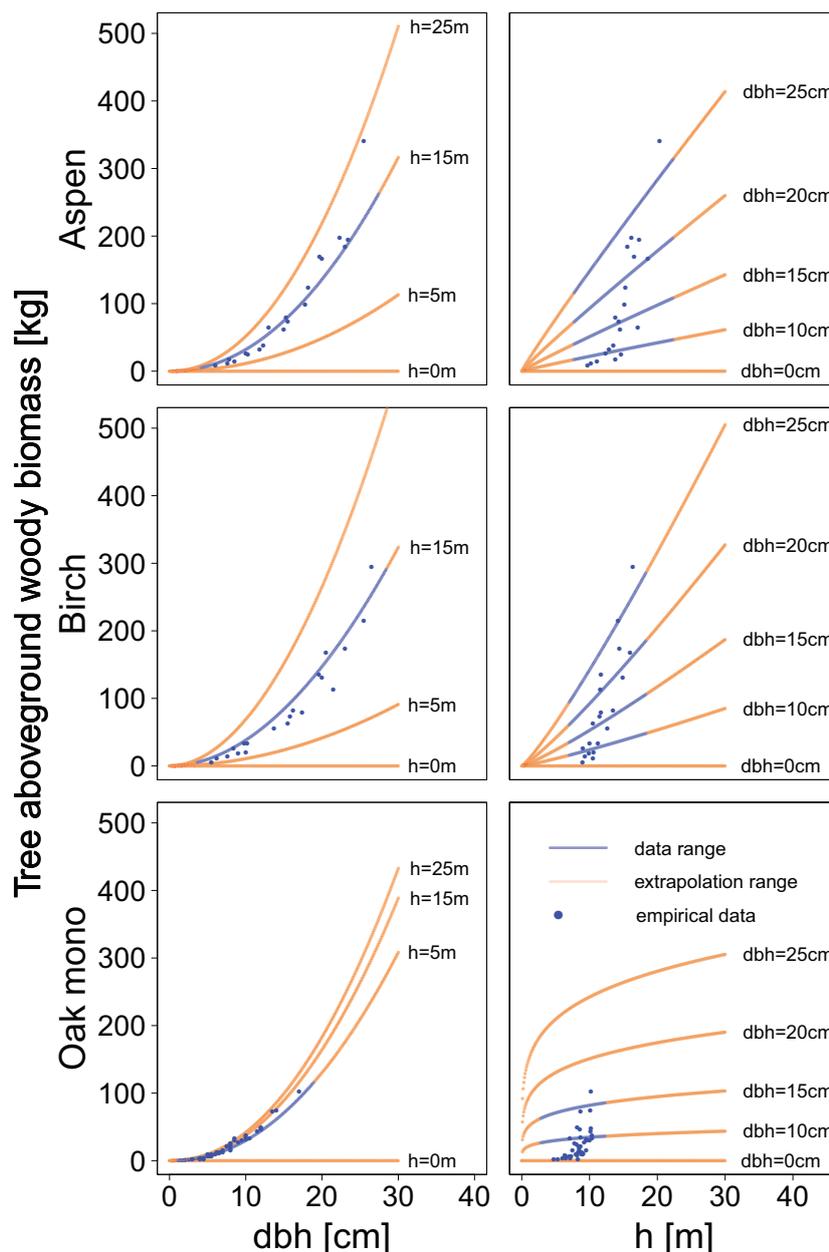


Table 4. Parameter estimates, *p*-values, residual standard errors (ResSE), and *R*² (calculated as one minus residual sum of squares divided by total sum of squares) for allometric biomass equations using diameter at breast height and tree height as explanatory variables [Equation (5)].

Species	Compartment	$\beta_1^{(4)}$			$\beta_2^{(4)}$			$\beta_3^{(4)}$			n	ResSE	ps. <i>R</i> ²
		Est.	St.Err.	<i>p</i> -value	Est.	St.Err.	<i>p</i> -value	Est.	St.Err.	<i>p</i> -value			
Aspen	stem wood	0.006	0.004	0.106	1.557	0.112	0.0	1.743	0.247	0.0	19	5.146	0.98
	stem bark	0.007	0.004	0.117	1.763	0.119	0.0	0.818	0.268	0.008	19	0.854	0.98
	branch	0.015	0.033	0.652	3.301	0.447	0.0	-0.684	0.908	0.462	19	7.948	0.91
	aboveground woody	0.021	0.016	0.211	2.084	0.152	0.0	0.936	0.326	0.011	19	10.587	0.98
Birch	stem wood	0.012	0.006	0.069	1.432	0.164	0.0	1.708	0.264	0.0	20	6.841	0.98
	stem bark	0.098	0.05	0.066	2.088	0.179	0.0	-0.486	0.272	0.092	20	1.49	0.96
	branch	0.001	0.001	0.149	2.862	0.237	0.0	0.779	0.301	0.019	20	5.063	0.98
	aboveground woody	0.019	0.008	0.036	1.944	0.147	0.0	1.154	0.217	0.0	20	10.521	0.98
Oak mono	stem wood	0.010	0.005	0.043	2.135	0.083	0.0	1.167	0.24	0.0	34	2.175	0.97
	stem bark	0.036	0.02	0.081	1.833	0.108	0.0	0.204	0.289	0.486	34	0.585	0.93
	branch	0.957	0.599	0.118	2.147	0.147	0.0	-1.098	0.349	0.003	40	2.444	0.89
	aboveground woody	0.161	0.056	0.007	2.122	0.069	0.0	0.21	0.183	0.258	40	3.319	0.98
Oak under nurse crops	aboveground woody	0.081	0.164	0.629	2.119	0.848	0.027	0.508	1.924	0.796	16	0.678	0.98

Figure 4. The behaviour of allometric biomass equations for aboveground woody biomass using diameter at breast height (dbh) and tree height (h) as explanatory variables [Equation (5)]. **(Left)** Predictions of aboveground woody biomass [kg] plotted versus diameter at breast height [cm] at a selection of fixed heights [m]; **(Right)** Predictions of aboveground woody biomass plotted versus height at a selection of fixed diameters at breast height. Blue line sections indicate the data range, orange parts indicate the extrapolation range. Points represent empirical aboveground woody biomass data.



The relative root mean squared error produced by allometric biomass equations using diameter at breast height as the only explanatory variable ranged between 18% and 20% for stem wood, between 23% and 37% for branches, and between 16% and 20% for the aboveground woody biomass (Table 5). The relative root mean squared errors produced by allometric biomass equations using diameter at breast height and tree height had approximately the same range but never exceeded 18% for stem wood and 16% for aboveground woody biomass (Table 6).

Confidence intervals based on bootstrap resampling usually increased towards the upper end of the diameter range and could inflate up to ± 25 kg; they were generally narrowest for stem bark and could be rather wide for stem wood or branches (Figure 3).

The grand mean allocation of biomass into branches of aspen and birch trees varied between approximately 8% to 38% and was negatively correlated with the diameter at breast height. In contrast, the allocation of branch biomass in oaks grown in monoculture remained constant at about 35% across the entire range of diameters at breast height (Figure 5).

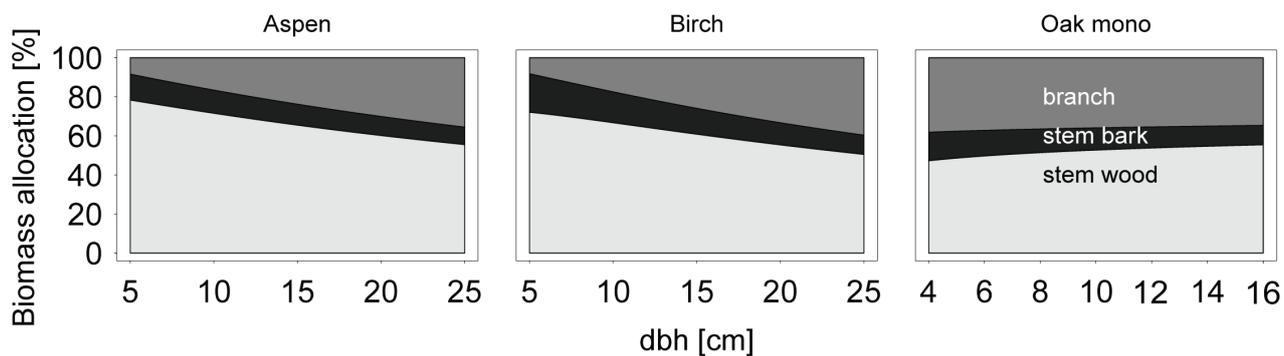
Table 5. Performance of our new allometric biomass equations using diameter at breast height as sole explanatory variable [Equation (4)]; absolute (RMSE) and relative (rel.RMSE) root mean squared errors were calculated for all models from jackknife resampling.

Species	Compartment	RMSE	rel. RMSE [%]
Aspen	stem wood	10.4	20.0
	stem bark	1.1	13.6
	branch	8.6	36.6
	aboveground woody	13.9	16.7
Birch	stem wood	9.5	19.7
	stem bark	1.6	16.7
	branch	6.8	23.3
	aboveground woody	16.8	19.3
Oak	stem wood	2.7	18.4
	stem bark	0.6	18.9
	branch	2.9	32.9
	aboveground woody	3.8	15.6
Oak under nurse crop	aboveground woody	1.0	20.8
Oak overall	aboveground woody	1.0	20.8

Table 6. Performance of our new allometric biomass equations using diameter at breast height and tree height as explanatory variables [Equation (5)]; absolute (RMSE) and relative (rel.RMSE) root mean squared errors were calculated for all models by means of jackknife resampling.

Species	Compartment	RMSE	rel. RMSE [%]
Aspen	stem wood	6.0	11.6
	stem bark	1.0	12.2
	branch	9.7	41.3
	aboveground woody	12.4	14.8
Birch	stem wood	8.8	18.2
	stem bark	1.8	18.3
	branch	6.2	21.3
	aboveground woody	13.6	15.5
Oak mono	stem wood	2.3	15.5
	stem bark	0.6	20.5
	branch	3.1	35.2
Oak under nurse crop	aboveground woody	2.7	57.5

Figure 5. Allocation of biomass across a range of diameters at breast height (dbh) and specified for the biomass compartments stem wood, stem bark, and branches as a fraction of total aboveground woody biomass. Data were estimated using the allometric biomass equations fitted to our sample tree data.



3.4. Comparison with Other Studies

Most allometric biomass equations from the literature (Table 1) produced a considerably larger bias and in all cases larger root mean squared errors compared to allometric biomass equations developed in this study (Table 7).

Regarding root mean squared errors calculated for aboveground woody biomass estimates of aspen trees, the allometric biomass equations provided by Ruark & Bockheim (1988) [46] and Wang (2006) [49] performed closest to the allometric biomass equations developed in this study (Figure 6). Their relative root mean squared error ranged between 19% and 21%, and was thus 40% to 50% higher compared to the root mean squared error produced by allometric biomass equations developed in this study. With respect to branch biomass all equations from the literature produced at least 18 kg and thus 150% larger root mean squared errors than equations developed in this study [49].

Out of all allometric biomass equations for birch those by Wang (2006) [49] and Uri *et al.* (2007) [36] produced a bias of 12 kg and relative root mean squared errors of 24% and 26%, which was 110% and 140% higher than the root mean squared error of our allometric biomass equations. Estimating branch biomass, the root mean squared errors produced by Wang (2006) [49] were by far smallest among equations from the literature and 60% larger compared to the error produced by equations developed in this study.

Regarding allometric biomass equation for oak, the equations published by Zell (2008) [52] produced a similar bias and a 31% larger root mean squared error compared to allometric biomass equations developed in this study, respectively. All other equations produced larger errors; the overall largest bias was 73 kg and the largest relative root mean squared error was 106% when predicting the biomass of aspen trees [47].

The root mean squared errors for aboveground woody biomass estimates at stand level were generally lower compared to tree level estimates (Table 8). Errors produced by equations from the literature decreased in four cases below the 10% level but in most other cases remained larger than 30% or even 50% in the case of branch biomass estimates; root mean squared errors produced by equations from the literature at stand level were thus 30% to 660% larger than the errors produced by our equations (Table 8).

Table 7. Bias and absolute (RMSE) and relative (rel.RMSE) root mean squared errors produced when predicting the aboveground woody biomass and branch biomass of our **sample trees** using our new allometric biomass equations or those from the literature. The RMSE ratio denotes the RMSE produced by allometric biomass equations from the literature divided by the RMSE produced by the corresponding allometric biomass equations fitted in this study, respectively.

Publication	Species	Aboveground woody biomass				Branch biomass			
		bias [kg/tree]	RMSE [kg/tree]	rel.RMSE [%]	RMSE ratio	bias [kg/tree]	RMSE [kg/tree]	rel.RMSE [%]	RMSE ratio
this study	<i>Populus tremula</i> × <i>P. tremulooides</i>	−1.4	13.1	13.6	1.0	0.2	7.4	27.4	1.0
Wang <i>et al.</i> (2002) [29]	<i>Populus tremulooides</i>	0.3	18.1	18.7	1.4	−18.9	28.2	104.4	3.8
Ruark & Bockheim (1988) [46]	<i>Populus tremulooides</i>	−5.6	20.0	20.7	1.5	−13.5	22.1	81.8	3.0
Johansson (1999) [41]	<i>Populus tremula</i>	−7.1	20.3	21.0	1.6	−20.0	31.4	116.2	4.2
Wang (2006) [49]	<i>Populus davidiana</i>	−8.0	21.5	22.3	1.6	−11.5	18.2	67.3	2.5
Pastor <i>et al.</i> (1984) [45]	<i>Populus tremulooides</i>	−12.4	27.1	28.1	2.1	−18.3	28.5	105.5	3.9
Johansson & Karačić (2011) [42]	<i>Populus nigra</i> L. × <i>P. doltooides</i>	−23.9	38.4	39.8	2.9	−16.2	25.3	93.6	3.4
Rock (2007) [34]	<i>Populus tremula</i> × <i>P. tremulooides</i>	−29.2	44.0	45.6	3.4	−10.1	20.2	74.7	2.7
Tullus <i>et al.</i> (2009) [48]	<i>Populus tremula</i> × <i>P. tremulooides</i>	−40.1	60.3	62.5	4.6	−15.4	25.8	95.5	3.5
Zabek & Prescott (2006) [51]	<i>P. trichocarpa</i> × <i>P. deltoides</i>	−49.7	72.9	75.5	5.6	−16.6	27.5	101.8	3.7
Telenius (1999) [47]	<i>Populus tremula</i> × <i>P. tremulooides</i>	−73.3	102.3	106.0	7.8	n.a.	n.a.	n.a.	n.a.
this study	<i>Betula pendula</i> × <i>B. pubescens</i>	−0.9	9.7	11.1	1.0	−0.7	4.7	16.0	1.0
Wang <i>et al.</i> (1996) [50]	<i>Betula papyrifera</i>	−12.0	20.8	23.8	2.1	−21.1	30.9	105.4	6.6
Uri <i>et al.</i> (2007) [36]	<i>Betula pendula</i>	−11.9	22.8	26.1	2.4	−9.7	15.8	53.9	3.4
Johansson (1999) [43]	<i>Betula pendula</i>	22.4	33.0	37.8	3.4	−14.4	22.5	76.8	4.8
Wang (2006) [49]	<i>Betula platyphylla</i>	25.7	37.8	43.3	3.9	−2.2	7.6	25.9	1.6
Johansson (1999) [43]	<i>Betula pubescens</i>	24.1	38.5	44.1	4.0	−11.8	19.5	66.5	4.2
Telenius (1999) [47]	<i>Betula pendula</i>	−37.8	52.7	60.3	5.4	n.a.	n.a.	n.a.	n.a.
Fatemi <i>et al.</i> (2011) [40]	<i>Betula papyrifera</i>	40.6	60.6	69.4	6.3	−14.9	24.5	83.6	5.2
this study	<i>Quercus spp.</i>	0.3	3.2	13.3	1.0	n.a.	n.a.	n.a.	n.a.
Zell (2008) [52]	<i>Quercus spp.</i>	−0.3	4.2	17.4	1.3	n.a.	n.a.	n.a.	n.a.
Suchomel <i>et al.</i> (2012) [28]	<i>Quercus petraea</i>	−2.4	4.6	19.1	1.4	n.a.	n.a.	n.a.	n.a.
Muukkonen (2007) [44]	<i>Quercus spp.</i>	1.2	6.3	26.1	2.0	n.a.	n.a.	n.a.	n.a.
André <i>et al.</i> (2010) [39]	<i>Quercus petraea</i>	4.3	8.6	35.7	2.7	n.a.	n.a.	n.a.	n.a.
Grote (2003) [22]	<i>Quercus petraea</i>	5.7	12.8	53.1	4.0	n.a.	n.a.	n.a.	n.a.

Figure 6. Empirical aboveground woody biomass data of our sample trees and the respective predictions from allometric biomass equations from the literature and this study (Tables 1 and 7); lines connect all predicted values of the respective models.

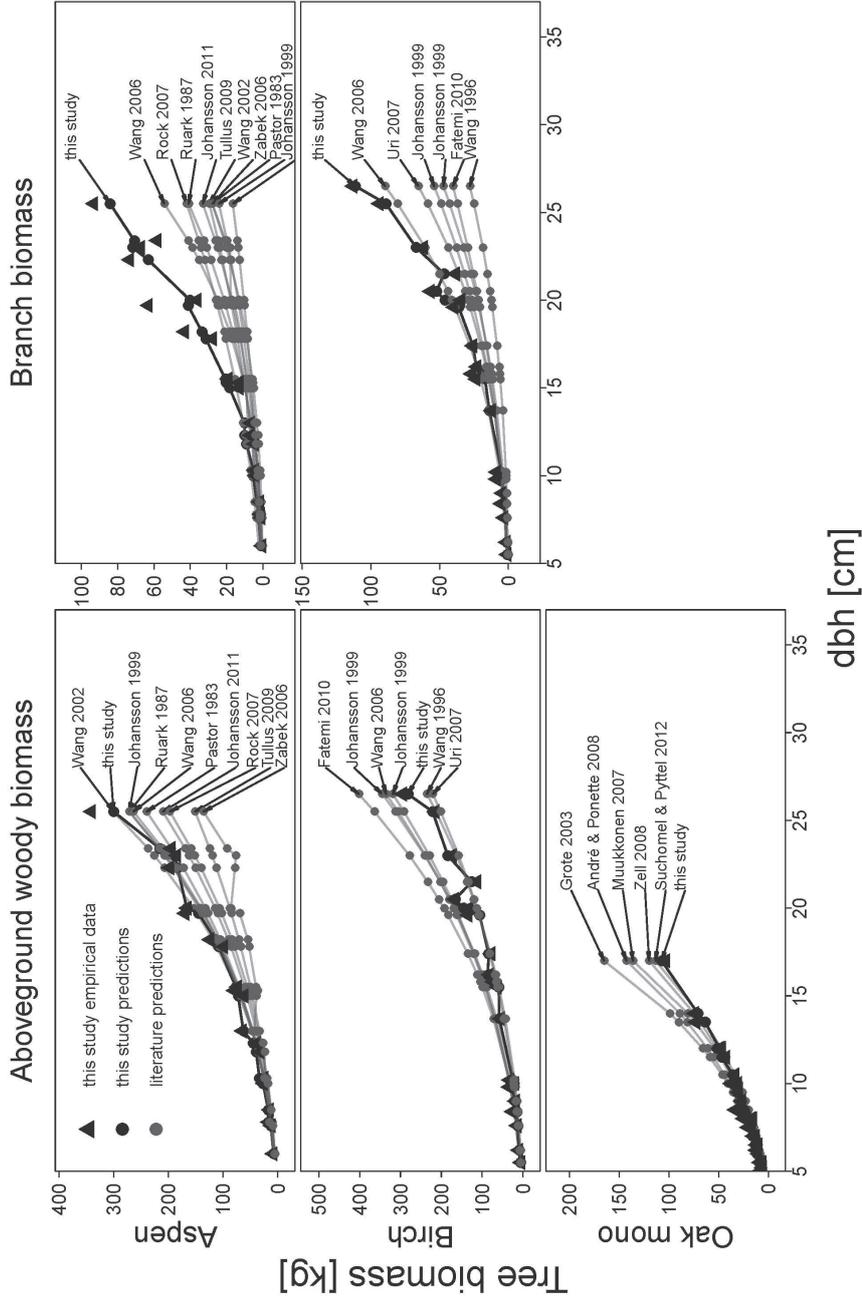


Table 8. Bias and absolute (RMSE) and relative (rel.RMSE) root mean squared errors produced when predicting the aboveground woody biomass and branch biomass of our sample data at **stand level** using our new allometric biomass equations or those from the literature. The RMSE ratio denotes the RMSE produced by allometric biomass equations from the literature divided by the RMSE produced by the corresponding allometric biomass equations fitted in this study, respectively.

Publication	Species	Aboveground woody biomass				Branch biomass			
		bias (Mg/ha)	RMSE (Mg/ha)	rel.RMSE (%)	RMSE ratio	bias (Mg/ha)	RMSE (Mg/ha)	rel.RMSE (%)	RMSE ratio
this study	<i>Populus tremula</i> × <i>P. tremuloides</i>	−1.4	1.4	1.8	1.0	−0.3	0.3	1.6	1.0
Wang <i>et al.</i> (2002) [29]	<i>Populus tremuloides</i>	0.9	1.0	1.3	1.4	−15.7	15.7	70.8	3.8
Ruark & Bockheim (1988) [46]	<i>Populus tremuloides</i>	−4.0	4.0	5.3	1.5	−11.4	11.4	51.6	3.0
Johansson (1999) [41]	<i>Populus tremula</i>	−5.1	5.1	6.7	1.6	−16.7	16.7	75.4	4.2
Wang (2006) [49]	<i>Populus davidiana</i>	−5.8	5.8	7.7	1.6	−9.7	9.7	44.0	2.5
Pastor <i>et al.</i> (1984) [45]	<i>Populus tremuloides</i>	−9.5	9.5	12.4	2.1	−15.2	15.2	68.6	3.9
Johansson & Karačić (2011) [42]	<i>Populus nigra</i> L. × <i>P. doltooides</i>	−18.5	18.5	24.3	2.9	−13.5	13.5	61.2	3.4
Rock (2007) [34]	<i>Populus tremula</i> × <i>P. tremuloides</i>	−22.8	22.8	29.9	3.4	−8.9	8.9	40.1	2.7
Tullus <i>et al.</i> (2009) [48]	<i>Populus tremula</i> × <i>P. tremuloides</i>	−31.7	31.7	41.5	4.6	−13.1	13.1	59.0	3.5
Zabek & Prescott (2006) [51]	<i>P. trichocarpa</i> × <i>P. deltooides</i>	−40.1	40.1	52.6	5.6	−14.1	14.1	63.6	3.7
Telenius (1999) [47]	<i>Populus tremula</i> × <i>P. tremuloides</i>	−57.9	58.0	76.2	7.8	n.a.	n.a.	n.a.	n.a.
this study	<i>Betula pendula</i> × <i>B. pubescens</i>	−0.1	0.3	0.5	1.0	−0.2	0.3	1.2	1.0
Wang <i>et al.</i> (1996) [50]	<i>Betula papyrifera</i>	−8.0	8.0	12.4	2.1	−15.0	15.0	71.2	6.6
Uri <i>et al.</i> (2007) [36]	<i>Betula pendula</i>	−7.7	7.8	12.0	2.4	−6.5	6.5	30.9	3.4
Johansson (1999) [43]	<i>Betula pendula</i>	18.2	18.2	28.2	3.4	−9.9	9.9	47.0	4.8
Wang (2006) [49]	<i>Betula platyphylla</i>	20.6	20.6	31.9	3.9	−0.8	0.8	4.0	1.6
Johansson (1999) [43]	<i>Betula pubescens</i>	19.0	19.0	29.5	4.0	−7.9	7.9	37.5	4.2
Telenius (1999) [47]	<i>Betula pendula</i>	−27.2	27.2	42.1	5.4				
Fatemi <i>et al.</i> (2011) [40]	<i>Betula papyrifera</i>	31.4	31.5	48.7	6.3	−10.1	10.1	48.1	5.2
this study	<i>Quercus spp.</i>	−0.1	0.1	0.4	1.0	n.a.	n.a.	n.a.	n.a.
Zell (2008) [52]	<i>Quercus spp.</i>	0.8	0.8	2.9	1.3	n.a.	n.a.	n.a.	n.a.
Suchomel <i>et al.</i> (2012) [28]	<i>Quercus petraea</i>	−1.4	1.4	4.7	1.4	n.a.	n.a.	n.a.	n.a.
Muukkonen (2007) [44]	<i>Quercus spp.</i>	3.0	3.0	10.5	2.0	n.a.	n.a.	n.a.	n.a.
André <i>et al.</i> (2010) [39]	<i>Quercus petraea</i>	6.6	6.6	22.7	2.7	n.a.	n.a.	n.a.	n.a.
Grote (2003) [22]	<i>Quercus petraea</i>	9.8	9.8	33.8	4.0	n.a.	n.a.	n.a.	n.a.

4. Discussion and Conclusions

4.1. Effects of Stand Density and Tree Age on Allometric Relationships of Trees

In accordance with the findings of other studies [20,27,59,60] our results suggested that the height-to-diameter ratio of aspen and birch individuals significantly increases with increasing stand density. However, height-to-diameter ratio was also affected by the age of trees [61,62].

Also, the younger the tree the more biomass was allocated into branches, and this effect was especially pronounced at low stand densities (Figure 2). Similar findings were reported by Sands & Landsberg (2002) [63] and Neilsen & Gerrand (1999) [64].

With increasing age, trees generally tend to invest more resources into radial stem growth and reproduction [65] rather than into height growth or the establishment of new branches. Hence, the modelled age dependency in aspen and birch trees is likely related to tree ontogeny [59,61] but also to changes in competition over time.

These findings underline the importance of considering tree age and stand density as important factors influencing allometric relationships of aspen or birch trees [27,34,40,66]. In particular, these findings indicate that allometric biomass equations developed in aspen or birch forests of high stand density would overestimate stem biomass and underestimate branch biomass when applied to forests of low stand density.

Although our models do not comprehensively assess all possible environmental effects on allometric relationships of trees, these results strongly support the development of specific allometric biomass equations for widely spaced nurse crops.

4.2. Allometric Biomass Equations

To avoid any bias related to data transformation [67], we employed non-linear least squares to fit power functions to our biomass data [20,68]. We fitted power functions using diameter at breast height as the sole explanatory variable, which generally performed well when predicting sample tree biomass.

The performance analysis based on jackknife resampling indicated relative root mean squared errors of up to 37% for predictions of branch biomass, which was comparable to reports from other studies [28,36,41–43]. However, the relative root mean squared errors for predictions of stem wood and aboveground woody biomass ranged between 11% and 20% and were thus considerably lower.

Such rather large errors can be attributed to our sampling scheme [54], because we sampled only one tree per diameter class. Therefore, reducing the set of sample trees by one particular tree during the resampling led to a relative large variation among the individual resampling curves. The variation was particularly high if the largest or smallest tree was removed during resampling. Therefore future efforts to develop or expand allometric equations should ensure that each diameter class is represented by multiple observations, preferably with a bimodal diameter distribution to produce equations of higher precision and robustness.

However, to extend the applicability of our allometric biomass equations to a broader range of stand densities, which for example may affect the proportion of branches and height-to-diameter ratios [27], we provided a second set of allometric biomass equations including tree height as an additional explanatory

variable. In accordance with other studies, the additional inclusion of tree height in allometric biomass equations could reduce the standard error of estimate particularly for predictions of stem wood and aboveground woody biomass [62,69]. Apart from these examples, the major improvement was the flexibility of such models to account for changing height-to-diameter ratios between our study plots. In contrast, the application of allometric biomass equations exclusively based on diameter at breast height should be restricted to a fixed range of height-to-diameter ratios in order to avoid a possible bias [34].

Stand density induced variation in height-to-diameter ratios may be one reason why most allometric biomass equations from the literature produced a rather large bias and root mean squared error when estimating the aboveground woody biomass of our sample trees. Thus, Table 7 shows that only one equation from the literature was able to produce a smaller bias than the respective equation developed in this study and that all equations from the literature produced 40% to 680% larger root mean squared errors per tree estimate than equations developed in this study.

When estimating tree branch biomass, root mean squared errors ranged between 25% to 116% and were additionally enlarged by at least 60% when equations from the literature were employed (Table 7).

Conclusively, a comparably low bias and root mean squared error, together ensuring a high precision of biomass estimation at tree level, could only be achieved by allometric biomass equations developed in this study (Table 7 and Figure 6).

However, relative errors were somewhat decreased at stand level but in many cases still constituted a considerable proportion of the overall stand biomass. Assuming 650 aspen trees per hectare with a mean tree aboveground woody biomass of 120 kg and an overall stand level biomass of 78,000 kg, an error equal or larger 15% as produced by many allometric biomass equations from the literature equals 11,700 kg and thus represents almost 3 years or 16% of the rotation length in our study. The respective branch biomass in the example accounts for approximately 23,400 kg (30%) and was often greatly underestimated by at least 40% or 9360 kg (Table 8 and Figure 6).

Therefore, considering these errors and the proportion of rotation length and overall biomass yield they represent, increasing the precision of biomass estimation is important to accurately predict the biomass accumulation in a comparatively short production cycle. In addition, it is crucial for the estimation of nutrient removal with biomass harvesting, a critical aspect of the sustainable management of these forests. Any additional error, as for example produced when biomass equations from the literature were employed, might lead to wrong assessments of the impact of biomass and nutrient removal [19,70]. This is particularly the case, when the error is largely attributable to inaccurate predictions of branch biomass, which has considerably higher nutrient concentrations than stem biomass [24].

4.3. General Conclusion

If nurse crops are to be used more widely to supply additional biomass from forests or from abandoned agricultural lands [36,71], nutrient sustainability will need to be considered, too [33,70]. However, only few studies have established replicate plot trials of nurse crops to examine growth, nutrient cycling, *etc.* [13,72,73]. Here, we provide specific allometric biomass equations for nurse crops as a foundation for the calculation of biomass production and nutrient sequestration. Biomass estimation in nurse crops

or other widely spaced forests [35] will benefit greatly from the use of allometric biomass equations that can account for stand density effects.

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Conflicts of Interest

The authors declare no conflict of interest.

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