

# Allometric biomass equations for Scots pine (*Pinus sylvestris* L.) seedlings during the first years of establishment in dense natural regeneration

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**Abstract** – A dense natural regeneration of Scots pine (*Pinus sylvestris* L.) exhibits a considerable biomass build-up in the first four years, with amounts of 7.03 Mg ha<sup>-1</sup> for aboveground biomass, and 0.88 Mg ha<sup>-1</sup> for coarse root biomass (> 1 mm). Power equations were developed, which relate collar diameter (ranging from 0.3 to 2.7 cm) and height to total aboveground and coarse root biomass of two, three and four-year-old seedlings in a regeneration of 16 seedlings m<sup>-2</sup> at one site in Belgium. During the first years of establishment, seedling allometry changes with age, whilst the density remains constant. Biomass equations developed for one of the three ages can produce biased predictions for the other ages. Even when an equation is based on data for all ages and information on height is included, age still has to be considered as a potential predictor variable. For pooled ages, linear regression after logarithmic transformation of the power equation, selected other predictors than weighted non-linear regression. The former approach indicated significant interactions between predictors, while the latter does not reveal interactions.

**allometry / aboveground biomass / coarse root biomass / seedling / *Pinus sylvestris* L.**

**Résumé** – Équations d'allométrie de biomasse pour semis de pin sylvestre (*Pinus sylvestris* L.) dans les premières années d'établissement d'une régénération naturelle dense. Une régénération naturelle dense de pin sylvestre (*Pinus sylvestris* L.) montre un accroissement considérable de biomasse dans les quatre premières années, avec des quantités de 7,03 Mg ha<sup>-1</sup> pour la biomasse aérienne et 0,88 Mg ha<sup>-1</sup> pour la biomasse des grosses racines (> 1 mm). Des équations de type puissance mettant en relation le diamètre au niveau du collet racinaire (intervalle de 0,3 à 2,7 cm) et la hauteur avec la biomasse aérienne et la biomasse des grosses racines de semis de pin sylvestre âgés de deux, trois et quatre ans ont été développées dans une régénération d'une densité de 16 semis m<sup>-2</sup> sur un site en Belgique. Entre la deuxième et la quatrième année, à densité stationnaire, la relation d'allométrie des semis change avec l'âge. Les équations de biomasse développées pour les semis d'un même âge, peuvent produire des prédictions erronées pour les autres âges. Même en utilisant des données de tous les âges et la variable hauteur, l'âge doit être considéré comme une variable potentielle dans l'analyse de régression. En utilisant des données de tous les âges, l'analyse de régression linéaire a retenu différentes variables que l'analyse de régression non-linéaire pondérée. La première désignait des interactions significatives, tandis que la dernière ne considère pas les interactions.

**allométrie / biomasse aérienne / biomasse racinaire forte / semis / *Pinus sylvestris* L.**

## 1. INTRODUCTION

Forest stand regeneration techniques based on spontaneous seedling establishment fit the needs of a low-energy and cost-efficient conversion of coniferous plantations into more natural forest types in Western and Central Europe [35]. This is particularly true for natural regeneration induced in gaps or under shelter, with an abundant seed source of the same species. Furthermore, if forest floor conditions are suitable then the seedling density is high [17]. In the establishment stage, densities are typically more than 1 seedling m<sup>-2</sup> (up to 10 and more), compared to less than 1 seedling m<sup>-2</sup> for plantations [5, 8, 9, 13, 21, 28, 29].

Most empirical allometric biomass equations are confined to pole-stage and mature stands of planted forests. Extrapolating these equations to smaller diameters far outside of the data range used to develop them is questionable [7, 36]. Moreover, the high density of a young natural regeneration must be taken into account to avoid underestimation of the belowground biomass. Litton et al. [15] found that smaller mean tree size associated with increased stand density, appears to result in an increased relative allocation of biomass below ground for young trees of the same age. It is difficult to investigate whether allometric relationships change with increasing age at a constant (high) density, since in most tree stands density decreases rapidly with increasing age due to self-thinning or thinning operations.

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**Table I.** Size characteristics of the sampled Scots pine seedlings.

Variable	Age (years)	<i>N</i>	Mean (cm)	s.d. (cm)	Range (cm)
Diameter	2	110	0.7	0.2	0.3–1.2
	3	134	1.0	0.3	0.3–2.0
	4	105	1.2	0.4	0.4–2.7
Height	2	110	20.0	6.6	6.0–36.0
	3	134	48.3	13.5	10.5–90.5
	4	105	84.3	20.7	27.5–131
Living crown length	2	110	17.6	6.5	3.8–33.0
	3	134	47.0	13.5	9.8–90.5
	4	105	57.3	15.8	21.5–99.0

In this paper our objectives are: (i) to develop allometric equations that enable the total aboveground biomass and coarse root biomass for two, three and four-year-old Scots pine (*Pinus sylvestris* L.) natural seedlings at high density to be predicted; (ii) to determine whether at a constant density, allometry changes with age between the second and the fourth year after emergence; and (iii) to compare resulting equations from non-linear and linear regression analyses.

## 2. MATERIALS AND METHODS

### 2.1. Study site

Field measurements were conducted in a spontaneous regeneration of Scots pine in Herentals, Northern Belgium (51° 11' N and 4° 48' E, elevation 20 m). The seedling cohort occupies a clearing in a 65-year-old Scots pine plantation on a level site. The soil is a Plagganthrept Inceptisol [31] with a 65 cm thick homogeneous, anthropogenic, sandy top layer on sandy mother material and a clay substrate at 100 cm depth. The top 5 cm of mineral soil has a pH-H<sub>2</sub>O 4.20 ± 0.19 and a pH-KCl 3.06 ± 0.16. The climate is Atlantic maritime. The site is moderately dry, but between 1999 and 2002 the annual precipitation (869, 946, 1032 and 993 mm year<sup>-1</sup> respectively) was well above the long-term average of 782 mm year<sup>-1</sup> [12]. In early 1999, the clearing was freed of debris and litter, but the mineral soil with pine stumps and dead roots was left undisturbed. In September 2000, an average of 16 seedlings m<sup>-2</sup> had germinated during the 1999 growing season. New seedlings germinated in 2000 and 2001, but these had a limited growing space because of the high initial density in 1999. As a result of this, a second or third seedling cohort did not develop during the study period. The litter layer was less than 1 cm thick with little moss cover (< 5%) and very sparse other vegetation. No mortality was observed until after the fourth growing season.

### 2.2. Data capture

Three square sample plots of approximately 7 m<sup>2</sup> were located in the centre of the clearing for homogeneous light conditions. After the growing season of 2000, the aboveground parts of 110 two-year-old seedlings were destructively sampled in the first plot. The collar diameter to the nearest 0.01 cm was measured over bark using an electronic calliper. The height between the root collar and the base of the terminal bud was measured to the nearest 5 mm. Sampled seedlings were cut

off at the root collar. Stem, branches, needles and buds were not separated. After the samples had been oven-dried for 2 days at 70 °C, the dry mass was determined on an electronic balance to the nearest 0.01 g. For 67 of these seedlings, all roots in the top 10 cm of the mineral soil with a diameter greater than 1 mm diameter were measured. For a study of root system geometry (not presented here), diameter measurements to the nearest 0.1 mm were made at intervals using an electronic calliper. Fresh root volume was calculated by approximating coarse root segments as cylinders with a diameter equal to the mean of both end diameters. A conversion coefficient from fresh coarse root volume to coarse root biomass was determined on a separate sample taken outside the plot, which consisted of 363 root segments that were pooled before weighing.

In 2001, similar procedures were used to measure aboveground biomass of 134 three-year-old seedlings in the second plot as well as the root systems of 71 of these seedlings. Finally, 105 four-year-old seedlings in the third plot were sampled in 2002. The coarse root system of 55 of these seedlings was collected, dried and weighed in the same way as the aboveground parts.

The seedling cohort is characterized in Table I.

Ground area based biomass for each of the three ages was obtained by dividing the measured aboveground biomass and the model-estimated coarse root biomass of all seedlings by the exact plot surface. Fine root biomass (< 1 mm diameter) and biomass shed to the litter layer were not included.

### 2.3. Regression analysis

Stem sapwood cross-sectional area (CSA) at crown base is presumed to be an excellent predictor of crown biomass [18] due to the functional role of sapwood in conducting water and nutrients between fine roots and leaves. In very young seedlings, sapwood CSA encompasses almost the total stem CSA [2], and in pine seedlings the stem taper between the root collar and the crown base is limited. Collar diameter is proportional to the square root of the CSA and because it is measured at the intersection of both plant halves, it may serve as a predictor of both aboveground and belowground biomass quantities [10, 11, 15, 32]. Other potential predictor variables include height *H*, and the derivate  $D^2H$  [19, 24, 33]. Living crown length is only marginally different from height for the seedlings at ages 2 and 3 years (Tab. I) [24].

The general allometric equation used is

$$Y = aX^b + \epsilon \quad (1)$$

where  $Y$  is oven-dry mass (kg),  $X$  is a tree dimension variable: collar diameter ( $D$  in cm), height ( $H$  in cm) or  $D^2H$  (cm<sup>3</sup>),  $a$  and  $b$  are parameters and  $\epsilon$  is a random normally distributed additive error term with constant variance [30, 34]. Estimating parameters while satisfying the assumptions of regression analysis can be achieved by using: (i) weighted non-linear least squares estimation or (ii) ordinary least squares estimation after logarithmic transformation to a linear model [6].

Weighted non-linear least squares estimation ensures that the more variable larger seedlings contribute less to the parameter estimates than the smaller ones. The weights were derived from the function  $X^{-w}$ , which is used to estimate the unknown variance  $\sigma_i^2$  for each level  $i$  of  $X$ . We chose  $w$  as the value that resulted in non-significant heteroscedasticity of the residuals, while minimizing the standard error of the estimate (SEE). We tested for significant heteroscedasticity with Levene's test statistic, comparing the variance of the residuals between four even-sized groups along the range of  $X$ . Initial parameter values for the non-linear regression (Gauss-Newton method) were taken from the fit of a logarithmic model (see below). Due to the non-linear nature of the power function and the use of weighted least squares estimation, the coefficient of determination ( $R^2$ ) has no clear-cut meaning and its use as a goodness-of-fit parameter is therefore questionable [20]. We therefore used SEE.

A second approach used was ordinary least squares estimation after logarithmic transformation of both sides of the power equation:

$$\ln Y = \ln a + b \cdot \ln X + \epsilon'. \quad (2)$$

This is not the exact logarithmic transformation of (1) due to the additive nature of the error term [18, 25, 36] and therefore we do not fully support this approach. However, as it is widely used, we present the parameter estimates for comparison. Furthermore, it enables the interaction between multiple predictors to be analysed. Logarithmic transformation allows the use of  $R^2$  and SEE as goodness-of-fit statistics, if  $\ln a$  is different from zero [32]. Comparison of SEE between both approaches (logarithmic units versus arithmetic units) is not possible [24, 30]. A logarithmic bias correction term,  $MSE/2$ , was added to the intercept before backtransformation, to ensure that the power equation estimates the mean of dry mass rather than the median for each diameter level [1].

The statistical analysis was carried out using the `nls` and `lm` functions in S-PLUS (version 6.0 Release 2, Insightful Corp.). Significance of the regression parameters was determined using  $t$ -tests. Residual diagnostics were examined in SPSS (version 11.0.1, SPSS Inc.).

## 2.4. Dependency of age

Bond-Lamberty et al. [3] and Reed et al. [27] added an indicator variable for age to a logarithmic equation in order to test if one biomass equation is appropriate for multi-aged data. Using pooled two, three and four-year-old seedling data, we added the variable  $A$ , i.e. age in years, to equations (1) and (2) to enable the parameter estimates of both approaches to be compared.

$$Y = aX^b A^c + \epsilon \quad (3)$$

$$\ln Y = \ln a + b \ln X + c \ln A + d \ln A \times \ln X + \epsilon'. \quad (4)$$

Another way of testing the appropriateness of equations for different ages is to use the percentage of mean observed values (PMOV), which is also a goodness-of-fit statistic in regression analysis [24]. The biomass of the seedlings of age  $A_i$  is estimated with the equation developed for age  $A_j$ . The mean of these estimations is then expressed as a percentage of the mean of the observed biomass values of the seedlings of age  $A_i$  [33].

**Table II.** Biomass stock (Mg ha<sup>-1</sup>) in two, three and four-year-old dense Scots pine seedling cohorts (percentages between brackets). Coarse root biomass estimates based on single-age  $D^2H$  equations in Table III.

Compartment	Age (years)		
	2	3	4
Aboveground	1.43 (85)	4.00 (89)	7.03 (89)
Coarse root	0.26 (15)	0.52 (11)	0.88 (11)
Total living	1.69	4.52	7.92

## 3. RESULTS

### 3.1. Living biomass stock

Between the ages of 2 and 4 years, there is a strong increase in the total living biomass of Scots pine seedlings, i.e. from 1.7 Mg ha<sup>-1</sup> to nearly 8 Mg ha<sup>-1</sup> (Tabl. II). This increase is mainly due to the aboveground biomass, which accounts for 85–89% of the total living seedling biomass, excluding fine root mass.

### 3.2. Regression equations

For the three ages studied, the estimated parameters for the weighted non-linear regressions (Tab. III) were fairly similar to the parameters for the linear regressions after logarithmic transformation (Tab. IV) for the three ages, if the same predictors were selected. Nevertheless, both approaches lead to different model selections when height is added to a model that already contains collar diameter or, when ages are pooled, age is added to a model that already contains height or  $D^2H$ .

### 3.3. Age dependence

In pooled equations, the natural logarithm of age ( $\ln A$ ) is a significant predictor term for both aboveground and coarse root biomass, whether or not information on height is included by means of  $\ln H$  or  $\ln D^2H$  (Tab. IV). Interaction terms between  $\ln A$  on the one hand and  $\ln H$  or  $\ln D^2H$  on the other are always significant in pooled equations. Using the weighted non-linear approach, age is not included when both diameter and height or  $D^2H$  are already included in the model for aboveground biomass (Tab. III). For belowground biomass both approaches confirm the significance of the age predictor.

Using the  $D^2H$  equations based on seedlings of a certain age to estimate the biomass of seedlings of other ages results in (i) estimated means that are between 38.3 and 129.7% of the observed mean biomass (Tab. V) for aboveground biomass, and (ii) estimated means between 27.6 and 338.6% of the observed mean (Tab. V) for coarse root biomass. Even the pooled equations based on seedlings of all ages do not accurately estimate the means of the observed biomasses in some of the ages considered. The aboveground biomass of two-year-old seedlings is underestimated by 26.3% and coarse root biomass of three-year-old seedlings is overestimated by 28.4%.

**Table III.** Weighted non-linear regression parameter estimates of allometric equation  $Y = aX^b$ . Parameters a, b and c (for the second predictor) are significant at the 0.01 level (*t*-test).

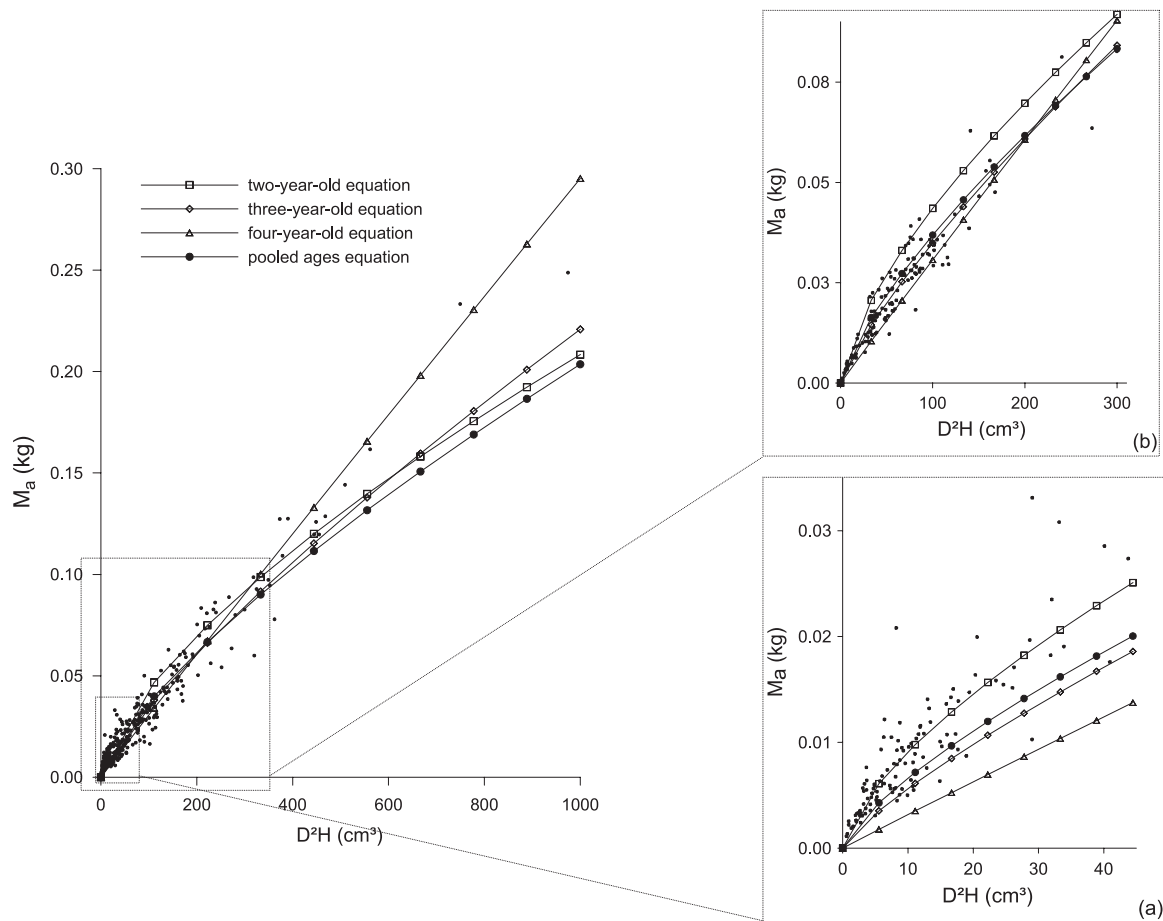
Age	Y	X	a	b	c	s.d. (a)	s.d. (b)	s.d. (c)	N	SEE	w	Levene's p	PMOV
2	$M_a$	$D$	0.0187	2.039		0.0006	0.081		110	0.00260	2.1	0.05	100.0
2	$M_a$	$D^2H$	0.00190	0.680		0.00011	0.029		110	0.00310	1.8	0.07	99.6
3	$M_a$	$D$	0.0189	2.287		0.0003	0.051		134	0.00473	4.0	0.22	100.8
3	$M_a$	$D,H$	0.00305	1.916	0.474	0.00099	0.081	0.084	134	0.00414	4.1	0.29	102.0
3	$M_a$	$D^2H$	0.000873	0.801		0.000070	0.019		134	0.00426	1.2	0.08	102.2
4	$M_a$	$D$	0.0233	2.556		0.0007	0.065		105	0.0112	4.0	0.05	100.7
4	$M_a$	$D,H$	0.000127	1.833	1.206	0.000087	0.112	0.158	105	0.00919	5.6	0.07	103.5
4	$M_a$	$D^2H$	0.000332	0.983		0.000033	0.021		105	0.00923	1.9	0.03	100.0
Pool	$M_a$	$D,A$	0.0163	2.343	0.247	0.0012	0.041	0.063	349	0.00822	4.1	0.06	97.6
Pool	$M_a$	$D,H$	0.00788	2.139	0.257	0.00114	0.056	0.037	349	0.00762	3.8	0.05	99.3
Pool	$M_a$	$D^2H$	0.00121	0.742		0.00007	0.012		349	0.00807	0.9	0.05	99.7
2	$M_r$	$D$	0.00414	2.828		0.00024	0.140		67	0.000599	3.5	0.06	99.1
2	$M_r$	$D^2H$	0.000184	0.929		0.000022	0.064		67	0.000734	2.2	0.09	97.9
3	$M_r$	$D$	0.00222	2.812		0.00008	0.137		71	0.000828	3.6	0.83	99.0
3	$M_r$	$D^2H$	0.0000601	0.934		0.0000119	0.053		71	0.000861	1.8	0.09	100.0
4	$M_r$	$D$	0.00283	2.549		0.00009	0.103		55	0.00142	5.9	0.06	100.4
4	$M_r$	$D^2H$	0.0000482	0.951		0.0000090	0.041		55	0.00127	2.1	0.07	101.6
Pool	$M_r$	$D,A$	0.00513	2.656	-0.547	0.00064	0.081	0.115	193	0.00106	3.4	0.06	99.1
Pool	$M_r$	$D^2H,A$	0.000615	0.929	-1.879	0.000066	0.035	0.173	193	0.00119	0.9	0.11	99.4

Pool: all ages,  $M_a$ : aboveground biomass and  $M_r$ : coarse root biomass in kg,  $D$ : collar diameter in cm,  $H$ : height in cm,  $D^2H$  in  $cm^3$ ,  $A$ : age in years, s.d. ( ): standard deviation of the parameter estimates,  $N$ : sample size, SEE: standard error of the estimate, -w: power of the weighting function (see text), Levene's p is the significance of the Levene's test statistic for equality of variances, PMOV: percentage mean observed value.

**Table IV.** Parameter estimates of allometric equation  $Y = aX^b$  using linear regression after logarithmic transformation. The parameters a, b and c, d, e (for multiple predictors) are significant at the 0.01 level (*t*-test).

Age	Y	X	Interaction	a	b	c	d	e	s.d. (a)	s.d. (b)	s.d. (c)	s.d. (d)	s.d. (e)	N	R <sup>2</sup>	SEE	MSE/2	PMOV
2	$M_a$	$D$		0.0189	2.068				0.0008	0.077				110	0.869	0.247	0.030	100.3
2	$M_a$	$D^2H$		0.00191	0.678				0.00012	0.030				110	0.826	0.284	0.040	99.1
3	$M_a$	$D$		0.0189	2.344				0.0003	0.050				134	0.943	0.191	0.018	101.8
3	$M_a$	$D,H$		0.00305	1.946	0.474			0.00100	0.085	0.085			134	0.954	0.172	0.015	102.6
3	$M_a$	$D^2H$		0.000831	0.813				0.000053	0.017				134	0.948	0.182	0.016	100.4
4	$M_a$	$D$		0.0230	2.629				0.0006	0.069				105	0.934	0.245	0.030	102.6
4	$M_a$	$H$		1.33E-08	3.362				7.6E-09	0.131				105	0.865	0.351	0.060	96.6
4	$M_a$	$D^2H$		0.000324	0.988				0.000032	0.021				105	0.957	0.199	0.020	99.8
Pool	$M_a$	$D,A$	$\ln D \cdot \ln A$	0.0138	1.228	0.336	1.035		0.0009	0.136	0.060	0.123		349	0.949	0.230	0.026	99.4
Pool	$M_a$	$D,H,A$	$\ln H \cdot \ln A$	0.140	1.999	-0.426	-3.615	0.850	0.041	0.057	0.091	0.312	0.078	349	0.957	0.210	0.022	99.4
Pool	$M_a$	$D^2H,A$	$\ln D^2H \cdot \ln A$	0.00934	0.400	-2.304	0.401		0.00113	0.040	0.137	0.036		349	0.951	0.225	0.025	99.5
2	$M_r$	$D$		0.00449	3.012				0.00037	0.157				67	0.850	0.377	0.070	104.3
2	$M_r$	$D^2H$		0.000179	0.947				0.000022	0.065				67	0.769	0.468	0.010	102.5
3	$M_r$	$D$		0.00224	2.856				0.00009	0.129				71	0.877	0.324	0.015	99.5
3	$M_r$	$D^2H$		5.53E-05	0.957				9.4E-06	0.049				71	0.850	0.359	0.064	101.0
4	$M_r$	$D$		0.00283	2.568				0.00009	0.090				55	0.939	0.217	0.023	101.2
4	$M_r$	$D^2H$		4.80E-05	0.951				8.1E-06	0.037				55	0.927	0.236	0.027	101.6
Pool	$M_r$	$D,A$		0.00550	2.790	-0.596			0.00072	0.087	0.123			193	0.881	0.369	0.067	103.8
Pool	$M_r$	$D,H,A$	$\ln H \cdot \ln A$	0.0827	2.599	-0.707	-4.299	0.928	0.0512	0.132	0.188	0.719	0.175	193	0.896	0.346	0.059	100.1
Pool	$M_r$	$D^2H,A$	$\ln D^2H \cdot \ln A$	0.00174	0.559	-3.054	0.375		0.00047	0.095	0.327	0.088		193	0.863	0.396	0.077	100.0

Symbols as in Table II; R<sup>2</sup>: adjusted coefficient of determination; MSE/2: correction term added to  $\ln a$  before backtransformation to a; numbers in italics are in logarithmic units and the rest are in arithmetic units.



**Figure 1.** Aboveground Biomass ( $M_a$ ) as a function of  $D^2H$ : equations of different ages and of pooled ages from Table III. The insets enlarge the figure for the two-year-old seedlings (a) and the three-year-old seedlings (b).

**Table V.** Percentage Mean Observed Value (%):  $D^2H$  equations (Tab. III) based on the respective ages applied to seedlings of other ages.

Y	Age	Age of the observations			
		2	3	4	Pooled
$M_a$	2		129.7	114.0	117.6
$M_a$	3	63.7		101.2	97.5
$M_a$	4	38.3	84.0		88.1
$M_a$	Pooled	73.7	106.8	99.8	
$M_r$	2		293.8	338.6	282.8
$M_r$	3	33.1		115.9	96.6
$M_r$	4	27.6	85.9		87.4
$M_r$	Pooled	91.7	128.4	86.2	

As can be seen in Figure 1, the relation between aboveground biomass and  $D^2H$  clearly differs between the three ages within the diameter and height range measured.

## 4. DISCUSSION

### 4.1. Single-age equations

The equations in Tables III and IV are applicable to Scots pine seedlings in a dense even-aged regeneration at the site in the present study from the end of the second growing season after seedling emergence until the end of the fourth season, when mortality appears due to intense competition. The relationships found here can be used for inferences nearby the origin, i.e. for small diameters of the allometric biomass curves for different ages [3]. Recently much emphasis has been placed on the small diameter classes when general equations for a wide range of ages and sizes are sought [37]. Crown sampling strategies did not influence the resulting allometric equations, because entire crowns and coarse root systems were sampled [18]. Fine roots (< 1 mm) were not considered. A better means of obtaining fine root biomass estimates at the stand level is to sample with a soil corer on a per soil surface or volume basis [22, 23]. Furthermore, seasonal fluctuations in root biomass of Scots pine are concentrated in the diameter class smaller than 1 mm [26].

Collar diameter proved to be the main predictor for estimating aboveground and coarse root biomass of seedlings of the same age. Although Litton et al. [15] proved that models based on outside bark basal diameter show a slight bias towards the overprediction of belowground biomass for diameters less than 3 cm, we did not observe such a systematic bias in the residuals of the regressions (PMOV in Tabs. III and IV).

If the same predictors are selected, parameter estimates and their standard deviations from both non-linear and log-linear approaches are quite similar. According to Långström et al. [16], even backtransformation with correction can produce bias if the untransformed variable is not log-normally distributed. For the single-age equations, we consider the parameter values in Table III to be the best fits. The aboveground biomass of three and four-year-old seedlings is best predicted by diameter and height or  $D^2H$ , while for two-year-old seedlings diameter alone gives a better fit. For two and three-year-old seedlings coarse root biomass is best predicted by diameter, while for four-year-old seedlings this is best predicted by  $D^2H$ .

#### 4.2. Multiple ages

Based on the equation parameters no conclusion can be drawn about the differences between ages when the same predictors are selected. Reed et al. [27] used standard deviations of the parameter estimates to test for significant differences between allometric equations. However, parameters  $a$  and  $b$  in equation (1) are well correlated [37] and therefore a separate comparison of these values is questionable.

The weighted non-linear regression approach (Tab. III), demonstrates that a multi-aged equation including  $D^2H$  or diameter and height, fits the aboveground biomass data of two, three and four-year-old seedlings. For coarse root biomass an age variable still has to be included. Using the linear regression approach after logarithmic transformation (Tab. IV), age and one interaction with another predictor are always significant for both aboveground and coarse root biomass. Accordingly, both methods lead to a different conclusion concerning the need to include age in multi-aged allometric aboveground biomass equations for the pine seedlings in this study. The percentage mean observed values confirm the above finding that allometric relationships for consecutive years are not equivalent. For example, equations for two-year-old seedlings underestimate mean aboveground biomass in three-year-old seedlings by more than the 20%, which Wang et al. [33] proposed as the limit for comparability.

Allometric relationships for seedlings seem to be species specific [32]. For Scots pine they do not seem to be specific for geographical seed origin if one age at one site is considered [22]. With respect to the dependence of size and age, Braekke [4] found that the slope of a linear relation which related squared diameter at breast height to the total aboveground biomass of young Scots pine trees growing in a dense natural regeneration, was different for trees above and below the limit of 7 cm stem diameter. Consequently he used two separate equations for smaller and larger trees. In a 46-year-old Scots pine stand, Lim and Cousens [14] found a systematic underestimation of biomass when allometric equations developed from data in a certain year, were applied to the trees in a successive year. This underestimation was 0.5 to 1 percent per year. There-

fore, the influence of age seems to be more important in the youngest stands. However, Reed et al. [27] concluded that relationships between collar diameter and aboveground and belowground biomass were consistent from the time of establishment through the onset of inter-tree competition. Indicator variables for age and the interactions with predictor variables  $D$  and  $H$  were not significant in a logarithmically transformed regression model, even though the young *Pinus resinosa* Ait. in their data set ranged from 1 to 8 years of age after planting and from 0.3 to 10.1 cm in collar diameter. The pines in the study of Reed et al. [27] were planted as three-year-old seedlings at a density of  $1 \text{ m}^{-2}$ , and the first aboveground physical interaction was observed 6 years later. For the Scots pine seedlings in our study, root system overlap was considerable at the age of 2 years, and in the third growing season crown contact was common. Mortality of the lowest branch whorls was common at the end of the fourth growing season (Tab. II) when first seedling mortality in the regeneration cohort also occurred. At the high densities common in natural regenerations of Scots pine, the pre-competitive state seems to be restricted to the first 1 or 2 years of establishment, which may account for the change in allometric relationships between the ages of 2 and 4 years.

#### 5. CONCLUSIONS

A dense natural regeneration of Scots pine exhibits a considerable biomass build-up during the first years of establishment. A general allometric equation for aboveground or coarse root biomass intended to be valid for these ages, with collar diameter, height or  $D^2H$  as predictors, should be based on observations of several ages and age should be tested as a predictor variable. Although weighted non-linear regression analysis is a statistically more reliable approach than linear regression after logarithmic transformation of an allometric power equation, the latter enables investigation of interactions between predictor variables.

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