Bedrock type significantly affects individual tree mortality for various conifers in the inland Northwest, U.S.A.

James A. Moore, David A. Hamilton, Jr., Yu Xiao, and John Byrne

Abstract: Individual tree mortality models for western white pine (*Pinus monticola* Dougl. ex D. Don), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western redcedar (*Thuja plicata* Donn ex. D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western larch (*Larix occidentalis* Nutt.) were developed using data from permanent research plots located throughout the inland Northwest. The proposed linear logistic models included the following independent variables: diameter at breast height, basal area in larger trees, basal area per hectare, individual tree diameter increment, and a set of dummy variables for the six bedrock types, which were granite, basalt, metasedimentary, sedimentary, mixed – glacial till, and deep deposit. The results show that rock type significantly affects individual tree mortality for western white pine, Douglas-fir, and western redcedar, while grand fir, western hemlock, and western larch were not affected. Western white pine and Douglas-fir growing on metasedimentary rocks exhibited greater mortality probabilities than on other rocks. Mortality probabilities for western hemlock were low across all rock types, including "nutrient-poor" rocks like metasedimentary types.

Résumé : Des modèles de mortalité des tiges individuelles pour le pin blanc de l'Ouest (*Pinus monticola* Dougl. ex D. Don), le douglas (*Pseudotsuga menziesii* (Mirb.) Franco), le sapin grandissime (*Abies grandis* (Dougl. ex D. Don) Lindl.), le thuya géant (*Thuja plicata* Donn ex. D. Don), la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et le mélèze de l'Ouest (*Larix occidentalis* Nutt.) ont été développés avec les données de parcelles permanentes de recherche localisées un peu partout à l'intérieur des terres dans le Nord-Ouest. Les modèles linéaires logistiques proposés incluent les variables indépendantes suivantes : le diamètre à hauteur de poitrine, la surface terrière des plus gros arbres, la surface terrière à l'hectare, l'accroissement individuel en diamètre et un ensemble de variables binaires pour les six types suivants d'assises rocheuses : le granite, la basalte, la roche métasédimentaire, la roche sédimentaire, le till glaciaire mixte ou le dépôt profond. Les résultats montrent que le type de roche affecte significativement la mortalité des tiges individuelles de pin blanc, de douglas et de thuya géant tandis que le sapin grandissime, la pruche de l'Ouest et le mélèze de l'Ouest ne sont pas affectés. Le pin blanc et le douglas qui croissent sur les roches de type métasédimentaire ont montré une plus grande probabilité de mortalité que sur les autres types de roches. Les probabilités de mortalité de la pruche de l'Ouest sont faibles sur tous les types de roches, incluant les roches pauvres en nutriments comme celles du type métasédimentaire.

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Introduction

Effective forest management decisions require accurate growth and yield models that provide reliable growth information. A typical growth and yield model usually includes three components: survivor growth, ingrowth, and mortality. Mortality is the most difficult of these components to accurately predict. Hamilton's (1986) work substantially advanced our ability to predict mortality by relating individual tree mortality probability to (*i*) tree size, (*ii*) stand density, (*iii*) individual tree competition, and (*iv*) tree growth rate. While these tree and stand variables are useful for explaining variation in mortality, substantial variation remains unexplained in most mortality prediction models.

Rock type has been shown to significantly affect the growth and mortality rates of individual trees following fertilization of Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) (Shen et al. 2000, 2001). Their results suggested that different rock types represented broad differences in the forest nutrient environment. We particularly wanted to learn about differences in nutrient ecology for conifers commonly occurring in inland Northwest forests. Therefore, we undertook the current study to determine if rock type could explain additional variation in

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mortality not accounted for by tree- and stand-level variables. Furthermore, we wanted to ascertain whether various tree species show different mortality rates on certain rock types.

Materials and methods

Data

Tree mortality data used in this study include the data described in Hamilton (1986). In addition, data from a regeneration development study established in the late 1970s (Ferguson et al. 1986) and data from unfertilized control plots described by Shen et al. (2000, 2001) and obtained from the Intermountain Forest Tree Nutrition Cooperative were combined with Hamilton's (1986) original data, thus expanding the range of conditions sampled, particularly for rock type. Collectively, the time periods included in the data span much of the 20th century, beginning in 1914 and continuing into the 1990s. Therefore, these data represent the wide range of climatic variation included in the more than 80-year time span. The average time period between successive measurements of these permanent sample plots was 6 years. Plots range in size from 0.02 to 0.87 ha. Hamilton (1986), Ferguson et al. (1986), and Shen et al. (2000) provided detailed descriptions of the data sets used in our current study. The combined data set consists of 194 permanent sample plots in the inland Northwest (Fig. 1). Site and stand conditions for the overall data set are summarized in Table 1. The range of conditions included in these data spans much of the natural variability encountered in the region.

Bedrock samples were collected from soil pits (from the C horizon if present) at each Intermountain Forest Tree Nutrition Cooperative location and, after examination by a geologist, each installation was assigned to one of six rock type categories: granite, basalt, metasedimentary, sedimentary, mixed – glacial till, or deep deposit. For the rest of the data, each plot was first located on the appropriate geology map (Burmester et al. 2001; Munts and Idaho Geological Survey 2000; Miller et al. 1999; Lewis and Derkey 1999; Lewis et al. 1999; Idaho Geological Survey 1996) and the plot assigned to one of the six categories. Then, a substantial number of plots, about 20% of the total in these two data sets, were field checked, particularly those located near rock type boundaries on the geology maps. Rock samples were also collected from soil pits and examined by a geologist to verify the rock type. The misclassification of bedrock geology based on the geology map identification compared with the field verification rock samples was about 15%. We used the geology maps to assign bedrock type for the remaining study plots.

The six bedrock categories are so broadly defined that each bedrock type can be fairly easily distinguished in the field, and thus, the categories are potentially useful for forest management applications. However, each rock type category includes substantial geochemical and mineralogical variation in the rocks. Furthermore, each bedrock category represents very large land areas spanning major watersheds in the region and each category includes wide variation in site attributes such as elevation and slope (Table 2). Misclassification of bedrock type derived from our use of geology maps coupled with variation within rock type categories will likely increase the magnitude of the error term in our subsequent statistical analyses, thus making it more difficult to demonstrate statistical significance for rock type as a classification variable.

As expected, since glacial deposits are usually located in valley bottoms, the mixed rock type showed the lowest average sample plot elevation (Table 2). Plots located on granite bedrocks had the highest average elevation as well as the most variability in elevation. Metasedimentary rocks were somewhat steeper than other rock types, while they, along with deep deposits, had the highest proportion of plots located on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) habitat series.

Deep deposits are really a collection of surficial deposits (not including glacial tills) that are not truly a bedrock type. They were generally deposited by water, have sandy texture, and are excessively well drained. They are so deep that we assume trees growing on them are little affected by the underlying hard rock, and thus, they formed a separate rock type category. Habitat type (Pfister et al. 1977) was determined on site for each plot and each plot was assigned to one of five habitat type categories: grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), western redcedar (*Thuja plicata* Donn ex. D. Don), and western hemlock.

The number of observations by species, rock type, and habitat type for the analysis data set is provided in Table 3. For all species, metasedimentary rocks were the most common. Sixty-four percent of the plots are on western hemlock habitat types. Western white pine (*Pinus monticola* Dougl. ex D. Don), Douglas-fir, grand fir, western redcedar, western hemlock, and western larch (*Larix occidentalis* Nutt.) had sufficiently large sample size to be analyzed separately. Other species were sampled so infrequently that they were grouped into a single category. Not all rock types were represented for each tree species. Western hemlock was not sampled on basalt or sedimentary rocks, while western white pine was not sampled on basalts.

Analysis: mortality model

Our primary objective was to test whether individual tree mortality rates differed significantly by rock type. The logistic function was chosen to model individual tree mortality in our study. Model development was based on both biological and statistical considerations. The RISK software (Hamilton 1974), which fits the linear logistic regression model for binary data by the method of maximum likelihood, was used to model individual tree mortality as a logistic function of site, tree size, and competition following the biological rationale of Hamilton (1986) and Monserud and Sterba (1999). Equation 1 was fit separately for each tree species:

$$[1] \qquad P = \frac{1}{\{1 + \exp[-(b_0 + \mathrm{SITE} + \mathrm{SIZE} + \mathrm{COMP})]\}^{\mathrm{LGP}}}$$

where P is the annual probability of tree mortality and

$$[2] \qquad \mathrm{SITE} = \sum_{k=1}^{5} b_{1k}\mathrm{RC}_k$$

Fig. 1. Permanent sample plot locations for a tree mortality study in the inland Northwest, U.S.A.

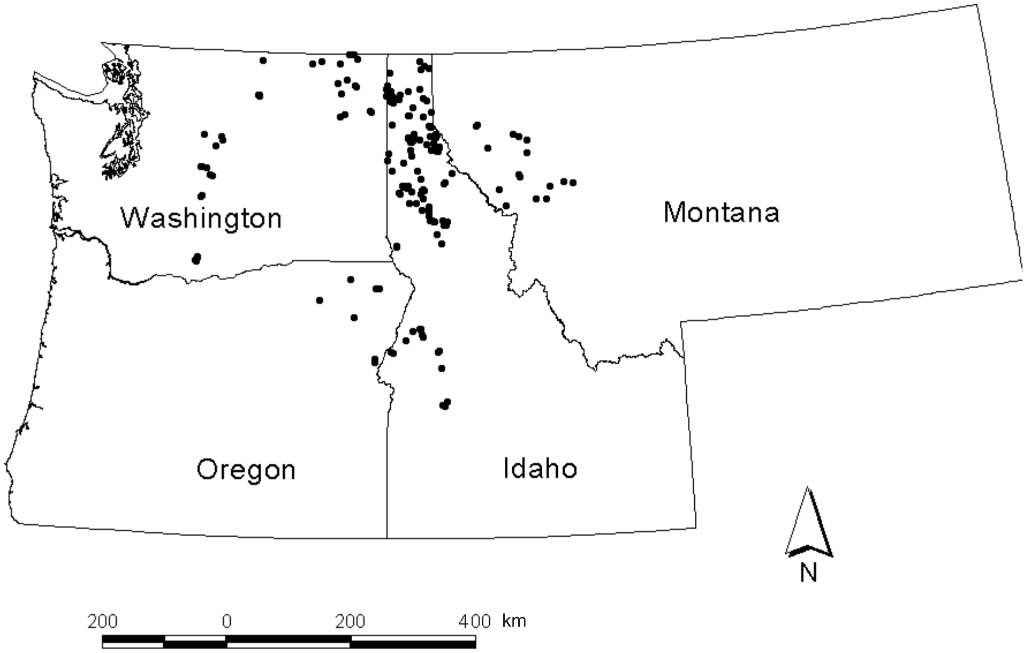


Table 1. Summary statistics of selected stand and tree attributes at the beginning of the observation period in the inland Northwest, U.S.A.

Attribute	Median	Minimum	Maximum
Age (years)	61	20	300
Elevation (m)	975	457	1798
Basal area ($m^2 \cdot ha^{-1}$)	45	1	98
Quadratic mean diameter (cm)	23.5	9.1	71.8

$$[3] \qquad \mathrm{SIZE} = b_2(1/\mathrm{DBH}) + b_3\mathrm{DI}$$

$$[4] \qquad \mathrm{COMP} = b_4\mathrm{BA} + b_5\mathrm{BAL}$$

and RC_k is a set of dummy variables for the six rock types (RC_1 was coded 1 on deep deposits and 0 otherwise, RC_2 was coded 1 on metasedimentary rocks and 0 otherwise, RC_3 was coded 1 on granite rocks and 0 otherwise, RC_4 was coded 1 on sedimentary rocks and 0 otherwise, and RC_5 was coded 1 on basalt rocks and 0 otherwise), DBH is tree diameter at breast height (centimetres), DI is the annual diameter increment of the subject tree in the previous measurement interval (centimetres), BA is basal area (square metres) per hectare, BAL is basal area in trees larger than the subject tree (square metres per hectare) (Wykoff et al. 1982; Wykoff 1990), LGP is the length of the growth period, defined as the time interval between successive measurements of each permanent sample plot, and b_0, b_{11}, b_{12}, b_{13}, b_{14}, b_{15}, b_2, b_3, b_4, and b_5 are parameters to be estimated.

Bedrock type has been shown to be an important factor affecting stand-level growth response to N fertilization (Moore et al. 1998) and could represent differences in the forest nutritional environment (Shen et al. 2000, 2001). Therefore, rock effects were included in the individual tree mortality model as a set of dummy variables (RC) (eq. 2).

In the size effect eq. 3, DBH is a useful and reliable measure of a tree's size. Generally, the larger the tree, the greater its chances of effectively competing for scarce resources, indicating that the probability of mortality decreases with increasing DBH. Thus, many mortality models include this variable (e.g., Monserud 1976; Buchman et al. 1983; Vanclay 1991; McTague and Stansfield 1994; Monserud and Sterba 1999). The 1/DBH term allows the mortality model to estimate accurately the large mortality rates for small trees (Hamilton 1986). Average annual individual tree diameter growth rate for the preceding measurement period is a measure of individual tree vigor and has been shown to be a significant predictor of tree mortality (Hamilton 1986) and is therefore included in eq. 3. Generally, the probability of mortality decreases with increasing individual tree growth rate.

In the combined competition effect (eq. 4), overall stand density effects are represented in the mortality model by BA (Hamilton 1986). Furthermore, the probability of a tree dying within the next growing period is also likely dependent on its competitive status relative to neighboring trees, represented in the model by the BAL term (Wykoff et al. 1982; Wykoff 1990). Variable measurement period lengths in the data were dealt with by treating survival as a compound interest phenomenon. This is accomplished by inclusion of LGP in eq. 1 (Monserud 1976; Hamilton 1986).

Results

The maximum likelihood parameter estimates, standard errors, and *p* values of the parameters for the mortality model (eq. 1) are listed in Table 4 for each species. Most coefficients associated with continuous variables are statistically significant at $\alpha = 0.05$. However, BA was significant only for western white pine and western hemlock. DI was not significant for western larch, western redcedar, and west-

Table 2. Distribution of individual tree observations and site characteristics by bedrock type in the inland Northwest.

				Percentage of observations by habitat type				
Rock type	No. and percentage of observations	Mean elevation (m)	Mean slope (%)	DF	GF	WRC	WH	SAF
Deep deposit	1 378 (7.4)	910±21	28±10	0	0	7.1	92.9	0
Metasediment	11 008 (59.1)	1044±161	41±17	0.8	13.6	5.6	77.3	2.7
Mixed	2 887 (15.5)	761±105	12±16	17.5	1.5	1.6	63.3	16.1
Granite	1 118 (6.0)	1225±318	27±16	37.3	31.8	0	30.9	0
Sediment	1 080 (5.8)	960±56	15±14	10.7	10.4	78.9	0	0
Basalt	1 155 (6.2)	1092±252	22±14	51.0	23.0	26.0	0	0

Note: Habitat type: DF, Douglas-fir; GF, grand fir; WRC, western redcedar; WH, western hemlock; SAF, subalpine fir.

Table 3. Number of individual tree observations by habitat type, rock type, and species for a mortality study in the inland Northwest.

Habitat type	Rock type	Species	No. of observations
Douglas-fir	Basalt	Douglas-fir	576
		Western larch	10
	Granite	Douglas-fir	420
	Metasedimentary	Douglas-fir	91
	Mixed	Douglas-fir	497
		Western larch	9
	Sedimentary	Douglas-fir	115
Grand fir	Basalt	Douglas-fir	236
		Western larch	28
	Granite	Douglas-fir	309
		Grand fir	28
		Western larch	21
	Metasedimentary	Douglas-fir	579
		Grand fir	591
		Western white pine	213
		Western larch	119
	Mixed	Douglas-fir	42
	Sedimentary	Douglas-fir	111
Western redcedar	Basalt	Douglas-fir	180
		Western larch	20
		Grand fir	88
		Western redcedar	11
	Metasedimentary	Douglas-fir	436
		Grand fir	101
		Western white pine	30
		Western larch	52
	Mixed	Douglas-fir	46
	Sedimentary	Douglas-fir	103
		Western larch	40
		Grand fir	240
		Western redcedar	23
		Western white pine	440
	Deep deposit	Douglas-fir	90
		Western larch	8
Western hemlock	Granite	Douglas-fir	60
		Western hemlock	77
		Western larch	40
		Grand fir	50
		Western redcedar	74
		Western white pine	46

Table 3 (*concluded*).

Habitat type	Rock type	Species	No. of observations
	Metasedimentary	Douglas-fir	706
		Western hemlock	1 255
		Western larch	349
		Grand fir	2 078
		Western redcedar	457
		Western white pine	3 667
	Mixed	Douglas-fir	52
		Western hemlock	96
		Western larch	310
		Grand fir	28
		Western redcedar	848
		Western white pine	497
	Deep deposit	Douglas-fir	60
		Western hemlock	56
		Western larch	86
		Grand fir	172
		Western redcedar	161
		Western white pine	748
Subalpine fir	Metasedimentary	Douglas-fir	113
		Grand fir	65
		Western white pine	107
	Mixed	Douglas-fir	127
		Western larch	22
		Grand fir	53
		Western white pine	263
Total			18 626

Table 4. Parameter estimates for mortality models (eq. 1) of different species.

Species	Variable*	Estimates[†]	*t*	Approximate *P* >*t*	Model-fitting χ^2
Douglas-fir	Constant	–4.7638	13.4712	0.0001	13.72
	RC$_1$	0.0514ab	0.1314	0.4483	
	RC$_2$	0.4202a	2.1697	0.0201	
	RC$_3$	–0.6349b	2.0687	0.0248	
	RC$_4$	–1.8632c	2.6534	0.0074	
	RC$_5$	–1.5764c	3.6487	0.0007	
	1/DBH	5.2648	3.5556	0.0008	
	BA	0.0006	0.0715	0.4719	
	DI	–0.4457	4.3612	0.0005	
	BAL	0.0256	3.3946	0.0009	
Grand fir	Constant	–4.0909	5.9866	0.0001	21.85
	RC$_1$	–0.3538a	0.5405	0.2969	
	RC$_2$	0.0618a	0.1084	0.4573	
	RC$_3$	1.0276a	1.4662	0.0778	
	RC$_4$	–0.2225a	0.3337	0.3710	
	RC$_5$	–0.0860a	0.0945	0.4628	
	1/DBH	2.9968	3.2055	0.0026	
	BA	–0.0106	0.9812	0.1693	
	DI	–0.3568	4.3430	0.0001	
	BAL	0.0170	1.7718	0.0446	

Table 4 (*concluded*).

Species	Variable*	Estimates†	t	Approximate $P > t$	Model-fitting χ^2
Western hemlock	Constant	–5.4995	6.0067	0.0001	22.53
	RC_1	–0.4506a	0.5343	0.2989	
	RC_2	0.2543a	0.5062	0.3088	
	RC_3	–0.9619a	1.1764	0.1273	
	1/DBH	2.2287	1.8374	0.0393	
	BA	0.0298	1.7173	0.0494	
	DI	–0.4929	3.3093	0.0019	
	BAL	–0.0062	0.4262	0.3384	
Western larch	Constant	–6.9561	8.1667	0.0001	11.76
	RC_1	0.0649a	0.1303	0.4487	
	RC_2	–0.3993a	1.3194	0.0998	
	RC_3	–0.1066a	0.1371	0.4461	
	RC_4	–1.0605a	0.9352	0.1806	
	1/DBH	19.5543	3.6009	0.0008	
	BA	–0.0019	0.1095	0.4569	
	DI	0.0578	0.3153	0.3779	
	BAL	0.0614	3.5966	0.0008	
Western redcedar	Constant	–7.1117	6.4334	0.0001	25.31
	RC_1	–0.4178ab	0.6821	0.2509	
	RC_2	–1.1557a	2.0806	0.0242	
	RC_3	–1.4274a	1.5105	0.0720	
	RC_4	1.4680b	0.8301	0.2078	
	1/DBH	5.1506	3.1326	0.0030	
	BA	–0.0252	0.3422	0.3678	
	DI	–0.1651	0.4904	0.3144	
	BAL	0.0637	0.8473	0.2028	
Western white pine	Constant	–5.9578	26.0779	0.0001	35.83
	RC_1	0.8821a	5.9399	0.0001	
	RC_2	0.6814ab	5.4644	0.0001	
	RC_3	–0.3676c	0.5450	0.2954	
	RC_4	0.5759b	3.0638	0.0034	
	1/DBH	4.6124	7.2777	0.0001	
	BA	0.0146	3.4296	0.0012	
	DI	–0.0546	1.3111	0.1013	
	BAL	0.0315	7.8115	0.0001	

*RC_1, deep deposit; RC_2, metasediment; RC_3, granite; RC_4, sediment; RC_5, basalt; DBH, diameter at breast height (cm); BA, basal area ($m^2 \cdot ha^{-1}$); DI, diameter increment (cm); BAL, basal area in large trees ($m^2 \cdot ha^{-1}$).

†Parameter estimates for rock types followed by the same letters are not significantly different at the 90% confidence level by one-tailed t test.

ern white pine, and BAL was not significant for western hemlock and western redcedar. The coefficients of 1/DBH are positive and either negative or not significant for DI, indicating that the probability of mortality will be less as tree diameter and growth rate increase, respectively. The coefficients of BA and BAL are positive or not significant, indicating that the probability of mortality will be higher, or not different, as overall stand density and basal area in larger trees increase.

Predicted and observed mortality rates, along with χ^2 goodness-of-fit statistics, by rock type and species for the fit data set are provided in Table 5. The χ^2 statistics for all bedrock types and overall for each species were nonsignificant, indicating that the predictions very closely matched the observed mortality for all species and bedrock types.

Predicted average annual mortality rates derived from eq. 1 and the parameters in Table 4 are shown for each species in Fig. 2. Western white pine has the highest average mortality rate, almost 4%·year^{-1}. Grand fir has the second highest mortality, but it is only about one half that of western white pine. Western redcedar showed the lowest mortality rate, about 1%·year^{-1}.

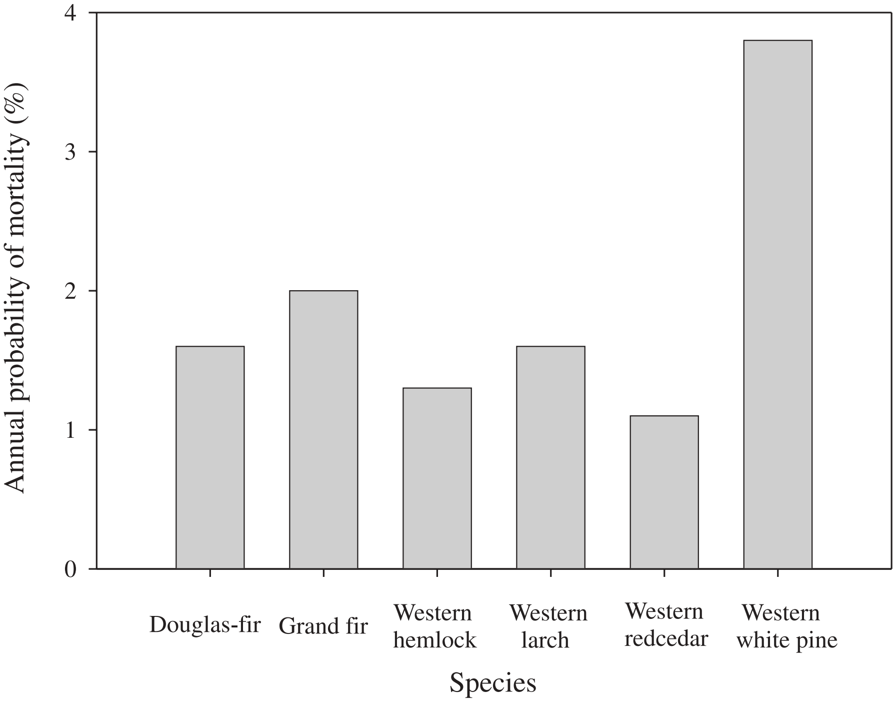
Table 5. Goodness-of-fit statistics for species mortality models (eq. 1).

			Dead trees		χ^2	
Species	Rock type	Total no. of trees	Observed	Predicted	Live trees	Dead trees
Douglas-fir	Deep deposit	150	11	10.3	0.0035	0.0476
	Metasedimentary	1925	219	221.9	0.0049	0.0379
	Mixed	764	36	36.6	0.0005	0.0098
	Granite	789	15	15.1	0.0000	0.0007
	Sedimentary	329	2	2.0	0.0000	0.0000
	Basalt	992	6	6.0	0.0000	0.0000
	Sum	4949	289	291.9	0.0090	0.0960
Grand fir	Deep deposit	172	16	16.3	0.0006	0.0055
	Metasedimentary	2835	385	386.9	0.0015	0.0093
	Mixed	81	5	5.1	0.0001	0.0020
	Granite	78	12	11.6	0.0024	0.0138
	Sedimentary	240	12	12.0	0.0000	0.0000
	Basalt	88	3	3.0	0.0000	0.0000
	Sum	3494	433	434.9	0.0046	0.0306
Western hemlock	Deep deposit	56	3	3.0	0.0000	0.0000
	Metasedimentary	1255	124	124.1	0.0000	0.0001
	Mixed	96	6	6.1	0.0001	0.0016
	Granite	77	7	7.2	0.0006	0.0056
	Sum	1484	140	140.4	0.0007	0.0073
Western larch	Deep deposit	94	8	8.1	0.0001	0.0012
	Metasedimentary	520	51	50.8	0.0001	0.0008
	Mixed	341	30	29.3	0.0016	0.0167
	Granite	61	4	3.9	0.0002	0.0026
	Sedimentary	40	1	1.1	0.0003	0.0091
	Basalt	58	0	2.0	0.0714	2.0000
	Sum	1114	94	95.2	0.0736	2.0304
Western redcedar	Deep deposit	161	10	10.0	0.0000	0.0000
	Metasedimentary	457	12	11.6	0.0004	0.0138
	Mixed	848	76	77.4	0.0025	0.0253
	Granite	74	7	7.2	0.0006	0.0056
	Sedimentary	23	1	1.0	0.0000	0.0000
	Basalt	11	0	0.1	0.0009	0.1000
	Sum	1574	106	107.3	0.0044	0.1447
Western white pine	Deep deposit	748	163	163.1	0.0000	0.0001
	Metasedimentary	4017	968	972.7	0.0073	0.0227
	Mixed	760	84	85.1	0.0018	0.0142
	Granite	46	3	2.9	0.0002	0.0034
	Sedimentary	440	53	53.0	0.0000	0.0000
	Sum	6011	1271	1276.8	0.0093	0.0404

Bedrock type effects on mortality for four of the tree species studied, representing a range of shade tolerance, are illustrated in Fig. 3. Douglas-fir and western white pine mortality rates are significantly affected by rock type, while western hemlock and western larch are not significantly affected (Table 4). Douglas-fir mortality rate is highest on metasedimentary rocks (2.8%·year^{-1}) and lowest on basalt and sedimentary rocks (each 0.3%·year^{-1}). Western white pine mortality is highest on deep deposits and also very high on metasedimentary rocks (4.2%·year^{-1}), while it is lowest on granites (1.3%·year^{-1}). Western hemlock mortality rates are relatively low across all four rock types sampled, ranging from 0.8% to 1.4% annually. Western larch mortality rates are about the same for all rock types. Although not presented in Fig. 3, grand fir mortality rates are not significantly affected by rock type, and western redcedar mortality rates are significantly higher on mixed and sedimentary rocks than on metasedimentary or granite bedrocks (Table 4).

Response surface diagrams representing the combined tree size and competitive status (BAL) effects on mortality rates are provided for four species growing on metasedimentary rocks in Fig. 4. A subject tree's competitive status decreases as BAL increases, assuming that other factors remain constant. Therefore, the upper right corner of each panel in Fig. 4 represents small, suppressed trees, while the lower left corner represents large, dominant trees (i.e., those with large DBH and low BAL). The response surface shapes correspond to the four species' relative shade tolerances. For the very shade-intolerant western larch, small trees with high BAL have a low chance of survival; however, large dominant western larch have low mortality rates (Fig. 4*a*). The response surface for shade-tolerant western hemlock is flat

Fig. 2. Predicted average annual individual tree mortality rates from eq. 1 for each species in the inland Northwest.



compared with the other species, indicating low mortality rate for all DBH and BAL combinations (Fig. 4*d*). Western white pine and Douglas-fir are intermediate in shade tolerance between western larch and western hemlock, as are their DBH and BAL response surface diagrams (Figs. 4*b* and 4*c*).

Discussion

The mortality prediction equations developed in this study could eventually be used with individual tree growth simulation models, such as the forest vegetation simulator (Wykoff et al. 1982), which is widely used to forecast growth and yield in the inland Northwest. However, before these equations could be used in the forest vegetation simulator, other component models, such as individual tree increment models, should also be modified to include rock type effects. Other statistical considerations, such as errors in variables, may also be important in evaluating model prediction properties.

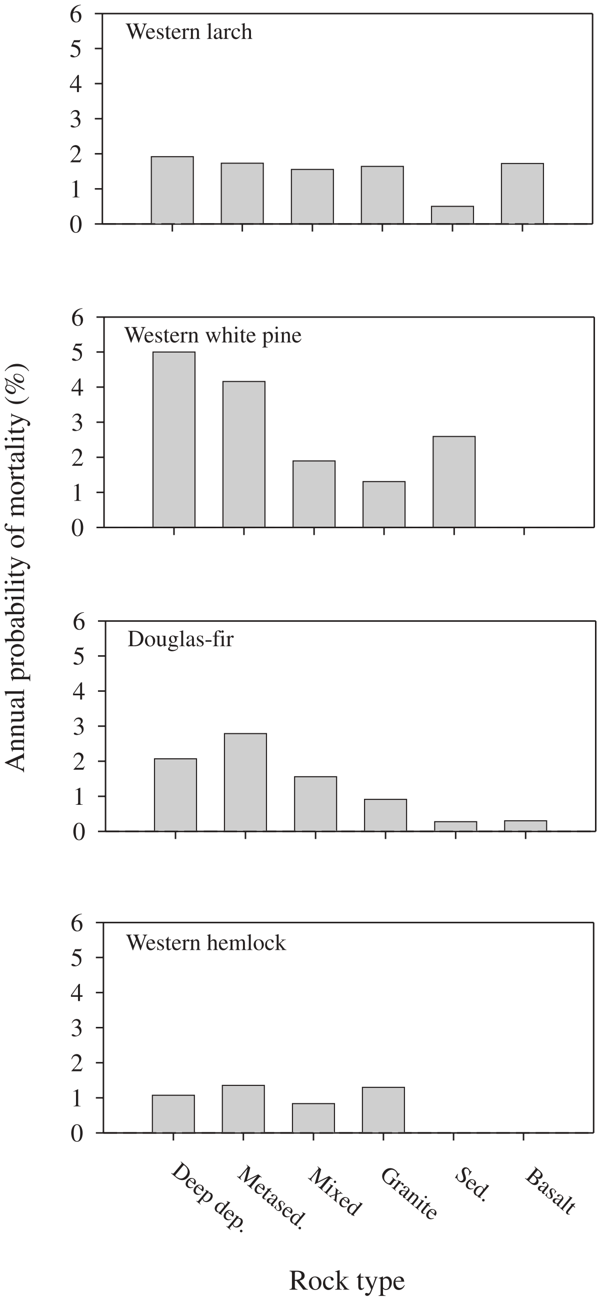
We are primarily interested in describing the quantitative ecology for the conifer species in our study rather than mortality prediction per se. Our results show that western white pine, Douglas-fir, and western redcedar mortality rates were significantly affected by rock type, while grand fir, western hemlock, and western larch were not affected. Why do some rock types produce different mortality rates for some species and not for others? The answer probably depends on both rock attributes and tree species characteristics. It is difficult to generalize about the high mortality rates on the deep deposit "rock" category, since it is composed of various surficial deposits. We speculate that these generally sandy soils provide a poor nutrient and moisture environment for tree growth.

Shen et al. (2001) and Moore et al. (2004) demonstrated that trees growing on different rock types have different foliar nutrient concentrations, particularly for K. Trees grown on metasedimentary rocks had the lowest foliar K concentrations, while trees on basalts and sedimentary rocks showed the highest foliar concentrations.

Geochemical analyses of rock samples collected from 10 Intermountain Forest Tree Nutrition Cooperative research sites distributed throughout the inland Northwest are noticeably different by rock type (Fig. 5). The SiO_2 content of metasedimentary rocks sampled is much higher than for basalts (83% versus 52%, respectively), while important mineral nutrients such as Fe, Ca, and Mg are proportionately lower for metasedimentary rocks. Some metasedimentary rocks have SiO_2 content in excess of 90%, with proportionately lower contents for other mineral nutrients. However, basalts have somewhat lower average K content than granite and metasedimentary rocks. Rock mineral nutrient content is important but not the only factor influencing forest tree nutrient availability. For example, rock weathering rates and different soil physical properties derived from different rocks are also important determinants of the forest nutrient environment. Soils derived from basaltic and sedimentary rocks tend to be richer in clay minerals and have a higher cation-exchange capacities, and granite rocks tend to weather to sandy soils, with low cation-exchange capacities (Buol et al. 1989). Many metasedimentary rocks weather very slowly due to high silica content and a mineralogic composition containing a high proportion of residual products from previous rock weathering (Birkeland 1999).

We believe that metasedimentary rocks provide trees with a poor nutrient supply, thus accounting for high mortality rates on these rocks. Our supposition that high mortality rates on metasedimentary rocks are nutritionally related rather than explained by some other site factor associated

Fig. 3. Predicted average annual individual tree mortality rates from eq. 1 by species and rock type in the inland Northwest.



with this bedrock type is supported by the data in Table 2. Although the slopes where sample plots occurred on metasedimentary rocks were somewhat steeper than for other rock types, the average elevation for the metasedimentary plots is near the mean elevation for all rock types. Importantly, the majority of metasedimentary plots were situated on western hemlock habitat series, which represent the moistest growing conditions in the region (Daubenmire and Daubenmire 1968; Pfister et al. 1977; Cooper et al. 1991). Therefore, in theory, trees on western hemlock habitat types should experience less moisture stress than those growing on other habitat type series. Even though metasedimentary plots are generally located in relatively high-moisture areas, they still produce significantly higher tree mortality rates for western white pine and Douglas-fir.

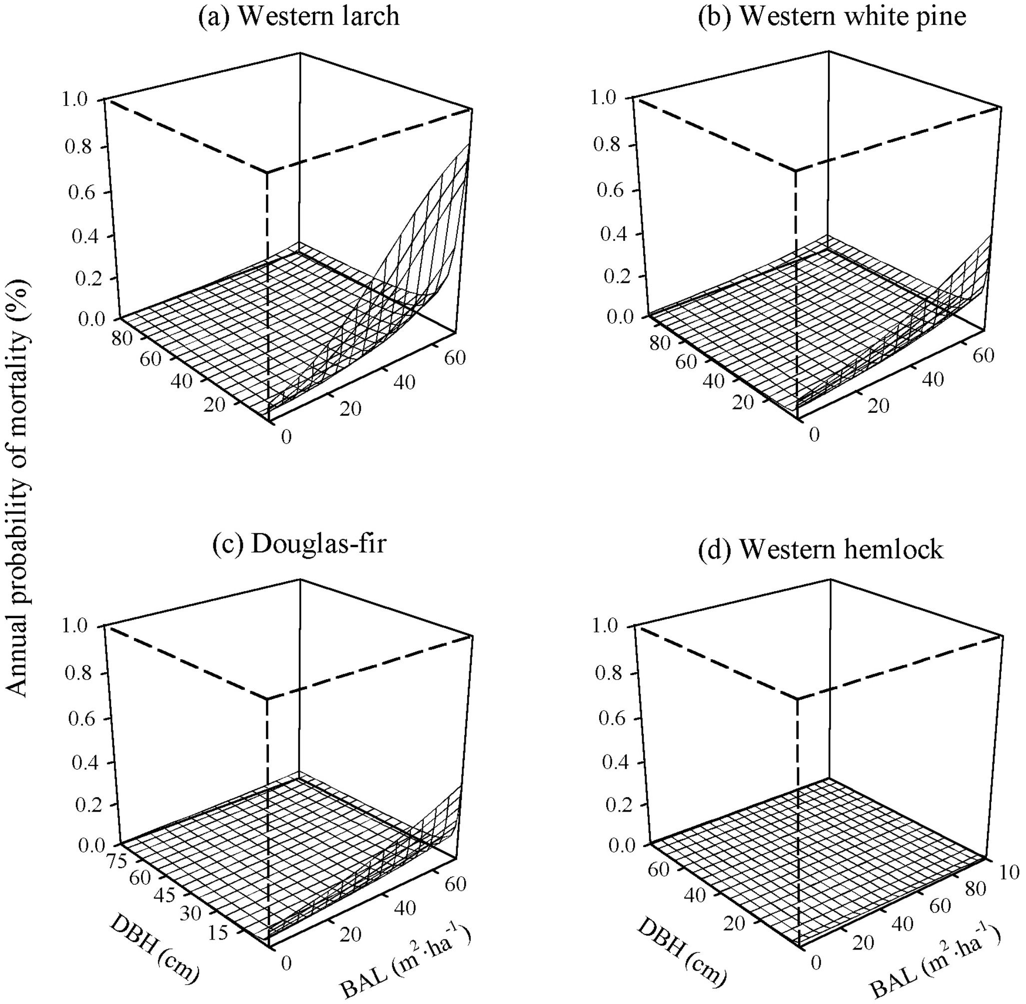
Our results, with respect to tree mortality differences by rock type, support those of Shen et al. (2001) and indicate that rock type represents broad differences in the nutrient environment where trees grow. A biological explanation for the mortality rate relationships may be that tree nutrient status differs by rock type, thus producing tree biochemical differences resulting in different tree susceptibility levels to diseases and insects (Mika and Moore 1991; Entry et al. 1991; Shaw et al. 1998; Shen et al. 2001).

Little has been published regarding the nutrient requirements of western white pine and western larch, particularly for forest-grown, mature trees. Some information regarding nutrient regimes used by seedling nurseries for growing the two species is available. Western white pine requires substantial nutrient inputs during a greenhouse growing regime, while western larch requires less nutrients than any other western conifer (D.L. Wenny, Professor, Forest Resources, College of Natural Resources, University of Idaho, personal communication). Interior Douglas-fir has been shown to be very responsive to nutrient status changes following fertilization (Shafii et al. 1989, 1990; Moore et al. 1991, 1994, 1998) and, by inference, should be a nutrient-demanding species. Western hemlock may have lower nutrient requirements than some species or be very efficient in acquiring required nutrients.

We surmise based on the above information that western larch and western hemlock would be less affected by the amount of nutrients available on a site, and thus by rock type, than western white pine or Douglas-fir. Regardless of the true nutrient requirement rankings of the species in our study, rock type affected western white pine and Douglas-fir more than western larch and western hemlock. Grand fir mortality rates across rock types had a pattern similar to hemlock. Sedimentary and mixed rocks produced the highest mortality rate for western redcedar, unlike the mortality pattern for other species.

The DBH–BAL mortality response surface shapes (Fig. 4) correspond to species relative shade tolerance rankings. The degree of upward sloping for the mortality surface decreases with increasing shade tolerance. For shade-intolerant western larch, large dominant western larch have low mortality rates, while suppressed western larch have very high mortality rates (Fig. 4*a*). The response surface for shade-tolerant western hemlock is flat, indicating low mortality rates for all DBH and BAL combinations (Fig. 4*d*). Our results show that both rock type and suppression substantially contribute to explaining mortality for western white pine and Douglas-fir, while most western larch mortality occurred in small suppressed trees across all rock types. Western hemlock mortality rates were low across all rock types, even for small, suppressed trees. In addition, our data suggest that western white pine blister rust may be more common on metasedimentary rocks (and deep deposits), since blister rust is the most common mortality factor for western white pine and mortality rates are highest for these rock types. Our data come from natural western white pine stands, not from selected genotypes bred for genetic resistance to western white pine blister rust. Western white pine's average annual mortality rate of 4.2% on metasedimentary rocks means that, on

Fig. 4. Combined tree size (DBH) and competitive status (BAL) effects on individual tree annual mortality probability from eq. 1 for four tree species in the inland Northwest.


(a) Western larch

(b) Western white pine

(c) Douglas-fir

(d) Western hemlock

average, only 34% of the western white pine would survive after 25 years. These remarkably high mortality rates are supported by the estimates provided by Fins et al. (2002) for unimproved western white pine across various rock types.

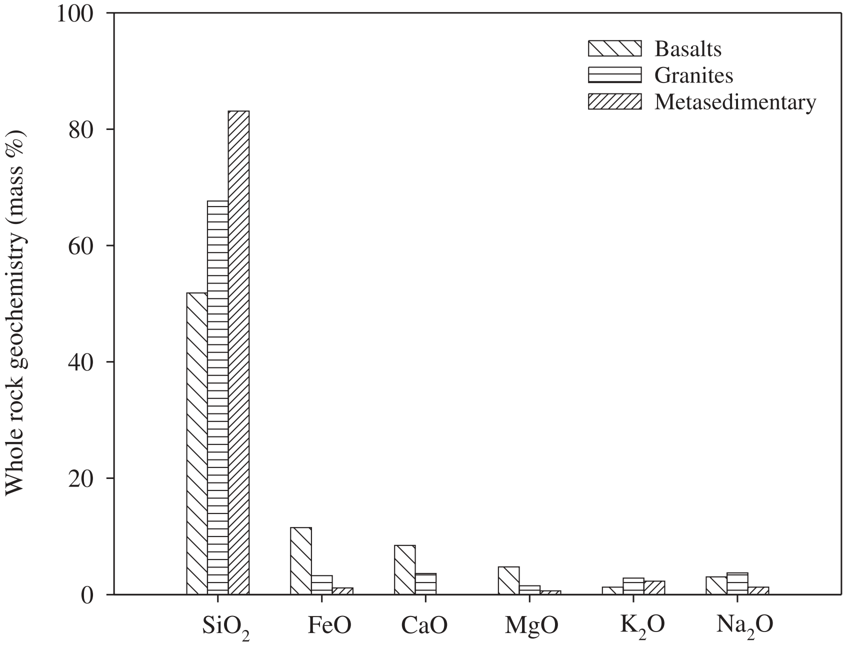
The ecological implications of our results are that western hemlock would eventually dominate stands where it occurs, particularly on "nutrient-poor" rocks like metasedimentary types, while other species (except for large dominant western larch and western redcedar) would have much lower survival. These generalities are confirmed by the composition of undisturbed older stands currently occurring in the inland Northwest. Perhaps rock type plays an important role, in addition to moisture and temperature, in determining climax vegetation on a site and therefore habitat type land classifications such as described in Pfister et al. (1977).

Conclusions

The combined tree size (DBH) and competitive status (BAL) effects on individual tree mortality rates correspond to species relative shade tolerance rankings. For shade-intolerant western larch, large dominant trees have low mortality rates, while small, suppressed trees have very high mortality rates. The mortality response surface for all DBH and BAL combinations for shade-tolerant western hemlock is flat, with low mortality rates. Western white pine and Douglas-fir response surface shapes are intermediate between those of larch and hemlock.

Western white pine, Douglas-fir, and western redcedar mortality rates were significantly affected by rock type, while western hemlock, grand fir, and western larch were not affected. Both rock type and suppression account for western white pine and Douglas-fir mortality, while most western larch mortality occurred in small, suppressed trees across all rock types. Western white pine and Douglas-fir growing on soils developed from metasedimentary rocks exhibited greater mortality probabilities than for other rock types. Our study quantitatively demonstrates differences in tree mortality across broad differences in the nutrient environment represented by different bedrock types. The relationships developed in this study, when combined with other individual tree growth component models modified to include the effect of rock type, should provide the capability to simulate substantially different stand development trajectories for various tree species and rock type combinations. Incorporating these new relationships into growth and yield

Fig. 5. Whole-rock geochemical analyses for silica, iron, calcium, magnesium, potassium, and sodium oxides for three common rock types from 10 sites in the inland Northwest. Whole-rock geochemical analyses were performed using X-ray fluorescence (Hooper et al. 1993).



simulators, such as the forest vegetation simulator, would provide land managers with the ability to include these effects in the management planning process.

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