

Estimation of optimal timing of early selection based on time trends of genetic parameters in *Abies sachalinensis*

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Abstract

Early selection is an imperative in ongoing forest tree breeding. This study estimated the optimal timing of early selection in *Abies sachalinensis* (F. Schmidt) Mast. based on time trends of genetic parameters obtained from two test sites. Tree height (H_t) at 5, 10 (11), 15, 20, 30, and 40 years of age and diameter at breast height (DBH) at 20, 30, and 40 years of age were analyzed. The efficiency of early selection per year (E) for performing early indirect selection relative to performing direct selection at the earliest rotation age (40 years of age) was estimated based on narrow-sense heritability (h^2) and age–age genetic correlation (r). The h^2 of H_t peaked at 10 or 15 years of age (0.52–0.71), and that of DBH was the highest at 20 years of age (0.19 or 0.22). The age–age genetic correlation between tree heights or between tree height and DBH at different ages decreased with increasing differences between ages (regression coefficients were -0.011 and -0.007 , respectively). The E values were highest at 10 or 15 years of age (0.84–1.74 and 1.42–2.24 for H_t and H_t -DBH, respectively), indicating the optimum selection timing. In Japanese forestry, the initial growth rate is considered important for reducing weeding costs. Selection at 10 or 15 years of age had more than $>65\%$ indirect genetic gain relative to the direct genetic gain at 5 years of age; thus, selection at 10–15 years of age is appropriate considering the initial and mature phases of tree growth.

Keywords: narrow-sense heritability, genetic gain, indirect selection, selection efficiency per year, Sakhalin fir, age–age correlation

Introduction

Quantitatively evaluating tree growth for breeding is challenging for boreal conifer species due to their long rotation time of more than 40 years. Early selection can reduce the need for field evaluations and enhance the breeding cycle gain (Wu 1998; Gonçalves et al. 2005). Therefore, early selection is an essential factor in the ongoing breeding of forest trees. It is essential to optimize the selection age in order to maximize genetic gain from early selection (Burdon 1989). Genetic gain from early indirect selection depends on heritability and age–age genetic correlation. To determine the optimum timing of early selection, it is crucial that the time trends of genetic parameters are considered. Heritability, age–age correlation, and feasibility of early selection have been shown in many tree species, such as *Pinus elliotii* (Hodge and White 1992), *P. sylvestris* (Happanen 2001; Jansson et al. 2003), *Picea taeda* (Gwaze et al. 1998; Lambeth and Dill 2001), and *Larix kaempferi* (Diao et al. 2016). These previous studies have successfully demonstrated the feasibility and advantage of early selection. However, studies have also revealed that the time trends of genetic parameters vary among species (Cornelins 1994); therefore, such trends must be verified carefully for each target species.

Abies sachalinensis (F. Schmidt) Mast. is the main forest species in Hokkaido Prefecture, Japan. Artificial forests cover approximately 1.5 million hectares in Hokkaido, with *A. sachalinensis* accounting for approximately 54 % of that area (Hokkaido Research Organization 2018). Therefore, *A. sachalinensis* has become one of the main target species of breeding programs in Japan, and tree growth is considered an important target trait. Since its cutting cycle is 40–80 years, tree size at 40 years of age is a significant target trait when considering a

breeding strategy. However, a growth evaluation period of 40 years or more is too long for choosing and using the next generation of select parents. Therefore, early selection should be adopted for the breeding strategies of the species. In *A. sachalinensis*, site index curves have been developed based on tree height data from many commercial plantations (Takiya 2014); however, little is known about the time trends of genetic parameters in this species. Thus, the optimal age for early selection and expected genetic gain from early selection should be determined to enhance breeding efforts for the species.

Studies have primarily investigated the selection efficiency for performing early indirect selection relative to performing direct selection at target (rotation) age. However, the behavior of initial height growth is also given weight in Japanese forestry, because the cost of weeding during long periods is another issue to be addressed (Forestry Agency 2010). The initial height growth of planted trees should exceed that of surrounding plants to save significant costs in establishment. For example, the duration of weeding in *A. sachalinensis* forests is 1–11 years (Nakagawa 2015); thus, the genetic gain of tree height (H_t) at a younger age, such as five years, is also an important breeding target in Japanese forestry. Therefore, both tree height at the initial phase and tree height or stem volume at the mature phase should be considered to determine the optimal timing for early selection.

In Japan, systematic breeding programs for Japanese forestry tree species started in 1954. Since the 1950s, the first generation of plus trees of *A. sachalinensis* has been selected and archived in Hokkaido Prefecture. Progeny tests derived from these plus trees were established in the late 1980s to the early 1990s. Therefore, the trees at most trial sites are less than 40 years old. However, some field progeny tests were established over 40 years ago. Thus, the time trends of tree growth and heritability can be estimated based on observed data from these older trials. In this study, the time trends of indirect genetic gain were estimated from originally collected height and diameter at breast height (DBH) data from 1965 to 2018 in two trials of *A. sachalinensis*, and optimum selection timing was suggested considering both initial and late growth phases.

Materials and Methods

Study sites

Two field trials of open-pollinated progenies of *A. sachalinensis* were established by the Hokkaido Regional Breeding Office, Forest Tree Breeding Center, Forestry and Forest Products Research Institute. In both trials, three blocks (replicates) were established, and 44 and 36 families derived from open-pollinated seeds of first-generation plus trees were planted for trials 1 and 2, respectively. Those sites were established in 1965 (trial 1) and 1967 (trial 2) and were located close together (Table 1). Plots, including 150 trees from a single family, were randomly arranged in each block. Therefore, 450 trees per family were planted in each trial.

Table 1

Basic information of each trial. Stand tree density was briefly calculated from the roughly estimated total area (ha) and the numbers of planted trees.

Trials	Location		Planting year	Planted tree	family	Tree density (/ha)
	N	E				
Trial 1	42.80°	141.45°	1965	19800	44	4519
Trial 2	42.80°	141.47°	1967	16200	36	3639

Data collection

Tree heights (H_t) were measured at 5, 10, 20, 30, and 40 years of age and 5, 11, 15, 20, 30, and 40 years of age for trials 1 and 2, respectively. In both trials, DBH was measured at 20, 30, and 40 years of age. Regarding H_t and DBH measurements, a sample survey was conducted, and some of the surviving trees were not surveyed in some years. In addition, we could not assess the tree growth of individual trees because tree ID was not recorded from 5 to 20 years of age. However, the mean number of surveyed trees per family was >50 in all measurement ages (for the number of trees surveyed per family, see Supplementary Tables 1 and 2). Therefore, we mainly assessed site or family-based data in this study. Table 2 shows the observed mean tree heights in each trial, and Supplementary Figure 1 shows their periodic annual increments (PAIs; Avery and Burkhart 2002) as a reference.

Analysis of trends of tree height growth

First, tree growth curves were produced in each trial to confirm the generality of tree height growth. The mean H_t was calculated for each family/block plot, then growth curves were estimated based on the calculated means. Because H_t growth was maximal between 20 and 30 years of age, and declined thereafter (Table 2, Supplementary Figure 1), we considered the left-right asymmetry shape of the function to be more appropriate for use in this study. Therefore, we adapted the Gompertz function (Equation 1) to produce the tree growth curves:

$$H_t = \beta_1 \cdot \exp(-\beta_2 \cdot \exp(-\beta_3 \cdot t)) \quad (1)$$

Here, H_t is the predicted tree height at age t . β_1 , β_2 , and β_3 are parameters estimated by Markov Chain Monte Carlo methods (MCMC) using Stan ver. 2.18.2 with a noninformative prior distribution. For MCMC, iteration was set to 3000, with 1500 of warm-up, and the Gelman–Rubin convergence diagnostic evaluated the convergence of four chains ($\hat{R}$; Gelman and Rubin 1992). The inflection point of the growth curve was also calculated as $\frac{1}{\beta_3} \cdot \log(\beta_2)$. Estimated tree growth curves and inflection points were compared with previously reported site index curves of *A. sachalinensis* (Takiya 2014).

Analysis of the optimum timing of early selection

To consider the optimum timing of early selection, we estimated the selection efficiency per year for performing early indirect selection relative to performing direct selection at the target age (Lambeth 1980) based on narrow-sense heritability,

Table 2

Mean tree heights and their standard deviations of all analyzed trees in each trial and age. Tree heights were observed at 10 years of age in trial 1, but it was observed at 11 years of age in trial 2. Others were observed at the same age.

Test site	Observed age (yr)					
	5	10(11)	15	20	30	40
Trial 1	1.07±0.31	2.61±0.52	-	5.68±1.78	11.57±3.51	14.03±3.47
Trial 2	0.77±0.26	2.47±0.86	3.99±1.21	6.44±1.37	12.54±1.60	14.94±3.97

age–age genetic correlation, and relative genetic gain of indirect selection to direct selection. Genetic variance and breeding values of each trial and age were estimated using the individual-based linear mixed model of Eq. (2) (Hiraoka et al. 2019):

$$y_{ij} = \mu + B_j + A_i + e_{ij} \quad (2)$$

where y_{ij} is the observed value for the i th individuals in the j th block, μ is a fixed effect of the overall mean, B_j is the fixed effect of the j th block, A_i is the random additive genetic effect of individual i , and e_{ij} is the residual. Narrow-sense individual heritability (h^2) was estimated for each trial/age subclass using Eq. (3):

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_e^2} \quad (3)$$

where σ_A^2 is the additive genetic variance and σ_e^2 is the environmental variance detected from the linear mixed model mentioned above. These terms were calculated using the breedR package (Muñoz and Sanchez 2016) of R (R core team 2016).

The estimated age–age genetic correlation ($r_{t,T}$) was calculated by obtaining the estimated correlation coefficient of the breeding values of parents at different observation ages ($t < T$) in each trial (Hiraoka et al. 2019). In this study, the age–age genetic correlation of tree height between different ages was estimated. Conversely, the age–age correlation of DBH was not analyzed because DBH was observed only at 20, 30, and 40 years of age. However, stem volume typically depends much more within an even-aged stand on DBH than tree height. Therefore, we assumed that the age–age genetic correlation between tree height and DBH at different ages could also be a useful criterion for considering early selection from tree height. To predict $\hat{r}_{t,T}$ in each trial, the relationship between LAG ($T - t$; Rweyongeza 2016) or LAR ($\ln(t/T)$; Lambeth 1980) and $r_{t,T}$ was estimated using a single regression model (Eqs. 4a and 4b):

$$\hat{r}_{t,T} = a_1 + b_1 \cdot \text{LAG} \quad (4a)$$

$$\hat{r}_{t,T} = a_2 + b_2 \cdot \text{LAR} \quad (4b)$$

where a and b are intercept and regression coefficient, respectively.

Direct genetic gain at age T (G_T) and indirect genetic gain from the selection at age t ($Gl_{t,T}$) were calculated using Eqs. (5) and (6), respectively (Falconer 1981). Then, the relative indirect genetic gain to direct genetic gain ($RG_{t,T} = Gl_{t,T}/G_T$) was simplified to Eq. (7) (Hallingbäck et al. 2018):

$$G_T = ih_T^2 \sigma_{phT} \quad (5)$$

$$Gl_{t,T} = ih_T h_t \hat{r}_{t,T} \sigma_{phT} \quad (6)$$

$$RG_{t,T} = \hat{r}_{t,T} \frac{h_t}{h_T} \quad (7)$$

where i is the selection intensity, h_T^2 and σ_{phT} are narrow-sense heritability and the phenotypic standard deviation at age T , respectively, and h_t and h_T are the square roots of narrow-sense heritability at ages t and T , respectively. From these estimated parameters, the selection efficiency per year (E ; Lambeth 1980, Hallingbäck et al. 2018) for performing early indirect selection relative to performing direct selection at target age was estimated as equation (8):

$$E = (\hat{r}_{t,T} \frac{h_t}{h_T}) \frac{10+T}{10+t} \quad (8)$$

In this study, we added 10 years to account for the establishment or improvement of seed orchards and seed production. Furthermore, T in Eq. (7) was fixed to 40 because rotation age is from 40 years of age, and it can be the target age of *A. sachalinensis*.

In Japanese forestry, initial height growth is an important breeding target trait. Therefore, the optimum selection age detected from the above method should have enough genetic gain at a younger age, such as 5 years of age. Therefore, the relative indirect genetic gain of H_t at older ages (10, 15, 20, 30, or 40 years of age) to direct genetic gain of tree height at 5 years of age (i.e., $RG_{T,5}$) was also confirmed in this study.

Results

Trends of tree height growth

Gomperz function (Eq. (1)) were successfully fitted, and $\hat{R}$ value of all parameters were less than 1.1, indicating sufficient convergence among the four chains. Detected growth curves were similar in both trials. They were $H_t = 19.34 \cdot \exp(-4.15 \cdot \exp(-0.07 \cdot t))$ and $H_t = 19.31 \cdot \exp(-4.16 \cdot \exp(-0.07 \cdot t))$ for trials 1 and 2, respectively (Figure 1). As a result, inflection points were similar in both trials and were estimated to be at age 22 years.

Estimation of optimum timing of early selection

Table 3 shows the estimates of narrow-sense heritabilities (h^2) of H_t and DBH. The highest h^2 value for H_t was 0.60 at 10 years of age in trial 1, and it was 0.71 at 15 years of age in trial 2, although there were no data at 15 years of age in trial 1. Regarding DBH, the highest h^2 values were 0.22 and 0.19 at 20 years of age for trials 1 and 2, respectively. After 20 years of age, observed h^2 values in both H_t and DBH tended to decrease. In addition, h^2 values were higher for H_t than for DBH for all observed ages.

Table 3
Estimates of narrow-sense heritability in each trial and age.

Age (yr)	Tree height		DBH	
	Trial 1	Trial 2	Trial 1	Trial 2
5	0.34	0.43	-	-
10(11)	0.60	0.52	-	-
15	-	0.71	-	-
20	0.36	0.46	0.22	0.19
30	0.14	0.26	0.10	0.10
40	0.51	0.20	0.14	0.06

Figure 2 depicts the relationship between detected age-age genetic correlation ($r_{t,T}$) and LAG or LAR in H_t among different ages. In the LAG-based model, fitted regression equations were $\hat{r}_{t,T} = 0.631 - 0.011 \cdot \text{LAG}$ and $\hat{r}_{1,2} = 0.771 - 0.012 \cdot \text{LAG}$ for trials 1 and 2, respectively. Their coefficients of determination were 0.24 and 0.42 for trials 1 and 2, respectively. In the LAR-based model, fitted regression equations were $\hat{r}_{t,T} = 0.462 + 0.019 \cdot \text{LAR}$ and $\hat{r}_{t,T} = 0.761 + 0.202 \cdot \text{LAR}$ for trials 1 and 2, respectively. Their coefficients of determination were 0.003 and 0.14 for trials 1 and 2, respectively. There was a better fit in the LAG-based model. Figure 3 depicts the $r_{t,T}$ between tree height

and DBH at different ages. In the LAG-based model, fitted regression equations were $\hat{r}_{t,T} = 0.648 - 0.007 \cdot \text{LAG}$ and $\hat{r}_{t,T} = 0.729 - 0.014 \cdot \text{LAG}$ for trials 1 and 2, respectively. Coefficients of determination were 0.23 and 0.56 for trials 1 and 2, respectively. In the LAR-based model, estimated correlation equations were $\hat{r}_{t,T} = 0.552 + 0.009 \cdot \text{LAR}$ and $\hat{r}_{t,T} = 0.598 + 0.132 \cdot \text{LAR}$ for trials 1 and 2, respectively.

Coefficients of determination were 0.002 and 0.26 for trials 1 and 2, respectively. A better fit of the LAG-based model was shown in both between tree heights and between tree heights and DBH. Therefore, we used the predicted values of $\hat{r}_{t,T}$ from the LAG-based model for subsequent analysis.

Tables 4 and 5 show the results of relative indirect genetic gain to direct genetic gain ($RG_{t,T}$). The $RG_{t,T}$ values for tree height among different ages were ranged from 0.21 to 0.40 and from 0.50 to 0.87 in trials 1 and 2, respectively (Table 4). Similarly, the values for DBH were ranged from 0.28 to 0.91 and from 0.07 to 0.79 for trials 1 and 2, respectively (Table 5).

Figure 4 depicts the selection efficiency per year for performing early indirect selection relative to performing direct selection at 40 years of age (E). Comparatively higher E values for H_t were detected when we selected trees between 5 and 15 years old, and the highest E values were detected at 10 and 15 years of age for trials 1 and 2, respectively. For DBH, E was especially high at 10 years of age in trial 1, and there were comparatively higher values at 15 and 20 years of age in trial 2 (Figure 4).

Relative indirect genetic gain of tree height at older ages (10, 20, 30, or 40 years of age) to direct genetic gain of tree height at 5 years of age ($RG_{t,5}$) was also estimated, and Figure 5 depicts the result. In this case, $RG_{t,5}$ decreased with increasing selection age, and more than 64.8 % of the genetic gain was maintained if the selection was done at 10 or 15 years old.

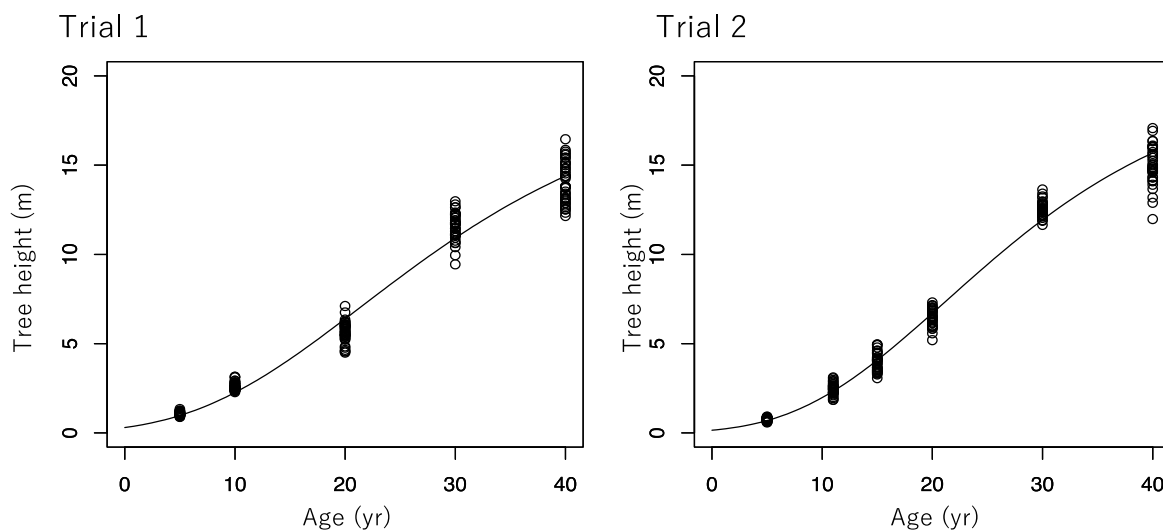


Figure 1
Tree growth curves with Gompertz function based on mean tree heights of each replicate/family block plot.

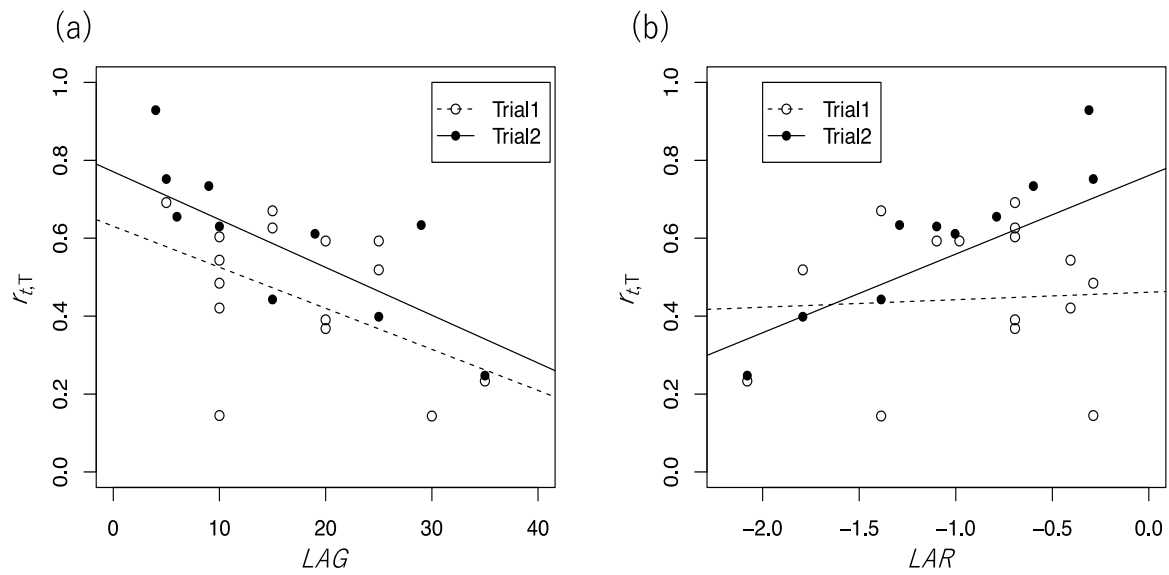


Figure 2
Relationship between LAG (a) or LAR (b) and estimated age–age genetic correlation values ($r_{t,T}$) of tree height for all combinations of different ages.

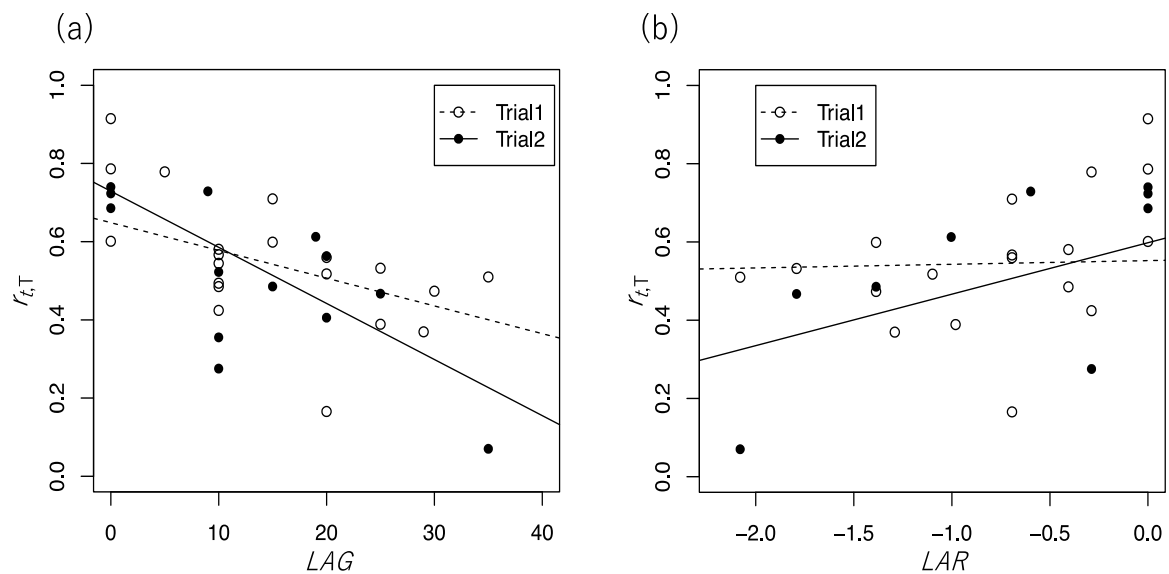


Figure 3
Relationship between LAG (a) or LAR (b) and estimated age–age genetic correlation values ($r_{t,T}$) between tree height and DBH for all combinations of different ages.

Discussion

Time trends of tree height growth

A previous study examined various artificial forests of *A. sachalinensis* ranging in age from 4 to 89 years, and the study derived site index curves from those data (Takiya 2014). The study showed that the inflection point of the site index curve is about 20 years of age, such that the height growth decreases after 30 years of age. In this study, the difference in mean tree height from 20 to 30 years of age was about 5.9 and 6.4 m for trials 1 and 2, respectively (Table 2, Supplemental Figure 1). Similarly, that for 30–40 years old was about 2.4 m in both trials (Table 2),

indicating reduced tree growth after 30 years. In addition, estimated inflection points were about 22 years of age. Observed growth trends corresponded to the previously reported site index curve. Therefore, we concluded that the two analyzed sites showed a broadly representative height growth trend for the species and both trials were suitable for estimating the optimum timing of early selection.

Trends of genetic parameters and suggestions for early selection

In this study, we attempted to determine the optimum timing of early selection from the selection efficiency per year for

Table 4

Estimated relative indirect genetic gain to direct genetic gain between tree heights at different ages.

Trial 1					
Selection age	Target age				
	10	20	30	40	
5	0.44	0.46	0.58	0.21	
10		0.68	0.87	0.34	
20			0.84	0.35	
30				0.27	

Trial 2					
Selection age	Target age				
	11	15	20	30	40
5	0.63	0.65	0.57	0.60	0.50
11		0.72	0.70	0.76	0.67
15			0.88	0.97	0.87
20				0.86	0.79
30					0.74

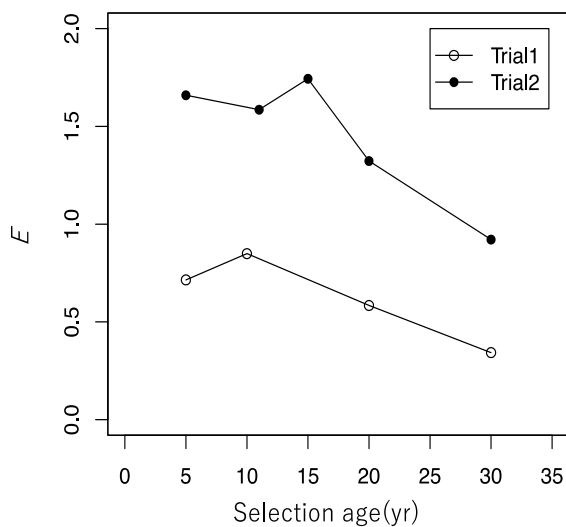
Table 5

Estimated relative indirect genetic gain to direct genetic gain between tree height and DBH at different ages.

Trial 1				
Selection age	Target age (DBH)			
	20	30	40	
5	0.60	0.53	0.51	
10	0.57	0.52	0.47	
20	0.91	0.49	0.56	
30	0.54	0.74	0.28	
40	0.41	0.36	0.72	

Trial 2			
Selection age	Target age (DBH)		
	20	30	40
5	0.49	0.47	0.07
11	0.73	0.61	0.37
15	0.78	0.71	0.39
20	0.79	0.58	0.17
30	0.49	0.60	0.42
40	0.56	0.52	0.69

(a) Tree height



(b) DBH

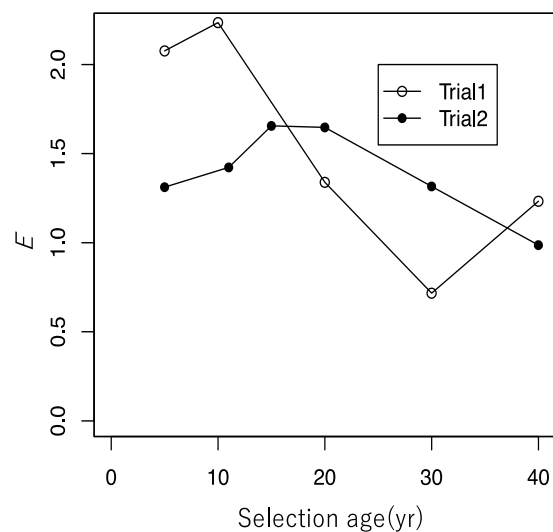


Figure 4

The expected selection efficiency per year (E) for performing early indirect selection relative to performing direct selection at 40 years of age.

performing early indirect selection relative to performing direct selection at a target age of 40 years (E). The 'index' age primarily depends on h^2 and $\hat{r}_{t,p}$, and it is crucial to reveal trends of them. Various levels and age trends of h^2 has been reported in some tree species, implying species complexity. For example, Kroon et al. (2011) studied h^2 from 5 to 20 years in *Picea abies* and discovered a declining trend with age (mean h^2 was 0.29). Mihai and Mirancea (2016) studied height and DBH growth of *Abies alba* from 6 to 36 years after planting and discovered that h^2 values were highest at 6 years in height (0.61) and DBH

(0.71), respectively. Conversely, Hiraoka et al. (2019) studied sites of *Cryptomeria japonica* throughout Japan, finding that h^2 of the tree height was relatively low (around 0.3) before 10 years. However, higher stable values (around 0.45) were maintained between 15 and 30 years. In this study, estimated h^2 of tree height peaked at 10 or 15 years of age, while h^2 of DBH decreased with increasing age after 20 years of age. Such trends were similar in *Pinus banksiana* (Weng et al. 2007). Our results are consistent with the postulate of Franklin (1979), who reported that genetic variance and heritability could

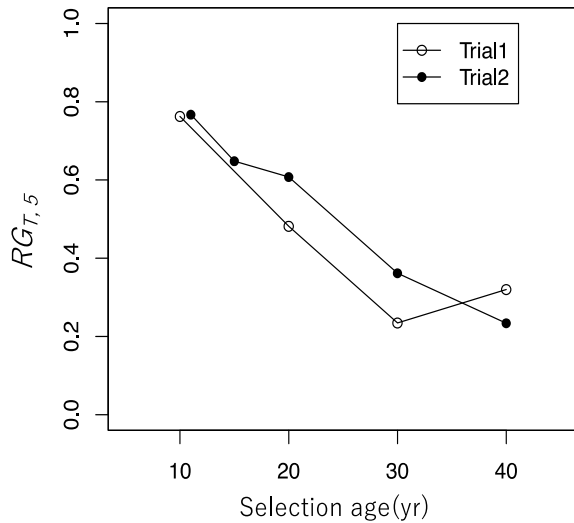


Figure 5
Expected indirect genetic gain from selection on H_t at 10, 15, 20, 30, or 40 years of age relative to direct genetic gain at 5 years of age ($RG_{T,5}$).

change depending on the stage transition from the juvenile-epigenetic phase and mature epigenetic phase to the competitive-suppression phase.

Heritability can be maximized in the mature epigenetic phase by adjusting for local microsite effects and/or competition with surrounding vegetation or planted trees. From the results of the abovementioned height growth trends and h^2 , we considered that from around 10 to 20 years of age represented the mature genotypic phase and that the transition to the competition-suppression phase occurred between 20 and 30 years of age. Abe (1989) supported our hypothesis, reporting that the canopy was just before closing at 18 years of age in the site of *A. sachalinensis* with 3000 individuals/ha. Stand tree density was about 4500 and 3600 individuals/ha for trials 1 and 2, respectively. Therefore, the onset of competitive influences was deemed to be much earlier than 18 years of age in both trials.

Regarding age–age genetic correlation, the range of detected $r_{t,T}$ values differed slightly between trials (Figures 2 and 3) but were of a similar range of age–age genetic correlation values for many forestry species, such as *Abies alba*, *Pinus banksiana*, *P. taeda*, *Cryptomeria japonica*, and *P. sylvestris* (Mihai and Mirancea 2016; Weng et al. 2007; Gwaze et al. 2000; Hiraoka et al. 2019; Jansson 2007, respectively). Those studies reported an increasing trend of $r_{t,T}$ with increasing LAR or decreasing trend of $r_{t,T}$ with increasing LAG. This study had the same results; a negative regression coefficient of $\hat{r}_{t,T}$ was detected in H_t for both trials. A similar trend was also observed between tree height and DBH, indicating that tree height at a certain age can predict DBH in different ages. Burdon et al. (1992) studied the age–age genetic correlation between tree height and DBH at different ages in *Pinus*

radiata and reported that early height could be a good predictor of a genotype's future diameter growth. The study also revealed that DBH sometimes correlates more with earlier height than with current height, and this is also detected in this study. In comparison with tree height, DBH growth is generally more sensitive to competition against surrounding trees (Naji et al. 2015; Bagchi 2007; Roberts and Harrington 2008). Decreased trends of h^2 after 20 years of age in both tree height and DBH, or higher genetic correlation of DBH with earlier tree height than with current tree height may occur by suppression due to increased competition. In any case, we revealed that early selection based on tree height at a younger age could adapt to the DBH and resulting stem volume at an older age.

The estimated E values were highest at 10 and 15 years of age in tree height and DBH (Figure 4). These findings reveal that early selection based on the tree height at 10 to 15 years, i.e., the selection from 1/4th to 3/8th of target age, is efficient in *A. sachalinensis*. Similar results have been reported in other tree species, i.e., they usually conclude that early selection is possible from quarter to half of targeted ages (Happanen 2001; Gunnar et al. 2003; White et al. 2007; Hiraoka et al. 2019).

This study confirmed relative indirect genetic gain from older ages (10, 15, 20, 30, or 40 years old) to direct genetic gain at a younger age (5 years old) to consider initial height growth performance. As previously stated, the selection at 10 or 15 years old was recommended for early selection. Indirect genetic gain at 10 or 15 years maintained 64.8 %–77.5 % of expected direct genetic gain at 5 years (Figure 5). Therefore, genetic gain at initial tree height was not significantly impaired when the selection was done at 10 or 15 years. Thus, selection based on the tree height in 10 to 15 years of age is thought to be the appropriate selection timing considering both initial and mature phases of tree growth in *A. sachalinensis*.

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