Incorporation of Genetic Gain into Growth Projections of Douglas-Fir Using ORGANON and the Forest Vegetation Simulator

Peter J. Gould and David D. Marshall

ABSTRACT

Growth models for coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) are generally based on measurements of stands that are genetically unimproved (or woods-run); therefore, they cannot be expected to accurately project the development of stands that originate from improved seedlots. In this report, we demonstrate how early expected gain and genetic-gain multipliers can be incorporated into growth projection, and we also summarize projected volume gains and other aspects of stand development under different levels of genetic gain, site productivity, and initial planting density. Representative tree lists that included three levels of productivity (site index = 100, 125, and 150 ft; base = 50 years) and three initial planting densities (302, 435, and 602 trees/ac) were projected from ages 10 to 60 years under three scenarios using two regional growth models (Stand Management Cooperative version of ORGANON and the Pacific Northwest variant of the Forest Vegetation Simulator). The two models projected similar percentage volume gains for improved seedlots. Seedlots with a genetic worth (*GW*) of 5% for height and diameter growth were projected to have volume gains of 3.3–5.8% over woods-run stands at 40 years and 2.1–3.2% at 60 years. Volume gains were projected to approximately double when *GW* was increased from 5 to 10%.

Keywords: tree improvement, growth and yield, growth models

Tree improvement programs in the Pacific Northwest are now producing improved seedlots of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) that are routinely used to regenerate stands following timber harvests (Jayawickrama 2005). Forest managers often want to use growth models to project growth and evaluate alternative silvicultural treatments. Most growth models, however, were developed from measurements of unimproved, woods-run stands and are therefore expected to underpredict the growth of improved seedlots. Owing to the absence of long-term growth data on improved stands, it is not currently possible to develop new empirical models or refit growth equations for improved seedlots. In addition, progressive tree improvement presents a moving target for forest modelers, as a new generation of seed orchards will likely be established before an improved seedlot completes its rotation (Silen and Wheat 1979).

An approach that is now available to forest managers is to incorporate genetic-gain multipliers into growth projections for improved stands. Genetic-gain multipliers represent the relative growth difference between woods-run and improved trees of the same size that are growing under the same conditions. Within individual tree growth models, the multipliers modify predicted periodic height and diameter increments but otherwise do not change how the models function. Genetic-gain multipliers for Douglas-fir height and diameter growth can be predicted from a seedlot's genetic worth (*GW*) for these traits at age 10 years (Gould et al. 2008). *GW* is the expected gain in a trait of a seedlot relative to the unimproved population (Xie and Yanchuk 2003) at a given age (10 years in this study). For example, if a seedlot with a *GW* of 10% for height was planted along side of a woods-run seedlot, its average height at age 10 years is expected to be 10% greater than the woods-run trees growing in the same environment. Estimates of *GW* are calculated from progeny test results from a limited number of test environments, and there is considerable uncertainty as to how well improved seedlots will perform in any particular situation. For the purpose of modeling growth, however, *GW* provides an important (and presumably unbiased) estimate of a seedlot's performance relative to woods-run. Genetic-gain multipliers are used to extend the genetic potential measured by *GW* into growth projections beyond the age when *GW* is calculated. Calculating genetic-gain multipliers from *GW* is a flexible approach that can be applied to seedlots from existing orchards and to future seedlots with progressively greater levels of gain.

Until more growth data become available, growth projections using genetic-gain multipliers are a viable method of estimating the amount of volume gain that can be expected from tree improvement programs for Douglas-fir in the Pacific Northwest. In addition, projecting stand development with genetic-gain multipliers can provide insight into how genetic gain may interact with other variables such as site index and stand density. The objectives of this study were (1) to demonstrate how forest managers can project stands planted from improved seedlots using existing growth models and (2) to summarize projected volume gains and other aspects of stand

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development under different levels of genetic gain, site productivity, and initial planting density. Two widely used individual-tree growth models for the Westside forests of the Pacific Northwest were used: Stand Management Cooperative version of ORGANON Edition 8.2 (Hann 2008) and the Pacific Northwest variant of the Forest Vegetation Simulator (FVS-PN) (US Forest Service 2008).

Methods

Five representative pure Douglas-fir stands were projected from ages 10 to 60 years under three scenarios: woods-run (WR; unimproved stand), GW5 (5% gain in height and diameter at age 10 year), and GW10 (10% gain in height and diameter). Initial tree lists representing 10-year-old Douglas-fir plantations were generated using the "presilvicultural" model component of FGROW (Flewelling and Marshall 2008), a growth model for Douglas-fir plantations that was developed using data on woods-run stands from the University of Washington Stand Management Cooperative. The presilvicultural model generates diameter distributions (approximated using the Weibull function) based on stand age, site index (SI), and planting density. Tree heights and crown ratios are also estimated from the stand variables. Stands 1, 2, and 3 represented three levels of productivity (SI = 100, 125, or 150 ft at 50 years; SI was measured according to King 1966) and a single initial planting density (435 trees/ac). Stands 2, 4, and 5 represented three initial planting densities at a single level of productivity (435, 302, and 600 trees/ac; SI = 125 ft) (Table 1).

The tree lists that were generated by FGROW did not include the early genetic gain (up to age 10 years) that would be expected under the two gain scenarios. For the purpose of modeling, we assumed that *GW* would translate into an increase in height and diameter of all trees in the stands. Therefore, the initial tree heights and diameters were multiplied by 1.05 for the GW5 scenario and by 1.10 for the GW10 scenario. Because of the young age of the stands and the fairly small changes in tree sizes, we assumed that any effect of increased size on early mortality would be negligible. Gain beyond age 10 years was projected using genetic-gain multipliers. Multipliers were calculated from equations developed using results from first-generation progeny tests coordinated by the Northwest Tree Improvement Cooperative in western Oregon and western Washington (Jayawickrama 2005). The equations predict genetic-gain multipliers for height (M_H) and diameter (M_D) using the 10-year *GW* for these traits (i.e., GW_H and GW_D) (Gould et al. 2008). The equations are

$$M_H = 1 + 0.0035 \cdot GW_H, \quad (1)$$

$$M_D = 1 + 0.0031 \cdot GW_D. \quad (2)$$

For the GW5 scenario, $M_H = 1.0175$ and $M_D = 1.0155$. For the GW10 scenario $M_H = 1.0350$ and $M_D = 1.0310$. The genetic-gain multipliers were assumed to remain constant over the 60-year projection period. Equations 1 and 2 were developed from growth data on trees up to 20 years old, and over this period the values of the multipliers did not change. This assumption currently remains untested for older trees; therefore, our results should be interpreted with caution.

ORGANON and FVS are both individual-tree distance-independent growth models. Both models use a set of equations to predict periodic height- and diameter-growth increments (ORGANON uses 5-year periods, and FVS uses 10-year periods).

Table 1. Summary of the initial tree lists used in the projections.

Stand	Site index (ft)	Planting density (trees/acre)	10-year density (trees/acre)	10-year dbh (in.)
1	100	435	374	0.8
2	125	435	374	2.0
3	150	435	374	4.7
4	125	302	260	2.1
5	125	600	584	2.0

The predicted growth increments are multiplied by genetic-gain multipliers to reflect the faster growth of improved seedlots. A test version of ORGANON, edition 8.2, that can incorporate user-defined genetic-gain multipliers into growth projections was used for this study. The multipliers are applied in ORGANON after the 5-year growth cycle is completed. Thus, the multipliers affect the predicted height and diameter increments for the current growth cycle directly and other model components, such as predicted mortality, only in subsequent cycles as a result of the growth increases. The test version of ORGANON will be publicly released in the near future (D. Hann, personal communication).

Genetic-gain multipliers were incorporated into FVS projections using the keywords FIXHTG (fixed height growth) and FIXDG (fixed diameter growth) (Dixon 2002, Van Dyck 2006). For example, the lines added to the keyword file for the GW5 scenario were

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FIXHTG    DF 1.0155
FIXDG     DF 1.0175
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These keywords are relatively recent additions to FVS and provide a more precise method for incorporating genetic gain than the multiplier keywords that had previously been included in the model (e.g., HTGMULT and BAIMULT) (Hamilton 1994). The keywords apply multipliers to all projection periods and to all tree sizes by default. FIXHTG and FIXDG function similar to the ORGANON multiplier; however, the multipliers may affect mortality within a growth cycle, as they are applied before mortality is estimated.

Total volume (ft^3/ac) projections from ORGANON and FVS were summarized and compared for each stand and each level of gain. To facilitate comparisons between models, the same volume equation (Walters and Hann 1986) was used for all projections. Mean annual increment (MAI) and periodic annual increment (PAI) were summarized for the GW10 scenario (SI = 125 ft) to evaluate the effects of multipliers on the culmination of MAI. The maximum stand density index (SDIMAX; Avery and Burkhart 1994) in FVS can strongly affect growth projections because of its effect on projected mortality (Hamilton and Rehfeldt 1994). Default SDIMAX is set by selecting a plant association; however, the recommended values vary widely among plant associations (Donnelly 1997). SDIMAX was set to 925 for all projections where volume gains were compared, which is the median value for plant associations in FVS-PN (US Forest Service Forest Management Service Center 2008). The effect of SDIMAX was evaluated in FVS-PN by comparing three levels of SDIMAX (750, 1,000, and 1,250) in the most productive stand and the highest gain scenario (GW10 with SI = 150 ft).

Results

Projections for the three levels of SI (stands 1, 2, and 3) are summarized in Figure 1. Total volume over the projection period is

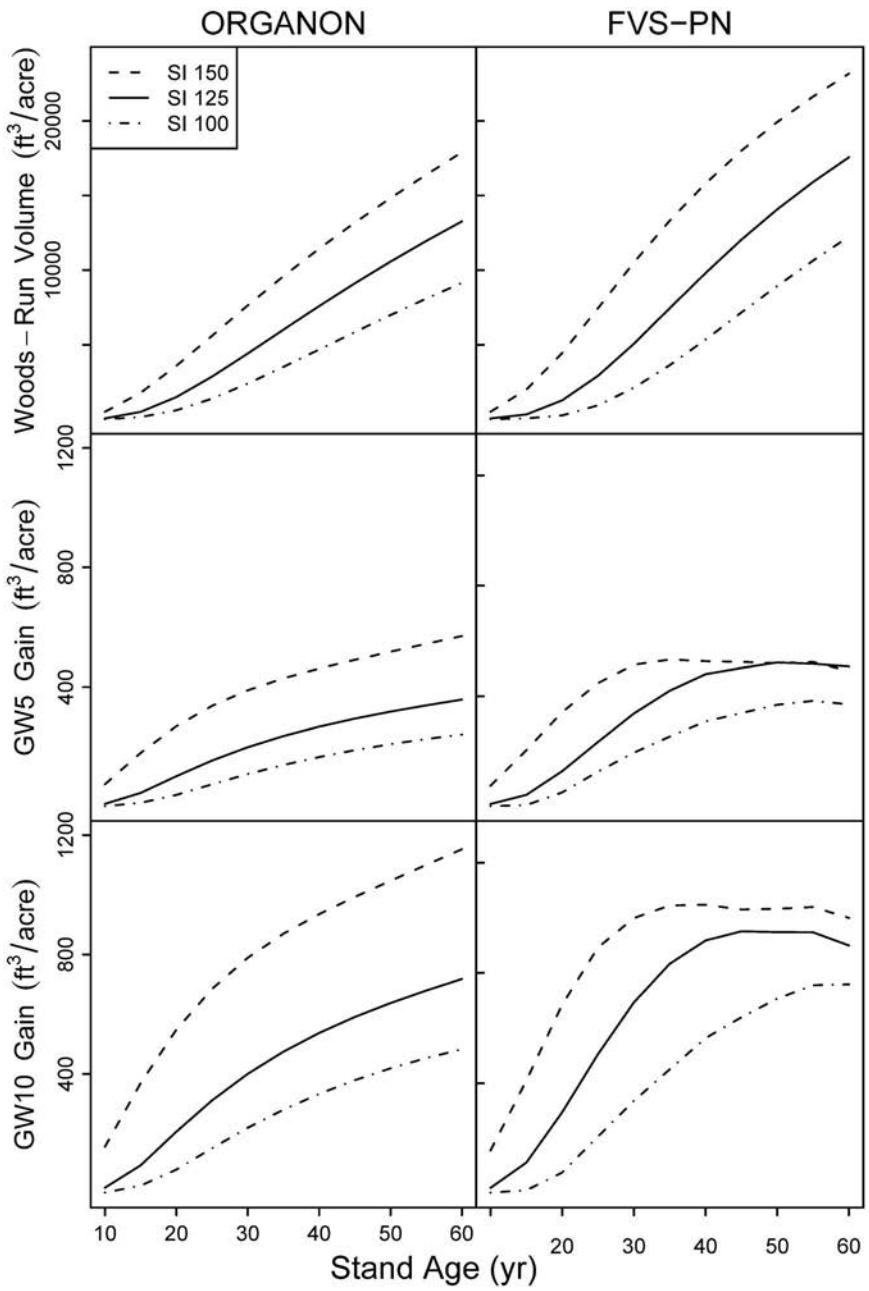

Figure 1. Projected volume of woods-run stands (top row) and volume gains (lower rows) under the two gain scenarios and three levels of site index (SI). GW, genetic worth; FVS-PN, Pacific Northwest variant of the Forest Vegetation Simulator.

shown for the WR scenario (no genetic gain) in the top row of Figure 1, and volume gains (the differences in total volume between the WR and gain scenarios) are shown in the lower rows. FVS-PN projected about 30% more total volumes at 60 years for the woods-run stands than ORGANON for all three levels of SI. Both models generally projected more volume gain as site productivity increased. ORGANON projected that volume gain would increase over the entire projection period for all three levels of SI. In contrast, volume gain tended to reach a maximum and then decline somewhat in FVS-PN, particularly for SI = 150 ft. The difference in volume gain between SI = 125 ft and SI = 150 ft also decreased; projected volume gains were about equal for the SI = 150 ft and SI = 125 ft for the GW5 scenario at stand age 50 years and older. The maximum volume gains projected by FVS-PN also occurred earlier in the projection period with increasing site productivity.

Projected woods-run volumes increased with increasing initial planting density in FVS-PN, but there was little effect of initial density in ORGANON (Figure 2). In FVS-PN, volume gains were initially greatest with 600 trees/ac, but greater volume gains were projected for the other two planting densities later in the projection period. Volume gains at 60 years were somewhat lower with an initial density of 600 trees/ac than with an initial density of 435 trees/ac for both gain scenarios projected by FVS-PN.

Despite the differences in total volume projected by the two growth models, volume gains were similar when expressed as a percentage of woods-run volume (Figure 3). The abrupt "spikes" in

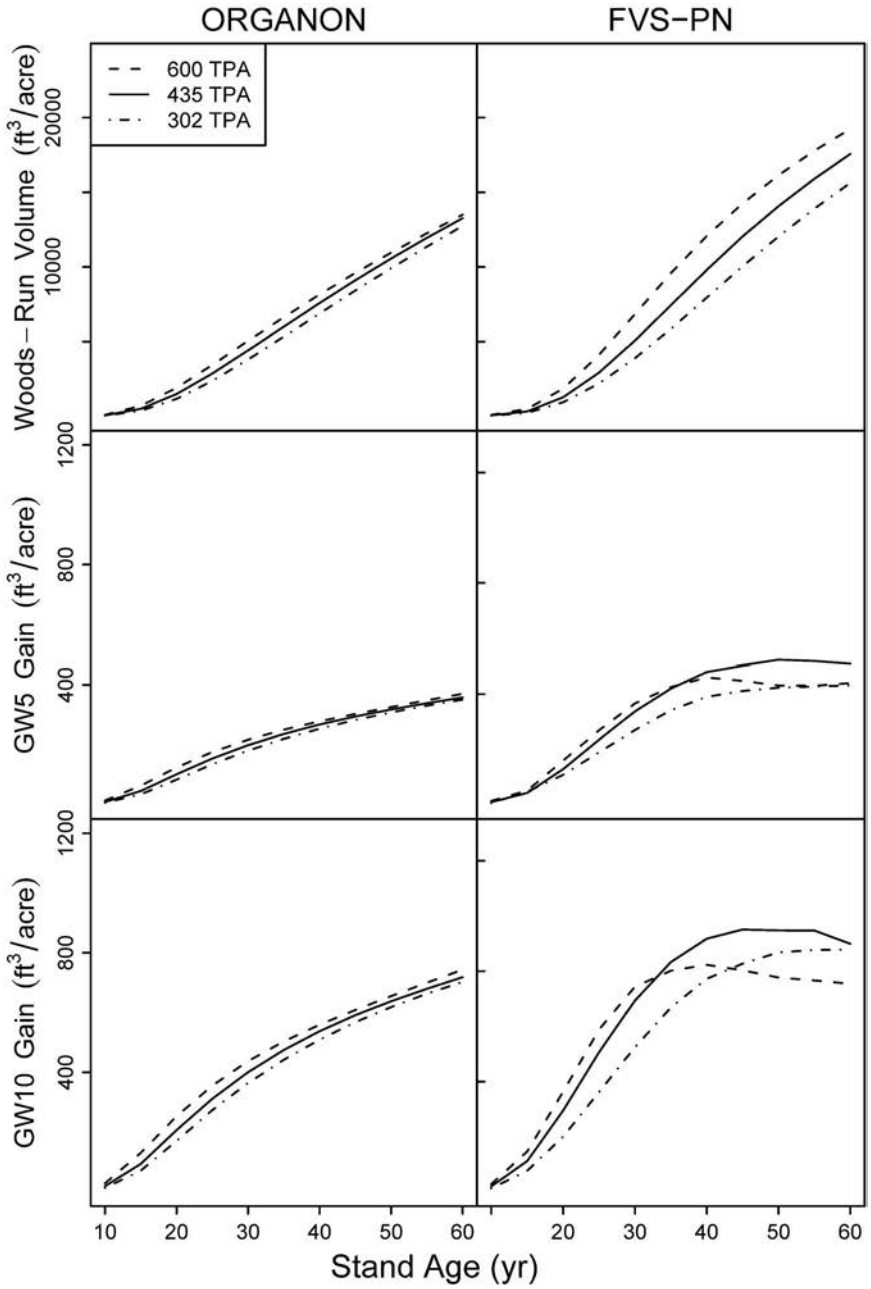

Figure 2. Projected volume of woods-run stands (top row) and volume gains (lower rows) under the two gain scenarios and three initial planting densities. GW, genetic worth; FVS-PN, Pacific Northwest variant of the Forest Vegetation Simulator; TPA, trees per acre; yr, years.

volume gain in the early part of the FVS projections were caused by the transition between the small-tree and large-tree growth equations used by the model and are not realistic. Assuming a 40-year rotation, projected gains ranged from 3.3 to 5.8% under the GW5 scenario and from 6.6 to 10.5% under the GW10 scenario. With a 60-year rotation, percentage gains ranged from 2.1 to 3.2% for the GW5 scenario and 4.3 to 6.4% for the GW10 scenario. Percentage gains were lower for a 60-year rotation because woods-run volumes had increased substantially beyond age 40 years, whereas volume gains increased at a lower rate, stabilized, or decreased. ORGANON projected somewhat greater percentage volume gains with increasing site productivity, whereas FVS-PN projected an opposite trend. For example, the volume projected by ORGANON at 40 years for the GW10 scenario was 8.2% greater than woods-run at SI = 150 ft versus 7.1% greater at SI = 100 ft. For the FVS-PN projections, the volume gains were 6.6 and 10.5% for SI = 150 and 100 ft, respectively.

The genetic-gain multipliers had only a small effect on the projected culmination of MAI (Figure 4). MAI and PAI were projected by ORGANON to be greater for the GW10 scenario than for the woods-run stand throughout the projection period. The difference in PAI between the two scenarios was projected by FVS-PN to disappear after age 35 years. Both models projected PIA to fall below MAI (marking the culmination of MAI) slightly sooner in the GW10 scenario than in the woods-run stand owing to the consistently greater MIA in the GW10 scenario.

SDIMAX had a considerable impact on projected volume and volume gain in FVS-PN under the GW10 scenario (Figure 5). Total volume in the woods-run stand and volume gain were not affected by the limit on maximum stand density up to age 20 years.

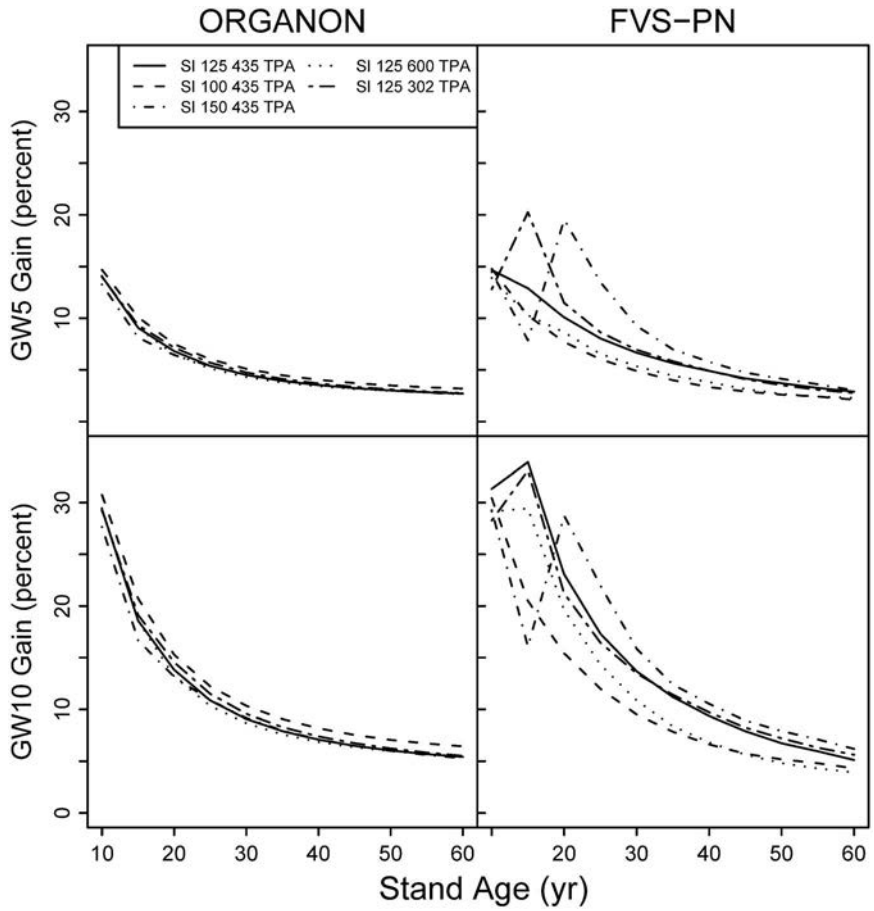

Figure 3. Projected volume gains as percentages of woods-run volume for the two gain scenarios and combinations of site index (SI) and initial planting density. GW, genetic worth; FVS-PN, Pacific Northwest variant of the Forest Vegetation Simulator.

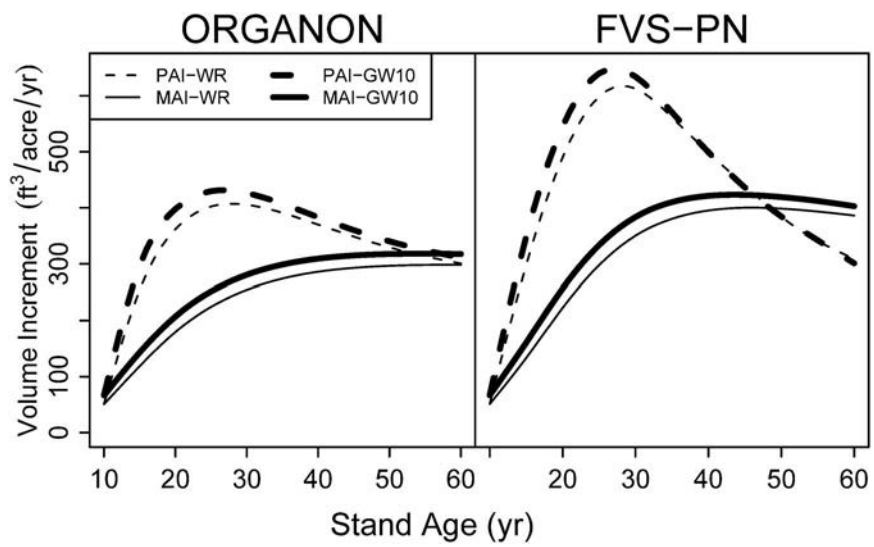

Figure 4. Rates of volume growth projected by ORGANON (left) and the Pacific Northwest variant of the Forest Vegetation Simulator (FVS-PN) (right) for the woods-run (WR) and genetic worth (GW) 10 scenarios. Mean annual increments (MAI) over the life of the stand are shown with periodic annual increments (PAI) for each projection period.

After 20 years, SDIMAX limited both total volume and volume gain. For a 40-year rotation, volume gain ranged from 5.4% for SDIMAX = 750 to 7.4% for SDIMAX = 1,250. For a 60-year rotation, volume gain ranged from 3.7 to 4.9% for the two levels of SDIMAX.

Discussion

The two growth models evaluated in this study were developed from independent data sets to project growth in the Pacific Northwest. Volume projections for woods-run stands differed

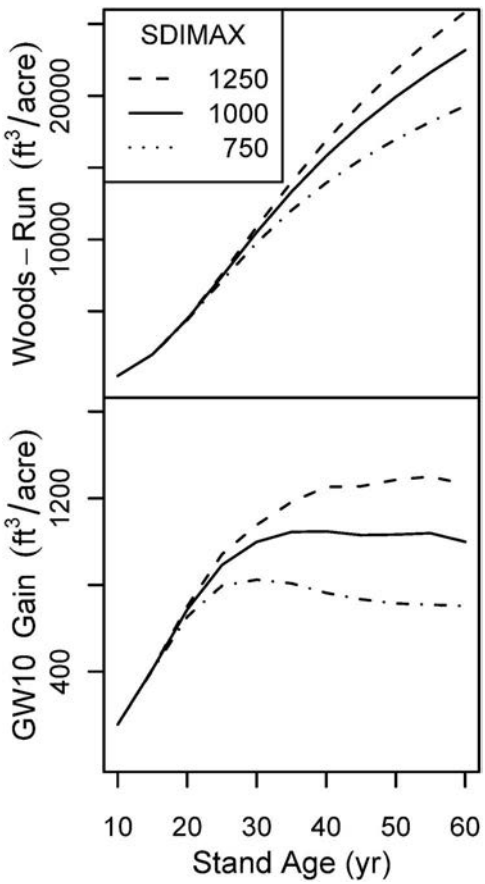

Figure 5. Woods-run volume of stand 3 (SI = 150 ft; initial density, 435 trees/ac) and volume gain under the genetic worth (GW) 10 gain scenario projected by the Pacific Northwest variant of the Forest Vegetation Simulator, with three levels of allowable maximum stand density (SDIMAX).

considerably between the models (Johnson 2002); however, the purpose of this study was to evaluate the effects of tree improvement on volume gain projections. From this perspective, the models provided a fairly narrow range of estimates. The models projected that seedlots with a *GW* of 5% for height and diameter will have about 3 to 6% more volume than woods-run stands growing under the same conditions at 40 years and 2 to 3% more volume at 60 years. With a *GW* of 10% volume gains were projected to approximately double to 7 to 11% at 40 years and 4.3 to 6% more volume at 60 years. Percentage volume gains decreased from 40 to 60 years because absolute volume gains increased at lower rates, reached asymptotes, or declined slightly after 40 years, whereas total volumes increased at a fairly constant rate throughout the projection period.

Our results suggest that the greatest potential for volume gain is on highly productive sites. This is a result of the way that the growth equations are specified in the two models, but the biological basis for it is less certain. The diameter-growth equations in ORGANON and the FVS-PN have positive coefficients for SI, and all three models predict height increments from site index curves and other factors (Donnelly 1997, Donnelly and Johnson 1997, Hann et al. 2006). Therefore, increasing SI caused the predicted height and diameter increments to increase, which also caused proportional increases in height and diameter gains when the genetic-gain multipliers were applied. The effect of multipliers on volume gain is counteracted to some degree in the models by stand-density coefficients in the mortality and diameter-growth equations. In contrast, predicted height growth is realistically insensitive to stand density. Unlike other factors that limit tree growth (e.g., water, nutrients, competition), the physiological basis for genetic gain in Douglas-fir is not well understood. The genetic-gain multipliers used in this study reflect the growth of seedlots across a range of sites and do not account for potential differences in growth with site quality (Gould et al. 2008). The models provide a first approximation of volume gains across a range of productivity classes, but empirical studies are needed to test whether the projections are realistic.

The range of stand densities evaluated in this study did not have as great an impact on volume gain projections as site productivity did. Gain projections in ORGANON were particularly insensitive to initial density. Initial density had a stronger effect on projected gains in the FVS-PN, as did changes to SDIMAX. Stand density can strongly affect both predicted diameter increments and mortality in both growth models. Constraints on maximum density, such as SDIMAX, are used in growth models to avoid projecting unreasonably dense stands. The constraints typically function by increasing mortality as stand density approaches the maximum. Edition 8.2 of ORGANON has a constraint on maximum density, but it is usually not imposed, because the individual-tree mortality equation alone keeps stand density from exceeding a reasonable maximum (Hann et al. 2006). In contrast, the choice of SDIMAX in the FVS-PN (and other FVS variants) can have a strong impact on both total volume in woods-run stands and volume gain in improved stands. When making projections, users need to carefully consider the appropriate SDIMAX for a given set of conditions. From a biological perspective, maximum density may constrain the level of volume gain that can be achieved with improved seedlots. Faster growth may cause stands to reach maximum density more quickly, and gains may be lost if mortality reduces volumes commensurate with gains (Long and Smith 1984). The question of how stand density will affect the growth and survival of improved seedlots is a critical part of estimating volume gain, but it has not yet been adequately addressed in empirical studies. In the present study, maximum density played a role in limiting volume gains but they were not entirely lost. Maximum density is typically measured as a function of tree density and diameter (e.g., stand density index), whereas volume also includes tree height. The height growth of Douglas-fir is rapid over the period projected in this study. Therefore, volume gains could increase or remain constant because of height gains even after maximum density is reached. This growth pattern is biologically tenable, but empirical studies are clearly needed to better understand the growth of improved stands.

Forest managers will likely apply genetic-gain multipliers when projecting established stands and when evaluating the potential for volume gain from improved seedlots prior to actual stand establishment. The latter approach was used in this study. Genetic gain expected prior to age 10 years was incorporated into the initial tree lists, and gain beyond 10 years was projected using genetic-gain multipliers. Representative tree lists for a particular site can be generated using a model such as FGROW or from data collected in young woods-run stands. Since *GW* is the relative gain in height or diameter at a specified age (10 years in this study), the initial tree list can be reasonably adjusted by increasing heights and diameters by the expected level of gain. The Stand Management Cooperative variant of CONIFERS, which is a growth model for young stands that can apply genetic-gain multipliers in projections that begin at the time a stand is planted, was recently released and could also be

used to generate the initial tree list (Ritchie 2008). Both prior gain and genetic-gain multipliers are important when projecting improved stands. In additional model runs (not shown) where the initial tree lists for the GW10 scenario were projected without genetic-gain multipliers, prior gain (at age 10) alone resulted in volume gains of 1–4% at 40 years and of 0.2–2% at 60 years. In some cases, young stands established from improved seedlots can be measured directly so that prior gain will already be reflected in the initial tree lists. Genetic-gain multipliers should still be used to project later growth.

Tree improvement is playing an increasingly important role in intensive silviculture in the Pacific Northwest. As forest managers become more interested in projecting the growth of improved stands, there is a greater need for managers of seed orchards to accurately estimate the *GW* of their seedlots and convey this information to their customers. Block-plot trials are needed to test how well the results of progeny tests translate into block plantings of improved seedlots. Several block-plot trials are under way (St. Clair et al. 2004, Jayawickrama 2006), and these studies may eventually help to address questions related to the consistency of genetic gain over time and maximum stand density. However, forest managers may find it valuable to establish operational experiments to test realized gain under their particular management regimes. Results from such trials could be used to estimate returns on investments in tree improvement and to fine tune whichever growth models that are used by a particular organizations. The focus of this study was on pure even-aged Douglas-fir stands without any intermediate treatments such as commercial thinnings. Projections of mixed-species, mixed levels of genetic improvement, and two-aged stands may provide some insight into how tree improvement may affect the development of these stands. We focused on total volume in this study to characterize the effects of genetic gain independent of markets for wood products. In many applications, projections of merchantable volume or net present value may be better measures of return on investments in tree improvement than total volume.

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