

Estimation of yield gains at rotation-age from genetic tree improvement in coast Douglas-fir



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ABSTRACT

Application of progeny test breeding values to forecast yield gains at rotation-age in genetically improved stands remains a very challenging yet crucial task for breeders of Douglas-fir and other long-rotation timber species such as western hemlock, white spruce, Norway spruce, and Scots pine. Evaluation of the economic returns on genetic improvement requires reliable estimates of yield gains at rotation age. Large-plot realized gain trials should provide more accurate estimates of yield gain than inferences from progeny tests, but are most dependable when they reach rotation age or at least approach rotation age.

A set of coastal Douglas-fir realized genetic gain trials in western Oregon, based on a first-generation breeding program, was measured most recently at plantation ages ranging between 17 and 21 years. The trial was established on five sites at a spacing wide enough (3.6×3.6 m) to assume that the trees could be grown to rotation age with no further silvicultural intervention. A growth model, CIPSANON v. 4.0, projected the current tree lists from these trials to plantation age 60 years to facilitate estimation of yield gains at various rotation ages up to 60 years. The following two simulation approaches were explored: (1) apply genetic-gain multipliers developed from a previous study for diameter and height growth, and (2) assume that genetic gain differences were fully represented by plot-level site index expressed at the most recent measurement. The two approaches resulted in similar estimates of realized yield gain at plantation ages up to 60 years. Relative gain decreased over time, but absolute gain (in cubic meters or board feet) increased over time. Relative stand volume gain simulated to the average current rotation age of 50 years was about 30% of the relative realized gain measured at plantation age 10/12 years (birth age 13/15 years) and about 38% of the relative realized gain measured at plantation age 17–21 years (birth age 20–24 years).

Several validation needs were identified including magnitude of genetic-gain multipliers, duration of annual multiplier application over the duration of a simulation, adjustment of multipliers as the stand ages, and most appropriate multiplier resolution (tree versus stand). A potentially critical knowledge gap remains about any genetic improvement effects on yield gains associated specifically with increased carrying capacity that would be consistent with the crop ideotype concept.

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) genetic improvement programs in the Pacific Northwest began in the 1960s with the establishment of first-generation progeny tests completed in 1993. The program has now progressed to a third-cycle of testing and selection (Howe et al., 2006; Jayawickrama et al., 2017). A typical progeny test contains trees that are completely interspersed with

regard to family origin. In contrast, operational plantations originate from seedlots containing a set of only the highest performing families from progeny tests, so they represent untested block plantings of relatively few families that compete more directly with each other. Accurate predictions of yield gain by genetically improved stands, therefore, require a comparison between improved and unimproved stands planted as block-plots (Carson et al., 1999; St. Clair et al., 2004; Ye et al., 2010). Dr. Tony Shelbourne of the New Zealand Forest Research

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Institute pioneered these realized gain trials by designing them to test how well gains predicted from individual-tree growth in progeny tests translated into stand-level yield gains at rotation age in block plantings of seedlings from only the highest performing families. The ultimate goal is to estimate realizable volume yield gains; however, obtaining estimates gain at the end of the rotation is challenging because: 1) first-generation progeny tests in Douglas-fir were established to measure the relative growth performance of individual trees only to relatively young ages (birth age 10–15 years); 2) progeny tests were normally established at relatively narrow spacings to promote inter-tree competition at an early stage, but the growth and competition pattern of young trees may continue to change with age; and 3) genetic gain is probably overestimated in 10- to 15-yr-old progeny tests because better performing trees will on average be competing with individuals from poorer performing families. Accurate projection of rotation-age gains is the most difficult task in tree improvement for these long-lived species such as Douglas-fir, western hemlock, white spruce, Norway spruce, and Scots pine, but the implications for wood production impact estimates from millions of hectares of genetically improved plantations. In contrast, rotation-age gains are much easier to obtain from block-plots in short-rotation species such as eucalypts (e.g., Callister et al., 2013).

Because realized gain trials in Douglas-fir have reached only about half the age of current rotations, forest managers need methods to estimate rotation-age stand volume gains by simulating genetically improved stands with growth and yield models. These projections would allow them to assess impacts on harvest schedules, allowable cut, and economic returns on genetic tree improvement. Three general approaches have been used to incorporate genetic gain into growth and yield models: 1) upward adjustment of site index (Nance and Wells, 1981); 2) application of genetic-gain multipliers to annual or periodic growth projections developed for unimproved trees or stands (Carson et al., 1999); and 3) application of genetic-gain multipliers to indices of both top height growth potential (site index) and total volume growth potential (Kimberley et al., 2015). The site index adjustment approach has involved increasing the stand site index to simulate the more rapid height growth of genetically improved trees (Nance and Wells, 1981; Buford and Burkhart, 1987). The genetic-gain multiplier approach has involved multiplication of predicted height and basal area (or DBH) increment of “unimproved” trees by the ratio of observed growth of trees from genetically improved seedlots to observed growth of trees from unimproved seedlots (Carson et al., 1999). Application of genetic-gain multipliers requires relatively little modification to existing growth models that represent average regional growth for genetically unimproved trees (Gould et al., 2008; Weiskittel et al., 2011). Although progeny tests can provide first approximations to genetic-gain multipliers for half-sib or full-sib families, large block-plots (e.g., realized gain trials) are ultimately needed to validate the growth gains estimated from progeny tests, particularly regarding reliable estimates of stand-level yield gains achievable by deploying untested groupings of families at rotation age (Dhakal et al., 1996; Gould and Marshall, 2010).

Consistent with this latter approach, Carson et al. (1999) calculated radiata pine genetic-gain multipliers from growth performance at mid-rotation (plantation age 15–17 years) in realized gain trials that contained seedlots of differing “Growth-Form” (GF) ratings (Jayawickrama and Carson, 2000). Stand volume growth gains at rotation age 30 years for open-pollinated orchard seedlots (GF14) were estimated at 13% relative to GF7 (“climbing select”) seedlots on which the current growth models were based, and rotation volume growth gains for GF22 (top-ranked) seedlots were 22% more than GF7 seedlots. Average percentage genetic gains decreased over the rotation, but average absolute genetic gains increased monotonically over plantation age. Kimberley et al. (2015) later analyzed the data from the radiata pine realized gain trials measured by Carson et al. (1999) to develop a new method that

modified site index (top height at age 20 years) and 300 Index (mean annual volume increment, MAI, for a stand with 300 trees/ha at plantation age 30 years). This approach represented superior genotypes as analogous to trees growing on sites that are more fertile, a logical modification for a growth model whose architecture drove growth from a combination of site index and 300 Index. The established GF rating, as well as a newer GF Plus rating system developed by the Radiata Pine Breeding Company, represented the level of genetic improvement in this later study. The GF Plus rating system provided a rating for diameter growth and several other traits separately. A positive relationship had been observed between GF Plus rating and the established site productivity measures (site index and 300 Index), with highly improved seedlots (GF Plus 25) yielding 25% greater stand volume and a 5.6% increase in site index at plantation age 30 years compared to unimproved seedlots (GF Plus 9.9). Volume growth rates increased by approximately 1.5% for each unit of increase in GF Plus rating.

In an approach similar to that applied by Gould et al. (2008), Haapanen et al. (2016) simulated Scots pine realized gain trials in southern Finland by adjusting parameters within the individual-tree growth model MOTTI (Salminen et al., 2005). In this case, genetic-gain multipliers adjusted the upper asymptote of Chapman–Richard diameter growth and height growth functions. Simulation of improved stands from two orchard types established in the first cycle of selection and testing suggested an average gain of 11.5% and 23.9% mean annual stem volume yield, respectively, compared to unimproved stands. In these same simulations, improved stands from first- and second-type seed orchard material reached peak mean annual increment (MAI) at 8.2% and 36.5% younger ages, respectively, than unimproved stands. Weng et al. (2010) projected realized genetic gain tests of large plots of black spruce and white spruce from age 15 years to 50 years using the individual-tree growth model STAMAN v. 5.5 (NBGYU, 2005). For both species, stand volume gains diminished at later ages. At age 50, four improved black spruce stands had changes in volume yield gains relative to unimproved stands that varied from a loss of 10.6% to a gain of 3.5%, while three improved white spruce stands gained 0.9–3.0% relative to unimproved stands.

In the U.S. Pacific Northwest, Douglas-fir is the most important timber species, so its tree improvement program is the most advanced in the region and has included over 1000 first-, second- and third-generation progeny tests. A subset of these progeny tests formed the basis for subsequent Douglas-fir realized gain trials (St. Clair et al., 2004; Jayawickrama and Ye, 2009; Stoehr et al., 2010; Ye et al., 2010). The oldest set of first-generation realized gain trials (Molalla realized gain trials) reached approximately half of average operational rotation age (50 years) by 2017. The Molalla trials included family mixes predicted from progeny test breeding values to yield three general levels of genetic gain, hereafter referred to as elite, intermediate, and woods-run populations defined more specifically below. Because the realized yield gains of the elite and intermediate populations have fluctuated throughout the first half of the full rotation (St. Clair et al., 2004; Ye et al., 2010; Joo, 2019), the eventual yield gain at full rotation age remains uncertain. However, an opportunity was open to project the most current tree lists to rotation age with growth models recently developed to accommodate genetic-gain multipliers on tree diameter and height growth. The objective of this study, therefore, was to forecast genetic gain in stem volume yields at rotation age in the Douglas-fir realized gain trials under various scenarios that included or precluded genetic-gain multipliers for the remaining years in the rotation. We ran simulations to total plantation age 60 years to provide insight into yield gains for any rotation age up to 60 years. Specifically, 45–55 years is currently a common range of operational rotation lengths, so much of the following analysis and discussion focuses on a 50-yr rotation, despite the fact that rotation ages vary considerably among landowners and sites, ranging up to as long as 80 years.

2. Materials and methods

2.1. Experimental design and data collection

The detailed experimental design and early results of the Molalla Douglas-fir realized gain trials were described by [St. Clair et al. \(2004\)](#) and [Ye et al. \(2010\)](#). Briefly, they established the realized gain trials at five sites in 1997 using a split-plot design with three-year-old seedlings representing three genetic improvement levels (elite, intermediate, and unimproved). Improved populations (both elite and intermediate) were produced by 20 single-pair full-sib crosses. In contrast, the unimproved ("woods-run") population consisted of a mix of progeny from 50 randomly selected trees across the breeding zone and was therefore assumed to represent a stand of naturally regenerated trees with no genetic improvement. Best linear prediction (BLP) procedures based on progeny data at birth age 15 years were applied to select parents for the realized gain trials. [St. Clair et al. \(2004\)](#) and [Ye et al. \(2010\)](#) outlined the selection process in detail. Briefly, an elite population was created using single-pair matings of 20 top parents (not the absolute best), and an intermediate population was created using single-pair matings of 20 parents of somewhat lower ranking than the top parents. The goal for the intermediate population was to achieve a genetic gain in stem volume that would be approximately half that of the elite population. There were no parents in common between the groups. These 40 parents were selected from 372 parents tested in the first-generation Molalla breeding program. As discussed below, the allocation of crosses to the two groups in the late 1980s proved somewhat faulty viewed retrospectively on the basis of best linear unbiased predictions (BLUP) of breeding values done in the early 2000s. At each site, six blocks were identified to receive one whole-plot planted on a 1.8×1.8 m spacing and one whole-plot planted on a 3.6×3.6 m spacing. These whole plots were further divided into three split-plots (subplots) receiving one of the three genetic improvement levels. Each square subplot was planted with 100 trees surrounded with one buffer row of trees from the same genetic improvement level. Each site, therefore, contained six blocks with two whole-plot density levels in each block, three split-plot genetic levels in each whole-plot, and 100 measurement trees per split-plot, totaling 3600 trees ($6 \times 2 \times 3 \times 100$). The latest measurement varied by site but yielded tree lists at one of the following four plantation ages: 17, 18, 20, or 21 years ([Table 1](#)). Contractors measured all five sites at plantation ages 17 or 18 years. Two sites, Colton and Mill City, were re-measured at plantation ages 20 and 21, respectively, by the senior author during the dormant seasons of 2016–17 (Colton) and 2017–18 (Mill City). All 100 measurement trees on each subplot

(excluding buffer rows) were recorded as dead or alive, and all live trees were measured for DBH (nearest 0.1 cm), total height (nearest 0.1 m), and height to crown base (nearest 0.1 m). Only the low density (3.6×3.6 m) plots were simulated in this study because they were close to operational plantation spacings (each plot is about 0.2 ha). The 90 widely-spaced plots from all locations contained 9000 ($5 \times 6 \times 3 \times 100$) measurement trees at the time of establishment.

2.2. Top height and site index

The first tree measurements were completed after 8 years of growth from seed or 5 years of growth from planting ([St. Clair et al., 2004](#)). Because [Bruce's \(1981\)](#) site index is based on breast height age, years required to reach breast height (1.37 m) had to be estimated for trees representing the top height component of each subplot ($HT100$ = height of the largest 100 trees/ha by DBH). This estimate was obtained by interpolation, but rather than simple linear interpolation between birth age zero ($HT100 = 0$ m) and birth age corresponding to $HT100$ at first measurement (birth age 8 years), the following regression model was fitted separately to each set of three *birthage- $HT100$* pairs (birth ages 0, 8, and 13/15 years) from each subplot and then was solved for birth age to breast height after setting $HT100$ to 1.37 m:

$$HT100 = \beta_0 + \beta_1 \cdot e^{(k \cdot birthage)} + \varepsilon_1 \quad (1)$$

where $HT100$ was top height of 100 largest trees/ha by DBH for each subplot (m); β_0 and β_1 were parameters to be estimated from the data; *birthage* was birth age for a given subplot; k was a constant between 0.01 and 0.30 for changing the shape of the curve; and ε_1 was the random error term with $\varepsilon_1 \sim N(0, \sigma^2)$. Because only three data points were available to smooth the trend of $HT100$ over birth age, k was optimized with respect to R^2 computed for each subplot testing in increments of 0.01 over the interval (0.01, 0.30) (average $R^2 = 0.99$). This equation form and fitting approach was selected to minimize potential bias in estimating *birthage* when $HT100$ reached 1.37 m. Likewise, the constraint $(\beta_0 + \beta_1) = 0$ at *birthage* = 0 was not imposed in estimating *birthage* when $HT100 = 1.37$ m, to minimize bias; instead, the point (0, 0) was included as one of the three measured *birthage- $HT100$* pairs. Even without forcing the regression line through the origin (0, 0), $HT100$ at *birthage* = 0 for the 90 subplots ranged between -0.11 to 0.12 m and averaged -0.008 m. The number of years between seed germination and attainment of breast height for the 90 subplots ranged between 3.4 and 7.1 years with a mean of 5.0 years.

[Bruce's \(1981\)](#) site index system defines site index as an estimate of

Table 1

Summary of initial conditions for simulating the five Molalla realized gain trials starting at plantation age 17–21 years. The following initial conditions vary by site and genetic improvement level: mean DBH (diameter at breast height), mean height, mean TPH (trees per hectare), mean SDI (stand density index; $SDI = TPH \cdot (Dq/25.4)^{1.605}$ where Dq is quadratic mean DBH; [Reineke, 1933](#)), mean stand volume (sum of individual tree volumes estimated from equations developed by [Hann \(2011b\)](#) expanded to a per-ha basis), and minimum (min) and maximum (max) of top height ($HT100$; height of the largest 100 trees/ha by DBH for each subplot).

Site	Plantation Age	Genetic Level	Mean DBH (cm)	Mean Height (m)	Mean TPH (trees/ha)	Mean SDI (25.4-cm TPH equivalence)	Mean Stand Volume (m ³ /ha)	Top Height (m; min–max)
Colton	20	Elite	21.4	16.5	668.7	522.4	159.4	16.6–18.8
		Intermediate	22.1	16.9	625.1	514.3	160.4	17.3–19.9
		Woods-run	20.8	16.0	632.6	476.8	140.0	16.4–18.6
Estacada	18	Elite	19.0	14.1	706.1	458.1	116.4	14.3–17.3
		Intermediate	18.6	13.9	684.9	429.1	106.4	13.4–17.0
		Woods-run	18.6	13.8	615.2	389.2	96.2	14.8–16.9
Mill City	21	Elite	23.2	18.2	635.1	561.4	197.1	18.5–20.9
		Intermediate	23.6	18.6	682.4	617.1	222.2	19.2–22.6
		Woods-run	22.9	17.8	647.6	559.9	191.8	18.1–20.3
Molalla	18	Elite	19.1	13.2	538.0	353.5	81.4	14.0–16.8
		Intermediate	19.0	13.3	561.6	366.9	84.8	14.1–17.0
		Woods-run	18.7	13.1	600.2	388.8	89.9	14.7–15.7
Silver Falls	17	Elite	14.2	10.7	696.1	283.4	48.7	12.3–13.6
		Intermediate	14.7	11.0	683.7	292.2	52.0	11.3–14.4
		Woods-run	14.1	10.5	627.6	251.2	42.4	11.4–13.5

expected *HT100* when age at breast height reaches 50 years. This site index was estimated for each subplot from the most recent *HT100* measurement and the corresponding average breast height age of the *HT100* trees computed by subtracting the *birthage* required to reach breast height from the average *birthage* of *HT100* trees at plantation ages 17–21 years (Table 1).

2.3. Realized and simulated gains

Realized gain (RG) and Simulated gain (SG) are typically computed relative to some standard such as an unimproved population (the woods-run population in this study). Realized gain (RG) was determined from direct tree measurements in the most recent measurement year for each site (Table 1); in contrast, SG was computed at plantation age 60 from the treelist projected with CIPSANON v. 4.0.0 (Mainwaring et al., 2020; Mainwaring et al., 2020). The model was initiated with the most recent tree measurements for each plot (plantation age 17–21 years) and the tree lists were projected out to 60 years. Both RG and SG were computed as percentages and absolute values based on arithmetic means (AM) for each subplot and the following equations (Carson et al., 1999):

$$\text{Percentage RG or SG} = \frac{\text{AM}_{\text{GI}} - \text{AM}_{\text{U}}}{\text{AM}_{\text{U}}} \times 100 \quad (2)$$

$$\text{Absolute RG or SG} = \text{AM}_{\text{GI}} - \text{AM}_{\text{U}} \quad (3)$$

where AM_{GI} was AM for the genetically improved (elite or intermediate) populations, and AM_{U} was AM for the unimproved (woods-run) population.

2.4. Genetic worth and genetic-gain multipliers

Genetic worth (GW) is the expected average genetic gain in a trait from improved stands relative to unimproved stands at a given age (Xie and Yanchuk, 2003). Genetic worth (GW) is traditionally estimated from progeny test data. For example, when woods-run seedlots are planted on sites adjacent to or similar to sites planted with genetically improved seedlots with estimated GW for diameter (GW_D) of 10% at age 8, the average diameter for these improved trees at age 8 is expected to average 10% greater than woods-run trees. Genetic-gain multipliers are used to extend the GW to growth simulations beyond the age at which GW is measured directly in progeny tests. The estimated GW_D is converted into a genetic-gain multiplier for diameter increment (M_D) by the following set of equations (Gould et al., 2008; Gould and Marshall, 2010):

$$M_D = 1 + A \times \text{GW}_D \quad (4)$$

with

$$A = A_1, A_2, \text{ or } A_3$$

$$A_1 = 0.0101054 \text{ (when initial age} \leq 5)$$

$$A_2 = 0.0031 \text{ (when initial age} \geq 10)$$

$$A_3 = A_1 - (A_1 - A_2) \times \frac{\text{Initial age} - 5}{5} \text{ (when } 5 < \text{initial age} < 10)$$

The estimated genetic worth for height growth (GW_H) is converted into a genetic-gain multiplier for height increment (M_H) by a similar set of equations (Gould et al., 2008; Gould and Marshall, 2010):

$$M_H = 1 + B \times \text{GW}_H \quad (5)$$

with

$$B = B_1, B_2, \text{ or } B_3$$

$$B_1 = 0.0062770 \text{ (when initial age} \leq 5)$$

$$B_2 = 0.0036 \text{ (when initial age} \geq 10)$$

$$B_3 = B_1 - (B_1 - B_2) \times \frac{\text{Initial age} - 5}{5} \text{ (when } 5 < \text{initial age} < 10)$$

Genetic-gain multipliers (i.e., M_D and M_H) are applied to diameter and/or height increments after each growth cycle is completed. For example, 10% GW in both diameter and height at age 8 would be converted into $M_D = 1.0590216$ and $M_H = 1.046708$, respectively, and 20% GW in both diameter and height at age 8 would be converted into $M_D = 1.1180432$ and $M_H = 1.093416$, respectively. The genetic-gain multipliers developed by Gould et al. (2008) were first incorporated into ORGANON (Hann, 2011a) and later into CIPSANON v. 1.0 (<http://cips.forestry.oregonstate.edu/cipsanon/>). These same multipliers were incorporated into CIPSANON v. 4.0.0 developed to project young small trees (total height < 1.37 m) and to simulate vegetation control responses. CIPSANON is an individual-tree distance-independent growth and yield model built on the ORGANON architecture and code but can simulate annual time steps and start at plantation age 0 years (Mainwaring et al., 2020; Mainwaring et al., 2020). The ORGANON model is widely used for Douglas-fir plantations in the Pacific Northwest (Gould and Marshall, 2010). There are more than 46 publications about equations and architecture for ORGANON, more than 37 studies used have applied ORGANON for growth and yield analyses, and innumerable users have fully vetted ORGANON performance (<http://www.cof.orst.edu/cof/fr/research/organon/orgpubr.htm>). Both ORGANON and CIPSANON constrain GW between 0% and 20%. In the Molalla Douglas-fir realized gain trials, estimated RGs from the latest measurement years were input as GW in the simulations (Table 2).

2.5. Simulations and scenarios

All five installations of the Molalla Douglas-fir realized gain trials were simulated under two different scenarios to estimate genetic gain in volume yield at rotation age, necessitated by the fact that genetic

Table 2

Initial conditions for two simulation scenarios starting at mid-rotation plantation ages listed in Table 1 for each installation of the Molalla Douglas-fir realized gain trials. Under the first scenario, the site index (SI) estimates (expected *HT100* at breast height age 50 years) from the mid-rotation data were averaged for all subplots on the site, and genetic worth for diameter (GW_D) and height (GW_H) were computed for each subplot from tree measurements at the mid-rotation plantation ages. Under the second scenario, subplot-level site index (PSI) represented genetic improvement level and no additional genetic-gain multipliers were applied. All subplots were simulated to total plantation age 60 years.

Site	Genetic Level	Scenario			
		With GW			Without GW
		SI	GW_D	GW_H	PSI
		Site index (m)	DBH (%)	Height (%)	Mean of subplot-level site index (m)
Colton	Elite	39.4	2.80	3.66	39.2
	Intermediate	39.4	6.36	5.52	39.5
	Woods-run	39.4	–	–	39.4
Estacada	Elite	38.8	2.02	2.80	39.4
	Intermediate	38.8	0.00	1.06	38.2
	Woods-run	38.8	–	–	39.0
Mill City	Elite	40.2	1.55	1.88	39.6
	Intermediate	40.2	3.25	4.06	41.9
	Woods-run	40.2	–	–	39.0
Molalla	Elite	39.3	1.98	0.35	38.1
	Intermediate	39.3	1.35	1.23	39.8
	Woods-run	39.3	–	–	39.9
Silver Falls	Elite	35.2	1.38	2.15	35.9
	Intermediate	35.2	4.46	4.70	34.9
	Woods-run	35.2	–	–	35.0

improvement effects were already represented in tree size measured at mid-rotation. The two different scenarios, therefore, aimed to separate the effects of estimable genetic worth and measurable site index differences. The GWR scenario applied estimated genetic worth, GW (GW = RG measured at plantation ages between 17 and 21 years) and location-average site indices (SI). The PSI scenario applied only subplot site indices (PSIs) to represent genetic gain, with no consideration of estimated GWs (PSI was computed from the latest measurements of each subplot between plantation ages 17 and 21 years). Any improved stands showing negative realized genetic gains (i.e., negative GW due to woods-run exhibiting better performance than improved stands) were assigned 0% GW (e.g., GW_D for the intermediate level of genetic improvement at Estacada; Table 2). Given ample evidence that the two improved seedlots had superior growth rate to the woods-run population, we assumed that plots with apparently negative gain had inherently lower site quality than the block or site average. The PSI scenario represented a standard projection protocol that assumes differences in multiple site productivity factors, including but not limited to potential genetic differences. The PSI scenario did not use GW and corresponding genetic-gain multipliers under the assumption that genetic improvement level has already been manifested in tree height growth, so was sufficiently represented in the subplot-level site index (PSI computed at plantation age 17–21 years), and that its future effects would also be adequately represented by these elevated site indices.

The simulations retained the initial tree list from each subplot, including the DBH, total height, crown ratio, and expansion factor (TPH) of each tree. Projection of measured tree lists ensured that projected rotation age yield gains represented the best estimate of actual subplot performance within each genetic level and site.

All scenarios were simulated with the Pacific Northwest (PNW) variant of CIPSANON (ver. 4.0.0) within the 'cipsr' (ver. 4.0.0) R package (Joo et al., 2020). All simulations were run from R ver. 3.5.1 (R Core Team, 2018). Joo (2019) previously tested the efficacy of genetic-gain multipliers and plot-level site index for simulating the growth of these Douglas-fir realized gain trials using CIPSANON v. 4.0.0. In this test, gains in height and diameter based on genetic worth from early measurement data (plantation age 5) were entered into CIPSANON to project growth to the latest re-measurement (plantation age 17/18). The gains predicted by CIPSANON were close to realized gains for both height and DBH at plantation age 17/18.

To address the objectives of this rotation age analysis, all individual plots were simulated from plantation age 17–21 years out to plantation age 60 years. The CIPSANON simulations incorporated calibrations for local crown ratio and, although a regional maximum size-density limit was toggled "ON" to the default maximum SDI of 1470 (see caption of Table 1) to guard against unrealistically high stand densities, the maximum size-density limit was never enforced for any of the simulations. This behavior may not be observed if users set the maximum size-density limit to a lower threshold. The initial condition of competing vegetation cover was set to 100% at the initiation of all simulations, but its growth effects were essentially zero due to the height of the Douglas-fir trees at initial plantation age 17–21 years.

Percentage and absolute SGs in stand volume (m^3/ha) for improved populations were summarized and compared between genetic levels. Simulated absolute and relative genetic gains at plantation age 50 years (assumed average rotation age) were tabulated for quadratic mean diameter (QMD), top height, tree density (TPH, trees per ha), stand density index (SDI) (Reineke, 1933; see caption for Table 1), and total cubic volume (m^3/ha). Standing live cubic volumes were also plotted over plantation age for each genetic level and under the alternative GWR and PSI scenarios, with computed relative (%) and absolute genetic gains labeled at each five-year interval. These graphs were intended to facilitate estimation of genetic gain at other rotation ages up to plantation age 60 years. Relative and absolute gains in standing live cubic volume (i.e., differences between genetically improved and woods-run volumes) were likewise plotted over plantation age for the two

levels of genetic improvement (i.e., elite and intermediate) under the alternative GWR and PSI scenarios. Finally, analyses of variance (ANOVAs) conforming to a nested randomized complete block design (six small blocks of all three genetic levels at each of five sites/locations/large blocks) were performed to test for genetic effects on plot attributes. The ANOVAs assumed the site effect was fixed and the block within site effect was random. The primary contrast of interest was the performance of genetically improved populations (i.e., elite and intermediate) relative to the unimproved woods-run population, and secondarily the relative performance between the two levels of genetic improvement. Analyses were performed only at plantation age 50 years (approximate rotation age for the region) based on the following linear mixed-effects model:

$$y_{ijk} = \mu + S_i + \eta_{k(i)} + G_j + (SG)_{ij} + \varepsilon_{k(i)j} \quad (6)$$

where y_{ijk} was subplot mean at plantation age 50 years (QMD, TPH, SDI, or stand volume) for the j th treatment in the k th block on the i th site; μ was overall mean; S_i was the fixed effect of the i th site ($i = 1, \dots, 5$); $\eta_{k(i)}$ was the random effect for the k th block (whole-plot) ($k = 1, \dots, 6$) nested in i th site; G_j was the fixed effect of the j th genetic improvement level ($j = 1, 2$) (genetically improved [elite + intermediate] vs. unimproved [woods-run]); $(SG)_{ij}$ was the fixed site by genetics interaction effect; and $\varepsilon_{k(i)j}$ was random subplot error. The ANOVA F-tests were performed using the 'lme4' (ver. 1.1-17) (Bates et al., 2015) and 'lmerTest' (ver. 3.1-0) (Kuznetsova et al., 2017) packages in R ver. 3.5.1 (R Core Team, 2018).

3. Results

The relative yield gains measured up to mid-rotation (plantation age 17–21 years; Table 1) provided a more robust basis for evaluating projections to plantation age 60 years than the potential gains estimated from either the progeny tests or from younger measurements of the realized gain trials, simply because they contain a longer record of relative performance and realizable gains. The measured relative stand volume gains of elite and intermediate populations over the woods-run population were 15.1% and 14.3%, respectively, at plantation age 5 years (8 years from seed); measured gains at plantation age 10/12 years (13/15 years from seed) were 13.1% and 16.2%, respectively; and measured gains at plantation age 17/18 years (20/21 years from seed) were 10.0% and 14.5%, respectively (Joo, 2019).

At a rotation age of 50 years (total plantation age), the elite population was predicted to achieve a 3.6% (28.1 m^3/ha) and 3.5% (22.4 m^3/ha) gain in stand yield over the woods-run population under the GWR and PSI scenarios, respectively (Fig. 1). However, the intermediate population was predicted to outperform the elite population by reaching volume gains of 5.0% (39.1 m^3/ha) and 5.5% (40.7 m^3/ha) relative to the woods-run population under the GWR and PSI scenarios, respectively. The latter gain by the intermediate population was 39% (11.0 m^3/ha) and 82% (18.3 m^3/ha) greater than the gain achieved by the elite population at plantation age 50 years under the two respective scenarios. Under the GWR simulation, 52.2% of the relative stand volume gain of the elite population measured at plantation age 25 years (6.9%) was predicted to persist to plantation age 50 years (3.6%), and similarly, 51.5% of the relative stand volume gain of the intermediate population measured at plantation age 25 years (9.7%) was predicted to persist to plantation age 50 years (5.0%) (Fig. 1). Absolute volume yield gains at plantation age 50 were predicted to reach 194% (28.1 m^3/ha) of the absolute gains measured at plantation age 25 (14.5 m^3/ha) for the elite population and 187% (39.1 m^3/ha) of the absolute gains measured at plantation age 25 (20.9 m^3/ha) for the intermediate population (Fig. 1).

The percentage of relative genetic gain measured at plantation age 25 that persisted to plantation age 50 under the PSI scenario did not differ much from that of the GWR scenario; i.e., 50.0% and 55.6% of the relative stand volume gains measured in the elite and intermediate

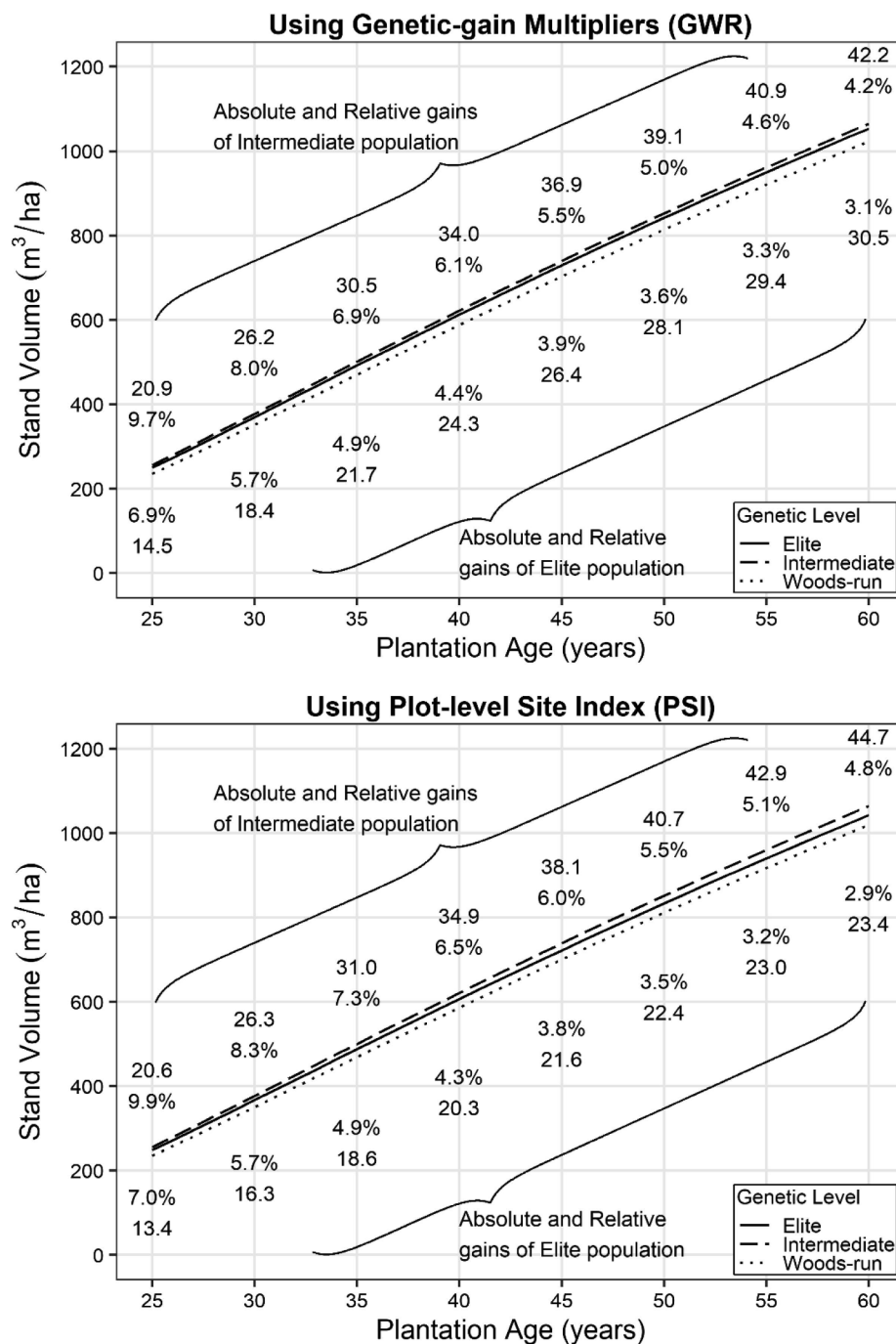


Fig. 1. Simulated cumulative growth in stand volume (m³/ha) for elite, intermediate, and woods-run genetic improvement levels under the assumption of continued realized genetic gain (GWR) observed at plantation ages 17–21 years and uniform site index (upper panel) and under the assumption that genetic gain is fully represented by subplot-level site index (PSI) measured at plantation ages 17–21 years (lower panel). Absolute and relative simulated stand volume gains were calculated relative to unimproved woods-run populations.

population, respectively (Fig. 1).

The GWR scenario projected only a slightly greater genetic gain in stand volume than the PSI scenario. On average, 1.03%, 0.15%, and 0.36% more stand volume was projected to plantation age 50 years under the GWR scenario than under the PSI scenario for elite, intermediate, and woods-run improvement levels, respectively. For the intermediate population, greater relative stand volume gains were achieved under the PSI scenario than under the GWR scenario from plantation ages 25 through 60 years. Conversely, for the elite population, greater relative gains were achieved under the GWR scenario than under the PSI scenario from plantation ages 40 through 60 years.

Relative simulated gains (SGs) in stand volume under the GWR scenario for both improved populations declined continuously from mid-rotation to 60 years plantation age, but the decline slowed with increasing age. On the other hand, absolute SGs increased continuously over the same range in plantation age (Fig. 2). Differences in relative volume gain between elite and intermediate populations under the GWR scenario decreased from 2.8% to 1.1% between plantation ages 25 and 60 years, while differences in absolute stand volume gain increased from 6.4 m³/ha to 11.7 m³/ha across the same simulation period (Fig. 2). Results from the PSI scenario were similar (Fig. 3), except that the magnitude of differences was larger, most likely due to the very

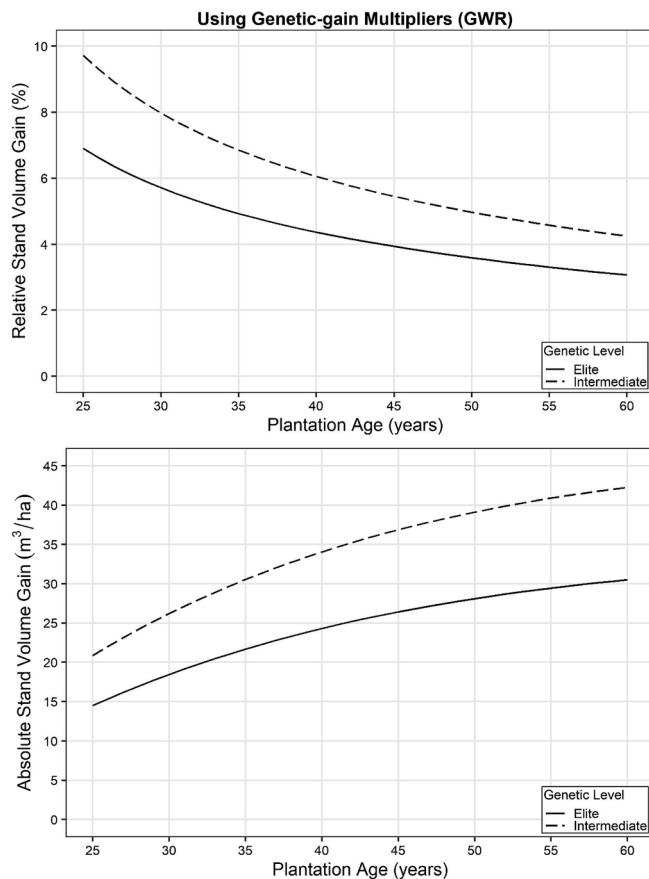


Fig. 2. Simulated gains in relative (%; upper panel) and absolute (m^3/ha ; lower panel) stand volume in elite and intermediate populations over unimproved woods-run population assuming continued genetic worth (GW) derived from observed realized gains at plantation ages 17–21 years.

different representations of genetic tree improvement effects between the PSI and GWR scenarios. Under the PSI scenario, differences in simulated relative volume gain between elite and intermediate populations decreased from 2.9% to 1.9% between plantation ages 25 and 60 years (Fig. 3), and differences in simulated absolute volume gain increased from 7.2 m^3/ha to 21.3 m^3/ha between plantation ages 25 and 60 years.

Periodic annual increment (PAI) in elite and intermediate populations peaked at plantation ages of approximately 32 years, 1–2 years earlier than the woods-run peak in both scenarios (Fig. 4). On the other hand, mean annual increment (MAI) increased continuously over the simulation. At plantation age 30, PAI for the intermediate and elite population gained 4.3% and 3.2%, respectively, over the woods-run population under the GWR scenario, and gained 5.0% and 3.0%, respectively, under the PSI scenario. PAI gains for both improved populations diminished over the projection period in both scenarios, although PAI gains of intermediate populations remained more constant to the end of the simulations under the PSI scenario. Simulated PAI and MAI gains declined from 4.2% to 1.4% and from 6.9% to 3.1%, respectively, in the elite population, and declined from 5.7% to 1.9% and from 9.7% to 4.2% in the intermediate population, respectively, between plantation age 25 and 50 years under the GWR scenario. Similarly, under the PSI scenario, the simulated PAI and MAI genetic gains in the elite population declined from 4.1% to 1.1% and from 6.9% to 2.9%, respectively, and in the intermediate population from 6.5% to 2.5% and 9.9% to 4.8%, respectively, over the same period. Intermediate populations had the greatest PAI and MAI, regardless of scenario.

Simulated gains (SGs) in QMD, top height, tree density (TPH), trees

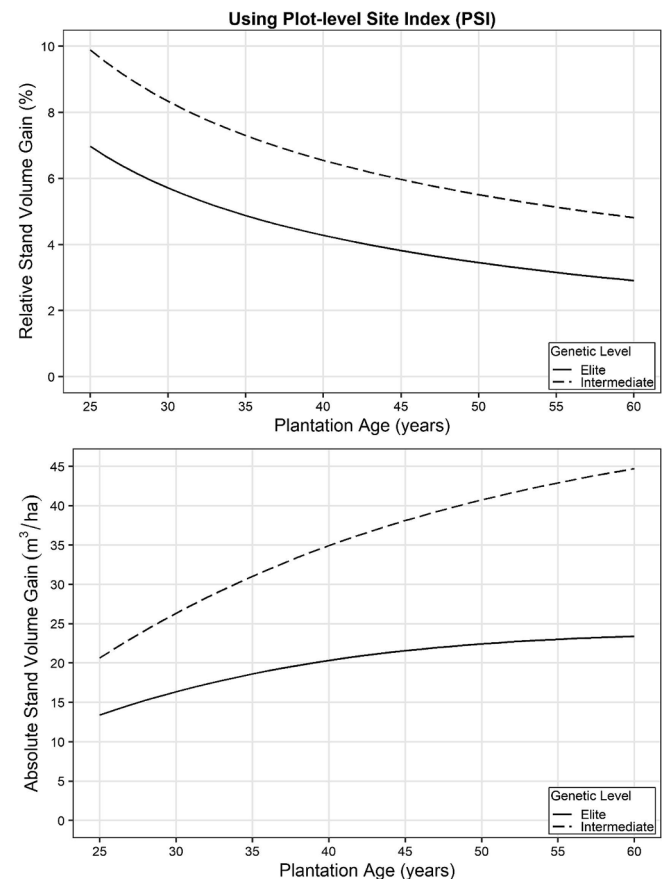


Fig. 3. Simulated gains in relative (%; upper panel) and absolute (m^3/ha ; lower panel) stand volume in elite and intermediate populations over unimproved woods-run population assuming genetic gain is accounted for by observed subplot site index at mid-rotation (PSI estimated at plantation ages 17–21 years).

per ha), stand density index (SDI) (Reineke, 1933), and stand volume at rotation age 50 years varied considerably among sites (Tables 3 and 4). Simulated volume gain of the elite over the woods-run populations under the GWR and PSI scenarios varied across the five sites from -1.8% ($-16.6 \text{ m}^3/\text{ha}$) to $+6.7\%$ ($52.4 \text{ m}^3/\text{ha}$) and from -6.5% ($-61.1 \text{ m}^3/\text{ha}$) to $+8.4\%$ ($55.4 \text{ m}^3/\text{ha}$), respectively. Stand volume gain of intermediate populations under the GWR and PSI scenarios varied from -0.1% ($-3.5 \text{ m}^3/\text{ha}$) to $+7.5\%$ ($58.6 \text{ m}^3/\text{ha}$) and $+0.4\%$ ($-8.9 \text{ m}^3/\text{ha}$) to $+13.3\%$ ($115.3 \text{ m}^3/\text{ha}$), respectively. The elite population in Molalla showed negative stand volume gain (i.e., net volume losses) relative to the woods-run population in both scenarios. On average for all five sites, the intermediate population showed positive genetic gains in QMD, top height, TPH, SDI, and stand volume, while the elite population had a net QMD loss. However, no significant differences between elite and intermediate were detected on these attributes at plantation age 50 years at $\alpha = 0.05$ (data not shown). No genetic improvement effects on QMD or top height emerged, but significant genetic improvement effects ($p < 0.001$ to $p = 0.055$) (improved [elite and intermediate] vs. unimproved [woods-run]), and in some case interaction effects between genetic improvement and site did appear ($p < 0.001$ to $p = 0.057$) in TPH, SDI, and stand volume under both scenarios (Table 5).

Mean heights by genetic improvement level within sites ranged from 10.5 m for the 17-yr-old woods-run population at Silver Falls to 18.6 m for the 21-yr-old intermediate population at Mill City (Table 1). Mean top heights by genetic improvement level at the last measurement (breast height ages 12.9 to 20.6 years) ranged from 11.3 to 22.6 m, so Bruce's (1981) 50-yr site indices at the subplot-level ranged from 32.2

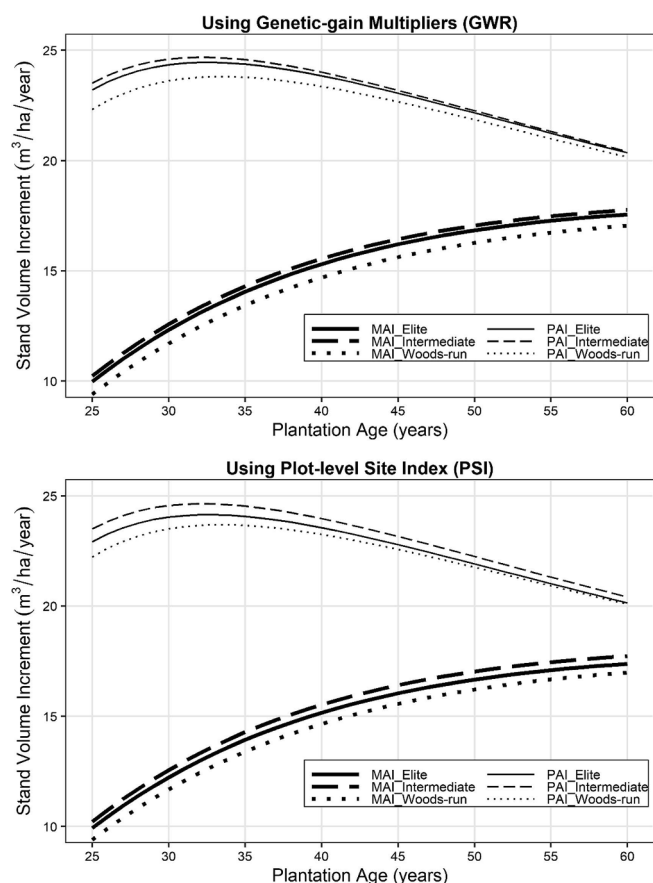


Fig. 4. Simulated periodic annual increment (PAI) and mean annual increment (MAI) under the assumption of continued realized gains observed at plantation ages 17–21 (GWR; upper panel) and under the assumption that genetic gain is totally accounted for by mid-rotation site index at plantation ages 17–21 years (PSI; lower panel).

to 45.8 m.

In these Douglas-fir realized gain trials, projected gains in quadratic mean diameter (QMD) covered a range centered on zero under the two simulation scenarios, from -0.98 cm to $+0.99$ cm, corresponding to a 2.7% loss and 2.6% gain, respectively (Tables 3 and 4). The elite level of genetic improvement averaged a very slight loss in final QMD and

the intermediate level a very small increase relative to the woods run population (Tables 3 and 4), although the two improved populations did not differ significantly (data not shown).

4. Discussion

The analyses presented here focused on extrapolating mid-rotation genetic gains on the five installations of the Molalla Douglas-fir realized gain trial sites to estimate yield gains at rotation age under various assumptions and methods. Yield gains at rotation age are critical to assessing returns on genetic tree improvement. Projections to rotation age were made possible by previous development of genetic-gain multipliers for diameter growth and height growth developed from progeny test data (Gould et al., 2008). These genetic-gain multipliers can be easily incorporated into individual-tree growth models (Gould and Marshall, 2010). A logical next step, therefore, was to test the accuracy of genetic gains predicted by insertion of these multipliers into an individual-tree growth model, with genetic worth of simulated seedlots based on breeding values from progeny tests. A key test of this system is to predict the stand-level growth of improved seedlots containing groups of superior families that had never been tested before in block plantings or realized gain trials. The initial five-year plantation growth of the Molalla realized gain trials showed that the elite population outperformed the intermediate population in cumulative diameter growth at breast height (DBH) and in cumulative height growth (St. Clair et al., 2004). However, yields at plantation age 10/12-yr revealed some surprising shifts in relative performance; i.e., the intermediate population started to perform better than the elite population in the wider spacing (3.6×3.6 m), although no statistically significant difference could be detected between the two populations (Ye et al., 2010). Mid-rotation results (plantation age 17–21 years) revealed even further departures from expectations based on progeny test breeding values (Joo, 2019). Simulated stand growth described in this paper projected conditions from mid-rotation out to plantation age 60 years, using realized gains at mid-rotation as the basis for projecting future growth, assuming that this approach would achieve the best projections possible with the tools currently available. However, future performance of the block plantings will almost certainly continue to depart to some degree from the growth model predictions.

Volume growth of individual trees ultimately depends on the rate of diameter growth and height growth. For stands that are not managed for optimal density, mortality or surviving tree density can also impact individual-tree and stand-level stem-volume growth. The Douglas-fir

Table 3

Simulated relative gains (%) in QMD (quadratic mean diameter), TPH (trees per hectare), SDI (stand density index), top height, and stand volume at rotation age 50 years for elite and intermediate populations under the following two scenarios on five sites: GWR (using realized gains observed at plantation ages 17–21 years) and PSI (assuming genetic gain is totally accounted for by subplot-level site index estimated at plantation ages 17–21 years).

Site	Genetic Level	Scenario									
		With Genetic Worth and Genetic-gain Multipliers (GWR)					With only subplot site index at plantation age 17–21 yrs (PSI)				
		Relative Gain (%)					Relative Gain (%)				
		QMD	Top Height	TPH	SDI	Stand Volume	QMD	Top Height	TPH	SDI	Stand Volume
Colton	Elite	-0.77	0.49	5.48	3.72	5.42	-1.04	-0.17	5.71	3.47	4.30
	Intermediate	2.09	0.79	0.15	2.71	5.81	1.73	0.41	-0.06	2.07	4.89
Estacada	Elite	-2.65	-0.21	11.61	6.82	6.67	-2.45	0.23	11.24	6.55	7.32
	Intermediate	-1.86	-1.25	8.60	5.34	5.21	-2.46	-2.53	9.03	4.70	3.22
Mill City	Elite	1.62	1.68	-1.18	1.14	2.68	1.89	2.68	-1.55	1.20	3.71
	Intermediate	-0.24	2.22	5.13	4.59	6.50	1.46	7.14	2.89	5.17	13.31
Molalla	Elite	2.58	0.02	-6.32	-2.72	-1.84	1.01	-3.29	-5.06	-3.79	-6.52
	Intermediate	1.24	-0.54	-2.70	-0.96	-0.14	1.02	-0.60	-2.85	-1.15	0.35
Silver Falls	Elite	-2.35	0.56	9.12	4.78	5.01	-1.62	2.53	8.31	5.31	8.43
	Intermediate	-0.89	0.42	7.56	5.74	7.47	-1.34	-0.44	7.67	5.03	5.78
All sites	Elite	-0.31	0.51	3.74	2.75	3.59	-0.44	0.40	3.73	2.55	3.45
	Intermediate	0.07	0.32	3.75	3.48	4.97	0.08	0.80	3.34	3.17	5.51

Table 4

Simulated absolute gains in QMD (quadratic mean diameter), TPH (trees per hectare), SDI (stand density index), top height, and stand volume at rotation age 50 years for elite and intermediate populations under the following two scenarios on five sites: GWR (using realized gains observed at plantation ages 17–21 years) and PSI (assuming genetic gain is totally accounted for by subplot-level site index estimated at plantation ages 17–21 years).

Site	Genetic Level	Scenario									
		With Genetic Worth and Genetic-gain Multipliers (GWR)					With only subplot site index at plantation age 17–21 yrs (PSI)				
		Absolute Gain					Absolute Gain				
		QMD (cm)	Top Height (m)	TPH (trees/ha)	SDI (25.4-cm TPH equivalence)	Stand Volume (m ³ /ha)	QMD (cm)	Top Height (m)	TPH (trees/ha)	SDI (25.4-cm TPH equivalence)	Stand Volume (m ³ /ha)
Colton	Elite	−0.32	0.18	27.26	37.3	46.67	−0.43	−0.08	28.43	34.6	35.06
	Intermediate	0.75	0.29	−2.38	26.5	49.76	0.61	0.14	−3.14	19.5	38.37
Estacada	Elite	−0.98	−0.08	60.88	65.4	52.39	−0.93	0.00	58.26	63.0	55.35
	Intermediate	−0.69	−0.46	45.88	51.5	41.12	−0.91	−1.03	48.30	45.3	21.72
Mill City	Elite	0.60	0.63	−7.20	11.3	24.44	0.69	0.97	−9.60	11.8	31.86
	Intermediate	−0.09	0.84	28.34	47.4	58.64	0.54	2.64	15.99	53.0	115.31
Molalla	Elite	0.99	0.01	−32.57	−27.7	−16.63	0.39	−1.27	−25.52	−38.8	−61.14
	Intermediate	0.47	−0.20	−15.40	−11.4	−3.46	0.38	−0.32	−15.31	−14.2	−8.89
Silver Falls	Elite	−0.84	0.19	49.75	44.4	33.54	−0.60	0.77	45.30	48.8	50.98
	Intermediate	−0.33	0.14	40.40	52.7	49.40	−0.50	−0.17	40.81	46.0	37.11
All sites	Elite	−0.11	0.19	19.62	26.1	28.08	−0.18	0.08	19.40	23.9	22.42
	Intermediate	0.02	0.12	19.37	33.3	39.09	0.02	0.25	17.30	29.9	40.72

realized gain trials at the 3.6-m spacing have not yet reached stand densities at which density-dependent mortality would be a factor (Table 1); however, differential self-thinning may be important on some high-quality sites when projecting out to 60 years, given the accelerated rate of stand development associated with faster height and diameter growth in genetically improved subplots. Earlier self-thinning may also occur by the time the 3.6-m spacing reaches the 50-yr rotation assumed in this realized gain analysis. The maximum recommended SDI (Reineke, 1933) for coastal Douglas-fir is 1470 (maximum number of 25.4 cm DBH trees/ha), but none of the plots had attained even half that SDI as of the latest measurement (Table 1).

The considerable genetic variation in diameter and height growth and the high heritabilities observed in Douglas-fir progeny tests have strongly suggested the opportunity to increase yields at rotation age by planting genetically improved trees (Howe et al., 2006). Selection of parent trees with greater diameter and height growth in second- and third-generation progeny tests has led to deployment of improved seedlings in operational plantings that subsequently achieve increased stem volume production, particularly when the tree breeding simultaneously screens for defect and heightened risk of damage (Howe et al., 2006). This type of genetic tree improvement has been corroborated by realized gain trials that deploy trees from seedlots collected from the best parents, whether half-sibs from open-pollinated superior trees or

full-sibs from controlled crosses between the best parent trees identified by progeny tests (Carson et al., 1999; St. Clair et al., 2004; Ye et al., 2010; Stoehr et al., 2010). Increases in stand-level production ensue from greater individual-tree diameter and height growth, perhaps from increased carrying capacity, and perhaps from improved stem form (Jack and Long, 1996; Haapanen et al., 2016).

The five installations of the Molalla Douglas-fir realized gain trials assessed in this analysis led to at least three major conclusions: 1) gains have shifted among three levels of genetic improvement between plantation ages five and ten years (Ye et al., 2010) and between plantation age ten years and mid-rotation (plantation age 17–21 years; Joo, 2019); 2) relative performances predicted from progeny tests do not transfer accurately to operational plantings of improved seedlots, in part because relative performance in progeny tests cannot be expected to correlate perfectly with growth behavior of families in block plantings of untested family mixes (Carson et al., 1999; Ye et al., 2010); and 3) achievable genetic gains at rotation age will remain the best guess based on simulations from well-formulated growth models, as particularly evident from the continuing shifts in relative performance of families and of designed levels of genetic improvement. In regard to the last point, the variability in results from the trials and apparent $G \times E$ interactions underscored that reliable estimates of realized genetic gain at rotation age require installation and maturation (to rotation age) of a

Table 5

Analysis of variance p-values based on subplot mean responses estimated from Eq. (6) on QMD (quadratic mean diameter), top height, TPH (trees per hectare), SDI (stand density index), and stand volume at plantation age 50 years for genetically improved (elite and intermediate) and unimproved (woods-run) populations under the following two scenarios on five sites: GWR (using realized gains observed at plantation ages 17–21 years) and PSI (assuming genetic gain is totally accounted for by subplot-level site index estimated at plantation ages 17–21 years). P-value in bold font indicates significance level at $\alpha = 0.06$.

Source of Variation	Degrees of Freedom	P-value									
		Scenario									
		With Genetic Worth and Genetic-gain Multipliers (GWR)					With only subplot site index at plantation age 17–21 yrs (PSI)				
		QMD	Top Height	TPH	SDI	Stand Volume	QMD	Top Height	TPH	SDI	Stand Volume
Site	4	0.032	< 0.001	0.057	0.268	< 0.001	0.111	0.524	< 0.001	0.254	0.254
Genetic Improvement (improved vs. unimproved)	1	0.826	0.104	0.013	< 0.001	< 0.001	0.756	0.695	0.019	0.003	0.057
Site × Genetic Improvement	4	0.094	0.015	0.016	0.026	0.055	0.243	0.331	0.021	0.044	0.313

larger number of realized gains.

Rotation-age yield gains achieved by several routine silvicultural activities are a key question to answer in intensively managed Douglas-fir plantations, particularly activities and treatments implemented early in the rotation like genetic tree improvement. These questions remain unanswered in part due to the relatively long rotation ages in Douglas-fir and the short-term nature of many silvicultural research trials, including progeny tests but also field trials on competing vegetation control, fertilization, and to a lesser extent thinning. CIPSANON v. 4.0.0 was refined specifically to facilitate simulation of genetic improvement effects on the realized gain trials (Joo, 2019). New measurements of the Douglas-fir realized gain trials allowed replacement of initial estimates of genetic worth for the two genetic improvement levels based on progeny test data with actual measurements of genetic worth achieved by the realized gain trials near mid-rotation (plantation ages 17–21). Given the shifts in relative performance of the elite and intermediate levels of improvement between plantation ages 5, 10/12, and 17–21 (St. Clair et al., 2004; Ye et al., 2010; Joo, 2019), and the departure of realized gains from those initially predicted from progeny tests (Ye et al., 2010; Joo, 2019), an opportunity was readily apparent for projecting the stands out to 60 years and estimating yield gains for the most common range of current operational rotation ages (approximately 45–55 years plantation age).

One striking result both from mid-rotation performance and from 60-yr simulations was the steady change in relative and absolute genetic gain over the initial 17–21-yr measurement periods (St. Clair et al., 2004; Ye et al., 2010; Joo, 2019) and over the subsequent 39–43-yr simulation periods (Figs. 2 and 3). These changes included rank shifts in genetic gain among levels of genetic improvement prior to the start of simulations. These rank shifts suggested the possible need to consider different modeling and simulation approaches, specifically by developing age-variant genetic-gain multipliers. If biological/genetic theory could identify mechanisms driving change in genetic-gain over stand age, then these mechanisms could be built into simulation models to strengthen confidence in projections to rotation age. However, rigorous assessment is needed to determine if changes in genetic gain over stand development and tree age are consistent with long-term data, and with hypothesized potential underlying mechanisms such as relative vulnerability to damage, environmental changes in weather or soil processes, or genetic mechanisms influencing gene expression. Genetic gain may even change, for example, in manner consistent with unique stand structures produced by different mixes of families as half- or full-sibs. If accumulating empirical evidence is sufficient to warrant a systematic change in genetic-gain multipliers as trees develop and stands mature, a compelling case can be made for understanding and modeling these patterns to facilitate projections to rotation age of seedlots designed from 15-yr-old progeny tests. Supplementation of empirical growth data with the intensive characterization of family traits and resulting stand structures on strategic subsamples of family mixes will provide better insights into mechanisms driving differences in family performance, in realizable gain of different family mixes, and in their shift over the course of stand development (Joo, 2019).

Given that the maximum difference in site index within any installation of the Molalla realized gain trials was about 3 m, annual height growth differences would be less than a decimeter, but cumulatively translate into a meter per decade. Prolonged volume growth potential in Douglas-fir has in fact been attributed to its maintenance of height growth well up to 100 years (Curtis, 2006), so height and related volume growth under the PSI scenario was potentially affected by the elevated site index evident by mid-rotation, especially in the improved populations. Also, Douglas-fir has been documented to hold a capacity for substantial diameter growth release for a very long period into its lifetime (Latham and Tappeiner, 2002). A relatively small difference in annual height, diameter growth, and resulting volume growth, if prolonged, would conceivably translate into diverging absolute growth. Conversely, because the trees are getting bigger, relative volume

growth would not be sustainable at a relatively fixed or slightly declining rate of volume growth. It is probably also important to keep in mind that current or periodic annual growth is the slope of the cumulative volume growth curves (curves depicting standing volume over time in Fig. 1). The slopes look stable, within the limits of the resolution of the graphs. Conversely, cumulative gain from mid-rotation (Fig. 2) indicated that the change or slope in relative gain is declining.

The question remains open regarding why the relative trend in yield gain over age under PSI remains “parallel” rather than converging and the trend in absolute volume yield gain continues to diverge more rapidly. At Mill City, the difference in SI between intermediate and woods-run is 7.4%, and Bruce’s (1981) curves would imply a continued larger height increment all the way through these simulations. The multiplier effect of this site index difference on diameter growth is a bit less direct, but based on the published ORGANON diameter growth equation (Hann et al., 2003), this degree of difference in site index would impose a difference in diameter growth of approximately 8.5% for a 5-yr growth period. However, unlike top height growth, individual tree diameter growth and stand basal area growth would have to reach some limit as they approach maximum density, but 50–60 years may not be sufficient to test this limit at a 3.6-m spacing.

Clearly, as realized gain trials can be measured closer to rotation age, estimated genetic gains become more reliable and upon reaching rotation age these gains can be measured rather than predicted. With ensuing refinements in methods for estimating and applying genetic-gain multipliers, predictions of relative growth and yield gains of untested family mixes should improve and confidence should be gained in our ability to design more optimal seedlots with the fastest-growing and most complementary families. Theoretically, more mechanistic or “hybrid” models that account for morphological or ecophysiological attributes of families could also improve our ability to predict the growth behavior of untested family mixes, but the marginal gains may not be worth the cost of measuring the driving variables (Gould et al., 2011). In short, as with other silvicultural strategies, the gains in yield, quality, and value determine the intensity, desirability, and feasibility of continuing the design and implementation of programs in genetic tree improvement (Haapanen et al., 2016).

The results from the Douglas-fir realized gain trials presented here differ in various ways from measured gains in other species. Although measured volume gains reached approximately 17% for the Douglas-fir trials at plantation age 10/12 years, measured mid-rotation volume gains in Douglas-fir averaged only about 10% at plantation age 17–21 years. In contrast, stand volume gains reached 15% and 34% for moderately and highly improved *Pinus radiata* at 15–17 years (Carson et al., 1999), respectively, 10% for 12-yr-old *Pinus elliottii* (Vergara et al., 2004), and 27.8% and 52.8% for mid-gain levels of genetic improvement and top crosses, respectively, of *Pseudotsuga menziesii* at birth age 12 years (Stoehr et al., 2010). Estimates of rotation-age volume yield gains and the methodologies for estimating these yield gains have varied tremendously with regard to complexity and sophistication (Table 6). In the current study, individual-tree growth models with genetic-gain multipliers based on a huge database of Douglas-fir progeny test data (Gould et al., 2008) were applied to estimate realizable gains at rotation age. However, genetic worth of the seedlots was based on gains already achieved by mid-rotation in the Douglas-fir realized gain trials, averaging about 4–5% in stem volume. In contrast, rotation-age gains from similar projections of ongoing realized gain trials reached 25.4% for stem volume in highly improved *Pinus radiata* (Carson et al., 1999), and 10.2% in stem volume of *Pinus elliottii* (Vergara et al., 2004). Growth increases from genetic selection in some species have been reported to decrease over time (Franklin, 1979; Hamilton and Rehfeldt, 1994), but as was the case in these coastal Douglas-fir trials, volume growth gains have been observed to increase over time in other species (Carson et al., 1999). When establishing patterns in genetic gain and its change over time, it is essential to consider the nature of the unimproved stands forming the basis of the

Table 6
Summary of estimates of rotation yield gains for various species.

Experimental design	Species	Estimated Rotation Yield Gains over unimproved stands	Initial Age	Rotation age	Method for representing genetic gain	Projection model	Reference
Realized gain trials, block-plot design	Douglas-fir	● 23% (top-cross) ● 12% (mid-gain)	Birth age 12 yrs	Birth age 60 yrs	Age-age correlation	–	Stoehr et al. (2010)
Realized gain trials, block-plot design	Radiata pine	● 22% (top-ranked, GF22) ● 13% (open-pollinated, GF14)	Plantation age 15–17 yrs	Plantation age 40 yrs	Genetic-gain multipliers	Growth models for <i>Pinus radiata</i> in New Zealand (Goulding, 1994)	Carson et al. (1999)
Realized gain trials, block-plot design	Radiata pine	● 25.4% (highly improved) ● 11.1% (moderately improved)	Plantation age 20 yrs	Plantation age 30 yrs	Site index and 300 Index	Forecaster (West et al., 2013)	Kimberley et al. (2015)
Realized gain trials, block-plot design	Black spruce	● – 1.6%	Birth age 15 yrs	Birth age 50 yrs	Implied by growth to birth age 15 yrs	STAMAN v5.5 (NBGYU, 2005)	Weng et al. (2010)
Realized gain trials, block-plot design	White spruce	● 1.9%	Birth age 15 yrs	Birth age 50 yrs	Implied by growth to birth age 15 yrs	STAMAN v5.5 (NBGYU, 2005)	Weng et al. (2010)
Realized gain trials, block-plot design	Slash pine	● 10.2%	Plantation age 5–16 yrs	Plantation age 25 yrs	Overall mean annual increment was extrapolated to 25-yr-old rotation age	–	Vergara et al. (2004)
First-generation progeny tests, row plots	Loblolly pine	● 12% (rogued seed orchards) ● 7% (unrogued seed orchards)	Plantation age 4, 8, and 12 yrs	Plantation age 25 yrs	Implied by growth to plantation age 4, 8 and 12	Model for unthinned loblolly pine plantations (Hafley et al., 1982)	Talbert et al. (1985)
Second-generation progeny tests, row plots	Loblolly pine	● 29.8% (top 30% of families in rogued orchards) ● 16.8% (unrogued orchards)	Plantation age 8 yrs	Plantation age 25 yrs	Use 8-yr height gains	Model for unthinned loblolly pine plantations (Hafley et al., 1982)	Li et al. (1999)
First-generation progeny tests, row plots	Slash pine	● 18.0% (1.5 generation orchards) ● 13.2% (first-generation rogued orchards) ● 7.0% (first-generation unrogued orchards)	Plantation age 10 yrs	Plantation age 20 yrs	Use average tree volume gains as stand volume gains	USLYCOWG (Baldwin and Feduccia, 1982)	Hodge et al. (1989)
First-generation progeny tests, single-tree plot & four-tree plot	Scots pine	● 8.3–10.7%	Birth age 19–33 yrs (mean age 27.4 yrs)	Full-rotation (not mentioned exact age)	Use mean height gains at age 19–33 yrs (mean age 27.4 yrs)	–	Andersson et al. (2007)

gain, the age of the stand due to different temporal growth patterns among species, differences in predicting gain from progeny tests and realized gain trials, differences between relative gain and absolute gain, and implications of relative and absolute gain given that steady or even increasing absolute growth may constitute a decreasing percentage of volume accrual.

A gradient in the nature of inter-tree competition clearly exists between the extremes of first-generation progeny tests with completely interspersed families to large block plots from controlled crosses of relatively few parents. The former represents an essentially unimproved stand of families that may have never grown together at any one location within a seed zone, and the latter represents offspring of relatively few elite families, so the resulting stand dynamics can be very difficult to predict and have a profound impact on the apparent stand-level genetic gain (Adams et al., 2006; Adams et al., 2008). As was the case for the Douglas-fir realized gain trials, shifts in relative size and position of the trees would be expected as competition sorts out the strongest competitors from the weakest. Growth and yield of managed stands and responses to many silvicultural treatments such as competing vegetation control, stock type, and fertilizer remains a highly empirical science, so it should not be surprising that breeding values based on progeny that are open-grown or just beginning to compete with surrounding trees are only a first approximation of growth multipliers appropriate for simulating widely varying mixes of families selected from progeny tests. In addition to the mean breeding value or genetic worth of a seedlot, it may be useful to also consider the range or variance in breeding values of families that contribute to a seedlot, given the implications for stand dynamics.

Based on the performance to date of this particular set of crosses made for the elite and intermediate populations vs. unimproved woods-run populations tested in the Molalla Douglas-fir realized gain trials, a genetic gain of approximately 10% appears to be a maximum value for mid-rotation. However, it is important to note that the elite crosses used in the Molalla realized gain trials are not the very best that could be made within the Molalla breeding program, given the advent of best linear unbiased prediction (BLUP) analysis in the early 2000s, long after the crosses for the Molalla realized gain trials were made (Table 7). Crosses (families) A and B showed the highest predicted gains from progeny tests and the highest realized gains in intermediate and elite populations, respectively. The A cross comprised 6% of the total number of trees in the intermediate populations, while the B cross comprised 14.7% of the total number of trees in the elite population when the realized gain trials were established. These two families are closer to a competition ideotype that tended to have wider crown widths and much higher DBH gain than height gain. The difference in the contribution of these two families to the respective intermediate and elite populations might be one cause of ranking changes between the elite and intermediate populations. At the tree-level, competition ideotype trees would have more tree-level volume than that of crop ideotype trees (those with narrower crown but longer crown). However, at the stand-level, stands with more crop ideotype trees should theoretically accommodate more trees per unit area and hence more volume than stands with competition ideotype trees. Competition ideotypes would tend to grow at the expense of neighboring trees, while crop ideotype would tend to occupy less growing space and use site resources less aggressively, resulting in higher growth efficiency, less inter-tree competition and greater carrying capacity on a given site (Dickmann, 1985; Dickmann et al., 1994; Martin et al., 2001).

In the Molalla realized gain trials, the growth responses from the elite and intermediate levels of genetic improvement at first glance may appear to have been inadvertently or at least indirectly imposed in part by selection of families conforming to the crop ideotype (Dickmann, 1985; Dickmann et al., 1994; Martin et al., 2001). Specifically, TPH at rotation age averaged 3.3–3.7% (Table 3) higher in improved populations (elite and intermediate) than in the unimproved woods-run populations ($p < 0.019$; Table 5). However, this apparent genetic

improvement effect on TPH may have been imposed to some degree by the poorer survival of the woods-run seedlings to plantation age five years (~3% or about 3 trees per 100-tree subplot). On the other hand, the combination of lower TPH and lower mean DBH and mean height of the woods-run trees at plantation age 17–21 (Table 1) underscore the superior diameter and height growth of the improved populations, even at a higher TPH. These results, therefore, strongly support the apparent dominance of superior individual tree growth in driving the projected yield gains by genetically improved populations at rotation age 50 years. TPH at rotation age 50 years averaged 3.3–3.7% higher for the genetically improved treatments (i.e., an increase over the ~3% at plantation age five years). Diameter growth among populations seemed to have converged at rotation age 50 years ($p > 0.76$ for QMD; Table 5), so the projected lower mortality and small projected gains in top height were apparently sufficient to estimate yield gains of 3.5–5.5% ($p < 0.057$). Given that the difference in five-year survival was only 3%, and evidence from spacing and thinning trials that yields converge within 50 years or less after much larger differences in initial or residual TPH, respectively, this small difference in initial TPH is not likely to have had a major influence on yield gains at rotation age. Regardless, the yield gains estimated in this study are the net effect of survival and growth differences together, but working in opposite directions. If any effect of a 3% difference in survival remains at plantation age 50–60 years, then genetic gain would have been overestimated in these simulations.

In addition to the change of rankings depending on methods for analyzing breeding values, the logistical reality that not all attempted crosses were successful should be kept in mind as well, especially because very large numbers of seed were required to ensure that each cross was equally represented (St. Clair et al., 2004; Ye et al., 2010). Although this equal representation was the ideal, the proportions of trees on each plot contributed by the 10 families were variable (Table 7), introducing source of variation in the targeted average breeding value for each treatment and the average actually attained. Landowners are currently planting seedlings grown from seed developed from second-cycle breeding programs that should produce higher average gains than those from first-cycle breeding. The treatments represented by genetic levels in the Molalla realized gain trials provide an interesting initial test of relative performance by seedlots of differing average breeding values. However, predicted levels of genetic gain are only approximate for many reasons, and the specific levels of genetic gain targeted or achieved should not be interpreted as the maximum possible for this or other breeding zones (unpublished gain estimates, Northwest Tree Improvement Cooperative). Empirical estimates of realized gain from necessarily long-term realized gain trials will always lag behind the best genetic material being planted.

Under the many necessary assumptions of the growth model and methodology applied for estimating genetic-gain multipliers, rotation length realized gains were projected to reach about 5–6% at rotation ages of approximately 50 years (Fig. 1). Because forest managers and/or geneticists often have measured genetic gain of relatively young stands (Zobel and Talbert, 1984; White et al., 2007), a need has arisen to estimate the proportion of this early measured gain that will persist to rotation age. In this study, relative simulated stand volume gain at plantation age 50 years for the intermediate population was 5.0% and 5.5% under the GWR and PSI scenarios, respectively. This was 31% and 34% of the realized stand volume gain measured at plantation age 10/12 years for GWR and PSI, respectively, and 34% and 38% of measured gain at plantation age 17/18 years under GWR and PSI, respectively. Given the similarity of trends in relative gain, absolute gain, and periodic/mean annual increment between direct observations and model simulations in other species (Carson et al., 1999; Adams et al., 2008), the pattern of decline in a relative genetic gain in Douglas-fir cubic volume yield observed in this study seems reasonable. Economic analysis in the U.S. Pacific Northwest has traditionally been based on Scribner board-foot yields. Scribner is a diagram log rule that aims to

Table 7
Summary of predicted gains from the Molalla progeny tests at birth age 15 years, and realized gains from Molalla realized gain trials at plantation age 17/18 by family (controlled crosses). Included for each cross in the five Molalla realized gain trials are total number of trees planted, survival, share of total stand volume, realized gains in 1.8 × 1.8 m and 3.6 × 3.6 m spacings, and correlations between predicted gains and realized gains for height and tree volume.

Cross Code (family)	Treatment in realized gain trials	15-yr birth age gains (%)			3.6-m spacing			1.8-m spacing			Average of 1.8-m and 3.6-m spacing	
		Height	DBH	Tree Volume	% of total planted trees	% gains achieved by realized gain trials at plantation age 17/18 (birth age 20/21)	Share of total stand volume (%)	% of total planted trees	% gains achieved by realized gain trials at plantation age 17/18 (birth age 20/21)	Share of total stand volume (%)	% gains achieved by realized gain trials at plantation age 17/18 (birth age 20/21)	% gains achieved by realized gain trials at plantation age 20/21
		Height	DBH	Tree Volume	Total number of trees planted	Survival	DBH	Tree Volume	Survival	DBH	Tree Volume	Tree Volume (%)
A	Intermediate	16.7	22.2	58.4	365	6.0	12.20	27.4	87.2	7.2	6.2	83.9
B	Elite	11.6	19.2	54.6	876	14.7	8.84	21.6	91.6	18.0	14.5	88.5
C	Elite	9.7	14.8	42.0	598	10.1	9.34	18.1	86.5	11.4	9.8	85.8
D	Elite	13.7	13.0	40.2	600	9.6	8.07	14.7	86.4	10.5	10.4	81.5
E	Elite	13.7	16.1	37.9	495	8.2	5.02	9.9	88.6	8.7	8.3	85.1
F	Intermediate	14.2	7.3	22.6	843	14.0	9.78	11.5	89.8	14.9	14.1	88.4
G	Elite	6.2	8.8	21.2	865	14.5	-2.00	-3.05	88.7	12.7	14.3	82.6
H	Elite	5.4	8.6	15.2	597	10.0	-2.36	-5.71	84.6	8.1	9.9	77.9
I	Elite	3.1	8.3	14.0	600	10.0	3.68	1.11	86.3	9.8	10.0	82.3
J	Intermediate	3.1	4.7	11.4	656	10.9	2.47	2.95	87.2	10.7	10.9	83.5
K	Elite	2.9	7.1	10.9	594	10.0	-0.86	0.78	84.9	9.3	9.8	90.8
L	Intermediate	2.2	3.2	8.7	168	3.2	4.16	0.19	87.6	3.1	2.4	84.5
M	Intermediate	-4.6	3.7	8.2	684	11.2	0.86	7.80	87.8	12.1	11.6	83.6
N	Elite	7.2	1.9	3.9	176	2.9	-0.47	-4.40	77.9	2.4	3.0	78.9
O	Intermediate	5.1	-1.8	1.9	471	7.8	1.91	6.07	82.9	7.7	7.9	85.2
P	Intermediate	5.1	-0.6	-0.5	666	11.1	1.02	-0.21	90.4	10.5	11.1	82.6
Q	Intermediate	1.1	-0.3	-1.4	845	13.9	4.08	5.40	85.9	14.4	14.3	87.6
R	Elite	2.9	0.5	-3.1	601	10.1	0.87	-3.06	86.5	9.1	9.9	81.5
S	Intermediate	-1.2	0.8	-6.8	643	10.8	1.58	-1.30	86.1	9.8	10.7	80.9
T	Intermediate	-10.3	-10.3	-19.7	659	11.0	0.78	-2.64	85.2	9.6	10.9	84.5
Cross-level correlations with 15-yr birth age predicted gains for the same trait from Molalla progeny tests						0.56	0.86	0.90	0.84	0.84	0.84	0.84

estimate the volume of sawn lumber recoverable from a log of given length and small end diameter (inside bark) based on rules about minimum and maximum board size and saw kerf (Avery and Burkhardt, 2015); in contrast, cubic volume includes total wood volume inside bark. Although board foot : cubic foot ratios typically increase with increasing log and tree diameter, board-foot genetic volume gains over the age range assessed were virtually identical in magnitude to the cubic volume gains (Figs. A.1–A.3) (Keegan et al., 2010).

A potentially important knowledge gap remains about potential genetic improvement effects on carrying capacity (Carson et al., 1999). If genetic improvement has a biologically and economically significant effect on carrying capacity in terms of basal area or relative stand density, the effects of family composition on the yield potential and associated genetic gains of forest plantations may be correspondingly different. Increased carrying capacity from genetic improvement is consistent with the crop ideotype concept (Cannell, 1978; Dickmann et al., 1994; Martin et al., 2001). Evidence up to mid-rotation in the Douglas-fir realized gain trials is not strong due to the relatively low density-dependent mortality (Table 1), but some increase in carrying capacity was apparent among the different levels of genetic improvement based on combined results for QMD, tree density (TPH), and relative stand density (SDI) (Tables 3–5). At the 3.6-m spacing, the data on survivorship will continue to accumulate and provide a more robust test of potential genetic gain in carrying capacity. Similarly, the more intense density-dependent mortality in the 1.8-m spacing, and associated tests on differences in QMD, surviving TPH, and temporal trends in SDI would probably provide some insight into expectations among the genetic treatment levels in the 3.6-m spacing (Joo, 2019); however, any significant treatment effects may not translate into the same difference among genetic gains in carrying capacity. Bruce's (1981) site index estimated at mid-rotation (i.e., PSI scenario) performed surprisingly well relative to the genetic-gain multiplier (GWR) approach. This result may not be too surprising because the genetic gain in height growth was measured at half rotation age. Likewise, DBH growth is a function of site index in the growth model CIPSANON. However, similar performance in SI (top height growth) but very significant differences in DBH growth and survivorship, can result in very significant differences in basal area carrying capacity for a given top height (e.g., Curtis, 2006). In the current analysis, average net losses in QMD have to be explained by increased tree survival if volume gains were positive (Tables 3–5). Even stand dynamics in the 1.8-m spacing strongly suggested that an increase in carrying capacity was imposed by the level of genetic improvement, particularly in cases where greater SDI or relative density keeps the average tree DBH slightly smaller.

Recognition must also be given to the challenges and inaccuracies presented by small-(subplot) to large- (site level) scale variation in site quality vis-à-vis random allocation of treatments. The U.S. Pacific Northwest is mountainous and environmentally heterogeneous (Howe et al., 2006), so 100-tree subplots at 3.6 × 3.6 m spacing can have a lot of variation within the site and between the sites. This variation and random allocation of treatments probably at least contributes to the

aberrant results like negative stand volume gain simulated for the elite population at the Molalla site (Tables 3 and 4).

The discrepancy between gains in the elite vs. intermediate treatments is difficult to explain but Ye et al. (2010) hypothesized that elite selections might have characteristics of high competitive ability and density tolerance expected of a competition ideotype, while the intermediate population might have been suppressed in progeny tests by competition ideotype trees. If so, intermediate trees may be able to grow faster in the absence of competition in stand structural conditions like those created in the 3.6-m spacing of the Molalla realized gain trials. Under the tighter 1.8 × 1.8 m spacing, the elite outperformed the intermediate populations by a large margin, in contrast to the results at the wider 3.6 × 3.6 m (Ye et al., 2010). Continued measurement of this trial will doubtless shed light on mechanisms driving these differences as the stands evolve. Questions also remain about the need to: modify the magnitude of the growth multipliers (upward or downward); refit the mortality model proportional to faster growth and higher carrying capacity of genetically improved trees (e.g., overestimation of mortality and underestimation of realized gain); and allowing for age-related modification of genetic multipliers. With the passage of nearly 30 years and the measurement of 9000 trees in this study, relatively few data points have been obtained, because the absolute or relative gain of one subplot containing one gain level at one age really provides just one data point. Likewise, we cannot assume that each Douglas-fir from each breeding zone would provide exactly the same result as observed in this set of realized gain trials. These knowledge gaps highlight the complexity, cost and difficulty of implementing genetic tree improvement, underscores the length of time it takes to measure its impact, and entices teams of geneticists, silviculturists, and biometricians to consider other analytical approaches that might expedite scientific and operational progress.

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Appendix A. Board foot volume gains

Board foot volume (bf/ac) gains from elite and intermediate levels of genetic improvement relative to the unimproved woods run population. Scribner volume estimates in CIPSANON were computed based on the following specifications:

- Log length = 32 feet
- Minimum log length = 8 feet
- Top diameter inside bark = 6 in.
- Stump height = 0.5 feet
- Trim allowance = 10 in.

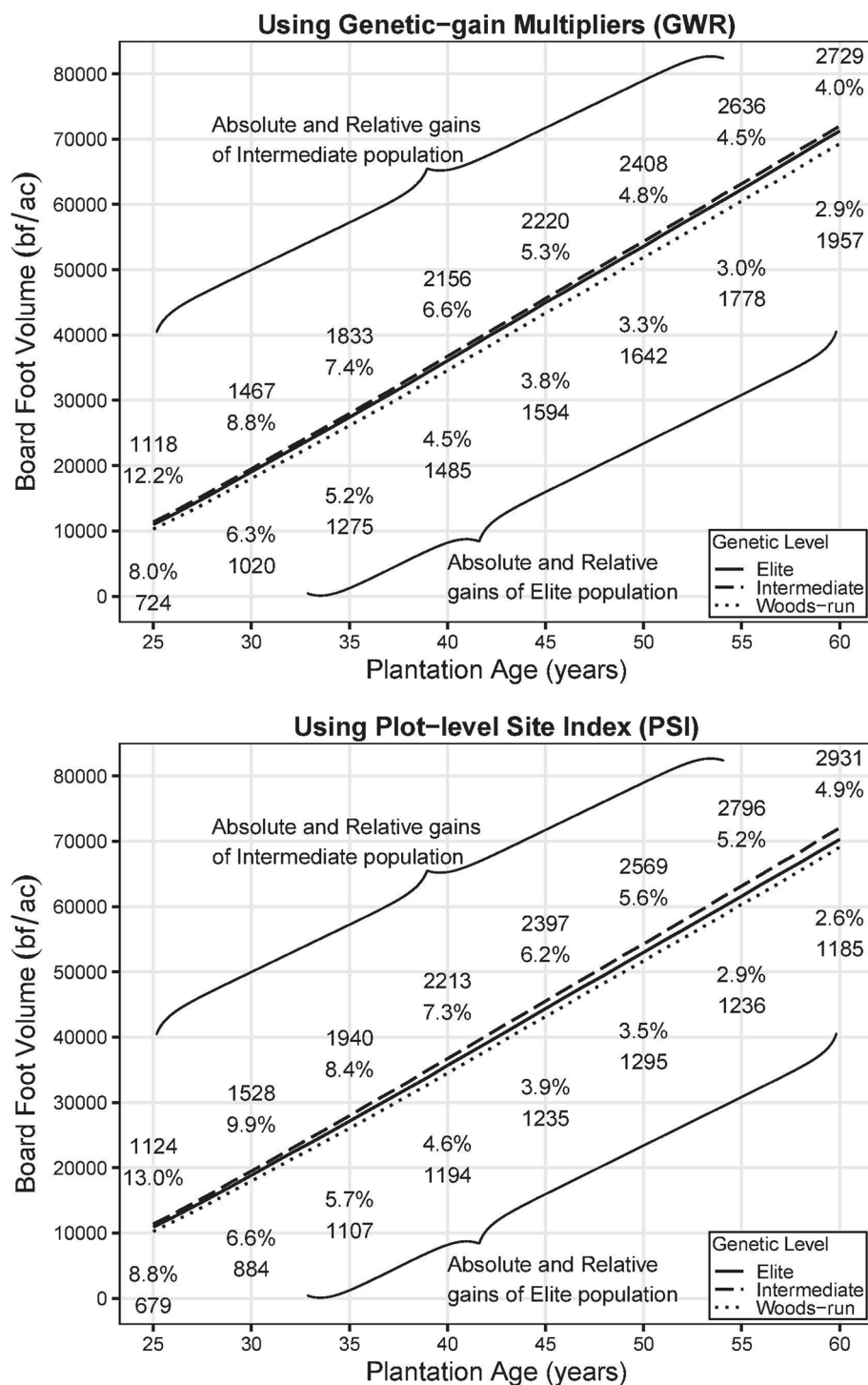


Fig. A1. Simulated cumulative growth in board foot volume (bf/ac) for elite, intermediate, and woods-run genetic improvement levels under the assumption of continued realized genetic gain (GWR) observed at plantation ages 17–21 years and uniform site index (upper panel) and under the assumption that genetic gain is fully represented by subplot-level site index (PSI) measured at plantation ages 17–21 years (lower panel). Absolute and relative simulated board foot volume gains were calculated relative to unimproved woods-run populations.

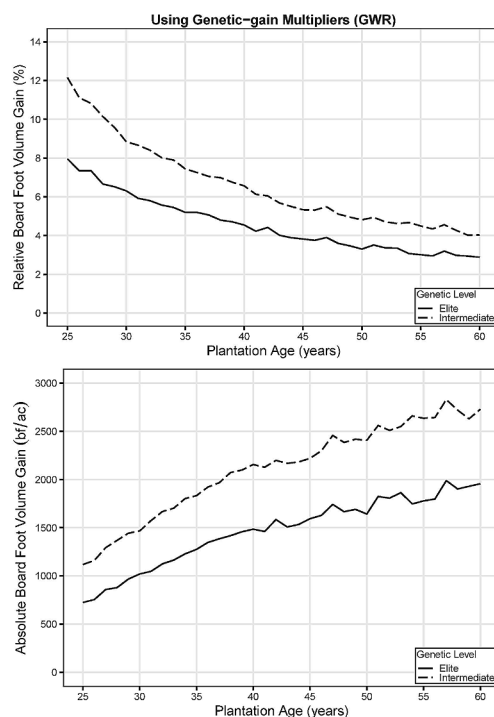


Fig. A2. Relative (% , upper panel) and absolute (bf/ac, lower panel) simulated gains of board foot volume averaged for the elite and intermediate populations relative to the woods-run population under the GWR scenario (using observed realized gains at plantation age 17–21 years to estimate genetic worth for computing genetic-gain multipliers).

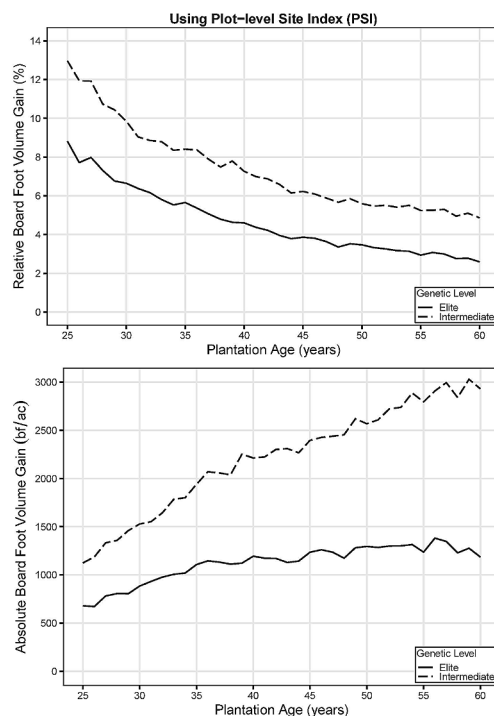


Fig. A3. Relative (% , upper panel) and absolute (bf/ac, lower panel) simulated gains of board foot volume averaged for the elite and intermediate populations relative to the unimproved woods-run population under the PSI scenario (without genetic-gain multipliers and using only subplot-level site index estimated at the latest measurement years to predict response to genetic improvement).

References

- Adams, J.P., Land, S.B., Belli, K.L., Matney, T.G., 2008. Comparison of 17-year realized plot volume gains with selection for early traits for loblolly pine (*Pinus taeda* L.). *For. Ecol. Manage.* 255 (5–6), 1781–1788.
- Adams, J.P., Matney, T.G., Land Jr, S.B., Belli, K.L., Duzan Jr, H.W., 2006. Incorporating genetic parameters into a loblolly pine growth-and-yield model. *Can. J. For. Res.* 36 (8), 1959–1967.
- Andersson, B., Elfving, B., Persson, T., Ericsson, T., Kroon, J., 2007. Characteristics and development of improved *Pinus sylvestris* in northern Sweden. *Can. J. For. Res.* 37 (1), 84–92.
- Avery, T.E., Burkhardt, H.E., 2015. *Forest Measurements*, fifth ed. Waveland Press, Long Grove, Illinois, USA, pp. 480.
- Baldwin Jr., V., Feduccia, D., 1982. Validation of the unthinned loblolly pine plantation yield model – USLYCOWG. Research Note SO-283. US Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48.
- Bruce, D., 1981. Consistent height-growth and growth-rate estimates for remeasured plots. *For. Sci.* 27 (4), 711–725.
- Buford, M.A., Burkhardt, H.E., 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33 (3), 707–724.
- Callister, A., England, N., Collins, S., 2013. Predicted genetic gain and realised gain in stand volume of *Eucalyptus globulus*. *Tree Genet. Genom.* 9 (2), 361–375.
- Cannell, M.G.R., 1978. Improving per hectare forest productivity. In: Hollis, C.A., Squillace, A.E. (Eds.), *Proceedings of the Fifth North American Forest Biology Workshop*. University of Florida School of Forest Resources and Conservation, pp. 120–148.
- Carson, S.D., Garcia, O., Hayes, J.D., 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *For. Sci.* 45 (2), 186–200.
- Curtis, R.O., 2006. Volume growth trends in a Douglas-fir levels-of-growing-stock study. *West. J. Appl. For.* 21 (2), 79–86.
- Dhakal, L., White, T., Hodge, G., 1996. Realized genetic gains from slash pine tree improvement. *Silvae Genet.* 45 (4), 190–196.
- Dickmann, D.L., 1985. The ideotype concept applied to forest trees. In: Cannell, M.G.R., Jackson, J.E. (Eds.), *Attributes of Trees as Crop Plants*. Institute of Terrestrial Ecology, Monks Wood, Huntington, UK, pp. 89–101.
- Dickmann, D.L., Gold, M.A., Flore, J.A., 1994. The ideotype concept and the genetic improvement of tree crops. *Plant Breed. Rev.* 12, 163–193.
- Franklin, E., 1979. Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genet.* 28 (5–6), 207–212.
- Gould, P., Johnson, R., Marshall, D., Johnson, G., 2008. Estimation of genetic-gain multipliers for modeling Douglas-fir height and diameter growth. *For. Sci.* 54 (6), 588–596.
- Gould, P.J., Marshall, D.D., 2010. Incorporation of genetic gain into growth projections of Douglas-fir using ORGANON and the forest vegetation simulator. *West. J. Appl. For.* 25 (2), 55–61.
- Gould, P.J., St. Clair, J.B., Anderson, P.D., 2011. Performance of full-sib families of Douglas-fir in pure-family and mixed-family deployments. *For. Ecol. Manage.* 262 (8), 1417–1425.
- Goulding, C., 1994. Development of growth models for *Pinus radiata* in New Zealand—experience with management and process models. *For. Ecol. Manage.* 69 (1–3), 331–343.
- Haapanen, M., Hynynen, J., Ruotsalainen, S., Siipilehto, J., Kilpeläinen, M.-L., 2016. Realised and projected gains in growth, quality and simulated yield of genetically improved Scots pine in southern Finland. *Eur. J. Forest Res.* 135 (6), 997–1009.
- Hafley, W.L., Smith, W.D., Buford, M.A., 1982. A new yield prediction model for unthinned loblolly pine plantations. Southern Forest Research Center, School of Forest Resources, North Carolina State University, Raleigh, North Carolina. Technical report No. 1.
- Hamilton, D.A., Rehfeldt, G.E., 1994. Using individual tree growth projection models to estimate stand-level gains attributable to genetically improved stock. *For. Ecol. Manage.* 68 (2), 189–207.
- Hann, D.W., 2011a. ORGANON user's manual edition 9.1. Department of Forest Engineering, Resources, and Management, Oregon State University, Corvallis, Oregon, USA. <http://www.cof.orst.edu/cof/fr/research/organon/download.htm> (accessed 12 February, 2019).
- Hann, D.W., 2011b. Revised volume and taper equations for six major conifer species in Southwest Oregon. College of Forestry, Oregon State University, Corvallis, Oregon, USA. Forest Biometrics Research Paper 2.
- Hann, D.W., Marshall, D.D., Hanus, M.L., 2003. Equations for predicting height-to-crown-base, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest, Forest Research Laboratory, Oregon State University, Corvallis, Oregon. Research Contribution 40.
- Hodge, G.R., White, T.L., Powell, G.L., De Souza, S.M., 1989. Predicted genetic gains from one generation of slash pine tree improvement. *South J. Appl. For.* 13 (1), 51–56.
- Howe, G.T., Jayawickrama, K.J.S., Cherry, M.L., Johnson, G., Wheeler, N., 2006. Breeding Douglas-fir. In: Janick, J. (Ed.), *Plant Breeding Reviews*. John Wiley & Sons, New Jersey, pp. 245–353.
- Jack, S.B., Long, J.N., 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. *For. Ecol. Manage.* 86 (1–3), 205–220.
- Jayawickrama, K., Carson, M., 2000. A breeding strategy for the New Zealand radiata pine breeding cooperative. *Silvae Genet.* 49 (2), 82–89.
- Jayawickrama, K.J.S., Ye, T., Truong, H., 2017. Northwest Tree Improvement Cooperative Annual Report: January 1, 2016 to June 30, 2017. Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR, USA <http://nwtic2.forestry.oregonstate.edu/nwtic-annual-reports> (accessed 27 September, 2018).
- Jayawickrama, K.J.S., Ye, T.Z., 2009. Northwest Tree Improvement Cooperative Annual Report: October 1, 2007 to July 31, 2009. Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR, USA. Available at <http://nwtic2.forestry.oregonstate.edu/nwtic-annual-reports> (accessed 27 September, 2018).
- Joo, S., 2019. Simulating Effects of Genetic Tree Improvement on Growth and Yield of Coastal Douglas-fir. Ph.D. Dissertation. Oregon State University, Corvallis, OR, USA, pp. 187.
- Joo, S., D.B. Mainwaring, D.W. Hann, N.L. Osborne, D.A. Maguire. 2020. User's Manual for CIPSR Version 4.0.0. Center for Intensive Planted-forest Silviculture (CIPS), College of Forestry, Oregon State University, Corvallis, Oregon, USA. Available at <http://cips.forestry.oregonstate.edu/cipsanon> (accessed 20 February, 2020).
- Keegan, C.E., Morgan, T.A., Blatner, K.A., Daniels, J.M., 2010. Trends in lumber processing in the Western United States. Part I: Board foot Scribner volume per cubic foot of timber. *Forest Prod. J.* 60 (2), 133–139.
- Kimberley, M.O., Moore, J.R., Dungey, H.S., 2015. Quantification of realised genetic gain in radiata pine and its incorporation into growth and yield modelling systems. *Can. J. For. Res.* 45 (12), 1676–1687.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82 (13), 1–26.
- Latham, P., Tappeiner, J., 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiol.* 22 (2–3), 137–146.
- Li, B., McKeand, S., Weir, R., 1999. Tree improvement and sustainable forestry-impact of two cycles of loblolly pine breeding in the USA. *Int. J. Forest Genetics* 6 (4), 229–334.
- Mainwaring, D.B., D.W. Hann, D.A. Maguire, N.L. Osborne, S. Joo. 2020. CIPSR Version 4.0 User's Manual. Center for Intensive Planted-forest Silviculture (CIPS), College of Forestry, Oregon State University, Corvallis, Oregon, USA. Available at <http://cips.forestry.oregonstate.edu/cipsanon> (accessed 1 February, 2020).
- Mainwaring, D.B., D.A. Maguire, D.W. Hann, N.L. Osborne, S. Joo. 2020. CIPSR Version 4.0. Center for Intensive Planted-forest Silviculture (CIPS), College of Forestry, Oregon State University, Corvallis, Oregon, USA. CIPS Technical Report 1. Available at <http://cips.forestry.oregonstate.edu/cipsanon> (accessed 27 February, 2020).
- Martin, T.A., Johnsen, K.H., White, T.L., 2001. Ideotype development in southern pines: rationale and strategies for overcoming scale-related obstacles. *For. Sci.* 47 (1), 21–28.
- Nance, W.L., Wells, O.O., 1981. Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. In: *Proceedings of 16th Southern Forest Tree Improvement Conference*. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, pp. 86–96.
- NBGYU, 2005. STAMAN v.5.5 user manual, New Brunswick Growth & Yield Unit, Fredericton, NB, Canada.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/> (accessed 29 September, 2018).
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46 (7), 627–638.
- Salminen, H., Lehtonen, M., Hynynen, J., 2005. Reusing legacy FORTRAN in the MOTTI growth and yield simulator. *Comput. Electron. Agric.* 49 (1), 103–113.
- St. Clair, J.B., Mandel, N., Jayawickrama, K., 2004. Early realized genetic gains for coastal Douglas-fir in the northern Oregon Cascades. *West. J. Appl. For.* 19 (3), 195–201.
- Stoehr, M., Bird, K., Nigh, G., Woods, J., Yanchuk, A., 2010. Realized Genetic Gains in Coastal Douglas-fir in British Columbia: implications for Growth and Yield Projections. *Silvae Genet.* 59 (5), 223–233.
- Talbert, J., Weir, R., Arnold, R., 1985. Costs and benefits of a mature first-generation loblolly pine tree improvement program. *J. For.* 83 (3), 162–166.
- Vergara, R., White, T.L., Huber, D.A., Shiver, B.D., Rockwood, D.L., 2004. Estimated realized gains for first-generation slash pine (*Pinus elliottii* var. *elliottii*) tree improvement in the southeastern United States. *Can. J. For. Res.* 34 (12), 2587–2600.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling*. John Wiley & Sons, Chichester, West Sussex, UK, pp. 430.
- Weng, Y., Tosh, K.J., Fullarton, M.S., 2010. Determining and projecting realised genetic gains: Results from early-stage spruce improvement programmes in New Brunswick, Canada. *N. Z. J. For. Sci.* 40, 5–17.
- West, G., Moore, J., Shula, R., Harrington, J., Snook, J., Gordon, J., Riordan, M., 2013. Forest management DSS development in New Zealand. Implementation of DSS tools into the forestry practice, pp. 153–163.
- White, T.L., Adams, W.T., Neale, D.B., 2007. *Forest Genetics*. Cabi, Cambridge, MA, pp. 704.
- Xie, C., Yanchuk, A.D., 2003. Breeding values of parental trees, genetic worth of seed orchard seedlots, and yields of improved stocks in British Columbia. *West. J. Appl. For.* 18 (2), 88–100.
- Ye, T.Z., Jayawickrama, K.J.S., St. Clair, J.B., 2010. Realized gains from block-plot coastal Douglas-fir trials in the northern Oregon Cascades. *Silvae Genet.* 59 (1), 29–39.
- Zobel, B., Talbert, J., 1984. *Applied Forest Tree Improvement*. John Wiley & Sons, New York, NY, pp. 505.