

# 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.

[Traduit par la Rédaction]

## 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 explain-

ing 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

Received 6 January 2003. Accepted 11 August 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 19 December 2003.

**J.A. Moore<sup>1</sup>** and **Y. Xiao**. Department of Forest Resources, University of Idaho, Moscow, ID 83844-1133, U.S.A.

**D.A. Hamilton, Jr., and J. Byrne**. Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Moscow, ID 83843, U.S.A.

<sup>1</sup>Corresponding author (e-mail: [jamoore@uidaho.edu](mailto:jamoore@uidaho.edu)).

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.

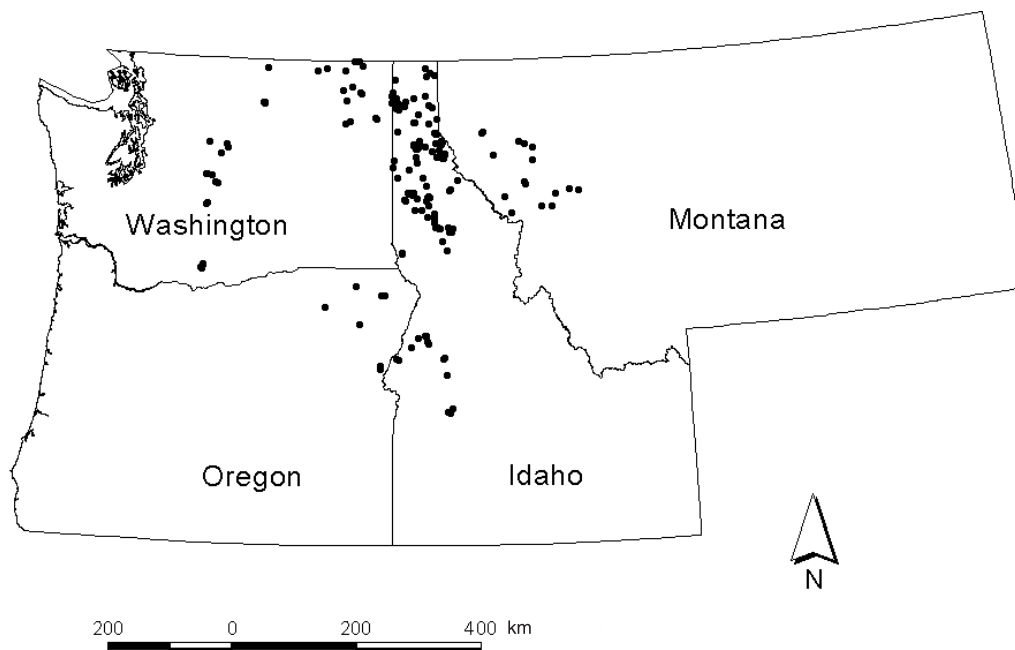
### Analysis: mortality model

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:

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

where  $P$  is the annual probability of tree mortality and

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

**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 ( $\text{m}^2\text{-ha}^{-1}$ ) | 45     | 1       | 98      |
| Quadratic mean diameter (cm)               | 23.5   | 9.1     | 71.8    |

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

$$[4] \quad \text{COMP} = b_4\text{BA} + b_5\text{BAL}$$

and  $\text{RC}_k$  is a set of dummy variables for the six rock types ( $\text{RC}_1$  was coded 1 on deep deposits and 0 otherwise,  $\text{RC}_2$  was coded 1 on metasedimentary rocks and 0 otherwise,  $\text{RC}_3$  was coded 1 on granite rocks and 0 otherwise,  $\text{RC}_4$  was coded 1 on sedimentary rocks and 0 otherwise, and  $\text{RC}_5$  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; Vancley 1991; McTague and Stansfield 1994; Monserud and Sterba 1999). The  $1/\text{DBH}$  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 North-west.

| Rock type    | No. and percentage of observations | Mean elevation (m) | Mean slope (%) | Percentage of observations by habitat type |      |      |      |      |
|--------------|------------------------------------|--------------------|----------------|--------------------------------------------|------|------|------|------|
|              |                                    |                    |                | 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                 |
|                  |                 | Douglas-fir        | 91                  |
|                  | Mixed           | Douglas-fir        | 497                 |
|                  |                 | Western larch      | 9                   |
| Grand fir        | Sedimentary     | Douglas-fir        | 115                 |
|                  |                 | Douglas-fir        | 236                 |
|                  | Basalt          | Western larch      | 28                  |
|                  |                 | Douglas-fir        | 309                 |
|                  | Granite         | Grand fir          | 28                  |
|                  |                 | Western larch      | 21                  |
|                  | Metasedimentary | Douglas-fir        | 579                 |
|                  |                 | Grand fir          | 591                 |
|                  | Mixed           | Western white pine | 213                 |
|                  |                 | Western larch      | 119                 |
|                  | Sedimentary     | Douglas-fir        | 42                  |
|                  |                 | 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                  |
|                  |                 | Douglas-fir        | 103                 |
|                  | Sedimentary     | 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 |
|---------------|-----------------|--------------------|---------------------|
| Subalpine fir | 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                 |
|               | Metasedimentary | Douglas-fir        | 113                 |
|               |                 | Grand fir          | 65                  |
|               | Mixed           | Western white pine | 107                 |
|               |                 | 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 <sup>†</sup> | <i>t</i> | Approximate <i>P</i> > <i>t</i> | Model-fitting $\chi^2$ |
|-------------|-----------------|------------------------|----------|---------------------------------|------------------------|
| Douglas-fir | Constant        | -4.7638                | 13.4712  | 0.0001                          | 13.72                  |
|             | RC <sub>1</sub> | 0.0514ab               | 0.1314   | 0.4483                          |                        |
|             | RC <sub>2</sub> | 0.4202a                | 2.1697   | 0.0201                          |                        |
|             | RC <sub>3</sub> | -0.6349b               | 2.0687   | 0.0248                          |                        |
|             | RC <sub>4</sub> | -1.8632c               | 2.6534   | 0.0074                          |                        |
|             | RC <sub>5</sub> | -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 <sub>1</sub> | -0.3538a               | 0.5405   | 0.2969                          |                        |
|             | RC <sub>2</sub> | 0.0618a                | 0.1084   | 0.4573                          |                        |
|             | RC <sub>3</sub> | 1.0276a                | 1.4662   | 0.0778                          |                        |
|             | RC <sub>4</sub> | -0.2225a               | 0.3337   | 0.3710                          |                        |
|             | RC <sub>5</sub> | -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 <sup>†</sup> | <i>t</i> | Approximate<br><i>P</i> > <i>t</i> | Model-<br>fitting $\chi^2$ |
|--------------------|-----------------|------------------------|----------|------------------------------------|----------------------------|
| Western hemlock    | Constant        | -5.4995                | 6.0067   | 0.0001                             | 22.53                      |
|                    | RC <sub>1</sub> | -0.4506a               | 0.5343   | 0.2989                             |                            |
|                    | RC <sub>2</sub> | 0.2543a                | 0.5062   | 0.3088                             |                            |
|                    | RC <sub>3</sub> | -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 <sub>1</sub> | 0.0649a                | 0.1303   | 0.4487                             |                            |
|                    | RC <sub>2</sub> | -0.3993a               | 1.3194   | 0.0998                             |                            |
|                    | RC <sub>3</sub> | -0.1066a               | 0.1371   | 0.4461                             |                            |
|                    | RC <sub>4</sub> | -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                             |                            |
| Western redcedar   | Constant        | -7.1117                | 6.4334   | 0.0001                             | 25.31                      |
|                    | RC <sub>1</sub> | -0.4178ab              | 0.6821   | 0.2509                             |                            |
|                    | RC <sub>2</sub> | -1.1557a               | 2.0806   | 0.0242                             |                            |
|                    | RC <sub>3</sub> | -1.4274a               | 1.5105   | 0.0720                             |                            |
|                    | RC <sub>4</sub> | 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                             |                            |
| Western white pine | Constant        | -5.9578                | 26.0779  | 0.0001                             | 35.83                      |
|                    | RC <sub>1</sub> | 0.8821a                | 5.9399   | 0.0001                             |                            |
|                    | RC <sub>2</sub> | 0.6814ab               | 5.4644   | 0.0001                             |                            |
|                    | RC <sub>3</sub> | -0.3676c               | 0.5450   | 0.2954                             |                            |
|                    | RC <sub>4</sub> | 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<sub>1</sub>, deep deposit; RC<sub>2</sub>, metasediment; RC<sub>3</sub>, granite; RC<sub>4</sub>, sediment; RC<sub>5</sub>, basalt; DBH, diameter at breast height (cm); BA, basal area (m<sup>2</sup>·ha<sup>-1</sup>); DI, diameter increment (cm); BAL, basal area in large trees (m<sup>2</sup>·ha<sup>-1</sup>).

<sup>†</sup>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  $\chi^2$  goodness-of-fit statistics, by rock type and species for the fit

data set are provided in Table 5. The  $\chi^2$  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<sup>-1</sup>. 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<sup>-1</sup>.

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

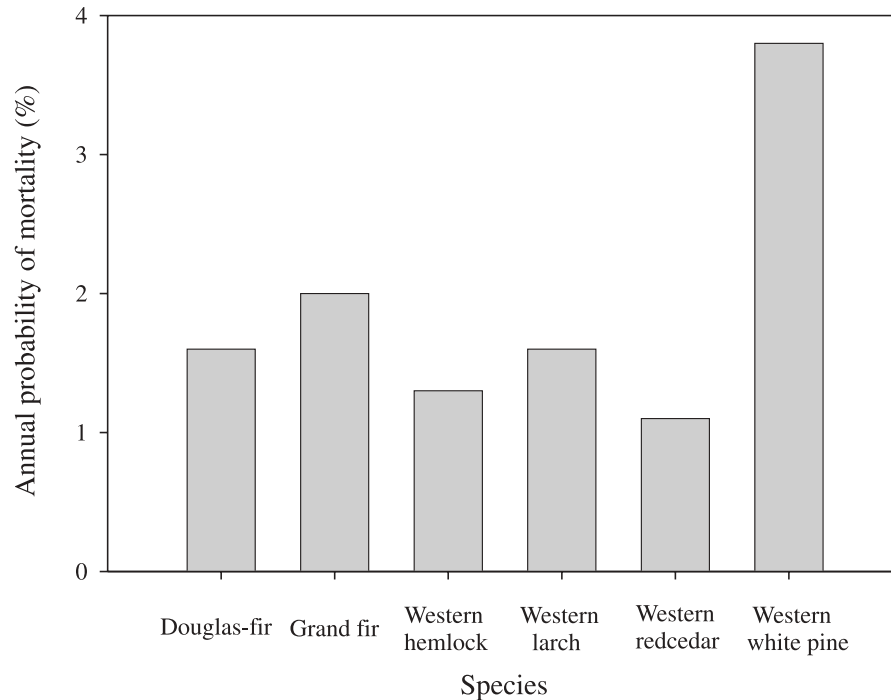
| Species            | Rock type       | Total no.<br>of trees | Dead trees |           | $\chi^2$      |               |
|--------------------|-----------------|-----------------------|------------|-----------|---------------|---------------|
|                    |                 |                       | Observed   | Predicted | Live<br>trees | Dead<br>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 ( $2.8\% \cdot \text{year}^{-1}$ ) and lowest on basalt and sedimentary rocks (each  $0.3\% \cdot \text{year}^{-1}$ ). Western white pine mortality is highest on deep deposits and also very high on metasedimentary rocks ( $4.2\% \cdot \text{year}^{-1}$ ), while it is lowest on granites ( $1.3\% \cdot \text{year}^{-1}$ ). 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. 4a). 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. 4d). 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. 4b and 4c).

## 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.

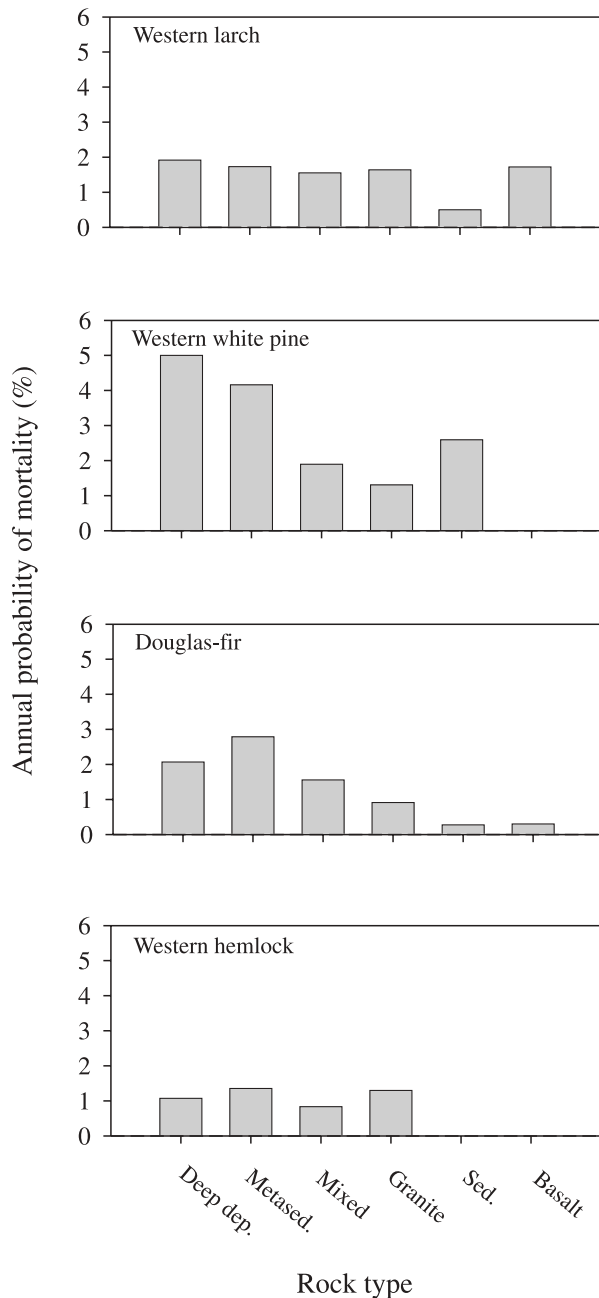
We are primarily interested in describing the quantitative ecology for the conifer species in our study rather than mortality prediction per se. Our results show that western white pine, Douglas-fir, and western redcedar mortality rates were significantly affected by rock type, while grand fir, western 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<sub>2</sub> 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<sub>2</sub> 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.

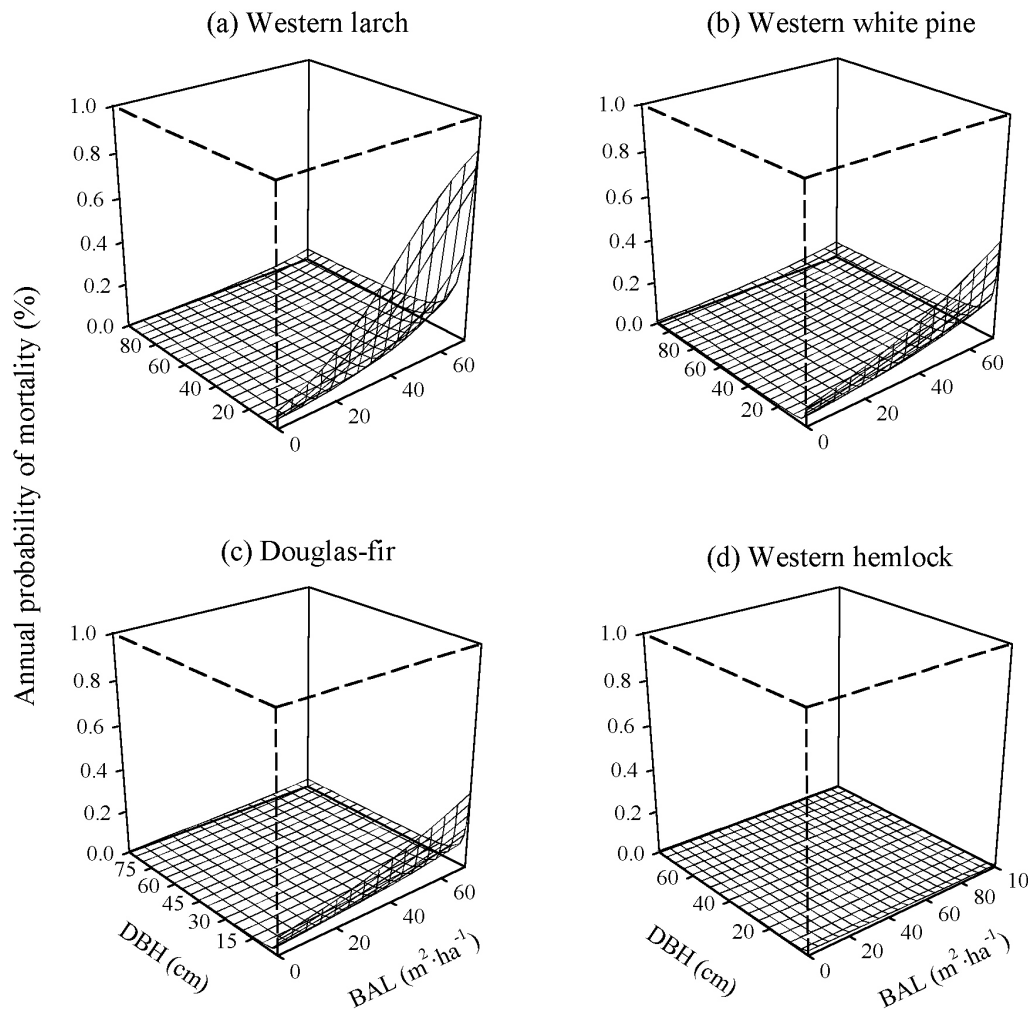
Our results, with respect to tree mortality differences by rock type, support those of Shen et al. (2001) and indicate that rock type represents broad differences in the nutrient environment where trees grow. A biological explanation for the mortality rate relationships may be that tree nutrient status 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. 4a). The response surface for shade-tolerant western hemlock is flat, indicating low mortality rates for all DBH and BAL combinations (Fig. 4d). 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.



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).

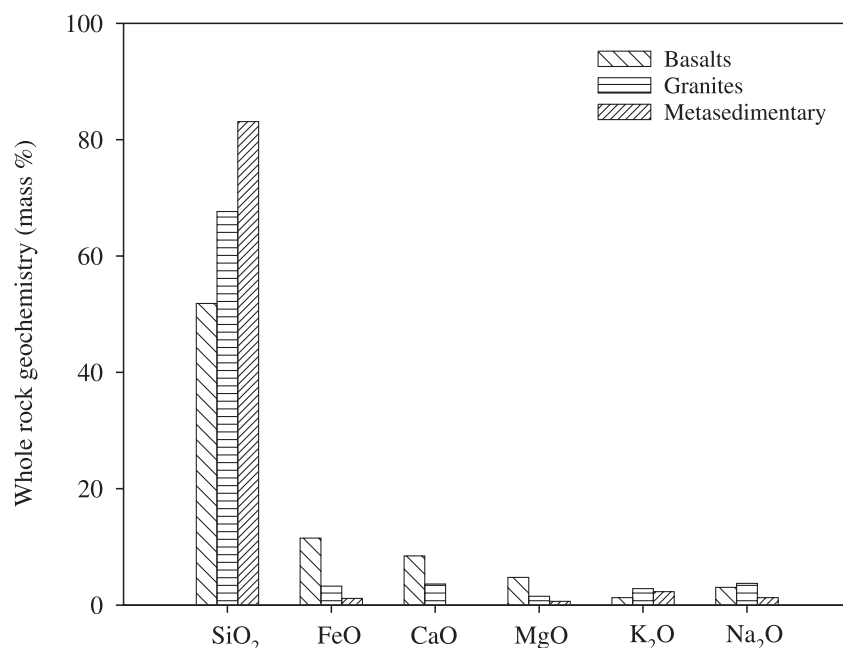
## Conclusions

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.

## Acknowledgments

The authors thank Intermountain Forest Tree Nutrition Cooperative members for their support. College of Forestry, Wildlife and Range Experiment Station, University of Idaho, contribution.

## References

- Birkeland, P.W. 1999. Soils and geomorphology. 3rd ed. Oxford University Press, Inc., New York.
- Buchman, R.G., Pederson, S.P., and Walters, N.R. 1983. A tree survival model with application to species of the Great Lakes region. *Can. J. For. Res.* **13**: 601–608.
- Buol, S.W., Hole, F.D., and McCracken, R.J. 1989. Soil genesis and classification. 3rd ed. Iowa State University Press, Ames, Iowa.
- Burmester, R.F., Frost, T.P., Kauffman, J.D., and Lewis, R.S. 2001. Digital geologic map of the St. Maries 30 × 60 min quadrangle, Idaho. Preliminary release 3/15/2001. Idaho Geological Survey, Moscow, Idaho.
- Cooper, S.V., Neiman, K.E., and Roberts, D.W. 1991. Forest habitat types of northern Idaho: a second approximation. U.S. For. Serv. Gen. Tech. Rep. INT-236.
- Daubenmire, R., and Daubenmire, J.B. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. Agric. Exp. Stn. Tech. Bull.* 60.
- Entry, J.A., Cromack, K., Jr., Kelsey, R.G., and Martin, N.E. 1991. Response of Douglas-fir to infection by *Armillaria ostoyae* after thinning or thinning plus fertilization. *Phytopathology*, **81**: 682–689.
- Ferguson, D.E., Stage, A.R., and Boyd, R.J. 1986. Predicting regeneration in the grand fir – cedar – hemlock ecosystem of the Northern Rocky Mountains. *For. Sci. Monogr.* 26.
- Fins, L., Byler, J.W., Ferguson, D.E., Harvey, A.E., Mahalovich, M.F., McDonald, G.I., Miller, D.L., Schwandt, J.W., and Zack, A. 2002. Return of the giants: restoring western white pine to the inland Northwest. *J. For.* **100**: 20–26.
- Hamilton, D.A. 1974. Event probabilities estimated by regression. U.S. For. Serv. Res. Pap. INT-152.
- Hamilton, D.A. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. *For. Sci.* **32**: 989–1000.
- Hooper, P.R., Johnson, D.M., and Conrey, R.M. 1993. Major and trace element analyses of rocks and minerals by automated X-ray spectrometry. Open file report. Washington State University Geology Department, Pullman, Wash.
- Idaho Geological Survey. 1996. Digital geologic map compilation of north central Idaho by 30 × 60 minute quadrangles [compact disc]. Idaho Geological Survey, Moscow, Idaho.
- Lewis, R.S., and Derkey, P.D. 1999. Digital geologic map of part of the Thomopson Falls 1:100,000 quadrangle, Idaho. U.S. Geological Survey, Washington, D.C. Open-File Rep. OF-99-390.
- Lewis, R.S., Burmester, R.F., McFadden, M.D., Derkey, P.D., and Oblad, J.R. 1999. Digital geologic map of the Wallace 1:100,000 quadrangle, Idaho. Geological Survey, Washington, D.C. Open-File Rep. OF-99-390. U.S.
- McTague, J.P., and Stansfield, W.F. 1994. Stand and tree dynamics of uneven-aged ponderosa pine. *For. Sci.* **40**: 289–302.
- Mika, P.G., and Moore, J.A. 1991. Foliar potassium status explains Douglas-fir response to nitrogen fertilization in the inland Northwest, U.S.A. *Water Air Soil Pollut.* **54**: 477–491.
- Miller, F.K., Burmester, R.F., Powell, R.E., Miller, D.M., and Derkey, P.D. 1999. Digital geologic map of the Sandpoint 1 degree × 2 degree quadrangle, Washington, Idaho and Montana. U.S. Geological Survey, Washington, D.C. Open-File Rep. OF-99-144.

- Monserud, R.A. 1976. Simulation of forest tree mortality. *For. Sci.* **22**: 438–444.
- Monserud, R.A., and Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* **113**: 109–123.
- Moore, J.A., Mika, P.G., and Vander Ploeg, J. 1991. Nitrogen fertilizer response of Rocky Mountain Douglas-fir by geographic area across the inland Northwest. *West. J. Appl. For.* **6**: 94–98.
- Moore, J.A., Zhang, L., and Newberry, J.D. 1994. Effects of intermediate silvicultural treatments on the distribution of within-stand growth. *Can. J. For. Res.* **24**: 398–404.
- Moore, J.A., Hanley, D.P., Chappell, H.N., Shumway, J.S., Webster, S.B., and Mandzak, J.M. 1998. Fertilizing eastern Washington coniferous forests. Washington State University, Pullman, Wash. Wash. State Univ. Coop. Ext. Bull. EB1874.
- Moore, J.A., Mika, P.G., Shaw, T.M., and Johnston, M.G. 2004. Foliar nutrient characteristics of four conifer species in the interior northwest United States. *West. J. Appl. For.* **19**(1). In press.
- Munts, S.R., and Idaho Geological Survey. 2000. Digital geologic map of the Coeur d'Alene 1:100,000 quadrangle, Idaho and Montana. U.S. Geological Survey, Washington, D.C. Open-File Rep. OF-00-135.
- Pfister, R.D., Kovalchik, B.L., Arno, S.F., and Presby, R.C. 1977. Forest habitat types of Montana. U.S. For. Serv. Gen. Tech. Rep. INT-34.
- Shafii, B., Moore, J.A., and Olson, J.R. 1989. Effects of nitrogen fertilization on growth of grand fir and Douglas-fir stands in northern Idaho. *West. J. Appl. For.* **4**: 54–57.
- Shafii, B., Moore, J.A., and Newberry, J.D. 1990. Individual-tree diameter growth models for quantifying within-stand response to nitrogen fertilization. *Can. J. For. Res.* **20**: 1149–1155.
- Shaw, T.M., Moore, J.A., and Marshall, J.D. 1998. Root chemistry of Douglas-fir seedlings grown under different nitrogen and potassium regimes. *Can. J. For. Res.* **28**: 1566–1573.
- Shen, G., Moore, J.A., and Hatch, C.R. 2000. The effect of habitat type and rock type on individual tree basal area growth response to nitrogen fertilization. *Can. J. For. Res.* **30**: 613–623.
- Shen, G., Moore, J.A., and Hatch, C.R. 2001. The effect of nitrogen fertilization, rock type, and habitat type on individual tree mortality. *For. Sci.* **47**: 203–213.
- Vanclay, J.K. 1991. Mortality functions for north Queensland rain forests. *J. Trop. For. Sci.* **4**: 15–36.
- Wykoff, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.* **36**: 1077–1104.
- Wykoff, W.R., Crookston, N.J., and Stage, A.R. 1982. User's guide to the stand prognosis model. U.S. For. Serv. Gen. Tech. Rep. INT-133.