



Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics

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ABSTRACT

To simulate stand-level impacts of climate change, predictors in the widely used Forest Vegetation Simulator (FVS) were adjusted to account for expected climate effects. This was accomplished by: (1) adding functions that link mortality and regeneration of species to climate variables expressing climatic suitability, (2) constructing a function linking site index to climate and using it to modify growth rates, and (3) adding functions accounting for changing growth rates due to climate-induced genetic responses. For three climatically diverse landscapes, simulations were used to explore the change in species composition and tree growth that should accompany climate change during the 21st century. The simulations illustrated the changes in forest composition that could accompany climate change. Projections were the most sensitive to mortality, as the loss of trees of a dominant species heavily influenced stand dynamics. While additional work is needed on fundamental plant–climate relationships, this work incorporates climatic effects into FVS to produce a new model called Climate–FVS. This model provides for managers a tool that allows climate change impacts to be incorporated in forest plans.

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1. Introduction

Climate change is expected to have pronounced ecological consequences in forested ecosystems. Projected impacts encompass a broad range of effects: the evolution of novel plant associations (Jackson and Overpeck, 2000), shifts in the spatial distribution of tree species (e.g., Iverson and Prasad, 1998), redistribution of populations adapted to local climates (e.g. Tchebakova et al., 2003), and changes in site index (Monserud et al., 2008). Studies (e.g., Bachelet et al., 2001b; Hansen et al., 2001; Melillo et al., 1995; Neilson et al., 2005; Shafer et al., 2001), in fact, have been unanimous in predicting widespread disruption of native ecosystems from the change in climate being portrayed by numerous General Circulation Models (GCM) (see IPCC, 2000). Many accounts illustrate the impact of climate change on the vegetation (see Breshears et al., 2005; Jump et al., 2009; Allen et al., 2010; Mátyás, 2010), such as the migration at high altitudes and demise and replacement at low altitudes of *Fagus sylvatica* (Peñuelas et al., 2007), or the dieback of *Populus tremuloides* due to a climate-induced stress (Rehfeldt et al., 2009).

Most forest managers use growth models to aid decision making. These models, like the widely used Forest Vegetation Simulator

(FVS, Crookston and Dixon, 2005; Dixon, 2008; Stage, 1973), were developed for use in a static climate. Because many component functions describing stand dynamics are dependent on climate, growth models in general are incapable of reflecting impacts of climate change. In this paper, we describe adjustments to the predictors in FVS to take into account the effects of climate on mortality, growth, and regeneration. The modified model, called Climate–FVS, is used to simulate impacts of climate change on three climatically diverse landscapes.

FVS is an individual-tree, semi-distance-independent growth model. Inputs include an inventory of site conditions and a set of measurements on a sample of trees (e.g., tree size, species, crown ratio, recent growth and mortality rates). Outputs include summaries of tree volume, species distributions, and growth and mortality rates that are often customized for specific user needs. The Fire and Fuels Extension of FVS (FFE–FVS, Rebain et al., 2009; Reinhardt and Crookston, 2003) outputs many indicators including a report on carbon loads used herein. FVS is used to support an array of management issues spanning silviculture prescriptions, fuels management, insect and disease impacts, and wildlife habitat management. Spatial scales range from a single stand to thousands of stands. The temporal scale has traditionally been about 200 years (400 years maximum), but here we limit ourselves to ~100 years, the period covered the GCM used for simulations.

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FVS is widely used in North America for project-level analyses and forest planning. Integrating climate change and species–climate relationships into FVS provides managers a familiar tool useful for addressing climate change issues. There are several variants of FVS that share the same core technology but differ in their treatment of growth and mortality. This paper deals only with those variants in use in the western United States.

2. Methods

The components of FVS most subject to climate and therefore needing adjustment are those dealing with mortality, carrying capacity, tree growth, and regeneration and establishment. Our approach to adjusting these components is to (1) define a species-specific viability score as a function of climate and (2) develop a means to compute climatically induced changes in site quality. The final model must also recognize that stand dynamics will depend on the adaptedness of the genetic system (physiological attunement to the climate, see Rehfeldt et al., 1999) as the climate changes.

2.1. Climate estimates and projections

Our analyses use spline climate surfaces (ANUSPLIN, Hutchinson, 2004) for providing 1961–1990 monthly normals of mean, maximum, and minimum temperature and precipitation for point locations (see Rehfeldt, 2006; Sáenz-Romero et al., 2010). The surfaces are indexed by latitude, longitude, and elevation, and because the splines are continuous rather than grids, point estimates can be generated rather than gridded estimates available from raster cells in many climate models (e.g., Daly et al., 2008). The spline climate estimates, available at URL <http://forest.moscowsl.wsu.edu/climate>, include algorithms to generate from monthly means 35 variables such as mean annual temperature and precipitation, degrees days above 5 °C, degrees days below 0 °C, and the length of the frost period, and interactions such as annual dryness index, which reflects the balance between growing season warmth and precipitation.

To estimate future climates, weather data used in developing the contemporary climate surfaces were updated using output from three GCM and three scenarios of the Special Report on Emissions Scenarios (SRES, IPCC, 2000) (Table 1). Downscaling from the GCM grids to the point locations of the weather stations used a weighted average of the monthly change for the GCM cell centers lying within 400 km of a weather station (see Sáenz-Romero et al., 2010). The inverse of the square of the distance from the station to the cell center was used for weighting. Monthly climate surfaces for average, minimum, and maximum temperature and precipitation were then fit anew for each GCM and each scenario for each of three 10-year periods, nominally, 2030, 2060, and 2090.

Table 1
General circulation models (GCM) and special report on emission scenarios (SRES) used herein.

GCM name	Center name
CGCM3	Canadian Center of Climate Modeling and Analysis
HADMC3	Met Office Hadley Centre (UK)
GFDLGM21	Geophysical Fluid Dynamics Laboratory (Princeton University, NOAA Research)
SRES scenario	Description
A2	High emissions, regionally diverse world, rapid growth
A1B	Intermediate emissions, homogeneous world, rapid growth
B2	Lower emissions, local environmental sustainability
B1	Lowest emissions, global environmental sustainability

2.2. Species-specific viability scores

As an index to viability, we use a species-specific estimate of the likelihood that the climate is suitable. The estimate is derived from the climate profile, a multivariate description of the climatic niche. The profiles are developed from bioclimate models, that is, regressions of the presence or absence of a species on climate variables. Modeling techniques generally follow Iverson and Prasad (1998) but most closely parallel Rehfeldt et al. (2006), described in detail in Rehfeldt et al. (2009).

To develop the climate profile, we used a data from permanent sample plots largely from Forest Inventory and Analysis (FIA, Bechtold and Patterson, 2005) but supplemented with research plot data to provide about 117,000 observations (see Rehfeldt et al., 2006, 2009) describing the presence and absence of numerous species. The Random Forests classification tree of Breiman (2001), implemented in R by Liaw and Wiener (2002), was then used to predict the presence or absence of species from climate variables. The Random Forests algorithm outputs statistics (i.e., vote counts) that reflect the likelihood (proportion of the total votes cast) that the climate at a location would be suitable for a species. We interpret this likelihood as a viability score: values near zero indicate a low suitability while those near 1.0 indicate a suitability so high that the species is nearly always present in that climate.

Random Forest classification trees were built for 74 tree species of the western United States (Table 2), about 70% of the species in the FIA database. Although the culling of species was somewhat arbitrary, those eliminated generally occurred at fewer than 50 plots. The statistical power of the analyses is reflected in the number of available observations, as many as 39,000 for *Pseudotsuga menziesii* and as few as 76 for *Populus deltoides* ssp. *monilifera*.

The climate profile was built on 3–30 forests, each with 100 trees. Protocols for selecting the sample of observations used in each forest and the stepwise variable elimination process followed Rehfeldt et al. (2006, 2009). The approach has been shown to be robust, working superbly for a variety of widely distributed species as well as the endangered spruce taxa of Mexico (Ledig et al., 2010).

2.3. Site Index and climate

Site index is a commonly used measure of the ability of a site to produce wood (Monserud, 1984). Ideally, it is a species-specific height at a base age reached by dominant trees that have always grown without competition. Site index is known to be a function of climate (see Monserud and Rehfeldt, 1990) which explained ~25% of variation in site index of *Pinus contorta* var. *latifolia* in Alberta, Canada (Monserud et al., 2006, 2008). In general, high site indices are correlated with long growing seasons and warm temperatures, provided that moisture is sufficient. The results show unequivocally that *P. contorta* site indices are altered by a change in climate.

Because FVS uses site quality to estimate tree growth, Climate–FVS requires a function relating site quality to climate applicable to all forest types and their ecotones to non-forest in all of western United States. This function, however, need not be species-specific because Climate–FVS used species viability scores to judge site suitability. To provide such a function, we defined S to be the proportionate change in site index caused by a change from one climate (called C_1) to another (called C_2), where C_i is a vector of climate metrics like those used to measure the viability scores.

Let f be a function of C_i that predicts the site index, or at least a number that is proportional to the site index, then $S = f(C_2)/f(C_1)$. Note that $f(C_1) > 0$ because FVS is initiated with sites that are suitable for forests. To construct f , we used the FIA collection of site trees for the western United States, in which 82,649 observations of height and age are spread over 21,553 plots in forested lands. Estimating site index for each tree, however, was hampered by

Table 2

Summary statistics of the random forest classification trees used to predict presence–absence of 74 western United States species.

Species	Number present ^a	Number random forests ^b	Average OOB error ^c	Average commission error ^d	Average omission error ^d	Lower viability threshold ^e	Percent scores ≥ 0.9 ^f
<i>Abies amabilis</i>	4106	10	0.031	0.054	0.0008	0.594	61
<i>Abies concolor</i>	8692	10	0.030	0.052	0.0017	0.565	60
<i>Abies grandis</i>	8220	10	0.037	0.066	0.0008	0.572	59
<i>Abies lasiocarpa</i>	11,294	5	0.042	0.075	0.0006	0.591	60
<i>Abies lasiocarpa</i> var. <i>arizonica</i>	370	30	0.027	0.045	0.0013	0.546	58
<i>Abies magnifica</i>	1248	10	0.038	0.067	0.0018	0.552	58
<i>Abies magnifica</i> var. <i>shastensis</i>	600	10	0.039	0.067	0.0020	0.536	57
<i>Abies procera</i>	1522	10	0.053	0.096	0.0014	0.554	56
<i>Acer glabrum</i>	712	30	0.047	0.082	0.0054	0.487	54
<i>Acer grandidentatum</i>	348	30	0.037	0.066	0.0012	0.554	57
<i>Acer macrophyllum</i>	3616	10	0.076	0.144	0.0011	0.550	51
<i>Aesculus californica</i>	228	24	0.091	0.180	0.0015	0.552	47
<i>Alnus rhombifolia</i>	208	30	0.077	0.146	0.0018	0.549	50
<i>Alnus rubra</i>	4882	10	0.065	0.121	0.0010	0.559	54
<i>Arbutus menzeisii</i>	3098	10	0.046	0.083	0.0008	0.575	58
<i>Betula papyrifera</i>	302	30	0.044	0.079	0.0019	0.554	56
<i>Betula papyrifera</i> var. <i>commutata</i>	328	30	0.022	0.038	0.0004	0.593	60
<i>Calocedrus decurrens</i>	4868	10	0.061	0.112	0.0017	0.551	54
<i>Castanopsis chrysophylla</i>	1810	10	0.051	0.092	0.0010	0.565	56
<i>Cercocarpus ledifolius</i>	1192	30	0.048	0.087	0.0012	0.555	55
<i>Chamaecyparis lawsoniana</i>	6152	10	0.014	0.024	0.0007	0.606	64
<i>Chamaecyparis nootkatensis</i>	472	16	0.059	0.107	0.0024	0.530	54
<i>Cornus nuttallii</i>	1050	11	0.076	0.144	0.0021	0.539	49
<i>Fraxinus latifolia</i>	206	30	0.071	0.132	0.0032	0.534	50
<i>Juniperus deppeana</i>	3046	10	0.032	0.055	0.0021	0.566	61
<i>Juniperus erythrocarpa</i>	84	23	0.110	0.223	0.0021	0.561	42
<i>Juniperus monosperma</i>	3866	18	0.041	0.072	0.0012	0.586	59
<i>Juniperus occidentalis</i>	3152	14	0.033	0.057	0.0007	0.568	60
<i>Juniperus osteosperma</i>	9262	10	0.045	0.080	0.0017	0.557	57
<i>Juniperus scopulorum</i>	3378	29	0.070	0.130	0.0019	0.549	52
<i>Larix lyallii</i>	102	30	0.063	0.118	0.0033	0.524	54
<i>Larix occidentalis</i>	9094	10	0.029	0.051	0.0006	0.600	61
<i>Lithocarpus densiflorus</i>	2158	10	0.035	0.062	0.0009	0.564	58
<i>Olivea tesota</i>	110	30	0.052	0.094	0.0046	0.521	55
<i>Picea breweriana</i>	348	8	0.025	0.042	0.0014	0.558	61
<i>Picea engelmannii</i>	10,460	5	0.047	0.085	0.0007	0.585	58
<i>Picea pungens</i>	328	30	0.068	0.126	0.0032	0.526	48
<i>Picea sitchensis</i>	946	10	0.052	0.093	0.0021	0.526	56
<i>Pinus albicaulis</i>	3112	20	0.028	0.049	0.0005	0.588	62
<i>Pinus aristata</i>	162	30	0.044	0.079	0.0004	0.577	54
<i>Pinus attenuata</i>	388	30	0.052	0.094	0.0011	0.546	55
<i>Pinus contorta</i>	15,386	5	0.048	0.086	0.0005	0.590	58
<i>Pinus coulteri</i>	116	29	0.074	0.148	0.0012	0.547	53
<i>Pinus edulis</i>	9102	10	0.042	0.074	0.0015	0.573	58
<i>Pinus flexilis</i>	1938	30	0.054	0.098	0.0010	0.562	56
<i>Pinus jeffreyi</i>	2394	10	0.050	0.090	0.0015	0.554	56
<i>Pinus lambertiana</i>	4032	10	0.060	0.110	0.0013	0.557	55
<i>Pinus monophylla</i>	3430	16	0.030	0.053	0.0005	0.595	60
<i>Pinus monticola</i>	3726	10	0.050	0.089	0.0010	0.561	57
<i>Pinus ponderosa</i>	24,280	5	0.044	0.080	0.0014	0.567	58
<i>Pinus strobiformis</i>	560	13	0.040	0.066	0.0065	0.438	59
<i>Populus deltoides</i> ssp. <i>monilifera</i>	76	30	0.067	0.134	0.0009	0.578	52
<i>Populus tremuloides</i>	6196	13	0.045	0.080	0.0014	0.553	57
<i>Prosopis</i> sp.	264	30	0.071	0.134	0.0011	0.562	52
<i>Prunus</i> sp.	724	30	0.049	0.088	0.0015	0.545	57
<i>Psuedotsuga menziesii</i>	39,490	3	0.043	0.079	0.0010	0.580	58
<i>Quercus agrifolia</i>	440	18	0.058	0.105	0.0024	0.541	55
<i>Quercus chrysolepis</i>	3310	10	0.067	0.124	0.0011	0.558	53
<i>Quercus douglasii</i>	778	10	0.073	0.137	0.0017	0.542	51
<i>Quercus emoryi</i>	758	18	0.051	0.092	0.0012	0.555	56
<i>Quercus gambelii</i>	4118	16	0.035	0.061	0.0010	0.573	59
<i>Quercus garryana</i>	1116	17	0.063	0.116	0.0017	0.553	54
<i>Quercus hypoleucoides</i>	218	26	0.040	0.070	0.0027	0.540	56
<i>Quercus kelloggii</i>	3500	10	0.054	0.098	0.0013	0.551	56
<i>Quercus lobata</i>	150	30	0.092	0.185	0.0025	0.523	46
<i>Quercus oblongifolia</i>	106	10	0.075	0.146	0.0028	0.528	51
<i>Quercus wislizeni</i>	752	13	0.078	0.148	0.0019	0.533	50
<i>Robinia neomexicana</i>	294	30	0.068	0.115	0.0153	0.372	53
<i>Salix</i> sp.	456	30	0.046	0.081	0.0024	0.536	57
<i>Taxus brevifolia</i>	2106	11	0.059	0.107	0.0014	0.540	54
<i>Thuja plicata</i>	6816	10	0.063	0.117	0.0006	0.574	54
<i>Tsuga heterophylla</i>	9992	10	0.050	0.089	0.0012	0.560	57
<i>Tsuga mertensiana</i>	2796	10	0.040	0.071	0.0013	0.557	59
<i>Umbellularia californica</i>	1034	10	0.063	0.116	0.0010	0.560	53

^a Number of observations in which the species was present in about 117,000 observations.^b Number of forests used in the analysis.^c Average out-of-bag error for observations not used as training data.^d Errors of commission, a prediction of presence when absent; errors of omission: predicting absence when present.^e Proportion of total votes above which 99.5% of the observations having the species received a higher voting proportion.^f Percent of predicted viability scores greater than or equal to 0.90 among observations where the species is present.

the several disparate regional models which, for instance, may use different base ages. We circumvented this problem by using Monserud's (1984) model calibrated for *P. menziesii* to estimate a site index for each tree. This equation was used for all species despite the well known differences in growth rates among species. Because Climate-FVS will use the ratio S instead of actual site index, bias introduced from using a single site curve for all species is expected to be alleviated while the noise associated with disparate site curves and underlying techniques is avoided. Approximately 39% of the observations in this dataset were *P. menziesii*, but the remainder included 61 other species.

Calibration data consisted of a random sample of 40,000 observations drawn without replacement from the full data set. To represent climates where there are no trees, a random selection of 5000 points were selected from lands in the western United States that are not capable of supporting forests. This sample was obtained from a systematic sampling of point locations within the digitized map of the Biotic Communities of North America (Brown et al., 1998). Technical procedures, described in detail in Rehfeldt et al. (2006), involved the use of ARCMAP software to procure the sample of point locations from each polygon on the file, and the digitized elevation model of the GLOBE Task Team (1999) to associate each point sample with an elevation. Of the 24 biotic communities that occur in western United States, 13 (e.g., desertscrub, grasslands, chaparral) contained neither forests nor woodlands. Our sample of 5000 was drawn from the group of about 28,000 lacking trees and to them a site index of zero was assigned.

These 45,000 observations were used to build a series of regression trees using the Random Forests algorithm and a set of 35 candidate climate variables (see Section 2.1) to initiate a stepwise elimination process (see Section 2.2). The regression model was developed from one forest with 150 trees.

Observations not used in fitting the regression were used to judge the quality of the fit. This dataset consisted of about 65,700 observations, of which about 22,000 were from the sample of biotic communities that contained no forests or woodlands.

2.4. Conversion of FVS to Climate-FVS

2.4.1. Mortality

In Climate-FVS, mortality is to be calibrated from species viability scores (Section 2.2). Our logic is that if viability scores drop below those at which the species occurs currently, mortality rates should be increased, eventually resulting in extirpation. Fig. 1a illustrates our conceptual view of a climate-based relationship between viability and mortality, plotted in the figure as survival. Experience in developing climate profiles of various species (e.g., Rehfeldt et al., 2006) has shown us that species rarely occur when viability scores are <0.5 . Indeed, most sites where *Abies amabilis* occurs receive viability scores >0.9 (Fig. 1b), while essentially no trees occur at viability scores <0.4 . Table 2 shows that the histogram for *A. amabilis* is typical of many species: of the sites in which a species is present, ~60% received $>90\%$ of the votes in favor of the climate being suitable, and 99.5% received at least 55% of the votes.

For Climate-FVS, we assume that at viability scores <0.2 , a species is absent and, therefore, survival is zero. For lack of information to the contrary, we use a linear relationship to describe the decline in mortality between scores of 0.5 and 0.2 (Fig. 1a). A comparison of Fig. 1a with Fig. 1b suggests that the mortality function in Fig. 1a overestimates survival and, therefore, is conservative. While a nonlinear regression could be fit in Fig. 1b, we suspect that our function is a more realistic balance between the fundamental niche in Fig. 1a and the realized climatic niche in Fig. 1b. Note also that no attempts are made to apportion mortality into causes, such as insect outbreaks, diseases, or climate-induced stress.

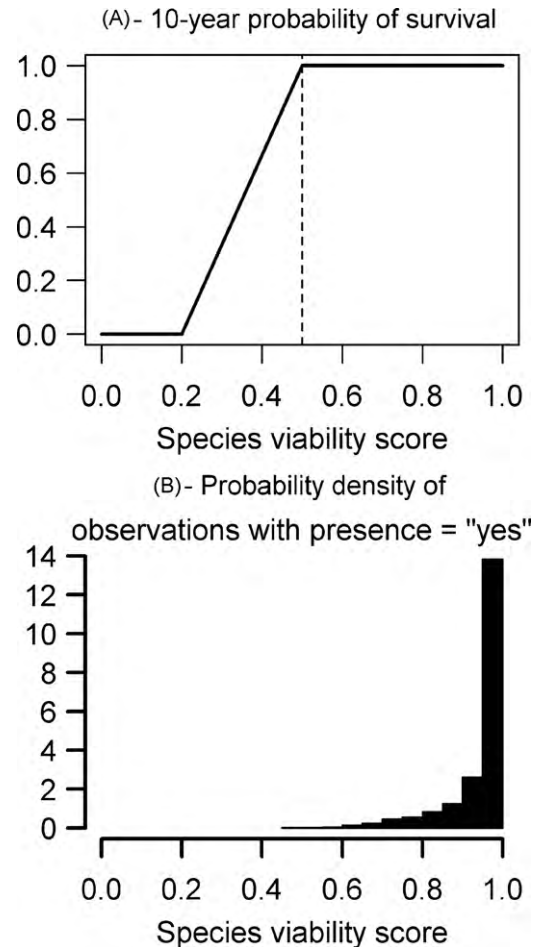


Fig. 1. Representation of the logic governing a rule-based relationship between species viability scores and 10-year survival (A), and a histogram of the observations in which *Abies amabilis* is present that supports the logic (B).

Mortality also occurs from density-dependent effects that are simulated in FVS (see Crookston and Dixon, 2005) and influenced by climate, as follows.

2.4.2. Carrying capacity

In FVS, carrying capacity is measured as a stand maximum basal area and as a maximum stand density index (Reineke, 1933)—an algorithm converts one to the other so that both are always defined. Changes in these maximum stand densities are computed over time by calculating a weighted average maximum density among the species growing in the stand. Each species is given a default maximum density used in this calculation (users can modify default values). Weights used in the calculation of the weighted average are the basal areas of the species present. This weighted average establishes the stand maximum in effect at a given point in simulated time.

Climate-FVS modifies the maximum carrying capacity computed by FVS by calculating a proportional change from two weighted average maximum densities, using the FVS maximum densities for all species in the FIA database. For the first of the two values, denoted D_1 , the weights equal the species viability scores at the beginning of the simulation period. For the second value, D_2 , the weights are the viability scores computed in simulated time. As for computing S (Section 2.2), D_1 is always greater than zero simply because FVS is initiated with data from sites that can support forests. The proportional change in carrying capacity is $r = D_2/D_1$, and maximum density in simulated time is calculated from the

product of r and the maximum value computed by FVS. According to this logic, maximum stand density will increase when the site becomes more suitable for species that carry high densities, but will decrease when the climate favors species that carry lesser density. The modified carrying capacity is then used in mortality calculations.

This approach, however, leaves two contingencies that must be addressed. First, the weighted average maximum density (D_2) could be high even though viability scores are all low. For example, if viability scores of all species were <0.2 but their maximum densities were high, then the weighted average maximum density would be unrealistically high simply because weighted averages are relative to the sum of the weights. To address this issue, an additional entry was made into the calculation of the weighted average maximum density to represent non-forests. This entry was given a carrying capacity of zero and a weight of one minus the maximum viability among the species.

Secondly, the proportional change in density (r) could become extraordinarily high if the denominator in the ratio was very small compared to the numerator. To circumvent this potential problem, the magnitude of r was limited to 1.5.

2.4.3. Growth

To address the effects of a changing climate on growth rates, Climate-FVS modifies the growth estimate of FVS. The modifier is multiplicative and is denoted as P_s , where the subscript indicates species specificity. There are three parts to the logic used to compute this modifier. The first part addresses the change in site quality, S , as defined in Section 2.3. The second part addresses the expectation that living trees whose viability is decreasing should exhibit declining growth rates (see Rehfeldt et al., 1999, 2001). For these trees, we added a species-specific viability, denoted by V_s and set equal to the survival rate for the species (Fig. 1a). The third part codes the adaptedness of trees as the climate changes. This component, denoted G_s , reflects intraspecific responses to a change in climate. Of these three effects, G_s requires elaboration before deriving P_s from S , V_s and G_s .

2.4.3.1. Genetic effects. It is well known from provenance tests conducted for most of the world's widespread tree species that seed sources exhibit different growth rates, but the expression of these differences depends on the environment. These tests provide the best source of data for estimating change in growth associated with a change in the climate. Indeed, provenance tests are climate change experiments (Mátyás, 1994). Unfortunately, however, the amount of provenance test data suitable for calibrating growth models is limited, largely because costs have constrained the scope of most studies. Notable exceptions include *Pinus banksiana* (Mátyás and Yeatman, 1992), *P. contorta* (Rehfeldt et al., 1999, 2001), and *Pinus sylvestris* (Rehfeldt et al., 2002, 2004), analyses of which have demonstrated that the growth of seed sources follows a quasi Gaussian response to climate.

In a recent reanalysis of common garden data (see Rehfeldt, 1989), Leites et al. (2009) quantified *P. menziesii* height growth as a function of mean annual temperature at the seed source and difference between the mean temperature of the coldest month at the seed source and the planting site. In *P. menziesii*, clines relating genetic differences among seed sources to environmental gradients are relatively steep, with differences in growth potential occurring at relatively short intervals along climatic gradients. Seed sources tend to be genetically attuned to relatively specific environmental conditions, and under those conditions are capable of expressing their growth potential (see Morgenstern, 1996). Rehfeldt (1994) used the term *specialist* to refer to species like *P. menziesii* in which clines are steep. In species with a *generalist* approach to adaptation (e.g., *Pinus monticola*), clines tend to be flat; seed sources are

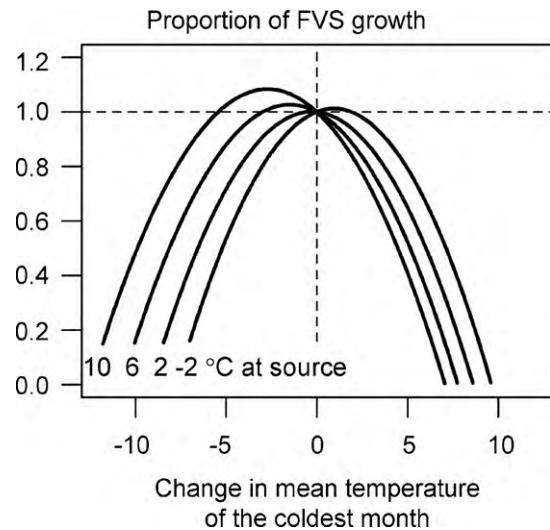


Fig. 2. Proportionate growth, the ratio of growth projected for a future climate to that of the contemporary, predicted by the change in mean temperature in the coldest month between the future and the present. Four regression lines are presented, each corresponding to a mean annual temperature of *Pseudotsuga menziesii* var. *glauca* provenances (which normally is the origin of the seeds) (redrawn from Leites et al., 2009).

capable of expressing their growth potential across a broad range of environments. Obviously, specialists and generalists require different sets of response functions to describe the relationship between growth and climate.

Fig. 2 illustrates the model of Leites et al. (2009) for *P. menziesii*, modified to express the proportion of growth expected if one were to move trees from one climate to another—a direct analog of a changing climate. Note that the work of Leites et al. (2009) predicted growth in absolute units, but for these predictions to be useful in Climate-FVS, they are expressed as a proportion of the growth FVS would predict under a static climate. G_s is defined, therefore, as the proportional growth expressed along the y-axis of Fig. 2. The function in Fig. 2 indicates that increasing winter temperatures would initially benefit trees growing where winters are cold but otherwise would cause a reduction in growth. Reducing winter temperatures provides a growth increase to trees from warm provenances. A change in climate sufficient to predict zero growth from in Fig. 2 could occur entirely within the contemporary climatic niche of this species. It is possible, therefore, that G_s could approach zero while the species viability (V_s) is near 1.0 and while site quality is improving ($S > 1.0$).

Similar, yet preliminary, response functions have been developed for *Larix occidentalis* and *Pinus ponderosa* (Leites, 2009, unpublished reports), two species in which clines in genetic attributes are moderately steep. In *L. occidentalis*, growth is also most sensitive to changes in winter temperature, while in the pine, growth is most sensitive to changes in a moisture index. In general, small changes in climate tend to cause either little effect or moderate increases in growth of existing populations while large climate changes, positive or negative, would reduce growth.

Although models are not yet available for many species, some species in the western United States besides *P. menziesii* have broad geographic distributions across which clines are steep. An example is *P. contorta* (see Rehfeldt, 1994), so for it we use the values of G_s calibrated for *P. menziesii*. For other *P. monticola*, *Picea engelmannii*, and *Tsuga heterophylla* for which clines tend to be flat, we use the values for *L. occidentalis*. For all species for which geographic patterns of genetic variation are poorly documented or unknown, G_s is 1.0, that is, maladaptation would never become the factor limiting growth.

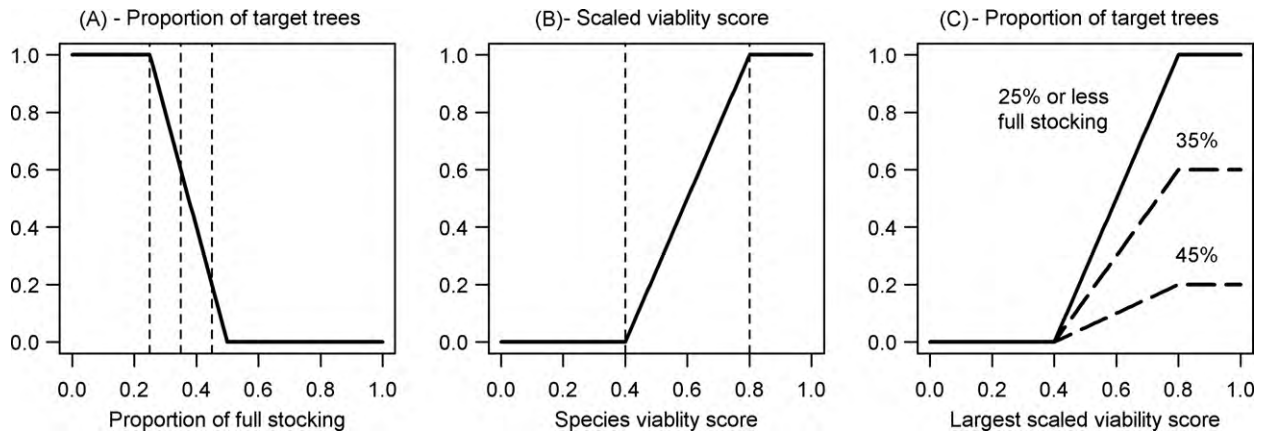


Fig. 3. Regeneration-establishment rules for determining the maximum number of trees to be established in relation to full stocking (A), the scaling of species-specific viability scores (B), and the proportion of target trees to be established as a function of the proportion of full stocking and the largest scaled score (C). Vertical hashed lines in A correspond to the three values (25, 35, and 45%) of full stocking illustrated in (C).

2.4.3.2. Growth modifier, P_s . With V_s , S , and G_s all defined, the growth modifier, P_s is chosen by the logic: if $\min(V_s, S, G_s) < 1.0$, then $P_s = \min(V_s, S, G_s)$, else $P_s = \max(V_s, S, G_s)$. The rationale is that if nothing is limiting growth, then the factor that results in the most growth is working in the ecosystem. Growth decreases if (1) the climate at the site becomes unsuitable to the species, (2) the site quality deteriorates, or (3) the seed source becomes maladapted to the climate.

2.4.4. Regeneration establishment

Climate-FVS uses three rules to compute number of trees to be added to an understocked stand. The rules consider species viability scores (Section 2.2) and stocking and they assume that seeds are available for regeneration or that the trees will be planted.

The first rule is that regeneration and establishment will be initiated when stand density falls below a threshold set by default to 40% of full stocking, but this setting can be adjusted by the user. Full stocking is commensurate with calculations of carrying capacity (Section 2.4.2), and as a result, the density that constitutes full stocking will change as the climate changes. The default setting simply reflects the choices made by FVS users who frequently established limits to control regeneration, episodes of which in western United States are largely dependent on disturbance. The second rule deals with the calculation of number of trees to be established. The process is begun by establishing a maximum number of trees that can be established. This number is controlled by the user (e.g., 1000/ha). From this maximum, the trees to be added are computed from the actual stocking and the viability scores of the species suited to the climate of the site. The proportion of the maximum number eligible for reforestation is determined by stocking levels (Fig. 3a), that is, by a linear function between zero for the stocking threshold (as set by the first rule) and 1.0 when stocking is <25% of full stocking. According to Fig. 3a, which assumes a reproduction threshold of 50% of full stocking, a stand that is only 45% of full stocking would be allowed to receive only 20% of the maximum number of trees that could be established.

However, the number of trees to be established should also depend on species viabilities. To use viability scores for this purpose, they are scaled between values of zero (all scores <0.4) and one (scores >0.8), as depicted in Fig. 3b. If the viability score is <0.4, then no trees will be established, regardless of allowable proportion; but, if viability is >0.8, all of the allowable trees will be established. These threshold values were selected in order to be consistent with the occurrence of species (Fig. 1 and the lower viability thresholds in Table 2). To compute the proportion of trees

that will be established, the allowable proportion (Fig. 3a) is multiplied by the scaled viability score of the species with the highest score (Fig. 3b) to arrive at the proportion to be established (Fig. 3c).

For example, if the target is 1000 trees/ha, the proportion of full stocking is 0.35, and the maximum of the scaled viability scores is 1.0, then the number of trees to be established is about 500/ha. But if the maximum scaled viability score is 0.6, the number to establish would be about 300/ha, and if the score is 0.4 or less, then no trees will be established.

In the third rule, the trees to be established are allocated among species. To accomplish this, all species with scaled viability scores less than 0.40 are ignored. From the species remaining, a maximum of four (by default) species are selected according to their viability scores. The number of trees to be established is apportioned among the species using the scaled scores as weights; the proportion allocated is determined by the ratio of the scaled score for a species and the sum of the weights. Fig. 4 provides four examples of applying these rules. In Fig. 4A and B the viability scores are the same, but because the percentage of full stocking differs, the number of trees to be established differ greatly. In Fig. 4C and D, the percentage of full stocking is low but equal, but species viability scores differ greatly. As a result, most of the trees to be established are those best suited for the climate of the site.

2.5. Simulations

To study the potential impacts of climate change on forest dynamics, we selected three geographically diverse landscapes in western United States (Table 3). For each, routine stand examination data sets were compiled from the U.S. Forest Service Field Sampled Vegetation database and processed for input into FVS. Because numerous stands were included in the data from each landscape, a range in elevation surround the means in Table 3, amounting to 1200 m for Clearwater, 1000 m for West Cascades, and 500 m for Black Mesa.

Species viability scores, climate estimates, and the growth modifier for each of the stands in the landscapes were computed according to Section 2, with Internet sites accessed in February 2010. These data were used as input to the regional Climate-FVS variant appropriate for the landscape (see Crookston and Dixon, 2005). Eight simulations were run for each landscape, one for each of the GCM and emission scenarios of Table 1, and one called the *base case* that assumes no climate change. No management regimes were simulated. Summaries of the runs were computed by averaging over all the stands in each landscape.

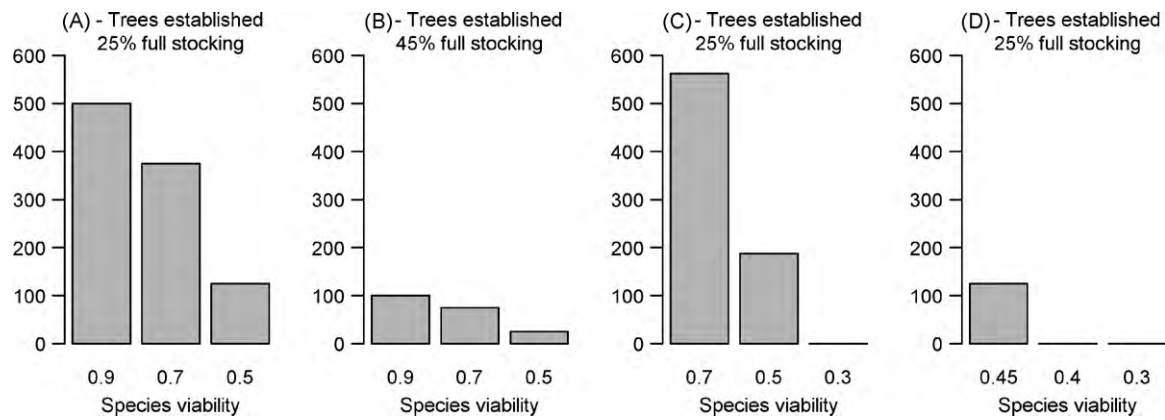


Fig. 4. Four examples of applying the establishment rules, each illustrating responses for three species according to their viability score.

Table 3

Characteristics of the forested landscapes chosen for simulations.

Name, state	Longitude ^a	Latitude ^a	Elevation ^a (m)	Number stands	Setting	Notable species
Clearwater, Idaho	–114.63	46.58	1588	135	Canyon along the Clearwater River in northern Idaho, moderate productivity	<i>Pseudotsuga menziesii</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Abies lasiocarpa</i> <i>Abies grandis</i>
Black Mesa, Colorado	–109.33	38.53	3004	214	High mesa in western Colorado, moderate productivity	<i>Populus tremuloides</i> <i>Picea engelmannii</i> <i>Abies lasiocarpa</i>
West Cascades, Washington	–121.76	46.53	839	310	Highly productive forested land southwest of Mount St. Helens	<i>Pseudotsuga menziesii</i> <i>Abies procera</i> <i>Tsuga heterophylla</i>

^a Averages over the stands in the landscape.

3. Results

3.1. Climate profiles and species viability

Species viability scores are based predictions of presence or absence by Random Forests classification trees, for which errors of prediction (the out-of-bag errors) were generally low, averaging 5.1% for the 74 species and reaching 10% for only one species (Table 2). The out-of-bag errors were composed almost exclusively of predictions of presence when a species was absent (commission errors). The model for *P. menziesii*, for instance, misclassified 39 observations out of the 39,490 observations where it was present. From the ecological viewpoint, this result is reassuring: while there are many ecologically sound explanations for the absence of a species when the climate is suitable (e.g., disturbance, soils, pests, lack of appropriate seed source), the most likely explanations for predicting absence when present are either data errors or modeling errors.

In addition to their superb statistical fit, the models demonstrated an unequivocal confidence in making predictions. Table 2 lists a variable called the lower viability threshold; 99.5% of the observations of presence received more votes than this threshold value. The average value of this threshold was 0.55. On average, therefore, all but 0.05% of the observations where species were present received 55% or more of the votes cast by the Random Forests algorithm. The distribution of votes was greatly skewed to the right as indicated by the high proportion of votes >0.9 (Table 2, Fig. 3b). This means that when votes are high, the confidence is correspondingly high that the species will be present. These results add credence to equating the proportion of votes to species viabilities in Climate-FVS and in using the viabilities to model mortality (Fig. 1a). In Climate-FVS, mortality commences at viability scores <0.5, a conservative threshold. Mortality rates are not increased

until there is assurance that the species does not occur in that climate.

3.2. Site index

The Random Forests regression trees explained ~86% of the observed variance in site index of the 65,766 observations that were not used to train the predictor. The distribution of residuals (Fig. 5) shows predictions generally were too high at both the low and at the high ends of the scale. At the low end, high predictions were

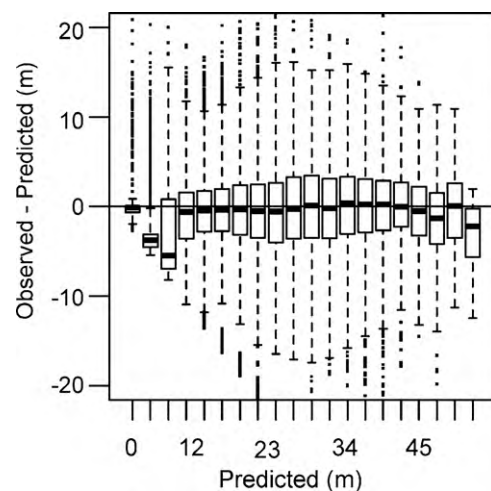


Fig. 5. Box and whisker plots of the residuals (observed minus predicted site index) plotted against the predicted site index for observations that were not used to build the Random Forests regression tree. Dots beyond the dashed lines are single observations.

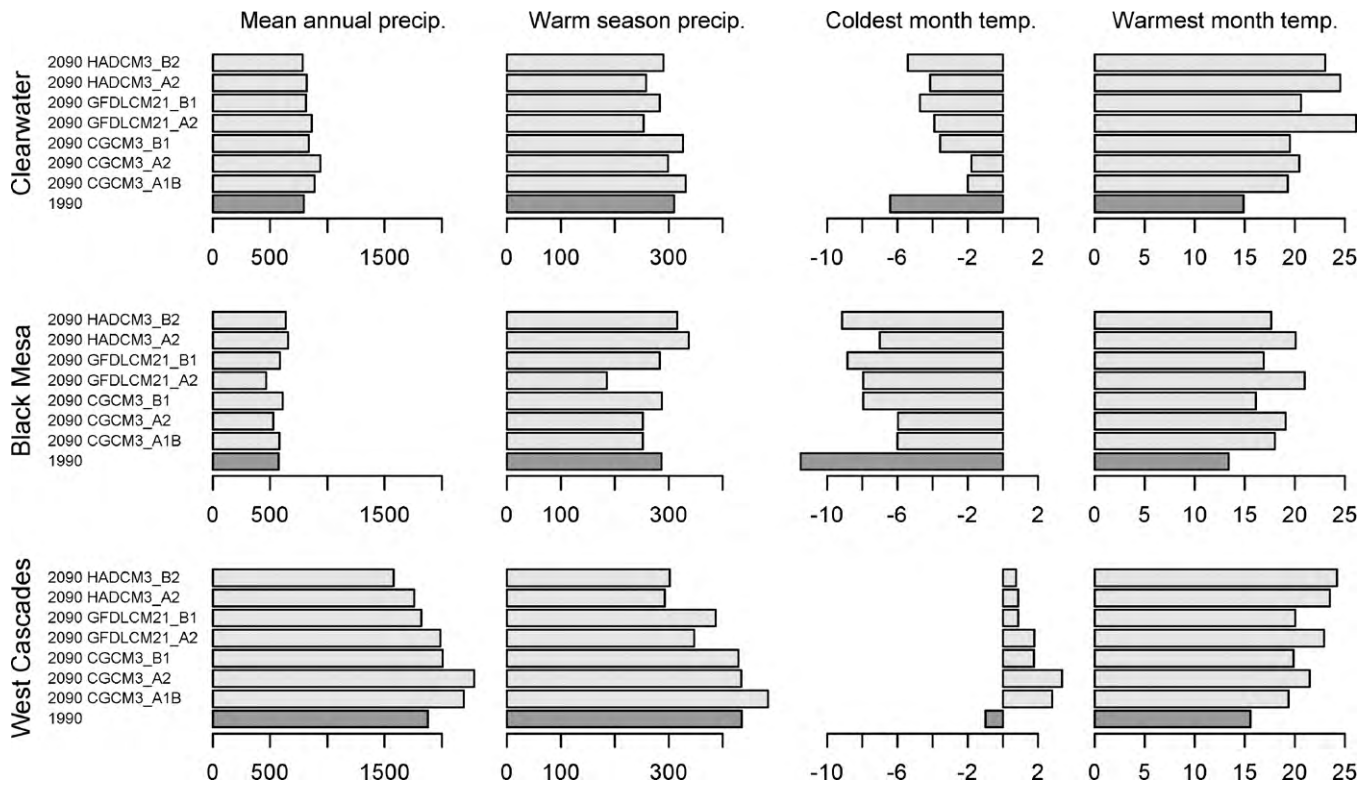


Fig. 6. Four climate variables plotted for three geographically disparate landscapes. Values for 1990 are the 1961–1990 climate normals, but otherwise the bars are 10-year averages surrounding the 2090 predictions from three general circulation models and three scenarios (see Table 1). Abbreviations: precip., precipitation (mm) and temp., temperature (°C).

attributable to the addition of non-forest locations to the training data. However, without these values of zero, the predictor was incapable of predicting low site indices for climates poorly suited or not suited for forests.

The predictors in the 7-variable were: (1) degree days above 5 °C (*dd5*), (2) warm season (April through September) precipitation (*wsp*), (3) mean temperature of the warmest month (*mtwm*), (4) product of mean annual precipitation (*map*) and the difference in *mtwm* and the mean temperature in the coldest month (*mtcm*), (5) ratio of *wsp* and *map* times *dd5*, (6) summer dryness index ($sdi = \sqrt{dd5/wsp}$), and (7) *sdi* times the number of degree days under 0 °C based on minimum temperatures (*mindd0*). Site index, therefore, is being predicted from variables describing the balance between temperature and precipitation, the warmth and amount of precipitation in the growing season, and the coldness of winter (weighted by moisture deficits of the previous summer).

Our attempts to produce a parametric model with these data resulted in models that explained as much as 60% of the observed variance, but residuals exhibited substantial localized biases over a wide range of site indices.

3.3. Simulations and projections

3.3.1. Climate

The three landscapes chosen for demonstration of Climate-FVS (Fig. 6) are climatically disparate for both the contemporary and projected climates. In general, the climate of the West Cascades is warm and moist, that for Black Mesa is cool and arid, while that for the Clearwater is intermediate. Climatic differences among the landscapes are most pronounced for total precipitation and winter cold but are surprisingly small for temperatures in the hottest month.

Projected climates of the landscapes were highly variable among the GCMs and scenarios, but the variability was insufficient to mask the overall climatic differences among the three landscapes. The variation is disconcerting for warm season precipitation, maximum temperatures in the warmest month, and the coldness of winters. The first two of these variables impact the summer dryness index (*sdi*, defined above) that has been shown to be influential in the segregation of species along altitudinal gradients (Rehfeldt et al., 2008). Winter cold, when weighted by the summer dryness index, frequently occurs as a component of species climate profiles.

Climate estimates for decades surrounding 2030 and 2060 that are not presented in Fig. 6 tend toward the interpolations that would be expected between the extremes. Variation among the projections was small for 2030, became pronounced by 2060, and continued to increase through 2090.

3.3.2. Growth: genetics and site

In Climate-FVS, impacts of climate on growth (Section 2.4.3) are mediated through an interaction of genetics (G_s) and site index (S). The box and whisker plots of Fig. 7 illustrates that these two effects may have opposing impacts on growth. While the impact of climate on site index would be positive throughout the coming century, the same climate trends would have a negative impact on adaptedness, particularly after mid-century. This negative impact would accrue as the trees inhabiting the site today become less and less attuned physiologically to the climates of the future.

To estimate growth, Climate-FVS uses the factor that results in the highest positive impact unless one factor has a negative impact. Fig. 7, for instance, shows that on average, the genetics component predicts ~25% decline in growth at 2060 while the site index component suggests a ~35% increase. Consequently, for species like *P. menziesii* for which genetic effects have been estimated, the effects of an improving site quality can be realized only if the proper

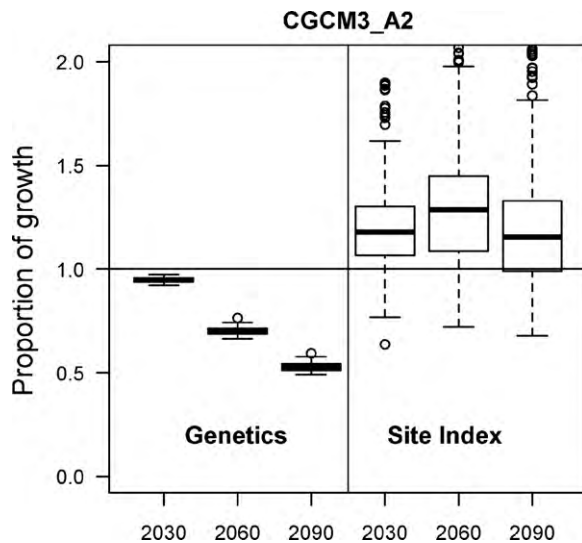


Fig. 7. Box and whisker plots showing the central tendencies and variation for proportionate changes in growth of *Pseudotsuga menziesii* attributable to the genetics component (left) and site index component (right) for 310 stands within the West Cascades landscape according to the A2 emissions scenario and the CGCM3 general circulation model.

genotypes are on the site (see Ryan, 2010). However, because we set $G_s = 1$ for species on which genetic effects are unknown, the model will accept the favorable of improved site quality when, in fact, the species and genotypes growing on those sites may not be able to take advantage of improved conditions.

3.3.3. Carbon

Fig. 8 summarizes carbon across a 100-year simulation starting with the date of the inventory for the three watersheds as reported by FFE-FVS. Estimates of carbon (metric tons/ha) in living trees, their roots, and in other living plant material is reported as *live* carbon, that in dead plants at various stages of disintegration (e.g., litter, duff, and coarse woody debris) is reported as *dead* carbon, while that stored in the soil is not considered.

According to the initial inventories, the Clearwater had the lowest carbon levels, followed by Black Mesa, and then West Cascades. When compared to projections for a static climate (the 2090 Base in Fig. 8), all climate change scenarios had negative effects on projected carbon loads in all landscapes, but the size of the impacts were much different. The largest negative impacts were projected for Black Mesa, particularly by the A2 scenario of the GFDLCM21. This scenario conveys the lowest warm season precipitation and hottest temperatures of the scenarios we used (Fig. 6), and this combination results in large summer moisture deficits. In terms of carbon, impacts on the West Cascades would be minor while those in the Clearwater would result in a reduction of live carbon by about 50%. Although variability in impacts was large for Black Mesa, projections for the Clearwater and West Cascades were surprising uniform.

3.3.4. Forest composition

When climate change alters viabilities, mortality will increase, eventually causing a change in composition of the landscapes (Figs. 9–11). In comparing impacts on the species in these figures, note that vertical axes are not the same for every species within a landscape.

3.3.4.1. Clearwater. Fig. 9 shows that *Abies grandis* should be only mildly affected by climate change except for one of the scenarios

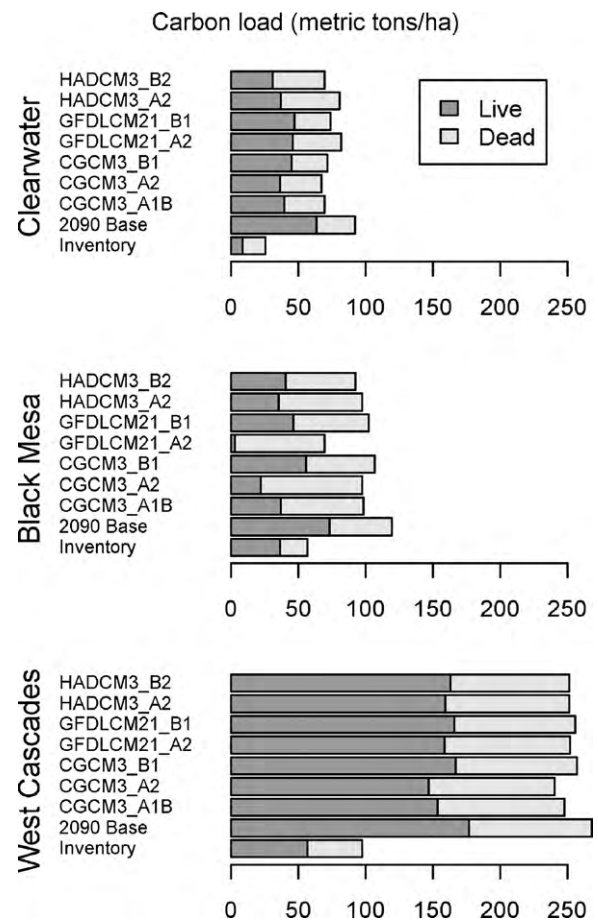


Fig. 8. Estimated and projected loads of carbon in live and dead material for contemporary stands (labeled inventory) in three landscapes, for 2090 projections as if climate was static (labeled 2090 base), and for 2090 projections from three general circulation models and three scenarios.

(HADCM3.B2), which shows it to nearly die out. All scenarios predict less total basal area in a changed climate than for the base run. Projections for *Abies lasiocarpa* suggest that suitability of climate should deteriorate sharply by about 2070 according to four scenarios, but all scenarios predict much less basal area than the base case. Basal area of *P. contorta* would also decline greatly while that for *Picea engelmanni* is projected to be highly variable. *P. menziesii*, however, would thrive under all scenarios, particularly for the GFDLCM21.A2 climate, under which growth should be better than in the base case.

Only one species, *T. heterophylla*, was absent in the initial inventory but would be introduced according to the establishment rules. The introduction would take place near the end of the simulation and would only occur under the B2 scenario of HADMC3.

3.3.4.2. Black Mesa. Forests of this region today are primarily comprised of *P. tremuloides*, *Picea engelmanni*, and *A. lasiocarpa* var. *lasiocarpa*. Five of the seven climate change scenarios predict the demise of *A. lasiocarpa*, all but one predict the demise of *P. engelmanni*, and one predicts the demise of *P. tremuloides*, the most dominant of the species (Fig. 10). Species not in the initial inventory that are added by the establishment model include *A. lasiocarpa* var. *arizonica*. This variety was added early in the simulation by about 2020 under six scenarios. *Picea pungens* was added late in the simulation under all three CGCM3 scenarios and under the B2 scenario of the other two GCMs. *Pinus edulis* was added late in the century under the CGCM3.A2 scenario. Because Climate-FVS does

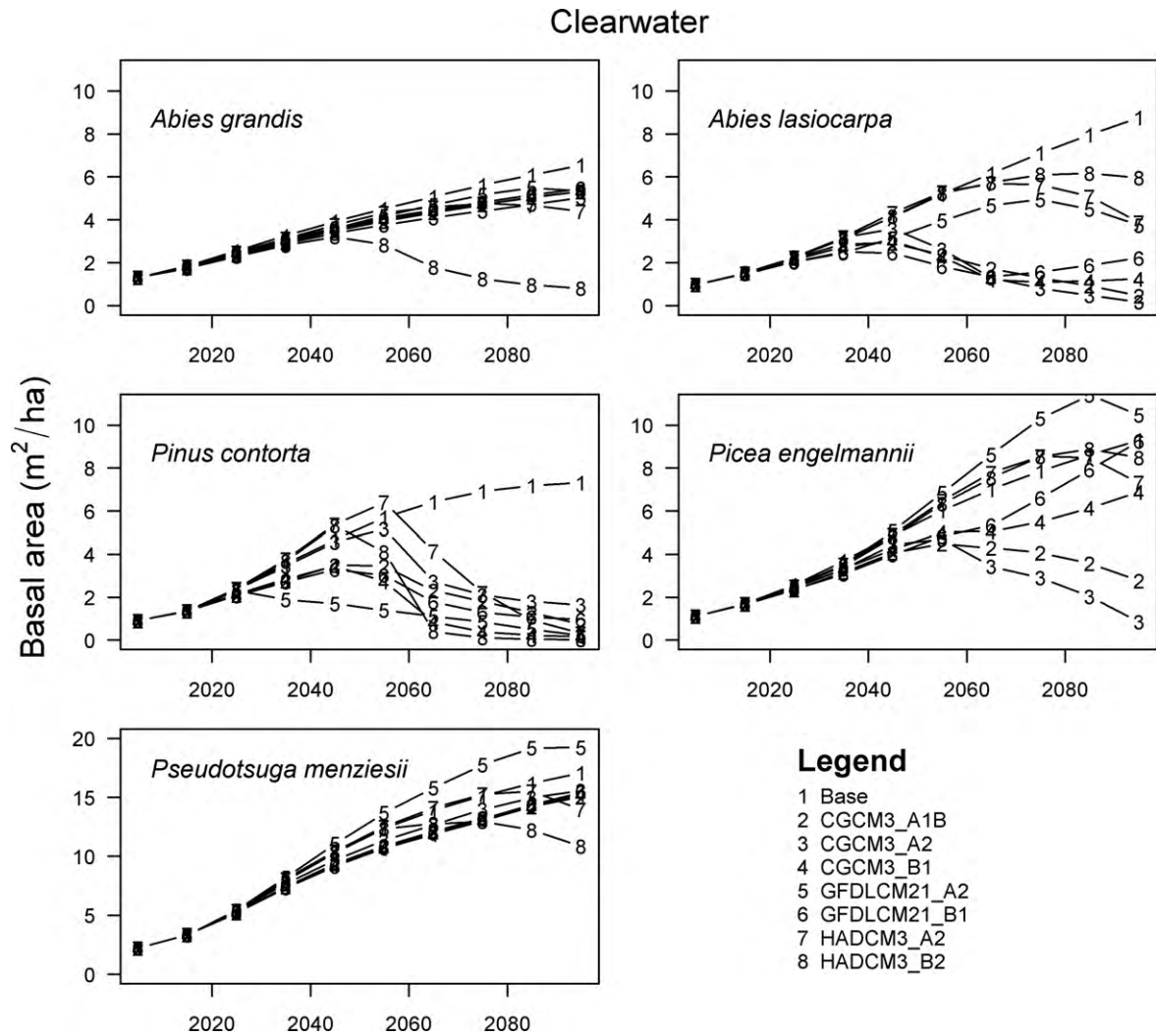


Fig. 9. Basal area (m^2/ha) by species for each of the scenarios run on the Clearwater data. Note that the vertical axis is scaled twice the height for *Pseudotsuga menziesii* than for other species.

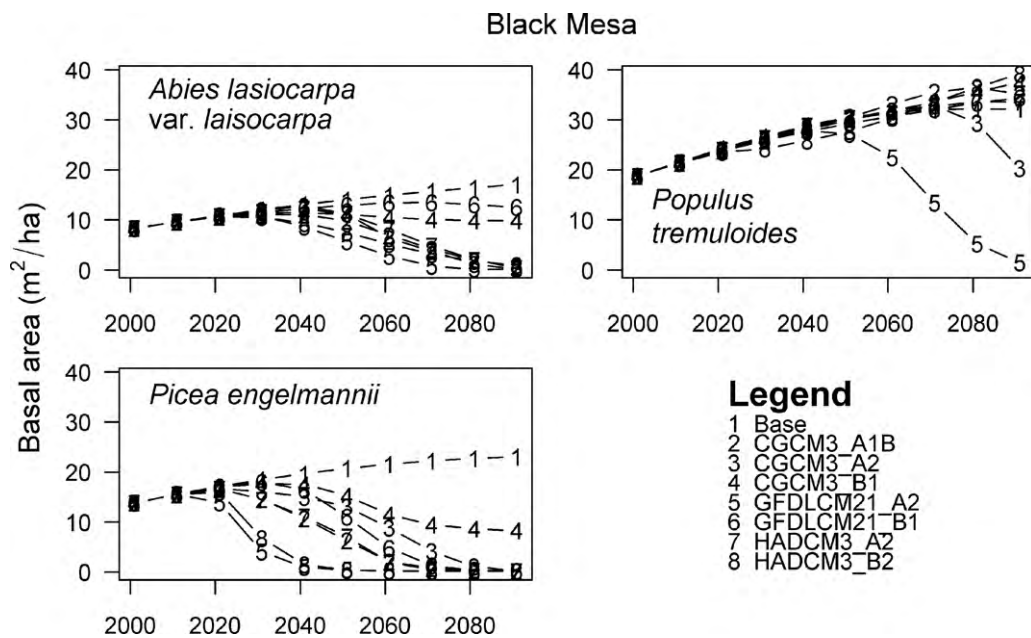


Fig. 10. Basal area (m^2/ha) by species for each of the scenarios run on the Black Mesa data.

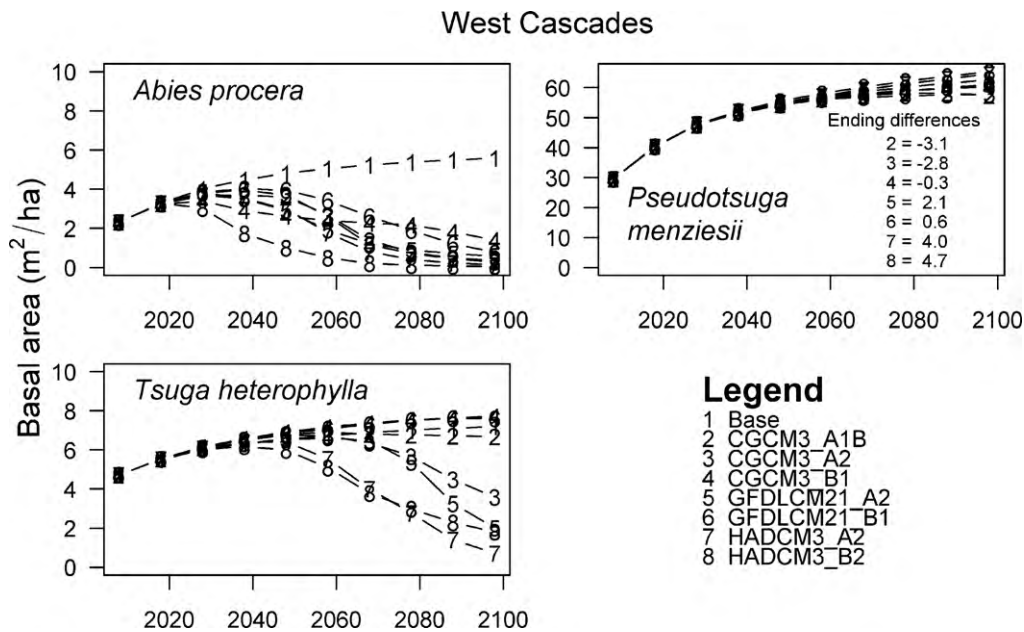


Fig. 11. Basal area (m²/ha) by species for each of the scenarios run on the West Cascades data. Note that for the *Pseudotsuga menziesii* plots, the vertical axis is six times higher than for the other species and that the final differences in basal area a scenarios and the base case are tabulated for each projection.

not consider migration rates, arrival of immigrant species at the appointed time likely would require planting.

3.3.4.3. West Cascades. Most obvious predicted impacts of climate change for the West Cascades (Fig. 11) are the losses of *Abies procera* (most scenarios) and *T. heterophylla* (four scenarios). These two species currently represent small portions of the basal area that is otherwise dominated by *P. menziesii*. The projections suggest that the dominance of the latter species should continue, with changes relative to the contemporary basal area ranging from -5% to +8%. *A. grandis*, *P. monticola*, *Cornus nuttallii*, *Acer macrophyllum*, and *Salix* spp. are all predicted to be added to this landscape late in the century.

4. Discussion

4.1. Mortality

Climate-FVS illustrates a potential impact of climate change on the three landscapes chosen for simulations. For all locations, one or more of the scenarios we used would result in the demise of one or more species. Clearly, the mortality component of Climate-FVS is the most influential part of the model. It is unfortunate, therefore, that there is little empirical evidence pertaining to rates of demise as the climate becomes unfavorable (see Ryan, 2010). As the climate changes, mortality on the trailing edge (Mátyás, 2010) will become better documented (e.g., Allen et al., 2010). These data will be indispensable for calibrating mortality estimates driven by climate effects.

Our approach to estimating mortality used species viability scores that were obtained from modeling presence and absence of species in contemporary climates. Because these viability scores are based on the realized niche rather than the fundamental niche, the ability of species to survive a change in climate may not be properly reflected by the scores. This argument is particularly valid where distributions are limited by competition rather than by the physical environment. Removal of the competition indeed may allow a species to flourish. However, the climate profiles can be considered as indicators of those future climates that are beyond the contemporary climatic niche. In the absence of data to the

contrary, Climate-FVS increases the mortality in such climates so that over time the species would disappear in the simulation. This impact is demonstrated for *P. tremuloides* at Black Mesa (Fig. 9): the species is predicted to die out under HADCM3.A2 and is headed toward demise under CGCM3.A2. The predictions of Rehfeldt et al. (2009) for this species recur in Climate-FVS forecasts.

If future climates have contemporary analogs, one can expect competitive interactions to remain unchanged. Consequently, whether the realized niche remains of constant breadth depends on the degree that future climates are novel (see Jackson and Overpeck, 2000). Rehfeldt et al. (2006) show that novel climates in western United States should increase in frequency as the current century advances, occupying about 25% of the land at the end of the century. It is in these novel climates that one can anticipate competitive relationships becoming re-assorted (see Jackson and Overpeck, 2000; Ibáñez et al., 2009).

Our viability statistics are a conservative representation of the realized climatic niche. At viability scores below 0.5, there is little chance of a species occurring (Table 2), and at scores between 0.0 and 0.2, there is essentially no chance. The rate of mortality and demise of stands after such scores are reached is a subject that requires a thorough assessment.

We recognize the importance of genetic effects on mortality (see Rehfeldt et al., 1999), but as of yet, these effects cannot be addressed by either statistical or mechanistic models. In the West Cascades, for example (Fig. 11), mortality of *P. menziesii* was projected to be low. We suspect, however, that this estimate underestimates the mortality rates that these forests will experience. The climate profiles on which the viability scores are based were computed at the species level and do not account for intraspecific genetic variation. However, for *P. menziesii* to maintain its current role in the ecosystem, that is, for the forecasted lack of mortality to be realized, the assortment of genotypes capable of thriving in the future climate will need re-assorting across the landscape (see St. Clair and Howe, 2007) and may even be different from those occurring there today (see Rehfeldt et al., 1999, 2002, 2003). If replacing the genetic stock of the site is required for the species survival, then size distributions and carbon loads would be greatly affected even if the species composition were to remain the same.

4.2. Growth

Our approach to predicting growth in a changing climate relies on results of ecological genetics studies in which trees were planted in common gardens in climates different from those in which they occur naturally. As a result these studies provide intraspecific analyses of growth as affected by a change in climate (Mátyás, 1994, Fig. 2). While of potential use in calibrating growth and mortality functions intraspecifically, suitable data are available for only a few species. However, Fig. 7 illustrates why genetics-related functions (*sensu* Fig. 2) are needed for many more species; quite simply, anticipated gains in growth resulting from improved site index cannot be realized if these are becoming less well attuned physiologically to the climate of the site (see Ryan, 2010).

Fig. 7 also suggests that field-collected measurements of growth in a changing climate may show, for instance, growth increases under moderate climate change at some sites and for some species but decreases for others; or increases in growth followed by decreases even when the climate seemingly appears to be improving for tree growth in general. Understanding the relationship between genetic variation and site index and thereby improving growth estimators in Climate-FVS would benefit greatly from observations across a wide range of conditions for a variety of species.

For present applications, we do not believe our treatment of genetic and site effects to be egregious. The simulations show that the model is much more sensitive to the mortality component than to the growth component. Also, the growth modifier we compute is applied to the FVS growth estimate which represents an expected realized growth under contemporary conditions rather than a potential growth. Climate-FVS focuses on the departure from these contemporary conditions to provide a framework that takes utmost advantage of current models and their embedded knowledge.

Nonetheless, we considered several other approaches to modeling growth. Perhaps most relevant is the approach of Milner et al. (2003) who developed FVSBGC, a model that linked FVS to the physiology-based model Stand-BGC (Milner and Coble, 1995), which in turn is based on the stand-level model FOREST-BGC (Running and Coughlan, 1988). We found, however, that genetic effects and species viabilities could be incorporated easily into FVS without resorting to the detail needed for FVSBGC. The mechanistic model MC1 (Bachelet et al., 2001a) and 3PG (Landsberg and Waring, 1997; Landsberg, 2003; Landsberg et al., 2003) also proved difficult for addressing the type of modifications we envisioned.

ForClim (Bugmann, 1996; Bugmann and Solomon, 2000) is a forest gap model that computes a potential growth and scales it with the product of two modifiers. One of the modifiers scales growth at the leading edge by equating a growth modifier to zero when degree days above 5 °C is zero and increases as this value increases to an asymptote index value of 1.0 when site conditions are optimal. A second modifier is used to reflect drying conditions and is computed as a ratio of actual water use to potentially available water. The product of these two indices scales potential growth. Although intriguing, the approach also requires soils data as additional input, and it is unclear to us how the strongly empirically based FVS predictions which operate at the species level can take advantage of this formulation.

We considered and rejected constructing a module dealing with CO₂ fertilization. Elevated concentrations of CO₂ have boosted growth in some situations, species, and age classes (Hättenschwiler et al., 1997), but Körner et al. (2005) suggest that positive effects have not been conclusively shown. Others (e.g., Norby et al., 2005) believe that forests will respond positively to increased CO₂ across a broad range of productivities. We prefer to procrastinate until the effects of CO₂ fertilization are unambiguous. In fact, FVS contains

options that would allow model users to posit these effects at their discretion. At present, we also are uncertain in which module CO₂ fertilization would be best expressed. If it is shown, for instance, that changes in atmospheric gas concentrations directly influence species–climate relationships, then CO₂ fertilization could alter the impact of a changing temperature and precipitation on mortality.

Another tempting approach to modeling growth responses to climate would involve re-fitting FVS component modules rather than provide adjustments to the algorithms already present. In a previous attempt to estimate climate impacts on basal area of *P. menziesii*, Crookston et al. (2007) re-fit Wyckoff's (1990) diameter growth equations by substituting climate variables for the site descriptors used originally while retaining predictors relating to tree size and competition. The best fitting regression model described a general increase in growth with increasing mean annual temperature and precipitation, but also suggested an absurd interaction whereby the negative impact of reduced precipitation would be offset by increasing temperatures. These results were largely due to the climatic distribution of data points. Highest growth rates occur in warm and moist conditions, but no data points exist where it is equally warm but dry or equally wet but cold. The results demonstrate the care that must be taken to assure that empirically based models are intuitively sensible as well as being of good statistical fit. The approach, therefore, was rejected.

4.3. Regeneration and establishment

For the regeneration and establishment module of Climate-FVS, we used a series of rules for controlling number of trees to be added to a site from a list of the species best suited for the climate. Absent in this approach were the modules accounting for effects of disturbance (e.g., time since disturbance, disturbance type) and composition of the previous stand that appear in some of the variants of FVS (Ferguson and Carlson, 1993; Ferguson et al., 1986). However, FVS and its regeneration component assume a static climate during the simulation period. Adding the effects of disturbance would require an establishment module that accounts not only for a change in species viability scores but also the impact of climate on the agents of disturbance, the latter of which is only beginning to be understood (see Morgan et al., 2008).

Also absent in Climate-FVS are effects such as migration rates that would attempt to account for the arrival (by natural means) of the seeds from species and seed sources that are suited to the new climate. Although ecological modelers currently are attempting to incorporate migration rates into the prediction of future distributions (e.g., Ibáñez et al., 2009), accounting for these effects in Climate-FVS output temporarily will remain the responsibility of model users.

The regeneration component of Climate-FVS provides managers a means of choosing among those species suitable to future climates. Selecting the appropriate seed source requires in-depth analyses such as that for *L. occidentalis* (Rehfeldt and Jaquish, 2010) and for now also will remain a responsibility of the users.

4.4. Variation among projections

The seven projections of climate we used produced consistent predictions for some species but highly variable projections for others. Fig. 9, for instance, suggests that Clearwater sites of today that contain *P. contorta* and *P. engelmannii* should continue to be climatically suited to them until mid century. Consequently, current timber management plans for the first half of the century may need little adjustment. In the long run, however, the simulations are unanimous in predicting a loss of climates suitable to *P. contorta*. A decision to regenerate this species today carries the expectation

that the trees will exist toward the end of the century, but such a decision clearly is not supported by Climate–FVS outputs.

By contrast to the consistent projections for *P. contorta*, results of the simulations for *P. engelmannii* for the Clearwater are highly variable, particularly in the second half of the century (Fig. 9). Projected impacts range from almost none to complete demise. The fact that the greatest negative impacts on this species are projected by three scenarios of the same GCM is not readily interpretable from the climate data in Fig. 6. Managers, however, must make decisions today despite the highly variable projections, relying perhaps on the consensus among projections (see Rehfeldt and Jaquish, 2010). Another choice might simply be the decision not to manage species with uncertain projected futures. Nonetheless, a lack of agreement among the GCM adds risk to managerial goals aimed at insuring a component of appropriate species for future Clearwater stands.

4.5. Viability scores and genetic responses

The bioclimatic models used to estimate species viability scores operate at the species level. Yet, provenance tests conducted on the world's economically important species have shown that growth and mortality varies among seed sources even when they are grown at the same site (see Morgenstern, 1996). Because climate-induced mortality is a genetic response (see Rehfeldt et al., 1999, 2002), genetic effects are necessary components of realistic models. Ideally, therefore, modeling should be done at the level of the population rather than the species. This would be especially relevant for widespread species like *P. menziesii* in which clinal variation among populations is steep (Campbell, 1979; Campbell and Sorenson, 1978; Rehfeldt, 1979, 1989). Doing so, however, is precluded by a lack of suitable data for all but a few species.

5. Conclusions

Climate–FVS provides forest managers a tool useful for considering the effects of climate change on forested ecosystems. The model relies on the original FVS growth equations to predict performance in the absence of climate change. To accommodate the effects of change, FVS components are modified rather than replaced with new estimators. In this respect, the primary intrinsic components of FVS and its empirical heritage remain intact.

The mortality and regeneration components of Climate–FVS both rely on species viability scores. These scores are based on thousands of observations of species presence and absence. As with FVS, a strong empirical basis is at the heart of the model. These empirical relationships, however, will need reviewing as climate-induced mortality becomes more widespread.

Our methods of computing changes in growth rates, particularly the genetic components thereof, are limited to a few species. Even though the simulations suggested that this factor was less important than the mortality component, improvement of the growth estimators would increase the reliability of model outputs. Improvement, however, will require the implementation of tests, collection of data, and analyses of many more growth measurements in situations where trees from one provenance are moved to different climatic regimes.

The climate change predictions that drive simulations are likely to change with the emergence of new information, new models, and new scenarios. For instance, efforts are currently underway to strengthen the spatial resolution of climate predictions to better account for slope, aspect, and other micro topographic factors. The internal mechanism of Climate–FVS relies on external models for predictions of climate and species viability. A means for making timely updates is available by having them linked on

Internet web services at URL: <http://forest.moscowfsl.wsu.edu/climate/customData/fvs.data.php>.

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