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Abstract

Many land managers are interested in maintaining or restoring plant communities that contain Oregon white oak (OWO, *Quercus garryana),* yet there is relatively little information available about the species' growth rates and survival to guide management decisions. We used two studies to characterize growth (over multi-year periods and within individual years) and to evaluate the main factors that affect growth and survival. The objective of the first study was to revise the OWO components of the Forest Vegetation Simulator (FVS), a widely-used growth model. We first compiled a large database on growth and survival to develop equations to revise FVS. Diameter growth and survival over multi-year periods were strongly affected by stand density, the competitive position of the tree, tree size, and site productivity. The height growth potential of OWO was predicted from site productivity, stand density and tree size. In the second study, intra-annual patterns of OWO growth were evaluated by precisely measuring stem diameters with band dendrometers. OWO experienced two periods of stem expansion, with the first period likely representing growth (the production of new wood and bark) and the second representing stem rehydration in the fall and winter. As in the first study, growth was strongly affected by the level of competition around each tree. Our results show the sensitivity of Oregon white oak to competition and highlight the need to restore low stand densities in many cases to improve growth and the likelihood of survival.

Introduction

Oregon white oak (OWO; *Quercus garryana* Dougl. ex Hook. also known as Garry oak) is valued in the Pacific Northwest for its contribution to biodiversity and for its cultural significance (Chappell and Crawford 1997, Wilson and Carey 2001). OWO and its associated plant communities were historically maintained in stands with relatively low tree densities (savannas and woodlands) through frequent burning by Native Americans (Thilenius 1968). Many areas where OWO historically occurred have been impacted by urban and agricultural development. Much of what remains is shifting in the absence of fire from savannas or open woodlands to closed conifer forests dominated by Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) (Crawford and Hall 1997, Thysell and Carey 2001, Foster and Shaff 2003). Managers have recognized that OWO communities in many places are threatened and management intervention is necessary to maintain or restore them.

The success of treatments to promote OWO communities can be evaluated in many ways, but tree growth and survival are often of primary interest. Tree growth is a good indicator of a tree's health, and in some respects, its capacity to contribute to the ecosystem. Growth and survival are both related to a tree's ability to capture limited site resources that are needed for photosynthesis and other physiological processes. Slow diameter growth is indicative of long-term stresses, such as those caused by excessive competition, that can make trees vulnerable to other agents that ultimately cause tree death (Pedersen 1998). Some minimum level of diameter growth is needed to maintain enough functional xylem to transport water to the foliage and other tissues. This may be a particular problem for oaks which have ring-porous wood structure as water transport only occurs in the outer one or two rings of the sapwood (Huber and Schmidt 1937, as cited in Rogers and Hinckley 1979). Diameter growth beyond the minimum necessary for survival is considered to be a low priority in the allocation of photosynthate (Oliver and Larson 1996). A high level of growth suggests that the tree has adequate access to site resources to meet its higher priority needs and still allocate photosynthate to diameter growth. Diameter growth has been associated with acorn production in other oak species (Goodrum et al. 1971) and stand conditions that promote high diameter growth (i.e., low tree densities) also have been found to promote acorn production in OWO (Peter and Harrington 2002).

Many forest growth models predict tree growth and survival over time scales of decades to centuries.

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These models are useful tools for testing management alternatives before they are implemented. The Forest Vegetation Simulator (FVS) is a collection of forest growth models that is widely used by forest managers (Crookston and Dixon 2005). Different variants of FVS have been developed for specific regions in North America. All variants are individual-tree models that predict height and diameter growth and the probability of survival of each tree in a stand, typically using a 10-yr time interval. OWO is not a major species in the variants of FVS developed for the Pacific Northwest (i.e., the west Cascade [WC] and Pacific Northwest [PN] variants). Large datasets were used to develop equations for major species, but only a small number of observations (12 trees) had been used to develop equations to predict the growth and survival of OWO (Donnelly and Johnson 1997). Prior to the revisions described in this paper, FVS could not be expected to accurately project the development of stands that contain OWO (Gould et al. 2008). FVS is an important tool that forest managers use to evaluate the effects of proposed treatments (or the decision not to do any treatments). With better algorithms to predict its growth and survival, FVS can be useful for evaluating treatments to promote OWO.

The purpose of this paper is to evaluate factors affecting the growth and survival of OWO. We use results from two studies. The aim of the first study was to revise the PN and WC variants of FVS to improve their usefulness for evaluating treatment alternatives and for projecting the development of stands that contain OWO. We assembled a large database of remeasured inventory and research plots for the model revision. Analysis of these data allowed us to draw some general conclusions about the factors affecting OWO growth and survival over multi-year periods. In the second study, we examined intra-annual patterns of OWO diameter growth to evaluate the timing of growth and how growth is affected by competition. Examining seasonal patterns of diameter growth can provide insight into how competition and seasonal changes in the availability of resources affect tree growth (Hinckley et al. 1976).

Methods

Oregon White Oak in FVS

The Forest Vegetation Simulator (FVS) predicts growth and survival of individual trees for a 10-yr period based on the condition of the tree and that of the surrounding stand at the beginning of the growth period. A modeling database was assembled to relate tree and stand characteristics to growth and survival. The database was assembled from measurements on inventory and research plots in Washington, Oregon, and California (Figure 1). The sources of plot data were: 1) the USDA Forest Service Forest Inventory and Analysis plot network (on private lands in Washington, Oregon, and California), 2) USDA Forest Service Current Vegetation Survey plots (on National Forest lands in Washington and Oregon), 3) Oregon State University McDonald-Dunn Forest Inventory plots (near Corvallis, Oregon) and 4) research plots established by the USDA Forest Service, Pacific Northwest Research Station (various ownerships near Olympia, WA). All trees had been remeasured, with the exception of 40 open-grown trees where diameter growth for the most recent 10 years was estimated from increment cores.

Tree and plot data from the first measurements were summarized to produce a set of variables to predict growth and survival (Table 1). The predictor variables measure tree attributes (*DBH, HT, CR*), stand density (*BA*), the tree's competitive position (*BAL, RHT*), and site productivity (*SI*, *SL, ASP, EL*). *SI* was based on King's (1966) curves for lowland Douglas-fir (base age = 50 years). *SI* for Douglas-fir is not an ideal predictor of site productivity for OWO as the two species may use site resources differently and different factors may limit their growth. However, *SI* for Douglas-fir is a convenient measure of site productivity as it was measured or imputed for all of the plots and it is already used within FVS as a predictor variable. Diameter growth was calculated for each OWO in terms of the difference in diameter squared (*DDS*), which is the difference in squared, inside-bark diameter between two measurements. Survival (*SURV*) was coded as 1 if the tree remained alive between measurements and 0 if it died.

All equations used in the FVS revision are given in the Appendix. The standard FVS equation form for diameter growth of large trees (> 8 cm *DBH*) was used (Equation 1 in Appendix). Nested diameter-growth equations were tested so that simpler equations (fewer predictors) were subsets of more complex ones (more predictors). Because the diameter-growth equation has an exponential form, each variable's relative contribution to growth is not affected by the values of the other predictor variables. This allows each variable's contribution to predicted growth to be evaluated by examining relative growth (i.e., the proportional change in predicted growth) across the variable's range. The mean-squared error (*MSE*), adjusted R^2 (R^2_{adj}), and Akaike's information criterion (*AIC*) were calculated for each equation fit (Akaike 1974). A total of 2144

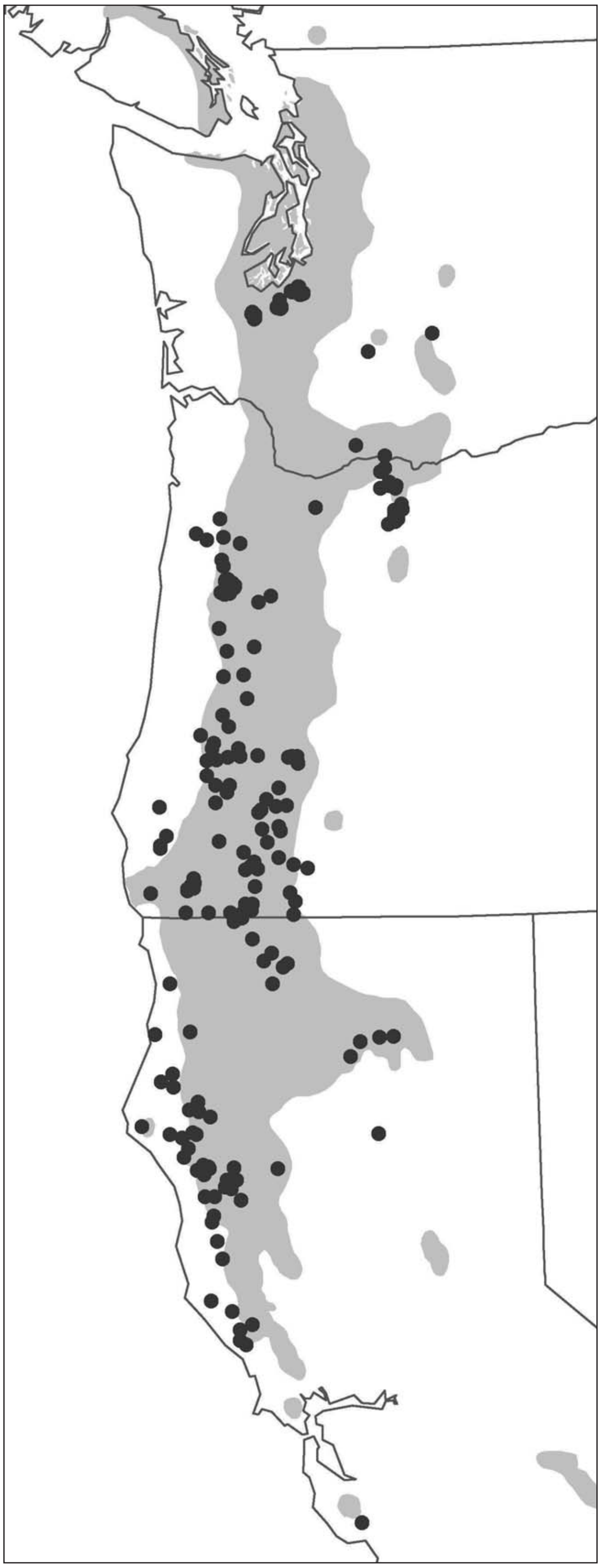

Figure 1. Locations of inventory and research plots used to develop the modeling database for Oregon white oak. The shaded area shows the species' range.

growth observations were used. A "holdout" dataset was removed from the model-fitting dataset so that it could be used to test the equations. To create the holdout dataset, 20% of measurement plots were randomly selected and all observations from these plots were removed. The holdout data were not used to fit the final model. Equations were fit using nonlinear least-squares regression in R (R Development Core Team 2006).

Height growth is usually predicted in FVS by first using a height-age curve to predict potential height growth (the fastest possible growth) and then reducing it based on the competitive position of each tree. A height-age curve has not been developed for OWO, and FVS previously used a placeholder curve for a miscellaneous species group that included OWO. The modeling database did not have enough information to create a new curve; therefore, a different method was developed using a three-part algorithm. The first part (Equation 2) predicts an overall maximum height (*MAXHT*) that cannot be exceeded by any OWO in the stand. *MAXHT* is predicted from *SI* for Douglas-fir. The second part (Equation 3) then predicts potential heights (*PHT)* of individual OWO trees based on *DBH* and stand *BA*. *MAXHT* from Equation 2 is the asymptotic height in Equation 3; consequently, *PHT* is always less than *MAXHT.* The third part predicts potential height growth (*PHTG*) which is the difference between *PHT* at the beginning and end of the growth period. *PHTG* is influenced by *DDS* since the difference in *PHT* at the beginning and end of the growth period is based in part on the difference in *DBH. PHT* and *PHTG* represent the upper limits on height and height growth rate, not the means. Therefore, the coefficients for Equation 2 and Equation 3 were fit using nonlinear quantile regression (Koenker and Hallock 2001) using the R package quantreg (Koenker 2009). Equation 2 was fit to the 95th percentile of *HT* and Equation 3 was fit to the 90th percentile as a solution could not be achieved for the 95th percentile. The model-fitting dataset for the height equations contained 1380 observations.

Mortality in the PN and WC variants of FVS is primarily determined by stand density (Dixon 2002). An alternative mortality algorithm for OWO was developed to better reflect its sensitivity to competition even when overall stand density is not near its maximum. Equations based on the logistic form (Sit and Poulin-Costello 1994) were fit using different combinations of variables to predict the probability of tree survival for a 1-yr period (Equation 4). The survival equation is then adjusted within FVS to predict the probability of mortality over a 10-yr period (Equation 5). The

TABLE 1. Variables measured or calculated in the Oregon white oak modeling dataset.

Variable	Description	Mean	Min	Max
ASP	Aspect (degrees)	--	--	--
BA	Plot basal area (m^2 ha^{-1})	32.9	<0.1	104.4
BAL	*BA* in larger trees based on *DBH* (m^2 ha^{-1})	20.8	0.0	78.1
CR	Crown ratio (proportion)	0.4	<0.1	1.0
DBH	Diameter at breast height (cm)	24.6	0.3	107.7
DDS	Difference in diameter squared, difference in the squared *DBH* between successive periods, normalized for a ten-year period (cm^2).	69.0	<0.1	868.4
EL	Elevation of the sample plot (m)	398.0	51.0	1511.0
HT	Height, total height of the tree (m)	16.7	0.2	40.2
HT40	mean height of the 40 trees $acre^{-1}$ in the stand with the largest diameters (or mean height of all trees when density ≤ 40 trees $acre^{-1}$) (m)	23.0	0.6	49.4
P	Period between measurements (years)	9.5	2.0	28.0
RHT	Relative height, tree height divided by *HT40*.	0.6	<0.1	1.5
SI	Site index, King's (1966) curve for Douglas-fir (m)	31.0	15.5	42.4
SL	Slope of the sample plot (%)	22.8	0.0	120.0
SURV	Survival between measurements (1 = survived, 0 = died)	0.9	0.0	1.0

logistic regression equations were fit using the maximum likelihood method as outlined by Flewelling and Monserud (2002). The model-fitting dataset contained 2327 observations. Candidate equations were evaluated by comparing observed and predicted mortality across the range of each predictor variable. The probability of mortality was also evaluated in terms of the number of years required for a population to be reduced to one-half its original size (half-life).

The revised version of the PN variant of FVS was demonstrated by projecting two stands. The first stand is part of a restoration project planned for the Oak Flats area on the Umpqua National Forest in the foothills of the central Oregon Cascades (Richard Abbott, personal communication). The stand is composed of OWO that is partially or completely overtopped by conifers, particularly Douglas-fir. The stand was projected without treatment, with partial conifer removal (similar to the actual prescription) and complete conifer removal. The second stand is a young, dense stand composed almost entirely of OWO on Joint Base Lewis-McChord (JBLM) in southwest Washington. Although competition with other species is not a concern in the JBLM stand, the high stand density is limiting the growth and vigor of individual trees. The JBLM stand was projected without treatment, with a single thinning, and with multiple thinnings (every 20 yrs) to maintain low basal area. All scenarios were projected for a 50-yr period.

Intra-Annual Growth (Dendrometer Study)

Growth was measured over a period of 33 months on 41 OWO trees at the Black River – Mima Prairie Glacial Heritage Preserve near Olympia, WA (46.9 °N, 123.0 °W, 60 m AMSL). Trees were selected so that there were about 10 individuals in each of four competition classes: 1) open-grown (either a lone stem or a stem within an open-grown clump) 2) moderate competition from conifers, 3) moderate competition from OWO or other hardwoods, and 4) overtopped by conifers. The average initial tree DBH was 30 cm (range = 22 to 47 cm). A band-style dendrometer (Environmental Measuring Systems Brno, Czech Republic) was installed on each tree on April 10, 2008 and remained fixed to the tree during the measurement period. Diameters were measured using the vernier scales on the dendrometers with a precision of < 0.05 mm. A soil moisture sensor (EC20, Decagon Devices, Pullman, WA) was installed diagonally at a depth of 10-30 cm near each subject tree to measure soil water content (volume · $volume^{-1}$). Readings from the dendrometers and soil moisture sensors were manually recorded every 14 to 30 days through the end of February 2011. The measurement frequency was greater during the growing season than during the dormant season.

More detailed measurements of the tree's competitive environment were taken in July 2010. These measurements included crown width, the percentage of the crown perimeter that was in contact with surrounding conifers (mostly Douglas-fir) or surrounding hardwoods, and the percentage of the crown that was overtopped by taller crowns. The relative height of the subject tree compared to surrounding competitors was also estimated. A competition index, free crown perimeter (*FCP*), was calculated as the length of crown perimeter that was free of contact.

Repeated-measures analysis of variance (Neter et al. 1996) was conducted to test whether growth differed significantly among competition classes. Relationships between growth and the more detailed measurements of competition were examined by calculating correlations between each measure of competition and tree growth. Relative height could not be calculated for trees without nearby competitors (n = 4 trees), so the analysis was conducted only for trees with some level of competition (n = 37 trees). Based on the results of the correlations, a repeated-measurement linear model (Neter et al. 1996) was fit to relate growth to *FCP*.

Results

Oregon White Oak in FVS

Variables describing tree size, crown ratio, competitive status, stand density, and site productivity were statistically significant predictors of diameter growth (Table 2). The fit statistics for the diameter-growth equations indicated that complex equations with many predictor variables were better than those with fewer variables. Fit 6, which included eight statistically-significant predictors, explained 43.2% of the variation in *DDS*. Closer analyses of the more complex equations revealed some shortcomings. In some complex equations, the relationship with *BA* was counter-intuitive in that greater growth was predicted as *BA* increased. When an equation contains variables that are correlated with one another (*CR, BA,* and *BAL* in this case), several problems can emerge including coefficient estimates that switch between positive and negative signs (Schabenberger and Pierce 2002). Equations with large numbers of predictor variables can also be overfit and are not as robust as simpler equations when they are applied to new data. When the equations were validated by predicting growth for the holdout data, equations with five or more predictor variables (Fits 4, 5, and 6) predicted growth less precisely (as measured by *MSE* and R^2_{adj}) than a simpler equation with four predictor variables (Fit 7).

The final selected model (Fit 7) predicts diameter growth from *DBH, BA, BAL,* and *SI* (Figure 2). All of the predictor variables have intuitive relationships with predicted growth. Predicted growth decreases monotonically with increasing *BA* and *BAL* and increases with increasing *SI*. *SI* has a smaller effect on predicted growth than *BA* or *BAL*. Predicted growth changes by only about 10% across the range of *SI* in the modeling database, compared with a change of about 30% across the range of either *BA* or *BAL*. Predicted growth increases as *DBH* increases up to about 40 cm and then decreases with larger values of *DBH*. The maximum growth rate is predicted when *DBH* is about 40 cm, stand *BA* is low (e.g., open-grown trees) and *SI* is high. Predicted diameter growth of an open-grown tree of 40 cm *DBH* on a site where Douglas-fir *SI* = 35 m is 2.8 cm over a 10-yr period.

Under the revised height growth algorithm, *MAXHT* increases with Douglas-fir *SI* but levels off to reflect the smaller maximum height of OWO (Figure 3). The value of the asymptote (α_0 in Equation 2) was 34.8 m, which acts as the upper limited on predicted height. *PHT* for individual trees increases with *DBH* and *BA*. Therefore, OWO in dense stands are predicted to have greater *HT:DBH* ratios than those that are in open

TABLE 2. Summary of fits for the diameter-growth equation.

Fit	Predictors	Model Fit MSE	Model Fit R^{2adj}	Model Fit AIC	Holdout MSE	Holdout R^{2adj}
	Mean only	322.2	0	NA	322.2	0
1	*DBH*	235.4	26.9	18812	267.6	16.9
2	*DBH ,CR*	196.9	38.8	17506	272.5	15.4
3	*DBH, CR, BA, BAL*	187.8	41.5	17414	259.7	19.4
4	*DBH, CR, BA, BAL, SI*	185.4	42.2	17251	256.6	20.4
5	*DBH, CR, BA, BAL, SI, EL*	182.5	43.0	17223	252.7	21.6
6	*DBH, CR, BA, BAL, SI, EL, SL, AS*	181.4	43.2	17211	257.7	20.0
7	*DBH, BAL, BA, SI* (final fit)	219.4	31.7	18487	251.4	22.0

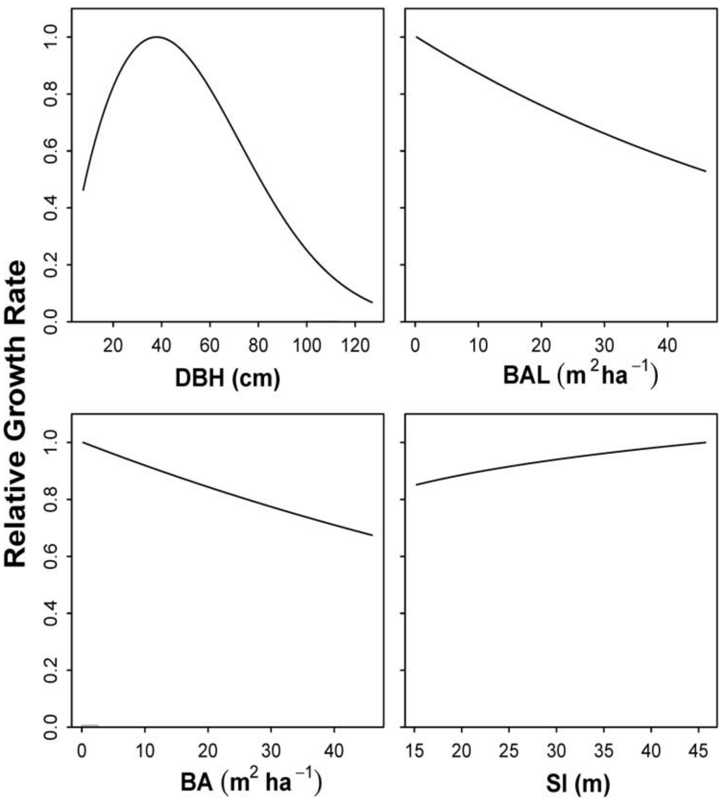

Figure 2. The effects of tree diameter (DBH), basal area (BA), basal area in larger trees (BAL), and Douglas-fir site index (SI) on predicted diameter growth of Oregon white oak. The relative growth rate shows the proportional change in growth when all other variables are held constant.

woodlands or are open-grown. Predicted *PHT* increases nearly linearly with *DBH* when *DBH* < 30 cm, and then increases at a lower rate when *DBH* is between 30 and 60 cm. Little additional height growth is predicted for OWO with *DBH* > 60 cm.

Although *DBH* and *SI* were important predictors of diameter growth, they were not found to be significant predictors of survival. *BA, BAL,* and *RHT* were significant predictors of survival, but not when all three variables were included in the model fit. Comparisons of predicted and observed survival indicated that *BA* and *RHT* performed best across the range of conditions in the modeling database. Predicted mortality over the 10-yr period (based on the survival equation) varies considerably within the range of *BA* and *RHT* where OWO is often found (Figure 4). Mortality is predicted to be low when OWO is competing with trees that are the same height or shorter; the 10-yr probability of mortality ranged from < 1% to about 6% when *RHT* ≥ 1.0. Mortality is predicted to be much greater in less favorable competitive positions. When *BA* = 45 m^2 ha^{-1} and *RH* = 0.5, the 10-yr probability of mortality is about 12% and the predicted half-life is 50 yrs (that is, one-half of the stems would die in the next 50 yrs).

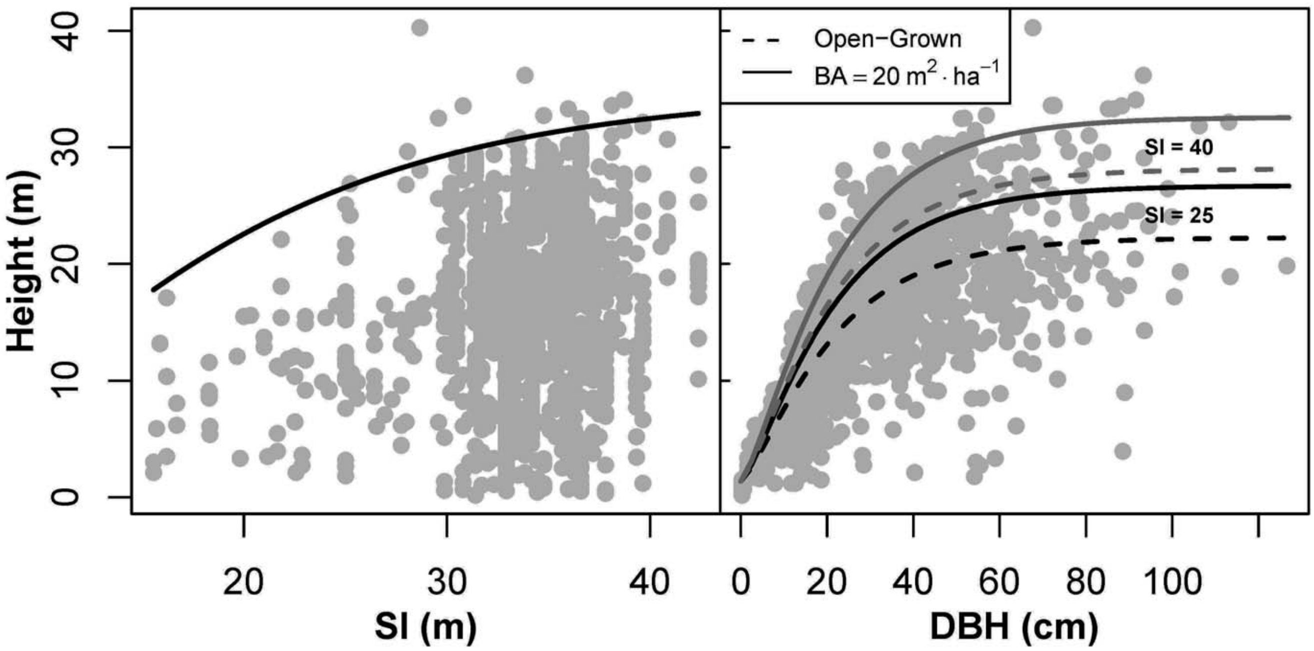

Figure 3. Prediction of maximum potential height for any Oregon white oak in a stand based on Douglas-fir site index (SI) (left), and prediction of potential height for individual trees based on their DBH and stand basal area (BA) (right). Lines show quantile regression fits for 95th quantile (left) and 90th quantile for two levels of stand density and site index (black lines show SI = 25 m, grey lines show SI = 40 m) (right).

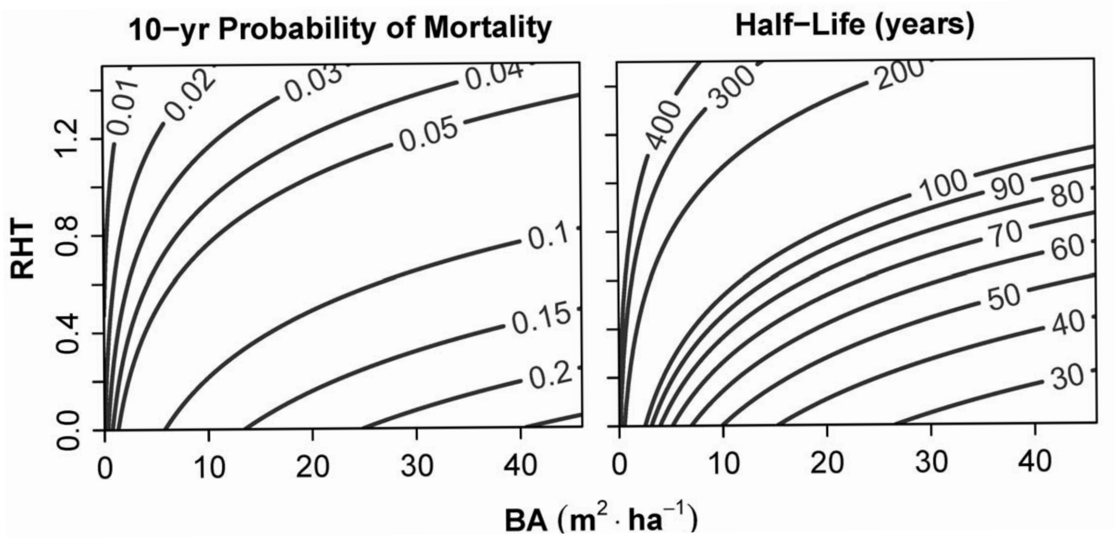

Figure 4. Predicted 10-yr mortality rates of Oregon white oak under a range of stand basal area (BA) and relative height (RHT). The lines in the contour plots connect points of equal values. The half-life is the number of years required for a population to be reduced to one-half its original size.

Based on the stand projections, treatments can be expected to have a large impact on the survival and growth of OWO (Figure 5). The Oak Flats stand had an initial basal area of 50 m^2·ha^{-1} of which 77% was Douglas-fir and 14% was OWO. Without any treatment, only 50% of OWO were expected to survive over the 50-yr projection period. Growth was slow as the quadratic mean diameter (*QMD;* the diameter of a tree of average basal area) increased by about 5 cm. Partial conifer removal reduced the initial stand basal area to about 19 m^2·ha^{-1} and full conifer removal reduced basal area to about 7 m^2·ha^{-1}. Partial conifer removal was projected to increase survival to about 70% and full conifer removal increased it to about 88% over the 50-yr period. *QMD* increased by about 7 cm with partial conifer removal and 9 cm with full removal. In the JBLM stand, the first thinning removed about 75% of stems and reduced initial basal area from 28 m^2 ha^{-1} to 12 m^2 ha^{-1}. The removal of small stems increased *QMD* initially and *QMD* continued to diverge among treatments as a result of different

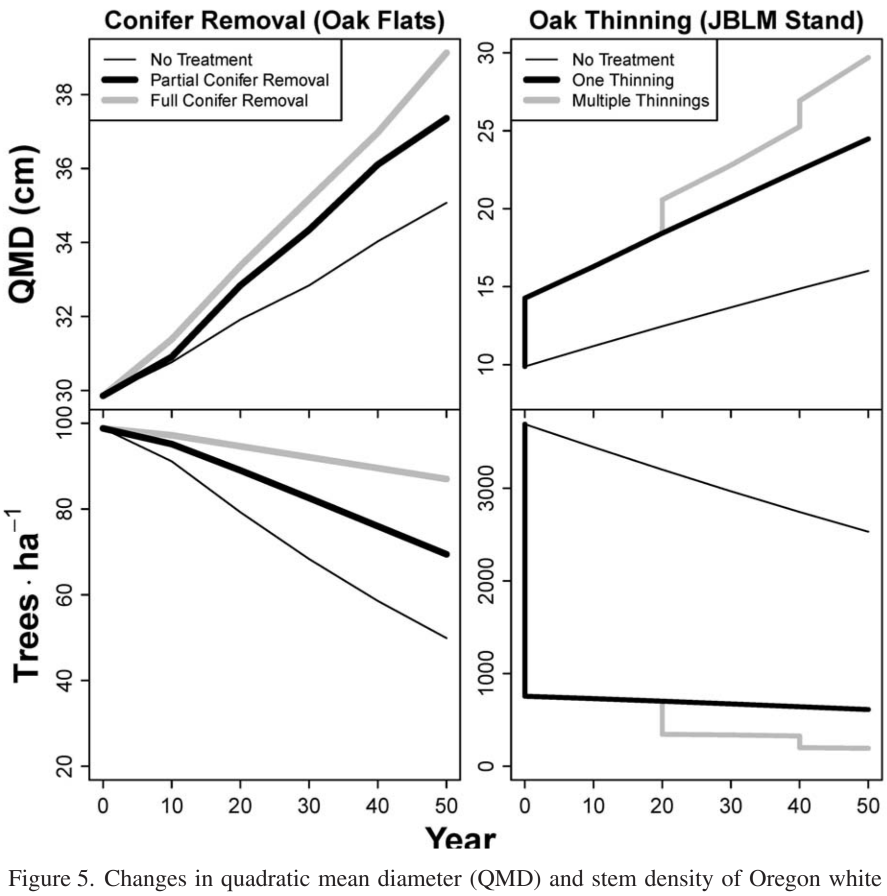

Figure 5. Changes in quadratic mean diameter (QMD) and stem density of Oregon white oak projected with the revised version of the PN variant of FVS for different management scenarios in two stands. The Oak Flats stand contains Oregon white oak trees that are overtopped by conifers; the JBLM stand started with a high density of small oaks.

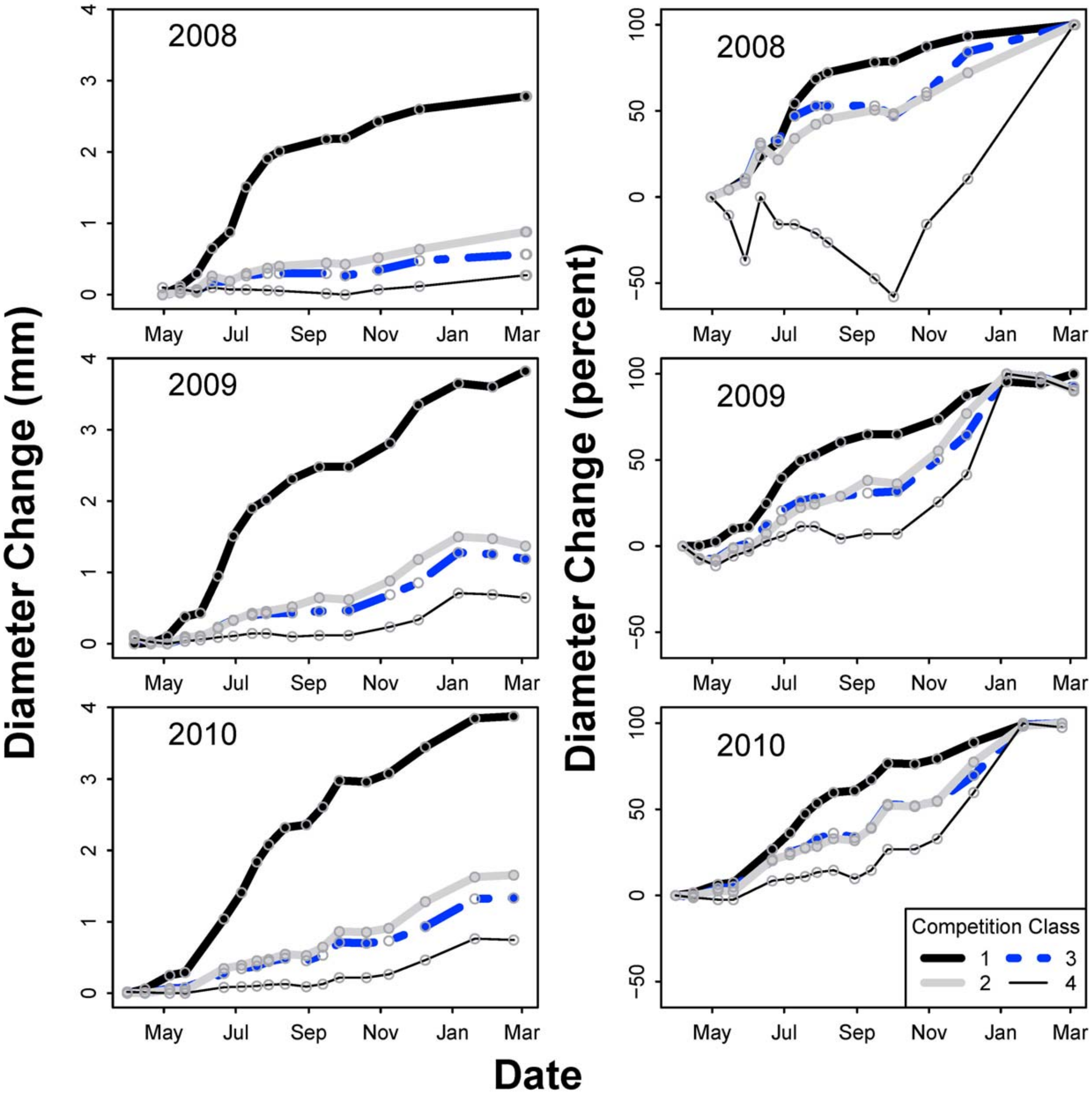

Figure 6. Diameter change measured with band dendrometers of Oregon white oak in four competition classes (1 = open-grown, 2 = moderate conifer competition, 3 = moderate hardwood competition, and 4 = overtopped by conifers). Diameter change (%) in the panels on the right is the cumulative % of total annual change in stem diameter from the beginning of the season.

growth rates. Thinning in years 20 and 40 to 12 $m^2 \cdot ha^{-1}$ boosted *QMD* and caused more rapid diameter growth. Compared with the no-thinning scenario, *QMD* at the end of the 50-yr projection was about 70% higher when the stand was thinned once and 100% higher when the stand was thinned twice.

Intra-Annual Growth (Dendrometer Study)

OWO with little competition (competition class 1) grew about four times more than those with moderate or high competition (Figure 6). Although growth was much less with competition than without competition, OWO with moderate competition (classes 2 and 3) grew about twice as much as those that were completely overtopped (class 4). The average growth rate was significantly greater in competition class 1 than in the other classes, and class 2 differed significantly from class 4 ($P < 0.05$ for the set of comparisons on the main effect of competition class).

In addition to differences in total growth, there were also differences from year to year and among competition classes in when stem expansion or contraction occurred. Stem expansion occurred in each year in two periods. The first period of stem expansion was from May 1 to

August 1. Stem expansion ceased until about October 1 in 2008 and 2009 and September 1 in 2010. The beginning of the second period of stem expansion appeared to be related to the recharge of soil water content, which began after October 1 in 2008, but around September 1 in 2009 and 2010. Stem expansion continued until about January 1 of each year. The first period of stem expansion was a much greater percentage of the total in open-grown OWO compared with those in the other three competition classes. About 70 to 80% of total stem expansion occurred during the first period in open-grown OWO, compared with 40 to 50% in competition classes 2 and 3 and about 20% in competition class 4. Stems in competition class 4 actually contracted between about July 1 and October 1, 2008.

Relationships between stem expansion and measures of competition were evaluated only for OWO that had some competition as measured by crown contact (4 trees had no crown contact so n = 37 trees) (Table 3). The measures of competition were more strongly correlated with stem expansion during the first period (May 1 to August 1) than during the second period (August 1 to March 1). Free crown perimeter calculated from conifer crown contact had the strongest correlation among the competition measurements. Crown contact of conifers, hardwoods, or both was less strongly correlated with stem expansion than *FCP*. Relative height and the percentage of the crown that was overtopped had fairly strong correlations with stem expansion, but not as strong as FCP based on conifer contact. Soil water content near May 1 was also evaluated as a predictor of stem expansion, but the correlations were relatively poor.

TABLE 3. Correlations between measures of competition and first-period stem expansion (May 1 to August 1) and second-period stem expansion (August 2 to March 1) measured by dendrometers.

Competition Measure	*r* 1st Period	2nd Period
Crown contact conifers (%)	-0.39	-0.30
Crown contact hardwoods (%)	0.14	0.21
Crown contact conifers + hardwoods (%)	-0.32	0.15
Free crown perimeter conifers (m)	0.65	0.39
Free crown perimeter hardwoods (m)	0.22	0.00
Free crown perimeter conifers + hardwoods (m)	0.49	0.24
Relative height (%)	0.50	0.42
Crown overtopped (%)	0.55	0.44
Soil water content on May 1 (m^3/m^3)	0.27	0.25

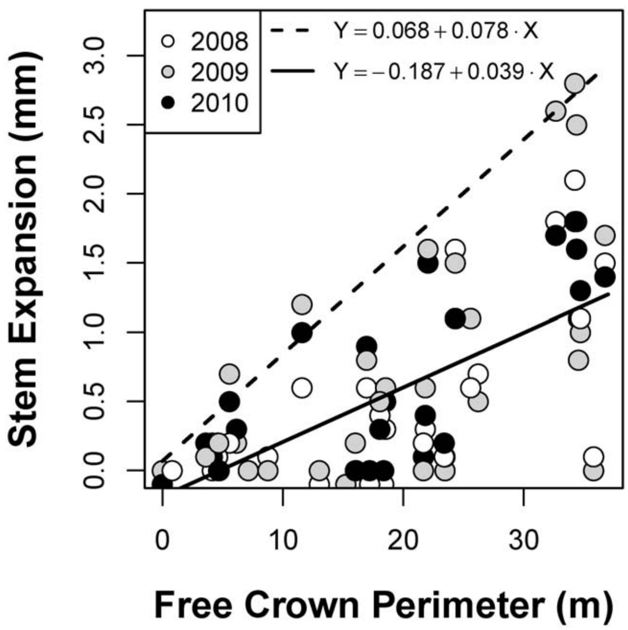

Figure 7. Relationship between first-period stem expansion (May 1 to August 1) and free crown perimeter, a measure of competition. The lower, solid line is a linear regression fit; the upper dotted line is a 95th quantile regression fit that represents the potential growth rate at a given level of competition.

Free crown perimeter based on conifer contact was evaluated further as a predictor of first-period stem expansion (Figure 7). A linear regression equation with *FCP* as the sole predictor variable was statistically significant ($P < 0.001$) and explained 41.8% of the variation in stem expansion. A second regression equation was fit with *DBH* and *FCP* as predictor variables. Both variables were statistically significant ($P < 0.001$), indicating that *FCP* provided information on the tree's size and competitive position in addition to *DBH* alone. The multiple-regression equation explained 68.4% of the variation in first-period stem expansion. Differences among years were not statistically significant ($P = 0.68$) and were not included in the models. The relationship between *FCP* and stem expansion suggested that a range of growth rates could occur at a given level of *FCP*, but that *FCP* created an upper limit on potential growth. A quantile regression line (Koenker and Hallock 2001, Koenker 2009) was fit to the 95th percentile of stem expansion to define the upper level of growth that could occur at a given level of *FCP*.

Discussion

The shift from open woodlands or savannas to denser woodlands or closed-canopy forests has greatly altered growing conditions for OWO. The relationships used in the new equations for FVS provide insight into how these changes are influencing the growth and survival of OWO throughout much of its range. OWO is considered to be intolerant to very intolerant of shade (Stein 1990). The sensitivity to competition is captured in the revised diameter growth and mortality equations. Stand density is represented in the diameter-growth equation by *BA,* and density in combination with the tree's competitive position is represented by *BAL.* Diameter growth is predicted to be reduced by 25% for all trees when $BA = 33$ m^2 ha^{-1} (the plot average from the modeling database) compared with an open-grown tree. *BAL* reduces growth further. In the same stand where $BA =$ 33 m^2 ha^{-1}, growth is reduced by 41% for a tree with 50% of basal area in larger trees and by 53% for the smallest tree in the stand. Competition also strongly affected growth of OWO in the intra-annual study. OWO in competition classes 2, 3, and 4 had about 75% less diameter growth than those in class 1. *FCP* was a useful measure of competition as it accounted for both tree size and the level of competition near each OWO. *FCP* was better correlated with growth when it was calculated only with conifer competitors, suggesting that hardwood competitors had a relatively small effect on growth.

In addition to crown competition, below-ground competition for water is an important factor affecting the growth of OWO. Most of the root area of OWO and competing conifers is in the upper 1 m of the glacial outwash soils that are found within the study area (Devine and Harrington 2005). As in other dendrometer studies, it is difficult to distinguish actual growth (i.e., cell division and expansion) from shrinking and swelling as stem water content changes (Deslauriers et al. 2007). The pause between the two periods of stem expansion, and the stem shrinkage recorded in some trees, indicates that growth stopped around August 1 or occurred at a rate less than the rate of stem shrinkage. Stem shrinkage occurred as OWO used water stored in the stem to meet some of their transpiration needs during summer (Phillips et al. 2003b). The second-period of stem expansion in the fall and winter indicates that water content of OWO was depleted during the summer. The second-period stem expansion was a particularly high percentage of total expansion among overtopped trees. This was likely the result of both low growth during the first period and a greater level of depletion of stem water than in the other competition classes. The recharge of soil water in September in 2009 and 2010 coincided with earlier and more stem expansion in the second period than in 2008, suggesting that growth can still occur in OWO in late summer or early fall when conditions are favorable. Conifer removal can delay the depletion of soil water (Devine and Harrington 2007) and may accelerate soil water recharge. These results reinforce the need for management actions that reduce the density of competitors, particularly taller conifers, to improve growth and survival of OWO. The pattern of stem expansion also has implications for measuring OWO diameters to estimate growth increments. Measurements should be made after stem expansion is completed and before new growth occurs (between January and March).

Tree size is also an important determinant of growth. As is the case for many species, the rate of diameter growth of small trees (< 40 cm for OWO) increases with increasing *DBH* and then decreases as the trees grow larger. Similarly, potential height was found to increase with *DBH* at an almost constant rate for trees < 30 cm *DBH* and then level-off so that little additional height growth is predicted for trees > 60 cm. The maximum potential height for OWO on a good site was 34.8 m, which is close to the maximum recorded height of 38.4 m reported by Stein (1990). Large (and often old) OWO are predicted to have no additional height growth and slow *DBH* growth, even with little competition. The growth reduction caused by competition may have a particularly strong impact on large OWO as they have been found to have less water transport capacity relative to their needs than smaller trees (Phillips et al. 2003a). Competition may be more likely to reduce diameter growth of large trees beyond the level needed to maintain adequate functional xylem, resulting in crown dieback and tree mortality.

Survival is predicted to be fairly high for trees of all sizes with low stand densities (e.g., < 10 m^2 ha^{-1}). At higher stand densities, survival is predicted to still be high when OWO are competing with shorter trees but it decreases sharply when competitors are taller than the oak. Measures of stand density used in growth models typically use *DBH* to represent tree size without considering height. Relative height was an important variable for describing the size disparity between OWO and competitors as Douglas-fir typically has a much greater height for a given *DBH* than OWO (Hanus et al. 1999). The revision to the height growth component of FVS ensures that it predicts reasonable values for OWO height so that relative height can be calculated more accurately.

The Oak Flats stand is representative of a common condition where OWO, some of which are centuries old, are overtopped by taller conifers. Many of these trees will die without management action. Reducing stand densities by selective conifer removal can increase growth and survival (Harrington and Devine 2006), but survival is expected to be greatest when very low stand densities are restored. The JBLM stand is representative of some stands that have established in the absence of fire. Thinning of OWO is expected to substantially increase the growth of the residual trees. The FVS projections indicate that *QMD* can be doubled over a 50-yr period with repeated thinning. OWO in thinned stands may have greater acorn production (Peter and Harrington 2002), thereby increasing their value to wildlife.

The revisions to FVS described in this paper have improved its usefulness for projecting stands that contain OWO; however, model validation with independent data is needed to ensure that all of the model components are working together to produce accurate projections. Long term data from growth plots would be useful for validation, but such data are not yet available. More permanent plots need to be established and remeasured for the purpose of model validation and to learn more about the dynamics of OWO stands. We did not revise some important algorithms, including those that predict the growth of small trees (< 8 cm *DBH*) and the reduction in potential height growth owing to competition. These algorithms need to be tested and revised if necessary. FVS does not include a short-term thinning effect so a stand that is thinned is assumed to grow like one that has had a low density for a long time. OWO may not respond to thinning immediately as time is needed for crowns and roots to take advantage of the growing space that is opened by thinning. The approach we took to predict potential height was different than the standard approach in FVS. The three-part algorithm used to predict potential height may also be useful for other species where height-age curves have not been developed. The authors welcome feedback from users that would help to identify problems that need to be addressed in future revisions.

Conclusions

The major factors that affect the growth and survival of OWO throughout its range are stand density, the relative competitive position of each tree, site productivity, and tree size. In many cases, the condition of OWO communities can be improved by restoring stands to the low densities that were historically common in oak woodlands and savannas. Although OWO can survive for centuries under favorable conditions (Stein 1990), its biological characteristics of shade intolerance and its reliance on the most recent two years of ring growth for water transport mean that it is very vulnerable to competition and it will not survive long under high competition. FVS was revised to incorporate the best-available information on the growth and survival of OWO. With the additional information, users can have greater confidence in the ability of FVS to accurately project stand development under different management alternatives. The current version of FVS contains the revised component and can be downloaded from the US Forest Service, Forest Management Service Center website (http://www.fs.fed.us/fmsc/fvs/).

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Appendix: Equations and Coefficient Estimates

FVS uses English units for all input and output data. The coefficient estimates shown here are the actual values used in FVS; therefore all input variables need to be in English units. The response variables are: change in squared diameter (*DDS* [in^2]), maximum tree height (*MAXHT* [ft]), potential tree height (*PHT* [ft]), the probability of tree survival for a period of one year (*SURV*), and the probability of tree mortality for a period of ten years (*MORT).* The input variables are: diameter at breast height (*DBH* [in]), stand basal area (*BA* [ft^2 acre^{-1}]), stand basal area in larger trees (*BAL* [ft^2 acre^{-1}]), site index for Douglas-fir using King's (1966) equation (*SI* [ft at age 50 yrs]) and tree height divided by the average height of the 40 largest trees per acre (*RHT* [unitless]).

Large-Tree Diameter Growth

$$DDS = e^{\sum_{i=1}^{n} \alpha_i \cdot \beta_i} \quad [1]$$

	Coefficient (αi)	
Variable (βi)	Estimate	SE (Estimate)
Intercept	-1.33299	0.30713
ln(*DBH*)	1.66609	0.11371
DBH^2	-0.00154	0.00019
BAL	-0.00326	0.00067
BA	-0.00204	0.00042
ln(*SI*)	0.14995	0.03657

Large-Tree Height Growth

$$MAXHT = \alpha_0 \cdot (1 - e^{(\alpha_1 \cdot SI)})^{\alpha_2} \quad [2]$$

Coefficient	Estimate	SE (Estimate)
α_0	114.24569	21.31973
α_1	-0.02659	0.03188
α_2	2.25993	4.63250

$$PHT = 4.5 + (MAXHT - \alpha_0 / 1n(2.71 \cdot BA)) \cdot (1 - e(^{\alpha_1 \cdot DBH}))^{\alpha_2} \quad [3]$$

Coefficient	Estimate	SE (Estimate)
α_0	18.60249	11.94532
α_1	-0.13743	0.00993
α_2	1.38994	0.08303

Mortality

$$SURV = \frac{1}{1 + \exp(\alpha_0 + \alpha_1 \cdot 1n(5 + BA) \cdot \alpha_2 \cdot RHT} \quad [4]$$

$$MORT = 1 - SURV^{10} \quad [5]$$

Coefficient	Estimate	SE (Estimate)
α_0	-6.67074	0.65839
α_1	0.51052	0.10691
α_2	-1.31832	0.19663

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