Making the Little Things Count: Modeling the Development of Understory Trees in Complex Stands

Peter J. Gould and Constance A. Harrington

Abstract

Forest growth models are useful for asking "What if?" questions when evaluating silvicultural treatments intended to increase the complexity of future stands. *What if we thinned to level A or B? How would it affect the growth rates of understory trees? How many trees would survive?* To answer these types of questions, a growth model needs to accurately predict the growth and survival of understory trees. Some users of the Forest Vegetation Simulator (FVS) growth model have commented that model predictions for understory trees do not match their field observations or data. To study the relationships which govern growth of understory trees, we assembled a large database from silvicultural experiments and operational inventory data. This database provided an opportunity to look at the major factors that affect the growth and survival of understory Douglas-fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), and Western Redcedar (*Thuja plicata*). Tree attributes like diameter and crown ratio were the best predictors of tree growth, followed by measures of stand density and competition. We found that the potential and average growth of all three species decreased as the density of larger trees increased, but the growth of Douglas-fir was reduced the most by increasing overstory density. Similarly, competition with larger trees reduced the survival of Douglas-fir more than the other species. Western Hemlock generally had greatest growth at moderate to high levels of overstory density. Survival of Western Redcedar was the highest of the three species. Overall, we found the effect of overstory density on understory tree growth was less, but the effects on mortality were greater, than predicted in earlier versions of FVS. Incorporating these new relationships into future versions of FVS should provide forest managers with better tools to evaluate alternative management scenarios.

Keywords: Growth and yield models, Forest Vegetation Simulator, thinning, competition, underplanting, regeneration.

Introduction

In recent decades, a goal of silvicultural treatments on some forest ownerships has been to increase the complexity of future stands. Forest managers often want to take "simple" even-aged stands that are dominated by a single species and create complex stands that are spatially heterogeneous and contain multiple species, canopy layers, and age classes. Silvicultural treatments to create complex stands include variable-density thinning, thinning with "skips and gaps" (Harrington et al. 2005), and planting trees in the understory. Since we have little experience in creating these types of complex stands by design, we often turn to growth models to ask "What if?" questions. What if we alter overstory density and species? How do we know when we have enough understory trees so that

Peter J. Gould is inventory lead, Washington State Department of Natural Resources, Olympia, WA; peter.gould@dnr.wa.gov; **Constance A. Harrington** is a research forester, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Ave SW. Olympia, WA 98512; charrington@fs.fed.us

at least some will survive to become big trees? To answer these questions, we need a growth model that does a good job of predicting the development of understory trees.

The Forest Vegetation Simulator (FVS) is a widely used growth model in the Pacific Northwest (Crookston and Dixon 2005). We have evaluated the performance of FVS with data from research trials and found that it generally under-predicts growth and over-predicts survival of trees in an understory position. We are in the process of developing new models of understory growth and survival that will be incorporated into FVS. These models will better reflect the growth rates and survival of small trees that have been observed throughout the Pacific Northwest. In addition, the understory environment for small trees is more variable, in terms of light and other environmental conditions, in complex stands than in simpler, even-aged stands. Thus, the new models will be more sensitive to variation in overstory density and predict greater variability in growth rates than previous models. We have assembled a large data set describing small-tree growth from many different silvicultural experiments, as well as operational inventory data. Part of developing models to predict growth and survival is evaluating how different factors affect these processes. This provides an opportunity to highlight which factors are generally important in the Pacific Northwest.

Our goal for this paper was to draw together different sources of information to make some general observations about the growth and survival of small trees under different conditions. We used the database that we assembled to revise FVS to address the following questions:

1. Which set of factors best predicts the growth of understory trees?
2. How is the growth of understory trees affected by stand structure?
3. How is the survival of understory trees affected by stand structure?

Methods

The database was assembled from measurements of seven large-scale silvicultural experiments in western Washington and Oregon and from measurements of the US Forest Service's current vegetation survey (CVS) plots (USDA Forest Service 2009) (table 1 and fig. 1). These data cover the ranges of the PN and WC variants of FVS. We defined small trees as those that were <16 cm dbh (diameter at breast height) at the beginning of a growth period. We only used data from trees which were measured at least twice, so that growth increments and survival could be calculated. The period between measurements ranged from 3 to 11 years. We calculated diameter and basal-area growth increments (at breast height) for all trees that were >1.3 m tall at the beginning of the growth period. For small trees where only height-growth increments were measured, we used a height-diameter equation to calculate equivalent diameter and basal-area increments from the height increments. Growth increments were normalized to a 5-year period by assuming constant growth during the period.

Each of the silviculture experiments (full names appear in table 1) includes treatments with different levels of overstory removal and, in some cases, different spatial patterns (e.g., gaps versus uniform thinning). In five of the experiments, seedlings were planted following overstory treatments. The small trees that were selected from the ODS, STUDS, and WOTUS experiments were almost entirely those that were planted after the overstory treatment. Trees were not planted in the OHDS experiment, but the stands were old enough that our selection criterion ensured that only trees that were in an understory position at the beginning of the experiment or established afterward were selected. Stands in the Blue River and Clearwater experiments were fairly young; therefore, only trees that were planted, established naturally, or were too small to measure at the beginning of

Table 1—Silvicultural experiments that provided data for modeling the growth and survival of understory trees. Additional sources of information on these experiments can be found in the cited references.

Experiment	Understory tree development	Overstory age (years)	References
Forest Ecosystem Study Transects (FES)	natural	50-65	Carey et al. 1999
Olympic Habitat Development Study (OHDS)	natural	40-80	Harrington et al. 2005; Comfort et al. 2010
Overstory Density Study (ODS)	planted	40-70	Curtis et al. 2004; Poage and Anderson 2007
Western Oregon Thinning and Underplanting Study (WOTUS)	planted	50-55	Cole and Newton 2009
Clearwater and Blue River	most natural, some planted	15	Poage and Anderson 2007
Siuslaw Thinning and Underplanting for Diversity Study (STUDS)	planted	30-35	Chan et al. 2006; Poage and Anderson 2007

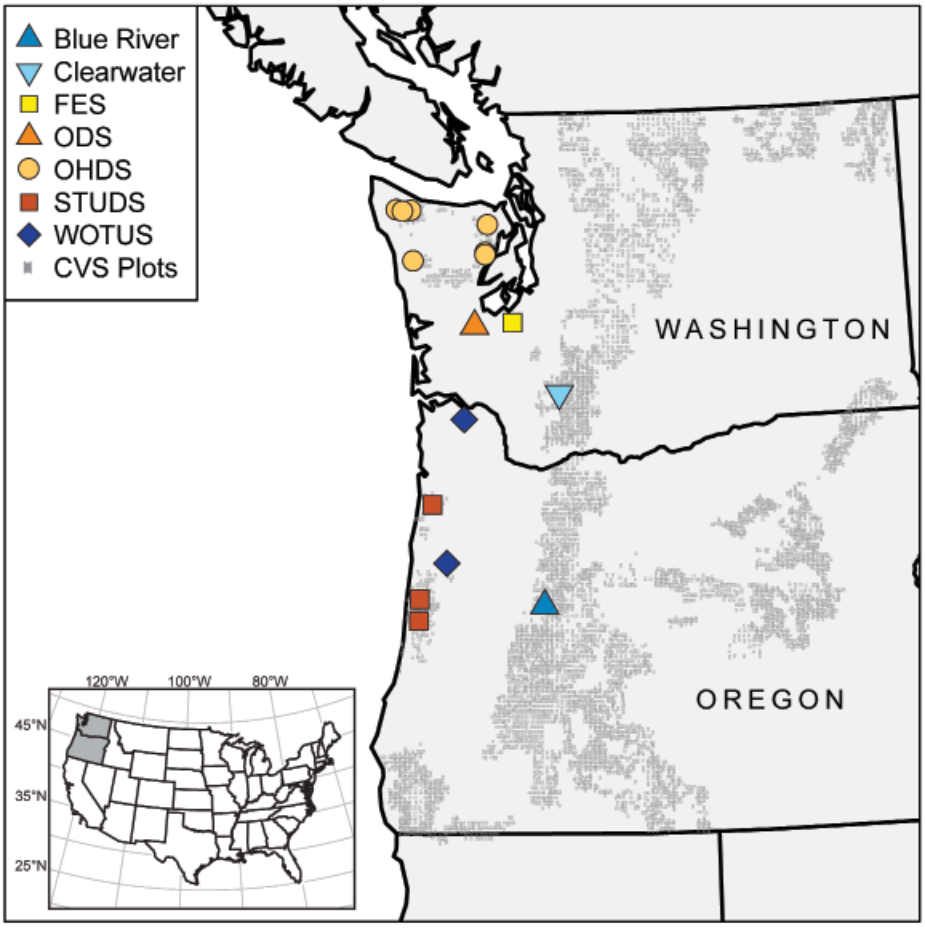

Figure 1—Locations of silvicultural experiments and CVS data in the modeling database.

the experiment (ingrowth) were selected for the database to avoid selecting overstory trees.

Small trees were selected from the CVS plots if they were <16 cm dbh at the beginning of the growth period. CVS plots were excluded from the database if there was evidence of thinning or another disturbance between measurements, leaving a total of 3988 plots. Unlike the large-scale experiments, the treatment histories and stand structures of the CVS plots were not known. We could not be sure which CVS plots were in complex stands. On the other hand, data from the CVS plots are valuable because they are representative of small-tree growth throughout much of the Pacific Northwest. For some analyses, we used only plots that had at least one tree >30 cm dbh to indicate the plot was located in a relatively complex stand. We compared results between the silviculture experiments and CVS plots to ensure our results would hold for both types of conditions.

A set of predictor variables was calculated from the database to explain small-tree growth and survival (table 2). There are three types of predictor variables:

1. Tree attributes such as dbh and crown ratio (*CR*);
2. Variables describing stand structure and the competitive environment, including basal area (*BA*) and crown-competition factor (*CCF*) (Krajicek et al. 1961); and
3. Variables describing site productivity and climate, such as site index (*SI*) and precipitation (*PPT*). Climate variables were derived from Rehfeldt's (2006) climate surfaces (Crookston 2011). Site index was measured on some of the plots and estimated for the remaining plots using nearest-neighbor imputation (Crookston and Finley 2008).

We chose to focus on Douglas-fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), and Western Redcedar (*Thuja plicata*) for this paper. Our database contained 32,534 observations for Douglas-fir, 22,593 observations for Western Hemlock, and 12,143 observations for Western Redcedar. We used the following methods to address each question:

Which set of factors best explains the growth of understory trees?

We looked at how well different combinations of predictor variables could predict 5-year basal-area growth of individual trees. We used a best-subset regression method to pick the best predictors for linear regression models that had between 1 and 10 coefficients (Lumley 2009). We repeated the subset selection process 100 times using data that were randomly selected from 25 percent of the plots each time. This iterative selection process helped to identify robust predictor variables that should work well in all of the different conditions found in the modeling data set. The predictor variables were ranked based on the numbers of times they appeared in a best regression model.

How is the growth of understory trees affected by stand structure?

The predictor variables that describe stand structure and the competitive environment are closely related, so we chose to look at only one of them, basal area of trees larger than the subject tree (*BAL*). This variable is a measure of the competitive position of individual trees, but it is also related to stand structure. For example, small trees that are growing in an understory position in complex stands will have high values of *BAL*, whereas those that are growing in gaps or even-aged stands will typically have low values of *BAL*. We looked at how *BAL* affected both average growth and potential growth by fitting cubic splines (Hastie and Tibshirani 1990). Spline fitting is a flexible modeling technique that is not constrained to produce a straight line or a particular curve shape; therefore, it allows for a detailed evaluation of the relationship between variables. Potential growth was evaluated by fitting a quantile spline (He and Ng 1999) to the 97th percentile of growth observed for each species.

Table 2—Abbreviations and descriptions for variables that were evaluated to predict the growth of understory trees.

Variable type	Variable	Description
Tree attributes	*CR*	Crown ratio (proportion)
	DBH	Diameter at breast height (cm)
	HT	Total tree height (m)
Stand structure / competitive environment	*BA*	Basal area ($m^2 \cdot ha^{-1}$)
	BA_I, BA_M, BA_T	*BA* of shade-intolerant, moderately tolerant, or tolerant species
	BAL	Basal area of trees larger than the subject tree ($m^2 \cdot ha^{-1}$)
	BAL/DBH	*BAL* divided by *DBH*
	BAL_I, BAL_M, BAL_T	*BAL* of shade-intolerant, moderately tolerant, or tolerant species
	CCF	Crown-competition factor: f(crown width, tree density) (%)
	CCF_{100}, CCF_{200}	Height above ground where *CCF* = 100% or 200% (m)
	CCF_D	*CCF* x crown depth
	CCF_R	*CCF* x *CR*
	CV_{DBH}, CV_{HT}	Coefficient of variation of *DBH* or *HT*
	DBHSUM	Sum of tree *DBH* (cm)
	HT100	Average height of 100 largest trees per hectare (m)
	HTSUM	Sum of tree *HT* (m)
	RELHT	*HT/HT100*
Productivity, climate	*DD100*	Date when sum of *DD5* = 100 (measure of spring warmth) (days)
	DD0, DD5	Degree-days <0°C, >5°C (°C·days)
	JUNEDRY	June temperature / June precipitation ($°C \cdot mm^{-1}$)
	PP, PPT_{GS}	Total precipitation, growing-season precipitation (mm)
	PSUMR	Ratio of summer-to-spring precipitation (proportion)
	SDAY, FDAY, FFP	Date of last spring frost, first fall frost, and frost-free period (days)
	SI	Site index (m)
	T_{AVE}, T_{MIN}, T_{MAX}	Average, minimum, and maximum temperature (°C)
	T_{COLD}, T_{WARM}	Average temperature in the coldest and warmest month (°C)

Some of the silvicultural experiments included thinning with gaps, which creates a different stand structure than uniform thinning. Where we had such information, we evaluated how gap creation affects growth by comparing growth of small trees in unthinned areas (skips), uniform (matrix) thinned areas, and gaps.

How is the survival of understory trees affected by stand structure?

Survival was evaluated across the range of BAL by examining survival rates graphically and fitting a logistic-regression equation (Schabenberger and Pierce 2002) for each species to compare average survival among species.

Results and Discussion

Which set of factors best explains the growth of understory trees?

Tree *DBH* at the beginning of the growth period was the most frequently selected variable to predict 5-year basal-area growth for each species (table 3). Crown ratio ranked second for Douglas-fir and Western Hemlock, and third for Western Redcedar. Measures of stand

density or the competitive environment such as *BAL*/*DBH* and CCF_D (*CCF* x crown depth) were the next most frequently selected predictor variables. Some of the predictor variables related to overstory height ranked highly for Douglas-fir and Western Redcedar. The climate variables were generally not as highly ranked as those that describe tree attributes, stand structure, and density; however, at least two climate variables were found to be good predictors of growth in some cases. Climate variables related to temperature (T_{MIN} , minimum temperature, and *DD100*, a measure of spring warmth) were among the top 10 predictors for each species. Growth was predicted to increase with increasing temperature, reflecting the lower productivity of cold, high-elevation sites. Site index ranked among the top 10 predictor variables for Western Hemlock and Western Redcedar but not for Douglas-fir.

Tree attributes are generally good predictors of future growth (Hann et al. 2006). The size and crown ratio of an understory tree is a good indicator of its growth capacity following thinning (Shatford et al. 2009). Maintaining a high crown ratio may be more important to Douglas-fir than to more shade-tolerant conifers. The presence of vigorous understory trees can indicate that things are going right when trying to create a complex stand, but it is not a factor that can be readily changed by forest managers. The competitive environment of understory trees as measured by *BAL* or *CCF* has an important impact on growth and can be changed through silvicultural treatments that reduce overstory densities. We suspected that BA_T (basal area of shade-tolerant species) would be a better predictor of growth than *BA* alone, as shade-tolerant species typically allow less light to reach the understory than intolerant species (Canham et al. 1994); however, it was not a frequently selected predictor. Measures of the competitive environment that account for dominant tree height (e.g., *RELHT*, height divided by the average height in meters) and differences in crown width among species (e.g., CCF_D) were important predictors in some cases, suggesting that understory growth is affected to some degree by stand composition and vertical structure.

Changes to the understory light environment are an obvious result of reducing overstory density, but competition between overstory and understory trees for soil moisture and nutrients is also important (Devine and Harrington 2008; Harrington 2006). Plants growing below the main canopy are in a more complex competitive environment than those in the main canopy, thus, tree responses may be more variable and models to predict response may require greater complexity (Harrington et al. 2002).

Table 3—Ranking of variables for predicting individual-tree basal-area growth of small Douglas-fir, Western Hemlock, and Western Redcedar. Ranks are based on how frequently the predictors were selected using best subset regression on 100 randomly selected subsets of the modeling data. Variables definitions are in table 2.

	Frequency of selected predictors by species					
Rank	Douglas-fir		Western Hemlock		Western Redcedar	
1	*DBH*	100	*DBH*	96	*DBH*	100
2	*CR*	91	*CR*	85	*BAL/DBH*	79
3	CCF_D	71	*BAL/DBH*	77	*CR*	69
4	*HT100*	53	*CV*	59	*HT100*	52
5	*RELHT*	52	*FDAY*	47	CCF_{100}	34
6	CCF_{100}	49	*SI*	44	*DD100*	24
7	*PSUMR*	45	T_{COLD}	24	*SI*	20
8	*DSUM*	38	*DD5*	23	*JUNEDRY*	17
9	T_{MIN}	18	T_{WARM}	20	CCF_{200}	15
10	*BAL/DBH*	13	*HTSUM*	18	*BA*	15

How is the growth of understory trees affected by stand structure?

Potential and average growth rates were negatively affected by increasing competition (as measured by *BAL*) but the species responded differently to competition (fig. 2). When *BAL* was low, potential and average growth rates of Douglas-fir and Western Hemlock were about equal and both species had higher growth rates than Western Redcedar. The average growth of Western Redcedar was much lower than that of the other species at low *BAL*. The potential and average growth rates of Douglas-fir decreased more than those of the other species with increasing *BAL*. When *BAL* was greater than about 20 $m^2 \cdot ha^{-1}$, the species' ranks for potential and average growth were Western Hemlock > Western Redcedar > Douglas-fir. When we looked at data from the silviculture experiments only, we found that the species' ranks were the same, but the potential and average growth rates were generally lower.

We predicted the growth of small Douglas-fir using the current (2011) version of FVS (before our revisions) and compared it with the average growth in our data set (inset in bottom left panel of fig. 2). Observed growth was greater than predicted growth (in the 2011 version of FVS) throughout the range of our data. Predicted growth at moderate to high *BAL* dropped to less than 1.0 $cm^2 \cdot 5\ y^{-1}$ while observed growth remained around 4.5 $cm^2 \cdot 5\ y^{-1}$. Although values for both observed and predicted growth were low, the difference has a big impact on growth projections. For example, it could take more than 3 times longer for an understory tree to move into a midstory position in an FVS projection than it should based on our data. Predicted growth

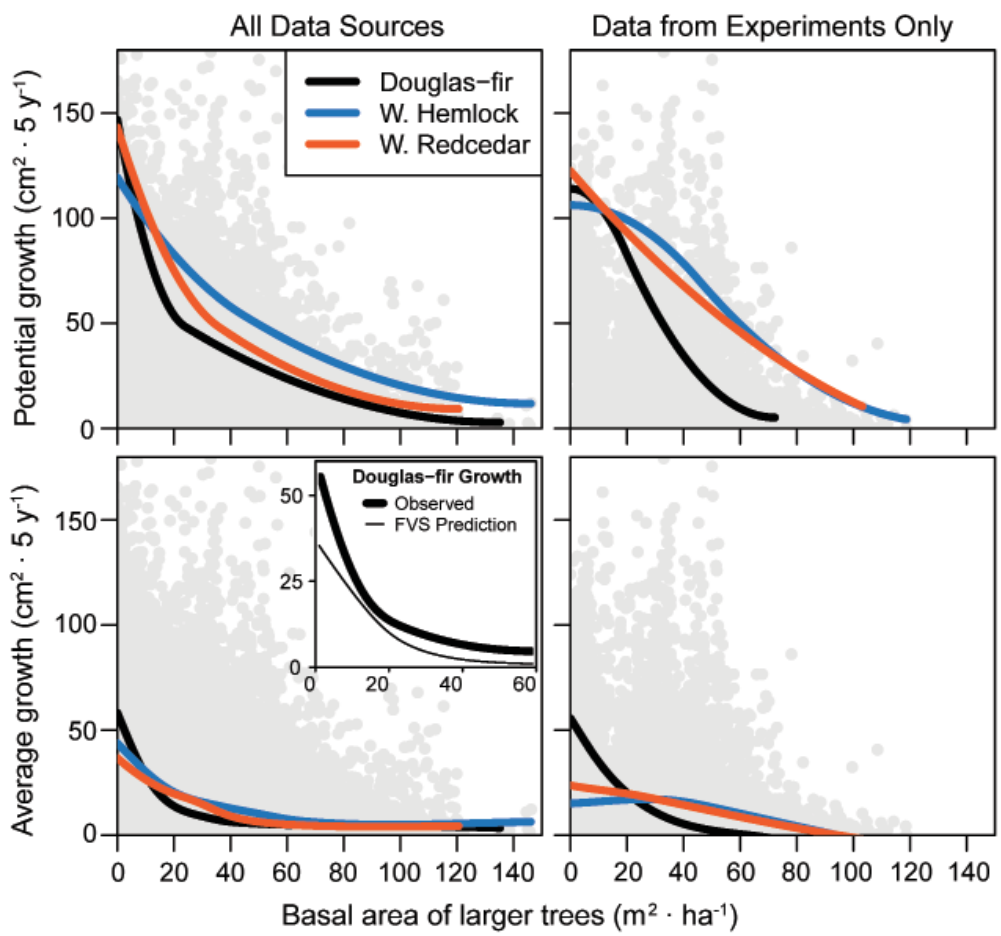

Figure 2—Potential basal-area growth (top row) and average basal-area growth (bottom row) of small trees across a range of basal area in larger trees (*BAL*). The potential growth curves show the 97th percentile of growth. Curves were fit to the entire modeling data set (left column) and to data from silvicultural experiments only (right column). The inset in the bottom left panel shows how the current version of FVS predicts the average growth of small Douglas-fir (observed growth is shown for comparison).

will more closely match observed growth in the revised version of FVS.

Our results agree with previous studies that have ranked Western Hemlock as the fastest growing species across a range of overstory densities (Chan et al. 2006; Cole and Newton 2009; Shatford et al. 2009), including complete overstory removal (Harrington 2006). Western Redcedar also showed greater potential growth compared to Douglas-fir at moderate to high overstory densities; however, its average growth was generally lower. Some of our data sets recorded high browse damage on Western Redcedar that hampered its growth (Cole and Newton 2009; Harrington 2006). The differences between average growth rates and potential growth rates highlight the variability in growth rates that can be found among trees in the same competitive position. The final FVS models will reproduce some of this variability by first predicting the average growth under a set of conditions and then adding a random component so that some trees are predicted to grow near their maximum rates.

Trees in gaps generally grew more rapidly than those in thinned and unthinned areas. Two installations of the OHDS experiment had large numbers of understory Western Hemlock within skips, matrix thinned areas, and 400-m^2 gaps (fig. 3). At the Rail installation, understory trees in gaps grew about 50 percent more than those in thinned areas and about 70 percent more than those in unthinned skips. Understory trees in both thinned areas and gaps at the Snow White installation grew about 40 percent more than those in skips.

Planted understory trees in the WOTUS experiment grew much more rapidly in gaps (600 m^2 or 1000 m^2 in size) than in uniformly thinned areas (fig. 4). Western Hemlock had the greatest growth of the three species in both thinned areas and gaps. The growth of Western Redcedar was damaged by browsing both in gaps and thinned areas.

Treatments to develop complex stands may be successful if they allow some trees to grow rapidly into midstory canopy positions, even if the average growth of understory trees is low. From this perspective, we looked at the range of growth rates within the OHDS experiment (fig. 5). Many of the trees in thinned areas and small gaps continued to grow at similar rates as in unthinned skips; however, the range of growth rates increased substantially. The range of growth rates in gaps was about twice that of unthinned skips.

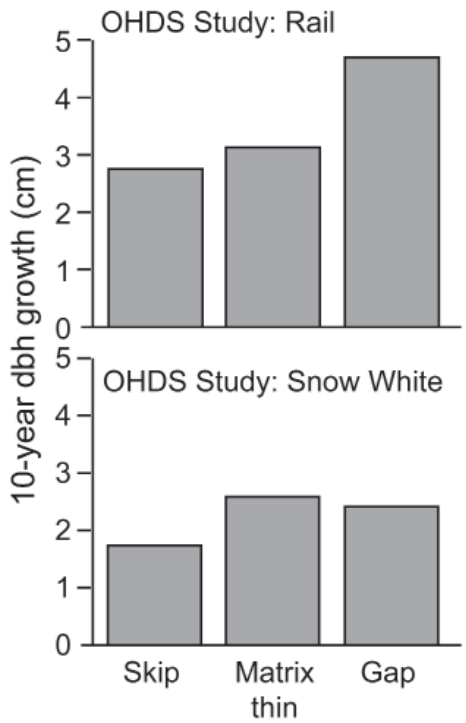

Figure 3—Diameter growth of understory Western Hemlock in skips (unthinned areas), matrix thinned areas, and gaps at the Rail and Snow White installations of the Olympic Habitat Development study.

How is the survival of understory trees affected by stand structure?

The survival of all three species was reduced in stands with high overstory densities, but the survival of Douglas-fir decreased much more than survival of the other species with increasing *BAL* (fig. 6). The mortality rate of Douglas-fir doubles between about 5 and 40 $m^2 \cdot ha^{-1}$ of *BAL*. Western Redcedar had the greatest survival across the range of *BAL*. Survival was generally higher

in the silvicultural experiments (not shown) than in the CVS plots, possibly owing to the effects of other treatments (e.g., vegetation control in some cases) and the initially high vigor of the planted growing stock. We also compared predicted survival in the 2011 version of FVS with observed survival of Douglas-fir (inset in fig. 6). Observed survival was lower across the range of *BAL* and it decreased more sharply with increasing *BAL* than predicted in the 2011 model. FVS will be revised so that predicted survival better matches the survival rates observed in our data set.

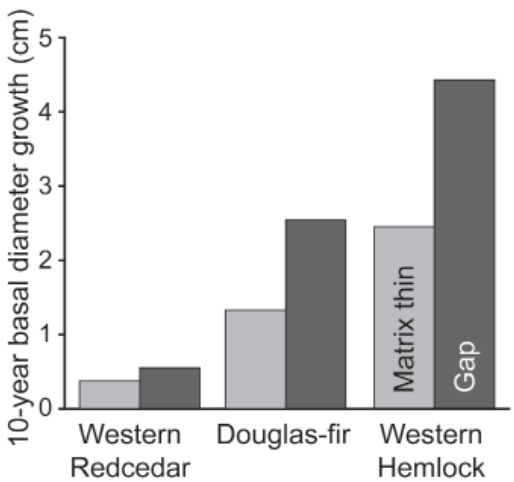

Figure 4—Basal diameter growth of understory Western Redcedar, Douglas-fir, and Western Hemlock in matrix thinned areas and gaps in the Western Oregon Thinning and Underplanting study.

The low survival of understory Douglas-fir in particular may require forest managers to maintain relatively low overstory densities or create large gaps if they want it to survive as an understory tree. In contrast, Western Hemlock and Western Redcedar may become established and survive across a much greater range of densities. For example, we have found that Western Redcedar can survive under dense overstory conditions for decades with very little growth (e.g., Harrington and Devine 2011). We did not account for mortality that can occur after planting in the understory owing to low seedling vigor or unfavorable environmental conditions (e.g., low soil moisture) (Cole and Newton 2009). Survival may be poorer than our

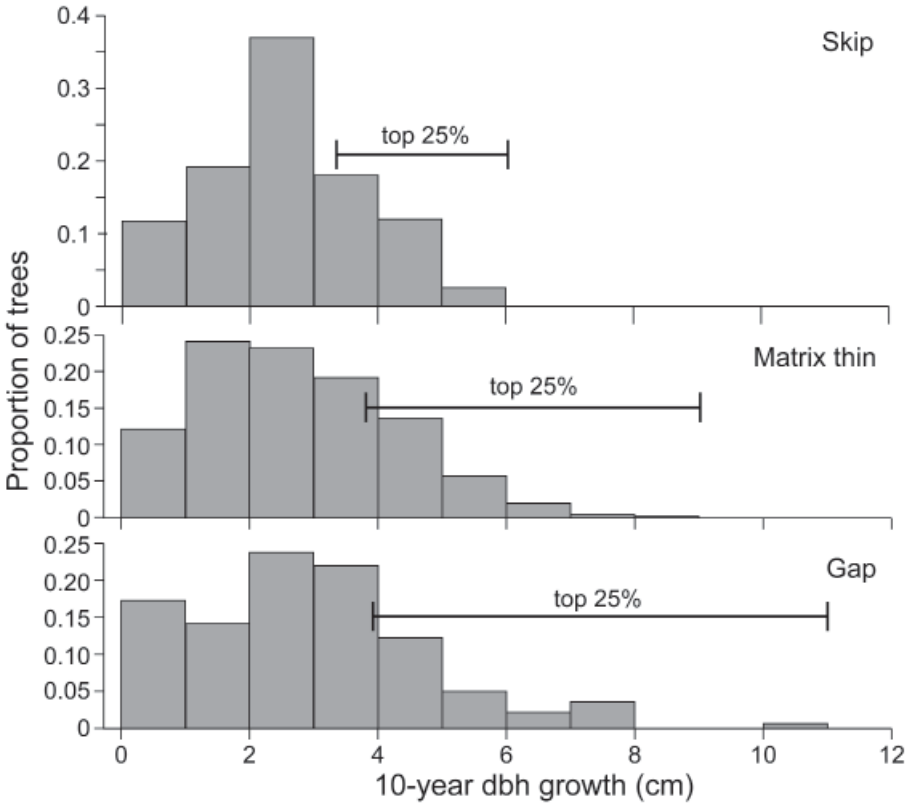

Figure 5—Range of diameter growth rates in skips (unthinned areas), matrix thinned areas, and gaps in the Olympic Habitat Development study. Thinning and gap creation greatly increased the range of growth rates among the fastest-growing 25 percent of trees, which should allow some trees to reach midcanopy positions rapidly.

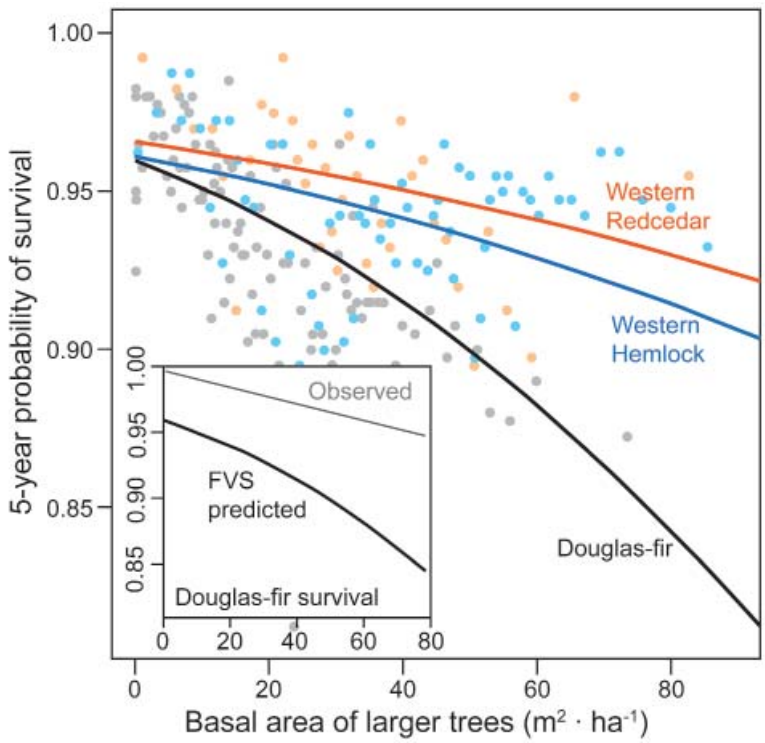

Figure 6—Survival of Douglas-fir, Western Hemlock, and Western Redcedar across a range of basal area in larger trees (*BAL*). Each point represents the survival rate of 400 trees; curves show fits of logistic regression equations. The inset shows how the current version of FVS predicts survival of small Douglas-fir.

data indicates during the first year or two after planting in some cases.

Management Implications

To create complex stands, forest managers need to create conditions that allow understory trees to establish, survive, and grow. Density management is an important tool for improving growing conditions for understory trees. Without thinning or other disturbances, most of the relatively young stands in the Pacific Northwest will maintain densities that will severely reduce the growth of understory trees (e.g., >40 $m^2 \cdot ha^{-1}$ of basal area). Uniform thinning can improve the growth and survival of understory trees, but thinning with gaps will create a wider range in understory tree growth rates, allowing some understory trees to grow more rapidly into the midstory. Treatments that create a range of overstory densities (i.e., thinning with skips and gaps) may be the best approach for creating conditions where some understory trees can thrive while meeting other management objectives.

Future Use of West-side FVS Variants

Our results will be incorporated initially into the PN and WC variants of FVS in 2012. Growth of understory trees will be predicted on a point basis, which will allow users to simulate variable thinning densities and gaps. FVS has a set of keywords (POINTREF, SETPTHIN, THINPT) that can be used to thin points to different densities or to simulate gaps. Because the variants of FVS used in the Pacific Northwest do not have full regeneration models, users will still need to add regeneration to the model runs to reflect understory planting or expected natural regeneration.

FVS can predict the average growth of understory trees under a given set of conditions, but it does not account for all factors that may be important in a particular case. Not every factor that is known to affect growth can be incorporated when developing the kind of data-based, empirical models that are used in FVS. This does not mean that these factors are not important. For example, competition with shrubs

and herbaceous vegetation may strongly affect growth of understory trees, but competition with vegetation other than trees is not modeled by FVS. Forest managers will always need to use their judgment and experience to determine whether conditions are favorable for the growth of understory trees. Stands should also be revisited periodically to determine if treatments have been successful and whether FVS projections were accurate. We invite users to provide feedback to us on how well they think the models perform.

Acknowledgments

We thank Paul Anderson, Elizabeth Cole, Mike Newton, and Leslie Brodie for generously sharing data from their silvicultural experiments, Robert Brown for making the CVS database available, David Thornton for his help in assembling the research database and Erin Smith-Mateja for her help in integrating our results into FVS. We also thank the Oregon State Office of the Bureau of Land Management and the Olympic National Forest for financial support.

Literature Cited

Canham, C.D.; Finzi, A.C.; Pacala, S.W.; Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research. 24: 337–349.

Carey, A.B.; Thysell, D.R.; Brodie, A.W. 1999. The Forest Ecosystem Study: background, rationale, implementation, baseline conditions, and silvicultural assessment. Gen. Tech. Rep. PNW-GTR-457. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Chan, S.S.; Larson, D.J.; Maas-Hebner, K.G.; Emmingham, W.H.; Johnston, S.R.; Mikowski, D.A. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. Canadian Journal of Forest Research. 36: 2696–2711.

Cole, E.; Newton, M. 2009. Tenth-year survival and size of underplanted seedlings in the Oregon Coast Range. Canadian Journal of Forest Research. 39: 580–595.

Comfort, E.J.; Roberts, S.D.; Harrington, C.A. 2010. Midcanopy growth following thinning in young-growth conifer forests on the Olympic Peninsula western Washington. Forest Ecology and Management 259: 1606–1614.

Crookston, N.L. 2011. Current climate data for western North America. Moscow, ID: USDA Forest Service, Rocky Mountain Research Station. http://forest.moscowfsl.wsu.edu/climate/. (September 15, 2011.)

Crookston, N.L.; Finley, A.O. 2008. yaImpute: An R package for kNN Imputation. Journal of Statistical Software. 23: 1–16.

Crookston, N.L.; Dixon, G.E. 2005. The forest vegetation simulator: A review of its structure, content, and applications. Computers and Electronics in Agriculture. 49: 60–80.

Curtis, R.O.; Marshall, D.D.; DeBell, D.S. 2004. Silvicultural options for young-growth Douglas-fir forests: the Capitol Forest study—establishment and first results. Gen. Tech. Rep. PNW-GTR-598. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Devine, W.D.; Harrington, T.B. 2008. Belowground competition influences growth of natural regeneration in thinned Douglas-fir stands. Canadian Journal of Forest Research. 38: 3085–3097.

Hann, D.W.; Marshall, D.D.; Hanus, M.L. 2006. Re-analysis of the SMC-ORGANON equations for diameter-growth rate, height-growth rate, and mortality rate of Douglas-fir. Oregon State University Forest Research Laboratory Research Contribution 49. 24 p.

Harrington, C.A.; Buermeyer, K.R.; Brodie, L.C.; Wender, B. 2002. Factors influencing growth and flowering of understory plants in conifer stands in western Washington. In: Johnson, A.C.; Haynes, R.W.; Monserud, R.A., eds. 2002. Proceedings of the Wood Compatibility Initiative Workshop. Gen. Tech. Rep. PNW-GTR-563. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 159–168. Number 17.

Harrington, C.A.; Devine, W.D. 2011. Stand development following precommercial thinning and fertilization treatments in a western redcedar (*Thuja plicata*) dominated forest. Canadian Journal of Forest Research. 41: 151–164.

Harrington, C.A.; Roberts, S.D.; Brodie, L.C. 2005. Tree and understory responses to variable-density thinning in western Washington. In: Peterson, C.E.; Maguire, D. A., eds. Balancing ecosystem values: innovative experiments for sustainable forestry. Proceedings of a conference. Gen. Tech. Rep. PNW-GTR-635. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 97–106.

Harrington, T.B. 2006. Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. Canadian Journal of Forest Research. 36: 2439–2453.

Hastie, T.; Tibshirani, R. 1990. Generalized additive models, 1st edition, London; New York: Chapman and Hall.

He, X.; Ng, P. 1999. COBS: Qualitatively constrained smoothing via linear programming. Computational Statistics. 14: 315–337.

Krajicek, J.; Brinkman, K.A.; Gingrich, S.F. 1961. Crown competition—a measure of density. Forest Science. 7: 35–42.

Lumley, T. 2009. Leaps: regression subset selection (with Fortran code by Alan Miller). R package version 2.9. http://CRAN.R-project.org/package=leaps

Poage, N.J.; Anderson, P.D. 2007. Large-scale silviculture experiments of western Oregon and Washington. Gen. Tech. Rep. PNW-GTR-713. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Rehfeldt, G.E. 2006. A spline model of climate for the Western United States. Gen. Tech. Rep. RMRS-GTR-165. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 21 p.

Schabenberger, O.; Pierce, F.J. 2002. Contemporary statistical models for the plant and soil sciences. Boca Raton, FL: CRC Press. 738 p.

Shatford, J.P.A.; Bailey, J.D.; Tappeiner, J.C. 2009. Understory tree development with repeated stand density treatments in coastal Douglas-fir forests of Oregon. Western Journal of Applied Forestry. 24: 11–16.

U.S. Department of Agriculture, Forest Service. 2009. Pacific Northwest Region, Current Vegetation Survey. http://www.fs.fed.us/r6/survey/index.htm. (December 2, 2009.)

Citation:
Gould, Peter J.; Harrington, Constance A. 2013. Making the little things count: modeling the development of understory trees in complex stands. In: Anderson, Paul D.; Ronnenberg, Kathryn L., eds. Density management for the 21st century: west side story. Gen. Tech. Rep. PNW-GTR-880. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 59–70.