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Year: 2021

Version: Published version

Please cite the original version:

Lee D., Beuker E., Viherä-Aarnio A., Hynynen J. (2021). Site index models with density effect for hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) plantations in southern Finland. Forest Ecology and Management 480, 118669. https://doi.org/10.1016/j.foreco.2020.118669.

Forest Ecology and Management 480 (2021) 118669

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Site index models with density effect for hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) plantations in southern Finland

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A R T I C L E I N F O

Keywords:
Clonal plantation
Initial planting density
Chapman-Richards function
Nonlinear mixed-effects model
Anamorphic site index curves

A B S T R A C T

This study was conducted to examine the characteristics of dominant height growth and develop site index models for clonal hybrid aspen plantations in southern Finland. Data were obtained from repeatedly measured clonal hybrid aspen trials with varying initial spacing: 2.5 m × 2.5 m (1600 trees ha^{-1}), 3.0 m × 3.0 m (1200 trees ha^{-1}), 3.5 m × 3.5 m (800 trees ha^{-1}), and 5.0 m × 5.0 m (400 trees ha^{-1}). The total number of data points in the analysis was 389 for the age of 3–20. Within the range of observed data, the dominant height grew linearly over age and was significantly different due to the initial planting density; growth was higher when the planting was denser. Using the initial density effect, dominant height growth models were developed based on the Chapman-Richards function through nonlinear mixed-effects modelling. The density variable was found to be statistically the best variable when modifying only the shape parameter of the Chapman-Richards function. All fixed-effects were significant for both models, with and without the density effect. The residual plots of the model did not show any bias over the predicted value, stand age or planting density. The predicted dominant height was higher with increasing initial density. The predicted dominant height increment was faster with higher planting densities until the age of 14 years. The anamorphic site index curves were presented with base age of 20 years including the planting density effect. The overall pattern of site index curves was consistent with those observed in previous studies. The models developed in this study can be used to estimate the dominant height and site index of hybrid aspen plantations in southern Finland.

1. Introduction

Hybrid aspen, a hybrid between the European aspen and North American trembling aspen (*Populus tremula* L. × *P. tremuloides* Michx.), was introduced in Finland at the beginning of 1950s in order to supply raw materials for the matchwood industry. From the start of the breeding activities the genetic variation and its effects have been studied using different hybrid progenies and clones (Beuker, 2000). In addition, experiments were established in southern Finland to study growth and yields (Oskarsson, 1962; Saloniemi, 1965; Hagman, 1971; Kallio, 1972). However, breeding and research activities with hybrid aspen decreased in the 1980s due to the decline of the matchwood industry (Tullus et al., 2012). Hybrid aspen received renewed attention during the 1990s, this time by the pulp and paper industry, because of its specific fiber characteristics and its predominant growth rate that was shown earlier (Beuker, 2000).

Besides paper production, hybrid aspen also provides suitable raw materials for plywood and veneer (Heräjärvi and Junkkonen, 2006). Due to its high growth rate and resulting short rotation period, hybrid aspen may also be considered suitable for bioenergy (Rytter and Stener, 2005). The ability of hybrid aspen to regrow from root suckers after harvesting the primary stand results in even higher growth rates during the second and following rotations (Hytönen, 2018). Because most of Finland's forested area is covered with Norway spruce and Scots pine, increasing the areas with other (broadleaved) species would increase the forest biodiversity. Hybrid aspen could be recommended as an alternative hardwood species for southern Finland.

In order to provide decision-making support for the establishment and management of hybrid aspen plantations in Finland, growth and yield models are needed to show the wood production potential of the species. The site index is a widely applied predictor for site productivity and is included in the majority of growth and yield models (e.g., Clutter

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https://doi.org/10.1016/j.foreco.2020.118669
Received 30 June 2020; Received in revised form 1 October 2020; Accepted 3 October 2020
Available online 22 October 2020

Table 1
Information on hybrid aspen clones included in the study. BC = British Columbia, CA = Canada, FI = Finland.

Clone/seed lot	Female parent	Male parent
E 10467[a]	E 1732 Tuusula, FI	U 2554 Ontario, CA
	E 969 Punkaharju, FI	U 2576, Aleza Lake, BC, CA
E 10476	E 295 Tuusula, FI	U 2502 Maple, Ontario, CA
E 10490	E 295 Tuusula, FI	U 2502 Maple, Ontario, CA

[a] The clone was selected from a stand including a mixture of two different progenies from controlled crossings, and its exact origin could not be identified.

et al., 1983; Vanclay, 1994; Burkhart and Tomé, 2012). The site index is usually represented by the dominant height of a stand at a given age based on a growth model for dominant height. The dominant height is commonly assumed to be independent of the stand density, as presented in many textbooks, based on numerous studies (Hiley, 1959; Sjolte-Jørgensen, 1967; Dahms, 1973; Schmidt et al., 1976; Clutter et al., 1983; Seidel, 1984; Lanner, 1985; Pienaar and Shiver, 1984; Smith et al., 1997; Avery and Burkhart, 2002; Harrington et al., 2009).

However, there are also studies reporting the effect of the initial spacing on the stand arithmetic height or dominant height, particularly for hybrid species grown in short-rotation plantations. The conclusions on the effect of density on height growth have differed in the studies and the effect has been reported to be either negative or positive (Knowe and Hibbs, 1996, Sharma et al., 2002, Harrington et al., 2009). In some studies, the effect of stand density has been included in site index models (MacFarlane et al., 2002, Sharma et al., 2002, Antón-Fernández et al., 2011).

In the Nordic countries, site indexes have been presented only for the major tree species, such as Scots pine, Norway spruce and silver birch. There are only few studies addressing height growth modelling for hybrid aspen (Johansson, 2013), but no growth and yield models for hybrid aspen in Finland have been published so far. No results on the effects of the initial planting density on the dominant height growth for hybrid aspen in northern Europe have been published.

The objectives of this study were to examine the dominant height growth of clonal hybrid aspen plantations. The factors affecting dominant height growth were analysed including the effect of the initial planting density. Dominant height growth models for site index assessment were developed. The predictability of the models was verified by comparing them to the results of previous studies.

2. Materials and methods

2.1. Experimental stands

During the mid-1990s, superior individual trees were selected from stands and experiments with hybrid aspen progenies in southern Finland that had been established during the 1950s and 1960s. The selections were made based on growth performance and form. Additionally, there should be no signs of any biotic or abiotic damage. From these selected genotypes only those that showed good vegetative propagation ability were included for further testing in field experiments.

The experimental stands used in this study were established using three clones (Table 1). At the time of the stand establishment, only a very limited number of clones with sufficient planting material were available. The clones were reported to be superior to the common European aspen in terms of height growth at an early age (Hynynen et al., 2002, 2004).

The experimental sites were located in Lohja, Lapinjärvi, and Pornainen in southern Finland (Table 2, Fig. 1). This region has a relatively mild climate for Finland with a temperature sum of 1300–1400 degree days (T ≥ +5 °C) and 600–700 mm of annual precipitation (Finnish Meteorological Institute, 2020). Experiments 2 and 3 were planted on a herb-rich heath forest (Oxalis-Myrtillus) site type (Cajander, 1949), while the experiments 1 and 4 were planted on former agricultural fields. Experiments 1, 2 and 3 were located on fertile sites, which are favourable for aspen. Experiment 4 was established on a clay-rich soil, which is not considered the best suitable for hybrid aspen.

The original objective of the trials was to study the growth and yield

Table 2
Description of the field trials and summary statistics of the measurements included in this study.

Plot design							Tree measurements		
Experiment No. and location	Planting year	Site	Clone	No. of blocks	Spacing, m (initial planting densities, trees ha^{-1})	No. of plots[a]	No. of measurements	Age range, year	Dominant height range at the last measurement, m
Exp. 1 Lohja, Jalassaari 60°12′47″ N 23°55′35″ E 50 m asl	1997	field	E10476 E10467	3	2.5 m (1600) 3.0 m (1111) 3.5 m (816) 5.0 m (400)	24	12	1–20	26.7 ± 1.8 (23.6–29.8)
Exp. 2 Lohja, Kirkniemi 60°10′44″ N 23°56′55″ E 40 m asl	1998	forest site OMT[b]	E10490	1	2.5 m (1600) 3.0 m (1200) 3.5 m (800) 5.0 m (400)	4	11	1–19	24.2 ± 1.5 (22.9–26.3)
Exp. 3 Lapinjärvi 60°39′26″ N 26°07′36″ E 50 m asl	1999	forest site OMT	E10490	2	2.5 m (1600) 3.0 m (1200) 3.5 m (800) 5.0 m (400)	8	9	1–18	22.5 ± 1.0 (20.6–24.2)
Exp. 4 Pornainen 60°32′21″ N 25°19′35″ E 60 m asl	1999	field	E10490	3	2.5 m (1600) 3.0 m (1200) 3.5 m (800) 5.0 m (400)	12	7	1–14	13.8 ± 1.1 (11.9–15.3)

[a] No. of plots = no. of clones × no. of blocks × no. of treatments.
[b] OMT is Oxalis-Myrtillus (a herb-rich heath forest) site type (Cajander, 1949).

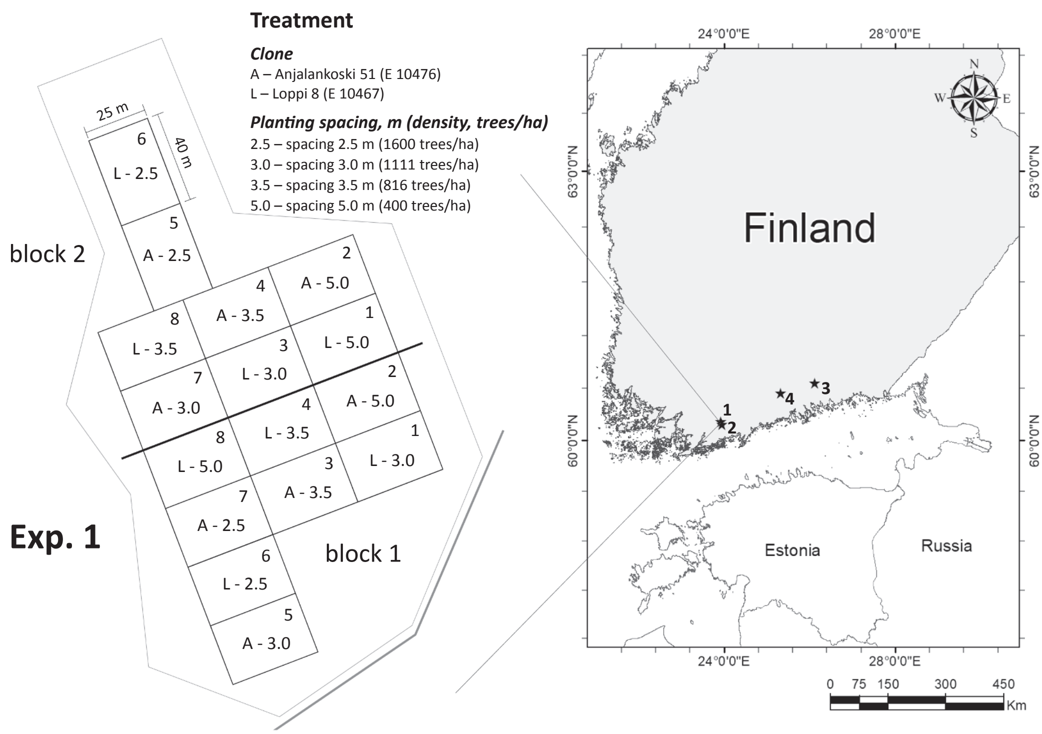

Fig. 1. Locations of the hybrid aspen density field trials and the design of blocks 1 and 2 in experiment 1 as an example.

Table 3
Analysis of covariance (ANCOVA) and parameter estimates of fixed-effects for stand age and initial spacing.

Source	Num DF	Den DF	F Value	Pr > F	Effect	Estimate	S.E.	t Value	Pr > |t|
Age	1	381	12716.40	<0.0001	Age	1.3773	0.0122	112.77	<0.0001
Spacing	4	381	16.78	<0.0001	Spacing 2.5 m	−1.4331	0.7028	−2.04	0.0421
					Spacing 3.0 m	−1.8970	0.7030	−2.70	0.0073
					Spacing 3.5 m	−2.4355	0.7030	−3.46	0.0006
					Spacing 5.0 m	−2.7407	0.7031	−3.90	0.0001

Note: The ANCOVA model was presented in Eq. (1).

of hybrid aspen clones under different site conditions and varying spacing. Each stand comprised of one to three blocks, each of which was planted using one or two different clones (Table 2). Each clone was initially planted with four different target densities: 2.5 m × 2.5 m (1600 trees ha^{-1}), 3.0 m × 3.0 m (1200 trees ha^{-1}), 3.5 m × 3.5 m (800 trees ha^{-1}), and 5.0 m × 5.0 m (400 trees ha^{-1}). The actual number of trees per ha varied slightly between experiments, because on forest sites it was not possible to plant in straight lines because of stumps or rocks. The experiments were established with a randomised block design for the clone and initial spacing (Table 2, Fig. 1). The plot size was 25 m × 40 m (0.1 ha) with a 5 m buffer zone to offset the random effects from adjacent plots.

The experiments were planted in 1997–1999 using one-year-old plants. Before planting, experiment 1 was ploughed during the previous autumn and harrowed during the spring just before planting. Patch scarification was carried out in experiments 2 and mounding in experiment 3 (Hynynen et al., 2002). There was no mechanical site preparation in experiment 4, but chemical weed control was conducted during the autumn prior to planting. After planting, the seedlings were protected from rodents and hares with 60 cm high Tubex tubes. In addition, experiments 1 and 3 were fenced against moose. Experiments 2 and 4 were not fenced because they were situated near a major road or in an agricultural area, where the risk of moose damage was low.

The first inventory of the experiments was made during the first autumn after planting. All measurements inside each plot were recorded at the single tree level. All experiments were annually assessed from year 1 to year 4, measuring the height with an accuracy of 1 cm. Thereafter, from age 5, they were measured every 2–4 years including height measurements at an accuracy of 10 cm and measurements of diameter at breast height (dbh) at 1.3 m from the ground with an accuracy of 1 mm. Single tree data were repeatedly collected 7–12 times from each experiment from the year of establishment until 2015. This resulted in a total number of 485 plot-level measurement instances. The summary statistics and information about the experiments and measurements are provided in Table 2. In addition to this, supplementary information on stand density trends and the size-density relationship is provided in Appendix A.

2.2. Statistical analysis and modelling approach

In the analysis, measurement data for all three clones were pooled together, because the experimental design did not allow the use of balanced data for each clone. Because a site index model was developed using dominant height over age, the dominant height has to be defined (Pienaar and Shiver, 1984). In this study, the dominant height was calculated as the average height of 100 trees with thickest dbh per hectare, which is the commonly used definition in northern Europe (Rantala, 2011).

In the measurements less than five years after planting, the dbh was not measured, and thus not included in the data. For these measurement data, the 100 tallest trees per hectare (10 tallest trees per plot) were used to calculate the stand dominant height. All the data points of age 1 and 2 were excluded from the modelling data in order to avoid the effect of varying initial seedling height at the time of planting on the height growth modelling. The total number of data observations eventually applied for model development amounted to 389 data points from 48 plots in 4 experiments with a total of 9 blocks with a range of 3–20 years for the age, 1.5–31.0 m for the dominant height, 400–1600 trees ha^{-1} for the initial planting density (Table 2).

Due to experimental design, the data had a hierarchical structure (multiple sample plots on each site), Therefore a mixed-effects model with random site effects was applied in the analysis. To examine the growth characteristics of hybrid aspen, a correlation analysis between the stand age and dominant height, and an analysis of the covariance between the stand age, dominant height, and initial spacing were carried out using the PROC MIXED procedure in the SAS 9.4 statistical analysis software prior to model development (SAS Institute Inc., 2015).

To develop the dominant height growth model in the early analysis, we considered several representative growth functions in forest biometrics such as Schumacher, Chapman-Richards, Hossfeld, and Gompertz. By comparing the growth patterns and fit statistics, the Chapman-Richards growth function was found to be the most suitable for application as a base equation to develop the site index model in the main results of the present study (Bertalanffy, 1957; Richards, 1959; Chapman, 1961). The function has been widely used especially for height growth modelling of plantation forests (e.g., Cao, 1993; Amaro et al., 1998; Palahí et al., 2004; Nord-Larsen, 2006; Huuskonen and Miina, 2007; Weiskittel et al., 2009; Johansson, 2013; Lee et al., 2015). To study additional effects on stand age, the parameters of the Chapman-Richards function have been expressed by modelling dominant height growth as a function of other stand characteristics such as soil and climate factors, or by comparing the significance of modified parameter terms in candidate models with F-test, full model vs. reduced model

Table 4
Parameter estimates and fit statistics of dominant height growth model depending on the application of the initial density effect for hybrid aspen. For the modelling approach, a nonlinear mixed-effect model was used based on the Chapman-Richards function. Equations were provided in Eq. (2) for the density-free and in Eq. (3) for the density-sensitive model.

		Density-free (Eq. (2))		Density-sensitive (Eq. (3))	
Class	Parameter	Estimates	S.E.	Estimates	S.E.
Fixed effects	a	44.8115 (0.0212)	6.6316	45.4616 (0.0098)	4.5230
	b	0.0540 (0.0182)	0.0074	0.0537 (0.0137)	0.0063
	c	1.5441 (0.0029)	0.0838	–	–
	c_0	–	–	1.6912 (0.0031)	0.0943
	c_1	–	–	−1.3356 (0.0219)	0.2008
Random effects	var(u_1)	0.0069		0.0105	
	cov (u_1,u_2)	−0.1738		−0.0987	
	var(u_2)	97.2330		18.7549	
Residual	var(ε)	1.4959		1.1787	
Fit statistics	AIC	1301.1		1209.9	
	BIC	1296.8		1205.0	
	R^2	0.9761		0.9812	
	RMSE	1.2127		1.0763	

Note: all fixed-effect parameters are significant indicating *P*-values in parenthesis. AIC is the Akaike information criterion. BIC is the Bayesian information criterion. R^2 is the coefficient of determination. RMSE is the root mean square error.

(Huuskonen and Miina, 2007; Smith et al., 2014). The effect of initial stand density has been studied with the help of modified parameters of the Chapman-Richards function (e.g. Pienaar and Shiver, 1984; Knowe and Hibbs, 1996; Sharma et al., 2002; Antón-Fernández et al., 2011).

In this study, the effect of initial density on growth pattern was analysed by adding the density effect to parameters terms of the Chapman-Richards function: asymptote, growth rate, shape, and all their combinations. Then, predicted growth patterns and fit statistics were compared among every possible combination of the density-sensitive candidate model.

Model parameters were estimated using the PROC NLMIXED procedure in SAS 9.4 (SAS Institute Inc., 2015). The suitability of these models was checked by fit statistics: the Akaike information criterion (AIC), the Bayesian information criterion (BIC), the coefficient of determination (R^2) and the root mean squared error (RMSE). Residual plots were diagnosed using all the independent variables as well as the predicted over the observed values. After the verification process, the site index curves were plotted as anamorphic equations, with a base age of 20 years, by transforming the developed dominant height growth model. A base age of 20 years was chosen based on references from previous studies (Johansson, 2013) and by taking into account the expected final harvest age and prospective yield models for Finland. Furthermore, the parameters and site index curves were compared with the results of earlier studies for northern Europe, which used the same base growth function (Johansson, 2013).

3. Results

3.1. Dominant height growth by initial stand density

The relationship between the stand age and the dominant height was basically linear up to the age of 20. The correlation coefficient between the dominant height and age was 0.98 ($P < 0.0001$). Thus, there was no obvious sign of an asymptote of height growth until the age of 20 years in the studied clonal hybrid aspen plantations. This strong linearity was the basis for the selection of the Chapman-Richards function for site index development in the later part of the analysis. An analysis of covariance was applied to examine the overall significance of the initial spacing on the dominant height development. In the analysis of covariance, the dominant height at the age of a stand at the time of each measurement instance was used as a dependent variable (Eq. (1)).

$$H = \mu + \tau_i + \gamma\left(A_{ij} - \overline{A}\right) + u + \varepsilon \quad (1)$$

where H is dominant height, μ is the global mean, τ_i is the effect of the ith initial spacing class, γ is the slope coefficient of the covariate, A_{ij} is the jth observation of the covariate, stand age (A), in the ith initial spacing class, $\overline{A}$ is the global mean for covariate, stand age (A). u is the random effect for the experiment, and ε is the error term.

The dominant height was significantly different for different initial spacing, which was categorised into four classes: 2.5 m × 2.5 m, 3.0 m × 3.0 m, 3.5 m × 3.5 m, and 5.0 m × 5.0 m (Table 3). Wider initial spacing resulted in slower dominant height growth. This significant result was valid regardless of the definition of dominant height (Appendix B).

3.2. Model fitting and validation

The growth models were developed by applying the Chapman-Richards function taking into account the strong correlation with age and the significant effect of the initial planting density on the dominant height. For the model with a density effect, every possible combination of candidates was examined using fit statistics to choose the best density-sensitive model (Appendix C). Two final model variants, a density-free (Eq. (2)) model and density-sensitive (Eq. (3)) model, were fitted to the data:

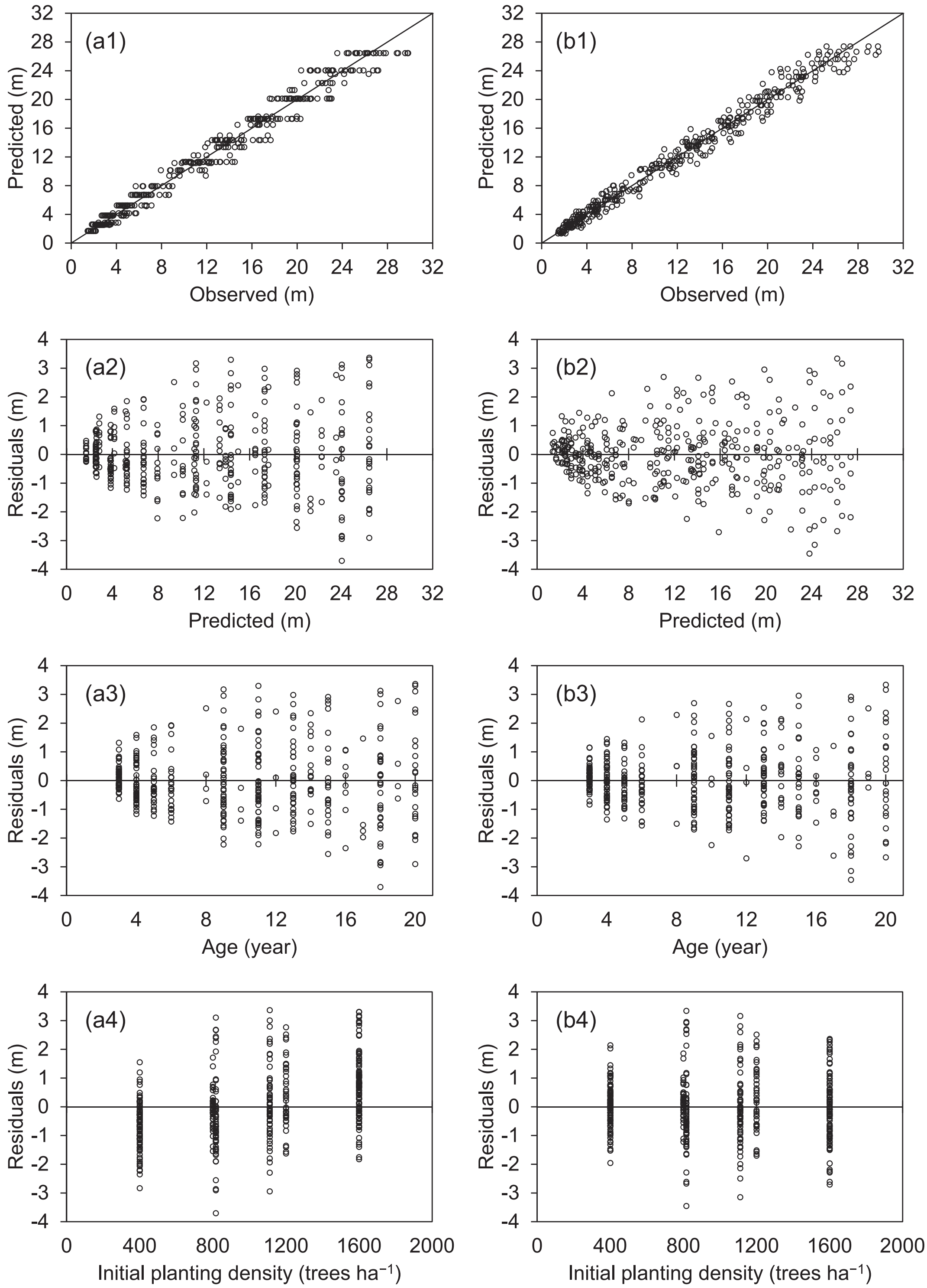

Fig. 2. Residual plots of the density-free (plot a1–a4) and density-sensitive (plot b1–b4) dominant height growth models for hybrid aspen. The residuals are derived from the model fitting of Eqs. (2) and (3) in Table 4.

$$H = (a + u_1)\left(1 - e^{-bA}\right)^{(c+u_2)} + \varepsilon \quad (2)$$

$$H = (a + u_1)\left(1 - e^{-bA}\right)^{(c_0 + c_1 \times D + u_2)} + \varepsilon \quad (3)$$

where H is the dominant height (m); D is the initial planting density (trees ha^{-1}) divided by 10,000 (m^2); e is the base of the natural logarithm. In both models, a and b are parameters, which refer respectively to the asymptote and the growth rate of the original Chapman-Richards function. In Eq. (2), the shape of the function is expressed as a single parameter c, but in density-sensitive model (Eq. (3)) the shape is affected by initial planting density ($c_0 + c_1 \times D$); u_1 and u_2 are random effects; ε is the random error term. Note that the growth rate parameter (b) is estimated as a fixed-effect and only the asymptote and shape parameters vary with random effects due to convergence problems when applying a random effect on the growth rate term (cf., Lappi and Bailey, 1988; Hall and Bailey, 2001; Huuskonen and Miina, 2007).

All the fixed-effect parameters were significant in both models ($P <$

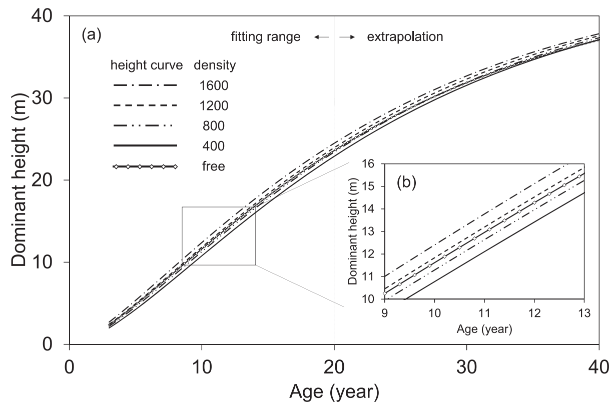

Fig. 3. Dominant height growth curves linked to the initial planting density based on density-free (density, free) and density-sensitive (density, 400–1600 trees ha^{-1}) models for hybrid aspen. Regression lines via Eqs. (2) and (3) are displayed using the fixed effects provided in Table 4. The age range fitted for model development was from age 3 to age 20 and thereafter the predicted curves were simulated for extrapolation. From the entire prediction (plot a), height curves at a certain range (plot b) were magnified to clarify the growth difference.

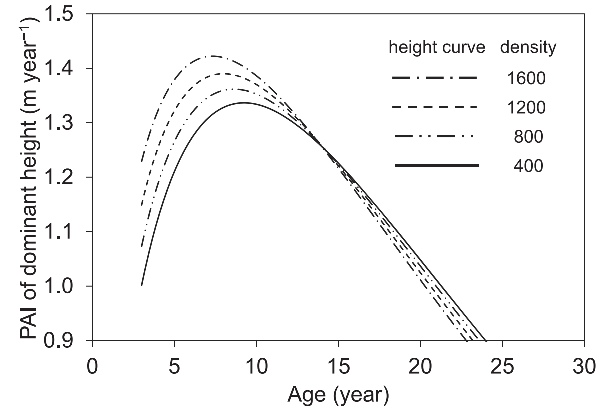

Fig. 4. The periodic annual increment (PAI) of dominant height linked to the initial planting density (400–1600 trees ha^{-1}) based on the density-sensitive dominant height growth models predicted using Eq. (3) in Table 4.

0.05) (Table 4). In both models, parameters *a* and *b*, referring to the asymptote and growth rate, respectively, were quite similar. However, standard errors of the parameters were lower in the density-sensitive model. In density-sensitive model, the effect of the initial planting density (parameter c_1) was included in the shape parameter. According to the density-sensitive model (Eq. (3)) fitted to the hybrid aspen data, the value of the shape parameter of the Chapman-Richards model varied from 1.6378 with 400 trees ha^{-1} to 1.4775 with 1600 trees ha^{-1}. Thus, for hybrid aspen stands with a low stand density, early growth was slower and the increment curve reached the inflection point later than for stands with a high stand density.

The model performance was also evaluated by residuals, AIC, BIC, R^2, and RMSE. All indices were better in the density-sensitive model than in the density-free model. For residuals and RMSE, the fit statistics of the density-sensitive model distinctly performed better than the density-free model. Residual plots were checked to verify the model behavior (Fig. 2). When comparing the observed and the predicted values, the residuals of the density-free model were plotted with a stepped, discrete distribution because the age was only considered as a predictor (Fig. 2, plot a1 and a2). On the other hand, the residuals of the density-sensitive model were dispersed more with various predictions even for the same age due to the variation in initial density, which was reflected in the predicted values of the density-sensitive model (Fig. 2, plot b1 and b2). The residual variation was slightly smaller in the density-sensitive model than in density-free model, which implies a better fit to the data. The same pattern was also observed in the residuals over age (Fig. 2, plot a3 and b3). Neither of the models showed abnormal trends or biases in the residuals. However, an obvious distinction between the two models was detected in the scatterplot of residuals for the initial density (Fig. 2, plot a4 and b4). In the density-free model, the mean of the residuals for the initial density increased from a negative value to a positive value showing a biased prediction with respect to the initial density. The residuals for the initial density implied a better fit of the density-sensitive model to the dominant height growth of hybrid aspen.

3.3. Exploratory growth description and site index application

In order to assess the growth patterns and the effect of initial density, models were used to simulate dominant height development with different stand densities (Fig. 3). The dominant height predictions varied between 2.0–2.7 m at age 3, and 22.9–24.5 m at age 20 with varying initial densities. The initial density influenced only the early dominant height growth rate resulting in an increasingly dominant height differentiation during the first 14 years. The largest difference of the dominant height growth was observed at age 14 when the dominant height was 17.7 m for a density of 1600 trees ha^{-1} while it was 16.0 m for a density of 400 trees ha^{-1}. Thereafter, the dominant height differences decreased, and it was predicted to be 0.7 m between 1600 trees ha^{-1} and 400 trees ha^{-1} at age 40. The predicted height curve of the density-free model remains in the middle of the range of density-sensitive model predictions (Fig. 3).

Furthermore, the periodic annual increment (PAI) of dominant height in the density-sensitive model was studied by calculating the growth difference according to the initial density over age to describe the general incremental pattern and age of the maximum PAI (Fig. 4). The annual increment of the dominant height was higher for high density and lower for low density, similar as shown for dominant height. The PAI annually increased up to 1.34 m year^{-1} at age 9 for a density of 400 trees ha^{-1} and up to 1.42 m year^{-1} at age 7 for a density of 1600

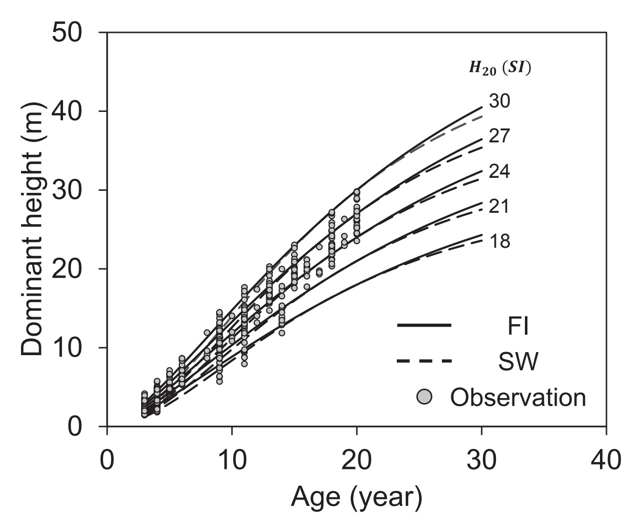

Fig. 5. The site index model curve of this study (solid line) from Finland (FI) with the data points (grey circle) used for model development was compared to the curve of a study (dash line) from Sweden (SW) reported by Johansson (2013). The density-free site index model via Eq. (4) was applied to compare with the Chapman-Richards model in the study by Johansson (2013). The site index (SI) in both studies indicates the dominant height at a base age of 20 (H_{20}).

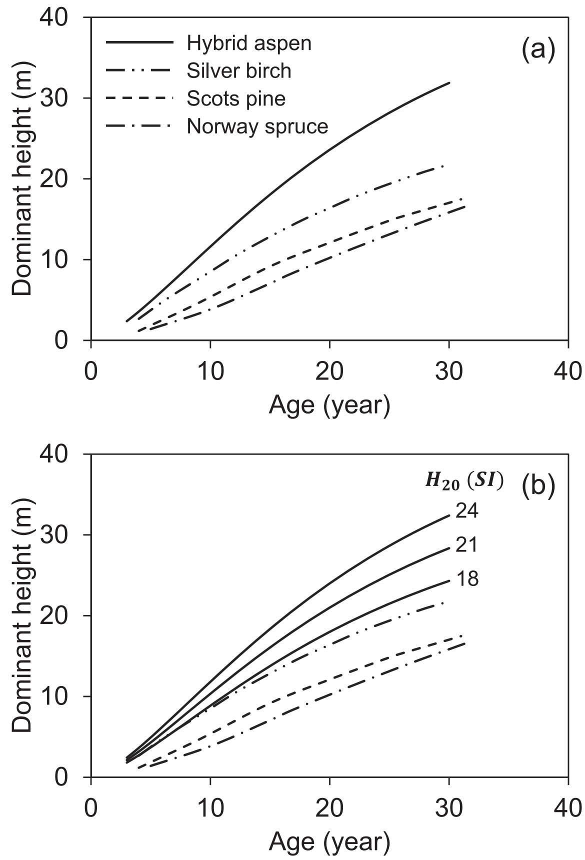

Fig. 6. Growth comparison between hybrid aspen and other major species in Finland at a herb-rich site (*Oxalis-Myrtillus* forest type) (Cajander, 1949; Tonteri et al., 1990). The density-free model of the present study was applied for hybrid aspen in a dominant height growth curve (plot a, solid line) via Eq. (2) and in site index curves (plot b, solid line) via Eq. (4). The site index (SI) for hybrid aspen indicates the dominant height at a base age of 20 (H_{20}). The data for Norway spruce and Scots pine was provided by the MOTTI simulator (Natural Resources Institute Finland, 2015). The dominant height model for silver birch was referenced from Oikarinen (1983).

trees ha^{-1}. The annual increment decreased after that, and subsequently the growth differences due to the initial density started to decrease. After age 14 the PAI was reversed for the density and the annual increment of the dominant height was lower for initially high density stands than for initially low density stands. Still, the difference in the annual increment for different initial densities was insignificant compared to the situation before the reversion.

Site index equations using the developed density-free and density-sensitive dominant height growth models can be expressed respectively in the density-free (Eq. (4)) and the density-sensitive (Eq. (5)) site index model of the anamorphic curve using the estimated parameters as follows:

$$H = S \times \left(\frac{1 - e^{-0.0540A}}{1 - e^{-0.0540A_0}}\right)^{1.5441} \quad (4)$$

$$H = S \times \left(\frac{1 - e^{-0.0537A}}{1 - e^{-0.0537A_0}}\right)^{(1.6912 - 1.3356 \times D)} \quad (5)$$

where S is the site index (m); A_0 is the base age at 20 years; and other terms are as defined earlier.

In the density-sensitive site index model (Eq. (5)), unlike the conventional site index models, the dominant height prediction at a given age varies according to the initial density. For instance, if Eqs. (4) and (5) are applied to predict the dominant height of a 15-year-old stand with a site index (H_{20}) of 27 m, the prediction from the density-free site index model (Eq. (4)) is 20.7 m. The dominant height prediction of density-sensitive site index model (Eq. (5)) is 20.3 m for a stand with an initial density of 400 trees ha^{-1} and 20.9 m for 1600 trees ha^{-1}.

So far, the only published site index model for hybrid aspen in the Nordic countries was developed in Sweden by Johansson (2013). It also used the Chapman-Richards function, but without a stand density effect. The density-free site index model (Eq. (4)) was compared with Johansson's model for deviated site indices with a base age of 20 years (Fig. 5). The dominant height development of stands with a site index from 18 to 30 m by 3 m intervals were predicted from age 5 to age 30. In general, the form of the predicted development for the dominant height was slightly higher than the model by Johansson (2013). However, the site index curves of both studies were identical from age 13 to 22. Before and after this, the site index curve from the present study was above the predicted dominant height of Johansson's model, the difference being 0.8–1.3 m at age 5 and 0.7–1.2 m at age 30.

4. Discussion

4.1. Effect of initial planting density on height growth

Site index models for hybrid aspen were developed based on data from repeatedly measured clonal plantations located in southern Finland. In this study, the characteristics of the dominant height growth linked to the initial density of the stand were studied and models were developed considering these characteristics. The general dominant height growth patterns observed in our study were similar to the findings from earlier studies in the Nordic and Baltic countries (Rytter and Stener, 2005; Heräjärvi and Junkkonen, 2006; Johansson, 2013; Zeps et al., 2016; Stener and Westin, 2017; Fahlvik et al., 2019). In the present study, nonetheless, it was shown for the first time that dominant height growth of hybrid aspen is affected by the initial stand spacing (Table 3). The dependence of height growth on spacing has been found for other tree species. There are several studies on hybrid poplar plantations on this (DeBell and Harrington, 1997; Johnstone, 2008; Benomar et al., 2012; Ghezehei et al., 2016). However, different studies report both negative and positive effects of spacing on height growth. Benomar et al. (2012) reported that, depending on the clone, the mean height growth of hybrid poplar trees increased with initial density.

A positive correlation between the mean height growth and initial planting density was also found in a study on ash by Kerr (2003). He proposes three hypotheses for the cause of the higher growth of closer spacing; an improved microclimate, reduced interspecific competition, especially from weeds, and altering of the red-far-red light reflected from foliage. If no weed control is carried out competition from weeds on former agricultural land is strong (Hytönen and Jylhä, 2005, 2013), and competition from weeds can have a significant effect on the survival and growth of *Populus* seedlings (Böhlenius and Övergaard, 2015). Although the effect of weed competition on height growth could not be verified in our study, it could be an explanation for the difference in the dominant height growth linked to the initial density, which is the reason why the effect was strongest during the early years of stand development.

4.2. Model evaluation with stand density effect

In this study the dominant height growth was modelled applying the widely used Chapman-Richards function including the age and initial planting density as predictors. A similar approach was tested by Pienaar and Shiver (1984) for slash pine plantations. They reported no significant effect of the initial stand density on the parameters of the Chapman-Richards function, and concluded using a model without an initial density effect. However, they also stated that the effect of the initial density may have had effect on the dominant height earlier than the range of stand age included in their data, which is consistent with our results that a significant distinction of dominant height growth was observed during early ages only (Fig. 3). In a study by Knowe and Hibbs (1996), the initial density effect was included in the growth rate parameter for red alder stands. The covered age was until 7 years. These results match those of our study that the annual height increment linked to the initial density inversed near the peak of its growth (Fig. 4).

In a model of loblolly pine by Antón-Fernández et al. (2011), the asymptote, growth rate, and shape parameters were all estimated using the initial spacing as a variable, and the effect proved to be significant for all three parameters. However, the dominant height growth model of our study gave the best fit using only the modified shape parameter for every possible combination of candidates (Eq (3), Table 4, Appendix C). Because we did not modify the asymptote and growth rate parameter in our model, it was not directly contradicted by the concept that the dominant height growth may not be affected by the stand density. The growth rate (parameter *b*) of hybrid aspen in our models (Eqs. (2) and (3)) was not affected by the initial planting density. However, the dominant height was strongly linear over age in the measured range. Our models did not indicate any obvious asymptote (parameter *a*). Therefore, the interpretation should be considered with care especially when extrapolating after the age of 20 (Table 4, Fig. 3). For higher ages additional field measurements and analysis are needed.

4.3. *Practicability and applicability of the final developed models*

The final models fitted well when using initial planting density as a predictor, but one should be cautious when applying these results. Hybrid aspen grow much faster than the native European aspen in Finland (Hynynen et al., 2002, 2004). For this study, the modelling data was collected from a clonal plantation of hybrid aspen. Hence, this model should not be applied to hybrid aspen plantations established with seedlings or second-growth plantations from root suckers because their growth characteristics clearly differ (Hytönen, 2018; Fahlvik et al., 2019). The clones originated from superior individual trees which were selected from progenies of controlled hybrid crossings. This is why in general clonal plantations grow faster than plantations from seedlings. In this study variation in growth between the clones was not acknowledged, which resulted in one single model for all clones. Clonal trials with hybrid aspen were conducted at the same time as the planting density trials as part of the Finnish national tree breeding program. They showed that at age 12 there is a significant difference in the height between clones. All three clones used here performed above the average of a total of 25 clones tested (unpublished data). However, in this study the clone effect might be biased with a possible site effect because the different clones were grown at different sites (Table 2).

The investigated initial planting density ranged from 400 trees ha^{-1} to 1600 trees ha^{-1}, which is common for fast growing tree species (such as poplars) in plantations, but wider than normally used in Finland for commercial tree species. Thus, the model should be applied with caution to stands with initial densities outside this range. In cases where the initial density is not known, nonetheless, the density-free model can be used only in cases when a small bias is acceptable in comparison to the density-sensitive model (Fig. 2, plot a4 and b4). Spatial coverage was confined within the region of southern Finland, but our models may be extended to neighbouring countries such as southern Sweden and Estonia, where geographical environment is similar, because the general growth pattern is quite similar to studies in those countries (Rytter and Stener, 2005; Zeps et al., 2016; Stener and Westin, 2017). Nonetheless, the models are not recommended for application in regions where the climate, soil, and/or topography are considerably different. In Finland, the models should be used only in the southern part of the country.

4.4. *Comparison of growth and model to earlier findings*

The models developed in the present study were similar to the dominant height growth and site index curves developed in earlier studies (Johansson, 2013; Fahlvik et al., 2019). Especially, the site index curves by Johansson (2013) were almost identical to the density-free site index model of our study for ages 13–22 (Fig. 5). Some differences between the two studies were detected outside this age range. This could be because the site quality of our experiments is expected to be more productive. In addition, due to progress in tree breeding, the present clones are expected to be more productive than those from the 1940s–1950s (Johnsson, 1953; Johansson, 2013). Fahlvik et al. (2019) reported, similar dominant height growth to our study beyond age 20. Hence, our models could be verified and applied for southern Sweden.

The developed models for the dominant height and site index were compared to those of other major tree species in Finland (Cajander, 1949; Oikarinen, 1983; Tonteri et al., 1990; Natural Resources Institute Finland, 2015). It was shown that hybrid aspen was remarkably higher in dominant height than silver birch, Scots pine, or Norway spruce (Fig. 6). *Populus* species are in general fast growing tree species and for species hybrids such as hybrid aspen, heterosis in combination with intensive clonal selection even increases this vigorous growth. This indicates the need for models developed specifically also considering a shorter rotation age. It is expected to use our models in studies to evaluate site productivity and for developing further growth and yield models of hybrid aspen.

5. Conclusion

Dominant height growth and site index models were developed using data from clonal hybrid aspen plantations in the range of 3 to 20 years of age in southern Finland. Dominant height growth was significantly affected by the initial planting density within the range of 400–1600 trees ha^{-1}: the higher the initial density, the higher the dominant height. Considering the effect of the initial density, dominant height growth models were developed using the Chapman-Richards function with modified parameters: a density-free model and a density-sensitive model. The density-sensitive model provided the best fit only when the shape parameter was modified in the Chapman-Richards function, and then it estimated the parameters following a modified equation with a biometrical concept and characteristics, projecting a higher dominant height with increasing initial density.

Anamorphic site index curves were explained properly with the density-sensitive model as well as with the density-free model. The developed models can be used for hybrid aspen plantations regardless of the clone used. However, it should not be used for European aspen and the secondary hybrid aspen stands grown from root suckers. The applicable geographical range should be limited to regions with similar environmental conditions as in southern Finland. One should be cautious when extrapolating to ages over 20 years and/or to initial densities outside the range of 400–1600 trees ha^{-1}. The developed dominant height and site index models including an initial density variable are to be used for clonal hybrid aspen plantations in southern Finland.

CRediT authorship contribution statement

Daesung Lee: Conceptualization, Methodology, Formal analysis, Software, Visualization, Writing - original draft, Writing - review & editing, Funding acquisition. **Egbert Beuker:** Writing - review & editing, Validation. **Anneli Viherä-Aarnio:** Writing - review & editing, Validation. **Jari Hynynen:** Conceptualization, Data curation, Writing - review & editing, Validation, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was also supported by the Basic Science Research Programme through the National Research Foundation of Korea (NRF) funded by the Korean Ministry of Education (Grant No. NRF-2019R1A6A3A03032912) in 2019. Research work was carried out in the Natural Resources Institute Finland (Luke), which also provided the empirical data for the analyses.

Appendix A. Stand density trend and size-density relationship

To support the concept that significant dominant height growth was not affected by different rates of mortality, stand density was plotted against the age and size-density relationship (Fig. A1). The analysis did not provide any distinct transitional points to imply a maximum size-density relationship. Signs of density-induced self-thinning were not found until the last measurement of the current analysis.

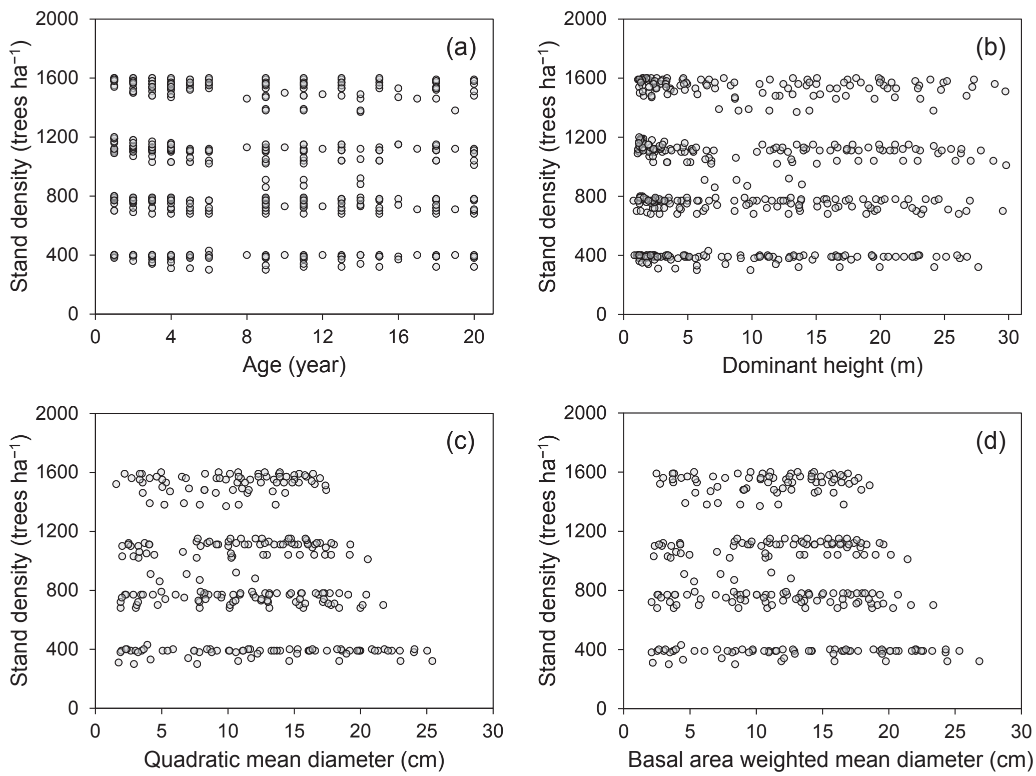

Fig. A1. Stand density trend with age (a) and the size-density relationship with the dominant height (b), quadratic mean diameter (c), and the basal area weighted mean diameter (d), which is commonly used in Northern Europe.

Appendix B. Significant height growth characteristics with initial spacing

In order to provide the general height distribution trend of hybrid aspen linked to the initial planting density, an exploratory data analysis was checked using a height distribution visualisation (Fig. B1). In all of the experiments, at the early stages, bell-shaped curves by initial spacing were shown with an identical center location, which indicated the same arithmetic mean height. The curve height was different due to the designed number of trees per ha per plot. Thereafter, from age 4, the height distribution of denser plots tended to shift more to the right, which indicated that the majority of the trees were higher in denser plots. This analytic result can support the significant height growth difference according to the initial density.

Still, one may question the current dominant height definition, calculated using the top 6.25% (100/1600), 8.33% (100/1200), 12.50% (100/800), 25.00% (100/400) sample trees per ha for different initial placing, respectively. One could doubt that the significant difference was not due to the initial spacing but because of the specific definition resulting in the selection of a higher dominant height in denser plots. In order to show that superior dominant height growth in denser spacing was not because of the definition of the dominant height (or specific dominant height selection method), an analysis of covariance (ANCOVA) was carried out for the most representative several definitions (Table B1). The result shows that, regardless of the definition, the dominant height growth was significantly different for initial stand densities. Therefore, the most common definition in northern Europe, Criterion B.1, could be chosen.

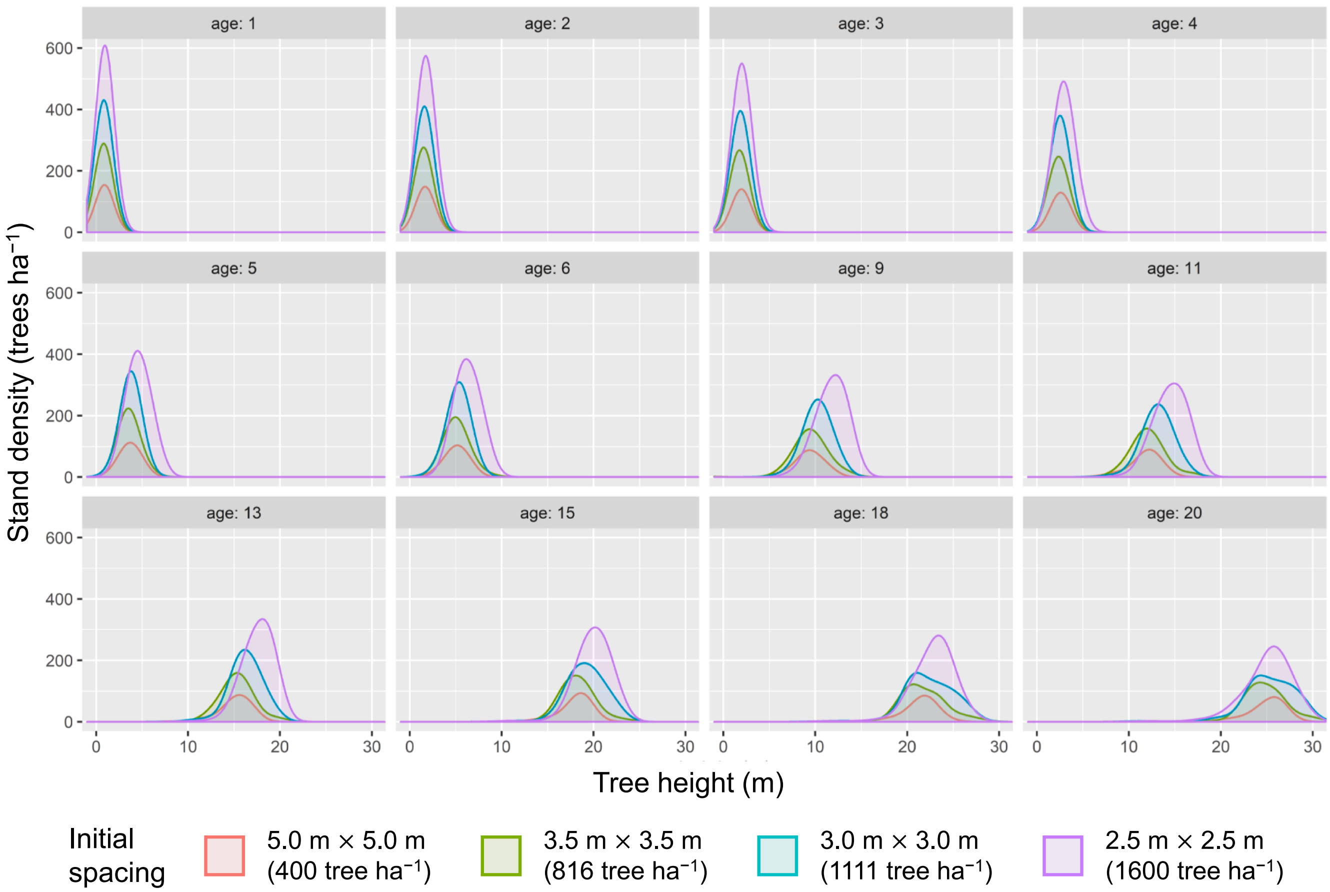

Fig. B1. Tree height distribution trends over time according to the initial spacing of experimental site 1 for different ages as an example. The distribution was displayed using the kernel density estimate with a bandwidth of 1 m, a smoothed version of the histogram and a non-parametric way to estimate the probability density function of a random variable for continuous data, through Gaussian approximation using the *ggplot2* package (Wickham, 2016) of the R statistical software (R Core Team, 2019). The area under each curve represents the number of trees per ha according to the initial spacing.

Table B1
Four kinds of analysis of covariance (ANCOVA) and parameter estimates of the fixed-effects for stand age and initial spacing with the different criteria to study the effect of the definition on significant dominant height growth. For Criterion B.1 the dominant height was calculated as the average height of 100 trees with thickest dbh per hectare. For Criterion B.2, the dominant height was calculated by averaging the tree height whose diameter was larger than the quadratic mean diameter. For Criterion B.3, the dominant height was calculated by sorting the tree dbh in an ascending order and averaging the height for the largest 20% of the trees. For Criterion B.4, the dominant height was calculated by sorting the tree height in an ascending order and averaging the height among the tallest 20% of the trees. The denominator degrees of freedom was different per method because there was no measurement of dbh before age 5.

Definition	Source	Num DF	Den DF	F Value	Pr > F	Effect	Estimate	S.E.	t Value	Pr > |t|
Criterion B.1.	Age	1	381	12716.40	<0.0001	Age	1.3773	0.0122	112.77	<0.0001
	Spacing	4	381	16.78	<0.0001	Spacing 2.5 m	−1.4331	0.7028	−2.04	0.0421
						Spacing 3.0 m	−1.8970	0.7030	−2.70	0.0073
						Spacing 3.5 m	−2.4355	0.7030	−3.46	0.0006
						Spacing 5.0 m	−2.7407	0.7031	−3.90	0.0001
Criterion B.2.	Age	1	286	7193.88	<0.0001	Age	1.4028	0.0165	84.82	<0.0001
	Spacing	4	286	11.28	<0.0001	Spacing 2.5 m	−2.9146	0.9459	−3.08	0.0023
						Spacing 3.0 m	−3.1916	0.9459	−3.37	0.0008
						Spacing 3.5 m	−3.8176	0.9459	−4.04	<0.0001
						Spacing 5.0 m	−3.9249	0.9463	−4.15	<0.0001
Criterion B.3.	Age	1	286	6971.72	<0.0001	Age	1.4060	0.0168	83.50	<0.0001
	Spacing	4	286	10.11	<0.0001	Spacing 2.5 m	−2.4509	0.9692	−2.53	0.0120
						Spacing 3.0 m	−2.7803	0.9692	−2.87	0.0044
						Spacing 3.5 m	−3.3731	0.9692	−3.48	0.0006
						Spacing 5.0 m	−3.4797	0.9696	−3.59	0.0004
Criterion B.4.	Age	1	381	12567.20	<0.0001	Age	1.4072	0.0126	112.10	<0.0001
	Spacing	4	381	8.57	<0.0001	Spacing 2.5 m	−1.9752	0.7044	−2.80	0.0053
						Spacing 3.0 m	−2.2014	0.7044	−3.13	0.0019
						Spacing 3.5 m	−2.6785	0.7044	−3.80	0.0002
						Spacing 5.0 m	−2.7381	0.7046	−3.89	0.0001

Note: the ANCOVA model was presented in Eq. (1) of the main manuscript.

Appendix C. Density-sensitive model candidates

To select the best density-sensitive dominant height growth model, every possible combination of candidates with initial density parameters were considered, as shown in Table C1.

Table C1
Model equations of dominant height growth for every possible combination of candidates with the effect of initial stand density.

Equation No.	Model equation	Parameters applied with density effect	Estimated parameters
C.1	$H = (a+u_1)(1-e^{-bA})^{(c+u_2)} + \varepsilon$	–	a, b, c
C.2	$H = (a_0 + a_1 \times D + u_1)(1-e^{-bA})^{(c_0+u_2)} + \varepsilon$	asymptote	a_0, a_1, b, c
C.3	$H = (a+u_1)(1-e^{-(b_0+b_1 \times D)A})^{(c+u_2)} + \varepsilon$	growth rate	a, b_0, b_1, c
C.4	$H = (a+u_1)(1-e^{-bA})^{(c_0+c_1 \times D+u_2)} + \varepsilon$	shape	a, b, c_0, c_1
C.5	$H = (a_0 + a_1 \times D + u_1)(1-e^{-(b_0+b_1 \times D)A})^{(c+u_2)} + \varepsilon$	asymptote and growth rate	a_0, a_1, b_0, b_1, c
C.6	$H = (a_0 + a_1 \times D + u_1)(1-e^{-bA})^{(c_0+c_1 \times D+u_2)} + \varepsilon$	asymptote and shape	a_0, a_1, b, c_0, c_1
C.7	$H = (a+u_1)(1-e^{-(b_0+b_1 \times D)A})^{(c_0+c_1 \times D+u_2)} + \varepsilon$	growth rate and shape	a, b_0, b_1, c_0, c_1
C.8	$H = (a_0 + a_1 \times D + u_1)(1-e^{-(b_0+b_1 \times D)A})^{(c_0+c_1 \times D+u_2)} + \varepsilon$	asymptote, growth rate, and shape	$a_0, a_1, b_0, b_1, c_0, c_1$

Note: the symbols were explained in the description of Eqs. (2) and (3) of the main manuscript.

The fixed-effects were significant ($P \leq 0.05$) when the density predictor was applied on none or one of the parameters (Eqs. C.1, C.2, C.3, and C.4), but not significant ($P > 0.05$) applied on more than one parameter (Eqs. C.5, C.6, C.7, and C.8). The best fit statistics were found in the application of the shape parameter (Eq. C.4), which was finally used in main manuscript (see Table C2).

Table C2
Parameter estimates and fit statistics for the candidate models provided in Table C1.

Class	Parameter	Estimates by candidate model no. described in Appendix C							
		Eq. C.1	Eq. C.2	Eq. C.3	Eq. C.4	Eq. C.5	Eq. C.6	Eq. C.7	Eq. C.8
Fixed effects	a	44.8115 (0.0212)	–	43.6145 (0.0093)	45.4616 (0.0098)	–	–	44.5188 (0.0098)	–
	a_0	–	41.1944 (0.0108)	–	–	47.8370 (0.0113)	44.7299 (0.0117)	–	47.8601 (0.0124)
	a_1	–	40.5028 (0.0180)	–	–	−39.4367 (0.1956 ^{ns})	4.2284 (0.7656 ^{ns})	–	−33.8921 (0.2904 ^{ns})
	b	0.0540 (0.0182)	0.0541 (0.0144)	–	0.0537 (0.0137)		0.0542 (0.0141)	–	–
	b_0	–	–	0.0515 (0.0124)	–	0.0467 (0.0153)	–	0.0532 (0.0131)	0.0481 (0.0179)
	b_1	–	–	0.0491 (0.0255)	–	0.0942 (0.0615 ^{ns})	–	0.0184 (0.4683 ^{ns})	0.0691 (0.2309 ^{ns})
	c	1.5441 (0.0029)	1.5608 (0.0028)	1.5716 (0.0027)	–	1.5657 (0.0025)	–	–	–
	c_0	–	–	–	1.6912 (0.0031)	–	1.6841 (0.0032)	1.6516 (0.0037)	1.6067 (0.0037)
	c_1	–	–	–	−1.3356 (0.0219)	–	−1.2221 (0.0890 ^{ns})	−0.8620 (0.2634 ^{ns})	−0.4875 (0.5074 ^{ns})
Random effects	var(u_1)	97.2330	18.1610	20.1723	18.7549	21.0139	18.6609	19.3371	20.8629
	cov (u_1,u_2)	−0.1738	−0.1055	−0.0838	−0.0987	−0.0878	−0.1000	−0.0930	−0.0857
	var(u_2)	0.0070	0.0107	0.0098	0.0105	0.0085	0.0106	0.0103	0.0091
Residual	var(ε)	1.4959	1.2096	1.1826	1.1787	1.1724	1.1783	1.1758	1.1705
Fit statistics	AIC	1301.1	1219.8	1211.4	1209.9	1210.1	1211.8	1211.1	1211.4
	BIC	1296.8	1214.8	1206.5	1205.0	1204.6	1206.3	1205.6	1205.3
	R^2	0.9762	0.9807	0.9812	0.9812	0.9813	0.9812	0.9813	0.9813
	RMSE	1.2127	1.0904	1.0780	1.0763	1.0733	1.0761	1.0749	1.0725

Note: the *P*-values of all fixed-effect parameters are provided in parentheses. AIC is the Akaike information criterion. BIC is the Bayesian information criterion. R^2 is the coefficient of determination. RMSE is the root mean square error. Superscript ns indicates the symbol for $P > 0.05$ (not significant).

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