The Effect of Nitrogen Fertilization, Rock Type, and Habitat Type on Individual Tree Mortality

Guanghong Shen, James A. Moore, and Charles R. Hatch

ABSTRACT. An individual tree mortality model for nitrogen fertilized Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) stands was developed using data from permanent research plots located throughout the inland Northwest. The proposed linear logistic model included the following independent variables: a dummy variable for the two habitat types, a set of dummy variables for the five rock types, a set of dummy variables for the three N fertilizer treatments, diameter at breast height, crown ratio, and crown competition factor. The results show that N fertilization, rock type, and habitat type significantly affect individual tree mortality. The probabilities of tree mortality on fertilized plots were greater than those on control plots and increased with increasing N fertilizer application rates. Trees growing on granitic and metasedimentary rocks had lower foliar potassium concentration and exhibited greater probabilities of mortality than did those growing on other rocks. The probabilities of mortality for trees growing on sedimentary rocks were very low. Moist sites had lower soil fertility and produced higher mortality rates than dry sites. Furthermore, the N fertilization response ratio, defined as the annual mortality probability of a fertilized tree over the annual mortality probability of a unfertilized tree with identical tree and stand characteristics, was estimated based on the mortality model. The response ratios were nearly constant (about 1.4) across a range of tree diameters for all rock types with the 224 kg N treatment. The response ratios were also nearly constant (about 2.1) across a range of tree diameters for all rock types with the 448 kg N treatment. Finally, the mortality prediction model passed a validation test on independent data not used in model development. For. Sci. 47(2):203–213.

Key Words: *Pseudotsuga menziesii* var. *glauca*, logistic function, mortality prediction, soil fertility, foliar potassium.

INTERIOR DOUGLAS-FIR (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) is important in a wide range of forest types for a wide array of nontimber values, and also plays a critical role in local and regional economies as a raw material for wood and paper products in the inland Northwest. Therefore, forest managers apply intermediate silvicultural treatments, such as cleaning, thinning, and fertilization, to Douglas-fir stands to achieve specific management goals.

In the inland Northwest, forest fertilization research began in the early 1960s (Loewenstein and Pitkin 1963, 1971). Early work focused on growth response of grand fir (*Abies grandis* [Dougl.] Lindl.) and Douglas-fir stands to thinning and nitrogen fertilization in northern Idaho (Olson 1981, Scanlin and Loewenstein 1981, Shafii et al.1989). Recently, considerable research has shown that N fertilization can significantly increase basal area or volume growth (Mika and Moore 1991, Shafii et al.1990, Stage et al. 1990, Mika and Vander Ploeg 1991, Moore et al.1991, 1994, Mika et al.1992, Mital 1995, Avila 1997). Larger trees in a stand showed greater diameter growth response

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to N fertilization than smaller trees, and individual trees in low-density stands exhibited more fertilization response than those growing in high-density stands (Shafii et al. 1990). Furthermore, rock type proved to be an important factor affecting stand-level growth response to N fertilization (Mika et al. 1992, Mital 1995), as well as the pattern of individual tree growth response within a stand (Shen et al. 2000). Forest habitat type (Daubenmire and Daubenmire 1968) and rock type are now used to guide operational fertilization programs in the region (Moore et al. 1998). However, there are no published individual tree mortality models that relate the probability of mortality to N fertilizer treatment, rock type, stand attributes, and tree attributes and that are compatible with growth simulation models, such as Forest Vegetation Simulator (FVS) (Wykoff et al. 1982), used in the region.

Informed forest management decisions need 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 predict accurately (Dobbertin and Biging 1998). Lee (1971) distinguished between regular and irregular tree mortality. Regular mortality can be defined as the mortality due to competition for scarce resources, or due to tree age, insects, and diseases at endemic levels. In contrast, irregular mortality is caused by some catastrophic event, for instance, fire, windthrow, or epidemic insect levels. In our study, only regular tree mortality was considered.

Current mortality-modeling approaches can be grouped into two categories: traditional parametric methods and modern computer-intensive statistical methods. For traditional parametric methods, parameters of a flexible nonlinear function bounded by 0 and 1 are estimated using maximum likelihood estimation or other procedures. The probability of a tree dying within the next growing period, given the individual tree and stand characteristics, is computed in terms of this function. Conceptually, any nonlinear function that is defined in the range of 0 to 1 can be used to model individual tree mortality. However, only a few functions have been used to model individual tree mortality. These functions include the negative exponential function (Moser 1972), the logistic function (Hamilton 1974), the Weibull function (Somers et al. 1980), the Richard's function (Buford and Hafley 1985), and the exponential function (Kobe and Coates 1997). Of these functions, the logistic function is the most widely employed (Hamilton 1974, 1980, 1986, 1990, Hamilton and Wendt 1975, Hamilton and Edwards 1976, Monserud 1976, Buchman 1979, Buchman et al. 1983, Hann 1980, Lowell and Mitchell 1987, Vanclay 1991a, 1991b, 1995, Avila and Burkhart 1992, Zhang et al. 1997, Monserud and Sterba 1999). Its widespread application is probably due to wide availability of logistic regression software and the logistic function's flexibility and robustness.

In addition, classification and regression trees (CART) (Dobbertin and Biging 1998) and neural networks (Guan and Gertner 1991) have been used to model individual tree mortality. Neither classification trees nor neural networks have led to significant improvement in our ability to predict mortality over analyses that use logistic regression methods (Hasenauer and Merkl 1997, Monserud and Sterba 1999). Therefore, we used traditional parametric methods in order to perform tests of hypotheses easily.

There are no published individual tree mortality models that relate fertilization response to rock type, habitat type, stand characteristics, and tree characteristics and are compatible with growth and yield simulation models used in the region (Wykoff et al. 1982). Therefore, the primary objective of this study was to develop an individual tree mortality model and assess the effect of N fertilization, rock type, and habitat type on tree mortality. We were particularly interested in exploring mortality differences following N fertilization on various rock types that we feel represent broad differences in the forest nutrient environment.

Data

Data used in the model development were obtained from Intermountain Forest Tree Nutrition Cooperative (IFTNC) study sites. The study area includes six geographic regions: northern Idaho, western Montana, central Idaho, northeast Oregon, central Washington, and northeast Washington. From 1980 to 1982, the IFTNC established a total of 94 fertilizer trials (installations) throughout the 6 regions.

Installations were located in second-growth, even-aged, managed Douglas-fir stands. Most stands had been thinned 5 to 12 yr prior to plot establishment; a few stands were unthinned, but naturally well spaced. Stands were selected to represent a range of stand density, tree age and size, and site productivity. We examined mortality in Douglas-fir, the dominant tree species in our stands.

Each installation contained six square plots ranging from 0.04 to 0.08 ha in size. The plot size was determined based on average tree size and stand density so that each plot contained at least ten Douglas-fir sample trees. The plots were selected to minimize between-plot variation in terrain, vegetation composition, tree stocking, and tree size at a site. Plots were grouped into two blocks of three plots based on similarity of these features to further reduce variation. Three fertilizer treatments—0, 224, and 448 N kg/ha—were randomly assigned to the plots within each block. Nitrogen in the form of urea was applied in the late fall utilizing handheld spreaders.

All live trees were measured for height (to the nearest 0.3 m) and diameter (to the nearest 0.25 cm) at the initiation of the experiment. Every plot was revisited every 2 yr over a 6 yr period after experiment establishment, and any incidence of tree mortality along with probable cause was noted. A total of 12,590 Douglas-fir trees located on 564 plots across 94 installations was used in the model development. Each tree was observed over a 6 yr period, and individual tree mortality over this period was the dependent variable in our analysis. In this experiment, 12,145 trees were classified as live and 445 (3.53%) were classified as dead. The annual mortality rate was 0.60% corresponding to a 6 yr rate of 3.53%. This annual rate was estimated in terms of a survival rate that is the complement of mortality. Our approach is a Markov process and assumes that annual survival rates over a 6 yr period are constant and independent.

Each plot was classified to one of five habitat types: grand fir (*Abies grandis*), dry Douglas-fir (*Pseudotsuga menziesii*), moist Douglas-fir, western redcedar (*Thuja Plicata*), and western hemlock (*Tsuga heterophylla*). Since there were limited observations within selected habitat types on some rock types, in our analysis, habitat type was specified at two levels: moist and dry. The moist level included grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types; the dry level included dry Douglas-fir habitat types. Moist Douglas-fir types occur in a region of north central Washington, where grand fir is completely absent in its geographic distribution. Thus, there can be no sites classified as grand fir habitat types in this geographic subregion (Williams and Lillybridge 1983). We assume that if grand fir occurred in this region, the sites would be similar to grand fir habitats elsewhere. Our assumption is consistent with the work of Williams et al. (1995). We therefore included the moist Douglas-fir sites in the moist site category in our analysis.

Rock samples were collected at each location and, after examination by a geologist, each installation was assigned to one of five rock type categories: granite, basalt, metasediment, sediment, and mixed—glacial till. Individual tree records included species codes, diameter at breast height, crown class codes, condition codes, crown ratio, and height. Individual plot records contained habitat type codes, rock type codes, treatment codes, slope, aspect, elevation, stand age, and Douglas-fir site index (Monserud 1984). Selected Douglas-fir stand and tree attributes are summarized in Table 1.

To test the mortality model on an independent data set, data were used from separate IFTNC experiments and from the Douglas-fir portion of the data analyzed by Shafii et al. (1990). These data were located on 40 plots across 7 separate installations. This validation data set comprised 879 Douglas-fir trees, of which 21 (2.39%) trees were classified as dead over a 6 yr period. The annual mortality rate was 0.40% corresponding to a 6 yr rate of 2.39%. Independent validation data such as these are difficult to obtain, and, as a consequence, the data do not span the entire range of conditions in the development data set (Table 1). Only moist habitats and two rock types are represented in the validation data, yet they provide a substantial and useful test of the predictive model.

Analysis

Mortality Model

Model development in our study was based on both biological and statistical considerations. The SAS PROC LOGISTIC procedure (SAS Institute 1989), 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 Monserud and Sterba (1999).

$$P = \frac{1}{1 + \exp(-(b_0 + SITE + SIZE + COMP))} \quad (1)$$

where

P = 6 yr probability of tree mortality

$$SITE = \sum_{K=1}^{4} b_{1k} RC_k + \sum_{t=1}^{2} b_{2t} TT_1 + b_3 HAB \quad (2)$$

$$SIZE = b_4 \, DBH / 100 \quad (3)$$

$$COMP = b_5 \, CR + b_6 \, CCF \quad (4)$$

and

RC_k = a set of dummy variables for the five rock types (RC_1 was coded 1 on granite rocks and 0 otherwise, RC_2 was coded 1 on basalt rocks and 0 otherwise, RC_3 was coded 1 on metasedimentary rocks and 0 otherwise, and RC_4 was coded 1 on sedimentary rocks and 0 otherwise.)

TT_t = a set of variables for the three treatment types (TT_1 was coded 1 with the 224 kg N/ha treatment and 0 otherwise, and TT_2 was coded 1 with the 448 kg N/ha treatment and 0 otherwise)

HAB = a dummy variable for the two habitat types (HAB was coded 1 for moist sites and 0 for dry sites)

DBH = tree diameter at breast height (cm)

Table 1. Summary statistics of selected Douglas-fir stand and tree attributes at the beginning of the 6 yr growth periods.

	Development data				Validation data			
Attribute	Mean	SD	Min	Max	Mean	SD	Min	Max
Site index[a] (m @ 50 yr)	19.2	3.2	13.1	27.7	27.6	4.1	19.5	32.3
Age (yr)	65	17	27	100	50	7	38	64
Number of trees (trees/ha)	658	308	210	2002	705	352	321	1,951
Basal area (m^2/ha)	32.3	10.6	7.3	77.0	45.2	11.5	24.0	71.9
Crown competition factor[b]	157	48	45	329	209	53	112	305
Quadratic mean diameter (cm)	26.14	5.92	13.26	49.00	29.87	5.02	17.80	41.34
Diameter at breast height (cm)	24.15	8.94	5.89	77.27	28.43	10.49	4.83	58.14
Crown ratio	0.45	0.14	0.10	0.99	0.51	0.08	0.21	0.75

[a] Monserud (1984).
[b] Wykoff et al. (1982).

CR = tree crown ratio

CCF = crown competition factor (Krajieck et al. 1961)

$b_0, b_{11}, b_{12}, b_{13}, b_{14}, b_{21}, b_{22}, b_3, b_4, b_5, b_6$ = parameters to be estimated

Site effect [Equation (2)] was estimated by three sets of dummy variables, one representing the five rock types, the second representing fertilizer treatments, and the third representing habitat types (moist or dry). Habitat type is a land classification based on expected climax vegetation (Daubenmire and Daubenmire 1968) and could represent a variety of moisture regimes and possibly broad differences in site fertility. Elevation and transformations of slope and aspect proposed by Stage (1976) were also tested. However, they were insignificant when habitat type was already included in the mortality model.

In size effect [Equation (3)], diameter at breast height (*DBH*) is an important and reliable measure of a tree's size. Generally, the larger the tree, the greater its chances of competing for scarce resources, indicating the probability of mortality decreases with increasing *DBH*. Thus, many mortality models include this variable (e.g., Monserud 1976, Buchman et al. 1983, Vanclay 1991a, McTague and Stansfield 1994, Monserud and Sterba 1999). Two transformations of *DBH*, $1/DBH$ and DBH^2, are useful to represent the nonlinear size effect. The $1/DBH$ term allows the mortality model to estimate accurately the large mortality rates for small trees (Hamilton 1986). The DBH^2 term allows the mortality model to represent the increased mortality rates for the largest and oldest trees [i.e., the senescence effect (Buchman 1983, Harcombe 1987, Monserud and Sterba 1999)]. However, both transformations were not included in the mortality model since they were insignificant in the presence of *DBH* likely due to the relative lack of very large or very small trees in the development data set.

In the combined competition effect [Equation (4)], tree crown ratio (*CR*) is a measure of foliage quantity indicative of tree vigor and is thus an important factor affecting the probability of mortality. Usually, mortality rates decrease with increasing *CR*. Many mortality models include this variable (e.g., Avila and Burkhart 1992, Zhang et al. 1997, Monserud and Sterba 1999). Although greatly dependent on tree vigor, the probability of a tree dying within the next growing period is also conditioned by competition with other trees for scarce resources. Crown Competition Factor (*CCF*) (Krajieck et al. 1961) represented stand density effects in the mortality model. Various other density measures and transformations were also tested: $BA^{0.5}$ (Hamilton 1986) and tree's percentile in the stand basal area distribution (*PCT*) proposed by Stage (1973). However, none of these variables improved the model's statistical properties or were significant once *CCF* was included in the model.

Interaction terms including all the categorical and continuous variables in Equation (1) were tested and found to be nonsignificant. Therefore, only main effects were included in the mortality model.

Model Evaluation

Predicted vs. observed mortality rates by diameter, crown ratio, and crown competition factor were examined to detect any deficiency in model fitting. Using the validation data set, predicted mortality was compared with observed mortality rates by rock type, treatment, diameter, crown ratio, and crown competition factor to assess the model predictions. The agreement of observed mortality distribution with predicted mortality distribution across all combinations of habitat type, rock type, and treatment for both development and validation data sets was evaluated using a chi-square goodness-of-fit test.

Effects of Fertilizer Treatment, Habitat Type, and Rock Type

Four hypotheses tested were: (1) there are no mortality differences between the control and fertilized plots, (2) there is no mortality difference between plots with application rates of 224 kg N/ha and 448 kg N/ha, (3) there are no mortality differences between rock types, and (4) there are no mortality differences between the two habitat type groups. Based on the mortality model [Equation (1)], the generalized likelihood ratio test (GLRT) method (Bain and Engelhardt 1991 p. 417–418) was used to separately test these hypotheses.

Fertilization Response Estimation

To quantify an individual tree's response to N fertilization, the response ratio (*R*) for annual probability of mortality is defined as

$$R_t = \frac{1-(1-\hat{P}_t)^{\frac{1}{6}}}{1-(1-\hat{P}_0)^{\frac{1}{6}}}, \quad t = 1 \ or \ 2 \qquad (5)$$

where

R_1 = response ratio for the 224 kg N/ha treatment

R_2 = response ratio for the 448 kg N/ha treatment

$\hat{P}_1$ = predicted value from the mortality model [Equation (1)] with the 224 kg N/ha treatment

$\hat{P}_2$ = predicted value from the mortality model [Equation (1)] with the 448 kg N/ha treatment

$\hat{P}_0$ = predicted value from the mortality model [Equation (1)] with no treatment

Equation (5) expresses predicted fertilized and unfertilized mortality as a ratio (*R*). When *R* is equal to 1, annual probability of mortality remains unchanged with the application of N fertilizer; when *R* is greater than 1, annual probability of mortality increases due to N fertilization; when *R* is less than 1, annual probability of mortality decreases due to N fertilization.

Results

The maximum-likelihood parameter estimates, standard errors, Wald Chi-Square statistics, and *P*-values of the pa-

Table 2. Parameter estimates for the mortality model [Equation (1)] using the maximum likelihood estimation method.

Variable	Estimate	SE	Wald chi-square	P > chi-square
Constant	–0.9405	0.3154	8.8913	0.0029
RC_1	0.3883	0.1537	6.3806	0.0115
RC_2	–0.3193	0.1517	4.4302	0.0353
RC_3	0.6500	0.1433	20.5624	0.0001
RC_4	–2.5411	0.5134	24.4988	0.0001
TT_1	0.3561	0.1362	6.8321	0.0090
TT_2	0.7635	0.1274	35.9134	0.0001
HAB	0.3214	0.1148	7.8383	0.0051
DBH/100	–9.4995	0.8345	129.5840	0.0001
CR	–4.4780	0.4615	94.1692	0.0001
CCF/100	0.3881	0.1188	10.6620	0.0011

rameters for the mortality model [Equation (1)] are listed in Table 2. All coefficients associated with continuous variables are statistically significant at $\alpha = 0.05$. The coefficients of *DBH* and *CR* are negative, indicating that the probability of mortality will be less as tree diameter and crown ratio increase, respectively. The coefficient of *CCF* is positive, indicating that the probability of mortality will be higher as overall stand density increases. The Wald Chi-Square Statistics in Table 2 show that of the continuous variables, the most important variable is *DBH*, *CR* is the second most important, and the third most important is *CCF*.

Mortality was significantly different on control plots compared to fertilized plots (GLRT Chi-Square = 37.96 with 2 df). There was a significant mortality difference between the two N application rates of 224 and 448 kg/ha (GLRT Chi-Square = 11.75 with 1 df). These results confirm the increasing mortality rate with higher N application rates shown in Table 2. Rock type also had a significant effect on Douglas-fir mortality (GLRT Chi-Square = 127.43 with 4 df). The sedimentary rock's coefficient is the smallest of all rock types (Table 2), resulting in the lowest predicted mortality rate, while the metasedimentary rock's coefficient is largest, producing the highest predicted mortality rate. The coefficients for granite and basalt rocks are statistically significant, indicating that their mortality rates are different from mixed rocks. Granite, mixed, and basalt predicted mortality rates are intermediate between metasedimentary and sedimentary rocks. Mortality rates were also significantly higher on moist sites than on dry sites (Chi-Square = 7.96 with 1 df).

Predicted and observed mortality rates for the development data with respect to the various predictor variables are displayed in Figure 1. The predictions were close to the observed mortality rates across all predictor variables. The model slightly overestimated the mortality rates in the 0–0.2 and 0.4–0.6 *CR* classes and slightly underestimated the mortality rates in the 0.2–0.4 *CR* class. The overall lack of a consistent error demonstrates that the model was well-behaved with respect to all predictor variables.

We compared our model predictions with observed mortality rates for the validation data. The overall predicted 6 yr mortality (2.28%) was only slightly lower than observed (2.39%). Predicted vs. observed mortality rates with respect to treatment (1.82% vs. 2.43% with control, 2.85% vs. 2.22% with 224 kg N/ha, and 2.14% vs. 2.56% with 448 kg N/ha) and rock type (1.84% vs. 1.97% on basaltic rocks and 5.56% vs. 5.13% on metasedimentary rocks) were in close agreement. We also compared predicted with observed mortality rates with respect to continuous predictor variables for the validation data in Figure 1. In general, predictions were close to the observed mortality rates across all these variables. Mortality was somewhat underestimated in the small diameter classes.

Table 3 shows chi-square goodness-of-fit statistics for the mortality model [Equation (1)] when it is applied to both development and validation data sets. Observations were summarized by habitat type, rock type, and treatment. The observed distribution of mortality was not significantly different from the predicted distribution of mortality across all combinations of habitat type, rock type, and treatment for each data set (Chi-Square = 48.69 with 48 df for the development data set and Chi-Square = 3.50 with 9 df for the validation data set).

The average Douglas-fir plot fertilization response ratios *R* for annual mortality rate by rock type and treatment based on the mortality model [Equation (1) and Equation (5)] and the development data set are provided in Table 4. The 448 kg N/ha treatment produced greater relative response (greater mortality) than the 224 kg N/ha treatment. For each combination of treatments and rock types, the response was significantly different than the null hypothesis that $R = 1$ at $\alpha = 0.01$ using a *t* test with degrees of freedom based on the number of plots.

Discussion

The results of this study could be useful for quantifying N fertilizer response of individual Douglas-fir trees in the region. Equation (1) is compatible with individual tree growth simulation models, such as Forest Vegetation Simulator (i.e., FVS, Wykoff et al. 1982), widely used to forecast growth and yield in the inland Northwest. However, to be completely useful, other component models in FVS, such as individual tree basal area and height increment models, should also be developed to include rock type effects. Alternatively, the parameters provided in Table 4 could be used as crude individual tree N fertilization response mortality rate multipliers until other component models that include rock type could be developed for the FVS model.

Interestingly, the coefficient associated with the moist habitat type had a positive sign, indicating that the probability

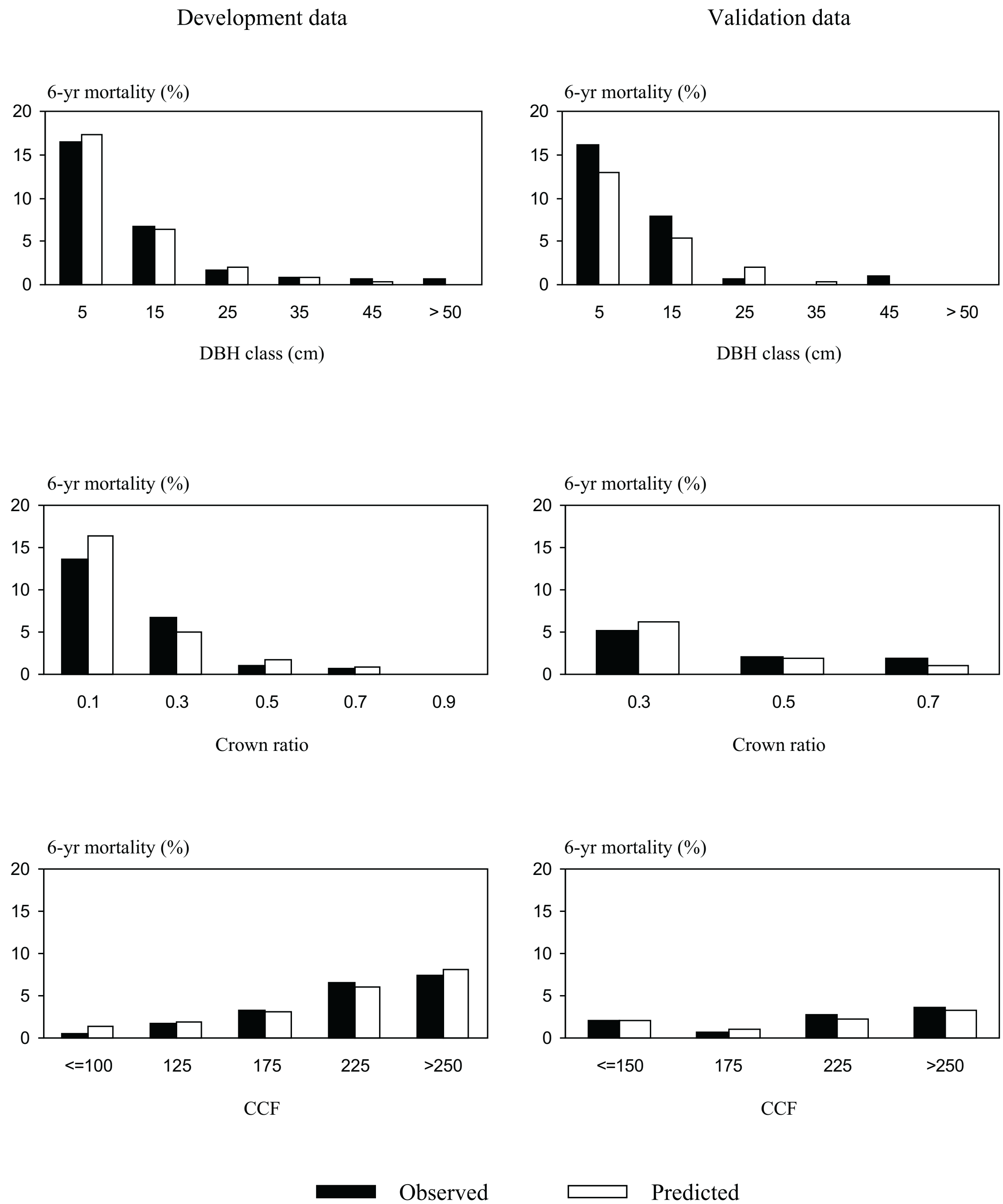

Figure 1. Observed vs. predicted 6 yr mortality rate by diameter (*DBH*) class, crown ratio (*CR*), and crown competition factor (*CCF*).

of tree mortality on moist sites is higher than on dry sites. We pursued several alternative explanations for this result. Soil samples were collected from the upper 10 cm of mineral soil for each plot at establishment prior to fertilization. Analytical methods used for soil ph, cation exchange capacity, base saturation, mineralizable N, exchangeable K, and available P are described in Carter (1993). One might expect that moist habitats are also more fertile; however, dry sites had significantly higher soil ph, cation exchange capacity, base saturation, mineralizable N, exchangeable K, and available P than moist sites (Table 5). Increased nutrient leaching on sites with higher precipitation amounts coupled with higher tree and stand growth rates that produce greater nutrient demands on moist sites could explain the observed lower soil fertility indexes on moist habitats. Nelson and Uhland (1995) showed that in regions where water percolation is high, the potential for leaching is also high. Wykoff (1990), among many, demonstrated that moist habitat types produce greater tree and stand growth than dry habitat types in the inland Northwest. Nutrient deficiencies could therefore be more common on moist habitat types than dry, thus contributing to higher Douglas-fir mortality rates on moist habitat types. This speculation is currently being tested in ongoing nutrient cycling research by the IFTNC.

The quantitative insights into the relationships between individual tree mortality and competition across a variety of

Table 3. Goodness-of-fit statistics for the mortality model [Equation (1)].

Data set	Habitat type	Rock type	Treatment	Trees	Observed dead trees	Predicted dead trees	Chi-square Dead trees	Chi-square Live trees
Development	Moist[a]	Granite	Control	267	18	15.8	0.3063	0.0193
			224 kg N/ha	266	32	20.7	6.1686	0.5206
			448 kg N/ha	234	14	21.3	2.5019	0.2505
		Basalt	Control	547	9	12.4	0.9323	0.0216
			224 kg N/ha	571	17	16.1	0.0503	0.0015
			448 kg N/ha	513	24	19.9	0.8447	0.0341
		Metasediment	Control	591	31	31.1	0.0003	0.0000
			224 kg N/ha	532	25	33.0	1.9394	0.1283
			448 kg N/ha	584	45	51.4	0.7969	0.0769
		Sediment	Control	243	0	0.5	0.5000	0.0010
			224 kg N/ha	270	1	0.9	0.0111	0.0000
			448 kg N/ha	240	2	1.4	0.2571	0.0015
		Mixed	Control	595	11	17.5	2.4143	0.0732
			224 kg N/ha	581	24	22.6	0.0867	0.0035
			448 kg N/ha	580	43	31.2	4.4628	0.2537
	Dry[b]	Granite	Control	329	5	5.9	0.1373	0.0025
			224 kg N/ha	324	5	7.8	1.0051	0.0248
			448 kg N/ha	360	14	16.4	0.3512	0.0168
		Basalt	Control	780	18	10.0	6.4000	0.0831
			224 kg N/ha	759	14	14.3	0.0063	0.0001
			448 kg N/ha	712	8	17.2	4.9209	0.1218
		Metasediment	Control	109	9	6.8	0.7118	0.0474
			224 kg N/ha	122	8	7.9	0.0013	0.0001
			448 kg N/ha	126	29	16.8	8.8595	1.3630
		Sediment	Control	176	0	0.2	0.2000	0.0002
			224 kg N/ha	184	0	0.4	0.4000	0.0009
			448 kg N/ha	189	1	0.6	0.2667	0.0009
		Mixed	Control	608	9	9.7	0.0505	0.0008
			224 kg N/ha	579	11	13.3	0.3977	0.0094
			448 kg N/ha	619	18	21.7	0.6309	0.0229
	Total			12,590	445	444.8	45.6119	3.0804
Validation	Moist[a]	Basalt	Control	268	6	3.3	2.2091	0.0275
			224 kg N/ha	260	3	5.1	0.8647	0.0173
			448 kg N/ha	234	6	5.2	0.1231	0.0028
		Metasediment	Control	61	2	2.8	0.2286	0.0110
			224 kg N/ha	56	4	3.8	0.0105	0.0008
	Total			879	21	20.2	3.4360	0.0594

[a] Includes grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.
[b] Includes dry Douglas-fir habitat types.

Table 4. Average plot response ratios *R* for annual mortality rate by habitat type, rock type, and treatment based on the mortality model [Equations (1) and (5)].

Habitat type	Rock type	Treatment 224 kg N/ha	Treatment 448 kg N/ha
Moist[a]	Granite	1.40115	2.04629
	Basalt	1.41580	2.09945
	Metasediment	1.40195	2.04950
	Sediment	1.42619	2.14001
	Mixed	1.41341	2.09041
Dry[b]	Granite	1.41581	2.09920
	Basalt	1.42150	2.12111
	Metasediment	1.39790	2.03332
	Sediment	1.42700	2.14302
	Mixed	1.41770	2.10657

NOTE: For each combination, the response was significantly different than the null hypothesis that $R = 1$ at $\alpha = 0.01$ using a t test with degrees of freedom based on the number of plots.
[a] Includes grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.
[b] Includes dry Douglas-fir habitat types.

mineral nutrient environments were developed by evaluating the individual tree mortality [Equation (1)] by rock type. Furthermore, the response ratios [Equation (5)] on moist sites for three treatment levels (control, 224 kg N/ha, and 448 kg N/ha) and five rock types (granite, basalt, metasedimentary, sedimentary, and mixed) were also evaluated across a range of tree diameters and crown ratios with the values of other independent variables being held constant at their means. The mortality surfaces for moist sites are shown in Figure 2.

As expected, suppressed trees (i.e., those of small diameter with low *CR*) showed higher probability of mortality over a 6 yr period than did dominant trees (i.e., those of large diameter with high *CR*) growing in the same stand (Figure 2). Two interesting features were revealed in Figure 2. The first is associated with the shapes of the mortality surfaces across a variety of mineral nutrient environments. The granite and metasedimentary rocks tend to weather to sandy soils, with low cation-exchange holding capacities (Buol et al. 1997, p. 147–150). Thus, the intertree competition for scarce resources is acute, resulting in the obviously upward-sloping shape of the mortality surface for granite and

Table 5. Least squares means of selected soil chemical characteristics by habitat type.

Habitat type	Soil ph	Mineralizable N	Available P	Exchangeable K (meq)	Cation exchange capacity	Base saturation (%)
		··········· (ppm)	···········			
Moist[a]	5.930	42	54.32	1.061	10.915	56.10
Dry[b]	5.977	49	67.36	1.198	13.411	63.02

NOTE: Least squares means were derived from the following model:

$Y_{ijk} = u + H_i + I_{(i)j} + e_{(ij)k}$ $\quad (i = 1, 2 \quad j = 1, 2, \ldots, n_i \quad k = 1, 2, \ldots, n_{ij})$

where:

Y_{ijk} = soil chemical characteristic of plot k in installation j on habitat i
u = overall mean
H_i = effect of habitat i (fixed)
$I_{(i)j}$ = effect of installation j on habitat i (fixed)
$e_{(ij)k}$ = effect of plot k in installation j on habitat i (random, $N(0, \sigma^2)$)
n_i = number of installations on habitat i
n_{ij} = number of plots in installations j on habitat i

The difference in least squares means of each soil chemical characteristic between moist and dry habitat types is significant at $\alpha = 0.01$ based on a t test.

[a] Includes grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.

[b] Includes dry Douglas-fir habitat types.

metasedimentary rocks. Soils derived from basaltic and mixed rocks, on the other hand, have a clay texture with a high nutrient holding capacity. As a result, the intertree competition for scarce resources is less, resulting in the slightly upward-sloping shape of the mortality surface for basaltic and mixed rocks. Sedimentary soils tend to be richer in clay minerals and have a higher nutrient holding capacity. Thus, the mortality due to competition for resources is very low, resulting in the nearly flat shape of the mortality surface for sedimentary rocks.

We propose that lower K availability on granite and metasedimentary rocks explains the higher mortality rates on unfertilized plots for these rock types. This explanation is supported by nutrient analysis of foliar samples collected from each installation 1yr after the experiment was initiated. Mika and Moore (1991) provide details of foliage sampling and analysis methodology. We reanalyzed only the portion of foliage data they described as collected from unfertilized control plots. These data provide a good sample of unfertilized foliar K concentrations for the rock types included in our study. Analysis of variance (ANOVA) results for Douglas-fir foliar K concentration by rock type are provided in Table 6. Least squares means derived from this ANOVA are shown in Figure 3. Douglas-fir growing on metasedimentary and granite rocks had significantly lower foliar K concentrations than Douglas-fir growing on basalt and sedimentary rock types.

Interestingly, the rank order of average foliar K concentration by rock type inversely matches the ranking of mortality parameters estimated for rock types (Table 3). Kobe (1996) observed sapling mortality differences for two sites in the eastern United States of differing soil mineralogy derived from schist/gneiss and calcareous bedrocks. Mika and Moore (1991) showed that sites with low foliar K levels prior to fertilization incurred substantially higher stand level mortality than those sites with adequate foliar K. The work of Shaw et al. (1998) suggests a biological explanation for these results. They found that Douglas-fir seedlings grown in a low K environment had significantly lower phenolic and tannin concentrations and lower ratios of these compounds to sugars in their roots than did seedlings with high K supplied. Further, Entry et al. (1991) demonstrated that low root phenol/sugar ratios were associated with higher incidence of *Armillaria* infection. Our results indicate that rock type represents broad differences in the nutrient environment where trees grow. We suggest that rock type, or a conceptually similar characteristic, should be useful for explaining variation in individual tree mortality in other geographic regions.

The second interesting feature of Figure 2 is associated with the shapes of the mortality surfaces associated with the different N application rates. The degree of upward-sloping for the mortality surface increases with increasing the N application rate. This indicates that N fertilization changes individual tree mortality, with higher probabilities of mortality associated with heavier N application. We

Table 6. Analysis of variance results for Douglas-fir foliar K concentration by rock type.

.	*df*	Sum of squares	Mean square	*F* value	*P* > *F*
Rock type	4	27080461.4	6770115.3	3.93	0.0045
Installation (in rock type)	79	325043854.0	4114479.2	2.39	0.0001
Block (in installation)	84	282082454.7	3358124.5	1.95	0.0001
Error	168	289359223.5	1722376.3		
Corrected total	335	923565993.6			

NOTE: Analysis of variance results were derived from the following model:

$Y_{ijkl} = u + R_i + I_{(i)j} + B_{(ij)k} + e_{(ijk)l}$ $(i = 1, 2, ..., 5 \quad j = 1, 2, \ldots, n_i \quad k = 1, 2 \quad l = 1, 2)$

where:

Y_{ijk} = Douglas-fir foliar K concentration of tree l in block k in installation j on rock type i
u = overall mean
R_i = effect of rock type i (fixed)
$I_{(i)j}$ = effect of installation j on rock type i (fixed)
$B_{(ij)k}$ = effect of block k in installation j on rock type i (fixed)
$e_{(ijk)l}$ = effect of tree l in block k in installation j on rock type i (random, $N(0, \sigma^2)$)
n_i = number of installations on rock type i

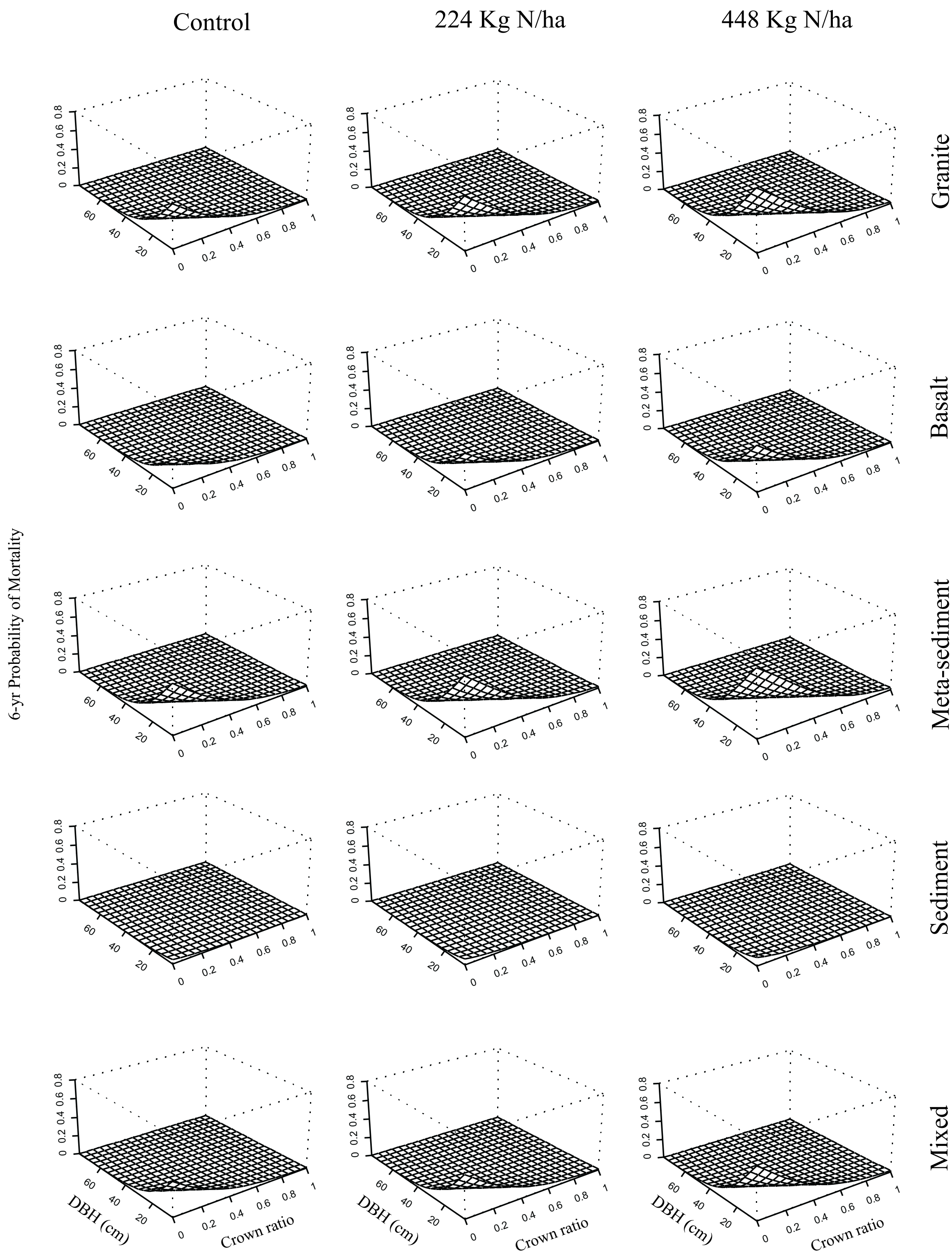

Figure 2. Six-year probability of tree mortality [Equation (1)] by tree diameter (*DBH*) and crown ratio (*CR*) for five rock types, and three treatments on moist sites.

feel there are three plausible reasons for these results. First, N fertilization increases individual tree growth. As trees become larger, competition increases, and fewer trees can be supported per hectare. Thus, an acceleration of growth due to N fertilization can produce increased stand density, resulting in increasing competition and mortality (Binkley 1986, p. 122). Second, N only fertilization may create nutrient imbalances, and thus create nutrient stress, such as for K discussed above, and therefore increase mortality. Adding other limiting nutrients in the fertilizer blend may reduce mortality levels observed in our study. Third, N fertilization may decrease the resistance of trees to wind, snow (Mika and Vander Ploeg 1991, Mika et al. 1992), and pathogens such as root rot as discussed above. Thus, the mortality due to wind, snow, and root rot increases as the N application rate increases.

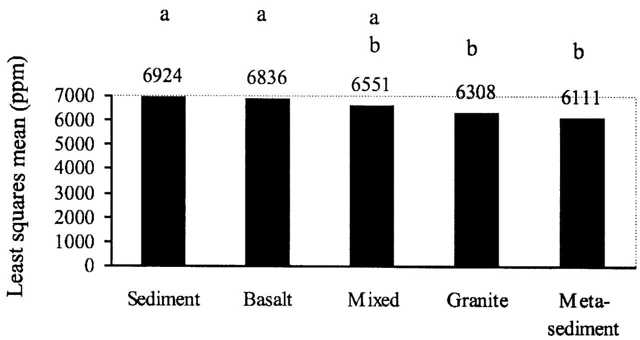

Figure 3. Least squares means for Douglas-fir foliar K concentration by rock type (least squares means with the same letter are not significantly different at $\alpha = 0.1$ based on pairwise comparisons using a *t* test).

The response ratios [Equation (5)] for annual probability of tree mortality across a range of tree diameters for all combinations of rock type and habitat type for each fertilizer treatment are almost identical (Table 4). However, the average response ratios of the 448 kg N treatment (about 2.1) are much greater than those of the 224 kg N treatment (about 1.4).

Conclusions

This study quantifies the effect of N fertilization, rock type, and habitat type on tree mortality. The probabilities of tree mortality on fertilized plots were greater than those on control plots and increased with increasing N fertilizer application rates. Trees growing on soils developed from granite and metasedimentary rocks exhibited greater probabilities of mortality than did those growing on other rocks. The probabilities of mortality for trees growing on sedimentary rocks were very low. Moist sites produced higher mortality rates than dry sites. Furthermore, the response ratios were nearly constant across a range of tree diameters for all rock types within a nitrogen treatment level. The mortality prediction model performed well on an independent data set. Our study quantitatively demonstrates differences in tree mortality across broad differences in the nutrient environment represented by different rock types. The mortality equations were formulated to be compatible with individual tree distance-independent simulation models. Incorporating these new equations into growth and yield simulators, such as FVS, would provide better representation of N fertilization effects on tree mortality and resultant stand development dynamics if other simulator components, such as individual tree increment models, also account for rock type effects.

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