The effect of habitat type and rock type on individual tree basal area growth response to nitrogen fertilization[1]

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Abstract: Individual tree basal area increment models for nitrogen fertilized stands were developed using data from permanent research plots located throughout the Inland Northwest. Results show that tree size, stand density, habitat type, and rock type significantly interact to affect individual tree basal area growth response to nitrogen fertilization. Suppressed trees growing on moist habitat types and all rock types, except metasedimentary, exhibited greater relative response than did dominant or codominant trees growing in the same stand. However, suppressed trees growing on dry sites or on soils derived from granite rocks did not show different relative response than dominant or codominant trees growing in the same stand. This study quantitatively demonstrates that individual tree competitive relationships are significantly affected by rock type. Rock types proved to be useful in representing broad differences in a site's nutrient environment. Incorporating the new equations into individual tree growth and yield simulators would provide better representation of N fertilization response differences within a stand.

Résumé : Des modèles d'accroissement en surface terrière d'arbres individuels dans des peuplements soumis à une fertilisation azotée ont été développés à l'aide de données provenant de parcelles expérimentales permanentes situées un peu partout à l'intérieur des terres dans le Nord-Ouest. Les résultats montrent que la dimension des arbres, la densité du peuplement, le type d'habitat et le type de roche interagissent de façon significative pour affecter la croissance en surface terrière d'arbres individuels en réponse à la fertilisation. Les arbres supprimés qui croissent sur des types d'habitat humide et tous les types de roche, à l'exception du type méta-sédimentaire, montrent une réponse relative plus forte que celle des arbres dominants et co-dominants qui croissent dans le même peuplement. Cependant, les arbres supprimés qui croissent sur des sites secs et sur des sols dérivés de roches granitiques n'ont pas montré de réponse relative différente de celle des arbres dominants ou co-dominants qui croissent dans le même peuplement. Cette étude quantitative démontre que les relations de compétition entre arbres individuels sont affectées de façon significative par le type de roche. Les types de roche s'avèrent utiles pour représenter de fortes différences dans l'environnement nutritif d'un site. L'introduction de nouvelles équations dans les modèles de croissance et de rendement d'arbres individuels permettrait d'avoir une meilleure représentation des différences de réaction à la fertilisation azotée dans un peuplement.

[Traduit par la Rédaction]

Introduction

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).

Considerable research (Shafii et al.1989, 1990; Mika and Moore 1990; Stage et al. 1990; Mika and Vander Ploeg 1991; Moore et al. 1991, 1994; Mika et al. 1992; Mital 1995; Avila 1997) has shown that nitrogen fertilization can significantly increase basal area or volume growth. Larger trees in a stand showed greater diameter growth response to nitrogen 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). 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).

In forest management planning, growth simulators are used for predicting the development of forest growth and yield. To forecast growth reliably for fertilized stands,

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growth simulators should include models for predicting growth response to fertilization. Recent examples of modeling the effect of fertilization on stand-level yield prediction are provided by Ballard (1984), Lowell (1988), and Bailey et al. (1989). At present, growth in most simulators is predicted using individual tree models. Thus, there is a continuing need to model growth response to fertilization at the tree level. Such an example was provided by Shafii et al. (1990), Stage et al. (1990), and Hynynen (1993). However, there are no published individual tree basal area growth models that relate fertilization response to habitat type, rock type, stand attributes, and tree attributes and that are compatible with growth simulation models used in the region (Wykoff et al. 1982). Therefore, the primary objective of this study was to develop an individual tree basal area growth model to quantify the effect of basal area response to nitrogen fertilization and assess habitat type and rock type effects on growth response. Since an accurate and precise model is critical for this assessment, efforts should be made to deal with issues surrounding model development appropriately, particularly collinearity (Belsley et al. 1980) and correlated errors.

Materials and methods

Data

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

Installations were located in second-growth, even-aged, managed Douglas-fir stands. Most stands had been thinned 5–years 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. The stands were dominated by Douglas-fir and included ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), western larch (*Larix occidentalis* Nutt.), and grand fir (*Abies grandis* (Dougl.) Lindl.).

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 contains at least 10 Douglas-fir sample trees. The plots were selected to minimize among-plot variation in terrain, vegetation composition, tree stocking, and tree size. 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 kg/ha of nitrogen) were randomly assigned to the plots within each block. Nitrogen in the form of urea was applied in the late fall utilizing hand-held spreaders. After 6 years, a variable number of plots were retreated at each installation. However, trees from these retreated plots are not included in the current analysis.

All live trees were measured for both height (to the nearest 0.03 m) and diameter (to the nearest 0.025 cm) at the time of the first treatment. For the first 10 years after plot establishment, diameters were remeasured on all trees every 2 years, and any incidence of damage or mortality along with probable cause was noted. Only trees alive at the end of the 10-year period, a total of 5065 Douglas-fir trees located on 257 plots across 94 installations, were used in this analysis. Thus, each tree had an observed 10-year growth period. Habitat was determined on site for each plot, and each plot was assigned to one of five habitat type categories: grand fir, dry Douglas-fir, moist Douglas-fir, western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Since there were limited observations within selected habitat types on some rock types, in our analysis habitat type is specified at two levels: moist including grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types and dry including 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). The moist Douglas-fir sites in our study are similar to grand fir types elsewhere, and we included them 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 were edited for species codes, diameter at breast height, crown class codes, condition codes, crown ratio, and height, and individual plot records were edited for habitat type codes, rock type codes, treatment codes, slope, aspect, elevation, stand age, and Douglas-fir site index (Monserud 1984). Distribution of plots and distribution of Douglas-fir trees by habitat type, rock type, and treatment at the beginning of the 10-year growth period are provided in Table 1. Selected stand and tree attributes are summarized in Table 2.

Analysis

Basal area increment model

Model development in our study was based both on biological and statistical considerations as follows.

The natural logarithm of 10-year periodic change in squared diameter, ln(DDS), was the dependent variable in the individual-tree basal area increment model for consistency with models in the forest vegetation simulator (FVS) (Stage 1973; Wykoff et al. 1982).

$$[1] \qquad \mathrm{DDS} = \mathrm{DIB10}^2 - \mathrm{DIB}^2$$

where DDS is the 10-year periodic growth in squared diameter at breast height, in square inches (1 in.^{2} = 6.4516 cm^2); DIB10 is the inside bark diameter at breast height 10 years after treatment, in inches (1 in. = 2.54 cm); and DIB is the inside bark diameter at breast height at the beginning of the growth period, in inches. Clearly, the growth rates of trees within a plot were spatially correlated. Because spatial information from mapped tree locations within a plot was not available, a mixed linear model containing both fixed-effects parameters and random-effects parameters with the compound-symmetry covariance structure suggested and employed by Hökkä and Groot (1999) was used to account for the correlated errors among trees within plots. Thus, the basal area increment model was specified as follows:

$$[2] \qquad \ln(\mathrm{DDS}_{ij}) = b_0 + \mathrm{SITE}_i + \mathrm{SIZE}_{ij} + \mathrm{COMP}_{ij} + u_i + e_{ij}, \qquad i = 1, 2, \ldots, 257;\ j = 1, 2, \ldots, n_i$$

where

$$[3] \qquad \mathrm{SITE}_i = b_1\mathrm{HB}_i + \sum_{k=1}^{4} b_{2k}\mathrm{RC}_{ki} + \sum_{p=1}^{2} b_{3p}\mathrm{TT}_{pi} + b_4(\mathrm{SL}_i/100)[\sin(\mathrm{ASP}_i)] + b_5(\mathrm{SL}_i/100) \times [\cos(\mathrm{ASP}_i)] + b_6(\mathrm{EL}_i/10\,000)^2$$

$$[4] \qquad \mathrm{SIZE}_{ij} = b_7 \ln(\mathrm{DBH}_{ij})$$

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Table 1. Distribution of Douglas-fir plots and trees by habitat type, rock type, and treatment at the beginning of the 10-year growth period.

Habitat type	Rock type	Control		224 kg N/ha		448 kg N/ha		Total	
		Plots	Trees	Plots	Trees	Plots	Trees	Plots	Trees
Moist[a]	Granite	6	121	6	116	5	94	17	331
	Basalt	12	226	12	255	10	165	34	646
	Metasediment	12	246	9	192	10	199	31	637
	Sediment	6	134	4	69	6	114	16	317
	Mixed	13	313	10	215	9	191	32	719
	Total	49	1040	41	847	40	763	130	2650
Dry[b]	Granite	9	150	7	117	7	122	23	389
	Basalt	21	414	14	259	15	261	50	934
	Metasediment	2	32	1	25	2	43	5	100
	Sediment	4	91	4	85	2	42	10	218
	Mixed	14	289	11	199	14	286	39	774
	Total	50	976	37	685	40	754	127	2415

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

Table 2. Summary statistics of selected Douglas-fir stand and tree attributes at the beginning of the 10-year growth period.

Attribute	Mean	SD	Minimum	Maximum
Slope (%)	24	17	0	85
Aspect (degrees)	177	120	0	357
Elevation (m)	1100	274	457	1798
Site index (m at 50 years)[a]	19.2	3.1	13.1	27.7
Age (years)	65	17	27	100
Number of trees (trees/ha)	650	297	210	2002
Mean tree height (m)	18.8	3.7	9.5	31.2
Top height (m)	20.3	4.2	11.3	36.9
Basal area (m^2/ha)	31.7	10.3	9.0	69.1
Crown competition factor[b]	155	47	52	304
Quadratic mean diameter (cm)	25.91	5.38	13.26	48.39
Diameter at breast height (cm)	24.99	8.33	5.89	77.27
Total height (m)	18.8	4.7	5.3	39.2
Crown ratio (%)	47	13	10	99

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

$$[5] \qquad \mathrm{COMP}_{ij} = b_8 \ln(\mathrm{CR}_{ij}/100) + b_9 \ln(\mathrm{TPA}_i/100) + b_{10}\mathrm{RHD}_{ij}/\ln(\mathrm{DBH}_{ij}+1) + \left(d_{11}D_{11i} + \sum_{r=1}^{5}\sum_{t=0}^{2} d_{1rt}D_{1rti} + \sum_{r=1}^{5} d_{2r}D_{2ri} \right) \times (\mathrm{BAL}_{ij}/100)/\ln(\mathrm{DBH}_{ij}+1)$$

and

DDS_{ij} is the 10-year periodic growth in squared diameter at breast height for tree j in stand i, in square inches; HB_i is a dummy variable characterizing habitat type for stand i (HB_i was coded 1 on moist sites and 0 otherwise); RC_{ki} is a set of dummy variables for the five rock types for stand i (RC_{1i} was coded 1 on granite rocks and 0 otherwise, RC_{2i} was coded 1 on basalt rocks and 0 otherwise, RC_{3i} was coded 1 on metasedimentary rocks and 0 otherwise, and RC_{4i} was coded 1 on sedimentary rocks and 0 otherwise); TT_{pi} is a set of dummy variables for the three treatment types stand i (TT_{1i} was coded 1 with the 224 kg N/ha treatment and 0 otherwise, and TT_{2i} was coded 1 with the 448 kg N/ha treatment and 0 otherwise); SL_i is the stand slope for stand i, in percent; ASP_i is the stand aspect for stand i, in degrees; EL_i is the stand elevation for stand i, in feet (1 ft = 0.3048 m); DBH_{ij} is the tree diameter at breast height for tree j in stand i, in inches; CR_{ij} is the tree crown ratio for tree j in stand i, in percent; RHD_{ij} is the ratio of the jth tree's height to the mean height of dominant and codominant trees in stand i; TPA_i is the number of trees per acre for stand i, in trees/acre (1 tree/ac = 2.47 trees/ha); BAL_{ij} is the basal area in trees larger than tree j in stand i, in square feet per acre (1 ft^2/ac = 0.2296 m^2/ha); D_{hri} and D_{hrti} are a set of dummy variables for the 18 combinations of habitat type, rock type, and fertilizer treatment for stand i, coded in Table 3; u_i is the random-effect parameter for stand i; e_{ij} is the random error for tree j in stand i; n_i is the number of trees used in the study on stand i; and b_0, b_1, b_{21},

…, b_{24}, b_{31}, b_{32}, b_4, …, b_{10}, d_{11}, d_{120}, …, d_{152}, d_{21}, …, d_{25} are the parameters to be estimated. The model assumed the growth observations of trees from the same stand to be correlated and all random parameters to follow independent multivariate normal distributions with zero means and constant variances and covariances at each level. All the model parameters were estimated simultaneously with the maximum likelihood estimation method using the PROC MIXED procedure on the SAS/STAT software (SAS Institute Inc. 1996).

In the combined site effect (eq. 3), habitat type (HAB) is a land classification based on expected climax vegetation (Daubenmire and Daubenmire 1968) and could represent a variety of moisture regimes. Thus, a dummy variable HB representing habitat effects was included in the increment model. Because rock type (ROC) 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, a set of dummy variables RC representing rock effects were included in the model. Fertilizer treatment (TRT) can raise site productivity by adding readily available sources of nutrients to increase a site's nutrient capital. Thus, a set of dummy variables TT representing treatment effects were added to the increment model. Slope (SL) and aspect (ASP) effects on tree growth were based on Stage's (1976) transformation modified by exclusion of the SL term, because it was not statistically significant. Although not significant, the (SL/100)(sin(ASP)) term was retained in the increment model, because the (SL/100)(cos(ASP)) term was significant. Stage (1976) recommends including both terms in the model even though one is statistically nonsignificant because doing so allows circular optima with respect to both slope and aspect to be expressed.

In the combined competition effect (eq. 5), tree crown ratio (CR) is a measure of foliage quantity indicative of tree vigor and is thus an important factor affecting tree growth. Although greatly dependent on tree vigor, the growth attained by an individual tree is also conditioned by competition with other trees for scarce resources. Overall stand density effects were represented in the increment model by the number of trees per acre (TPA). Furthermore, the growth attained by an individual tree is also dependent on its competitive status relative to neighboring trees. The ratio of a tree's total height to average height of dominant and codominant trees (RHD) is a measure of relative tree size with respect to the vertical position of a tree within the population. Daniels et al. (1986) demonstrated a correlation of RHD with individual tree growth. As a measure of the social cross-sectional ranking of a tree within the population, basal area in larger trees (BAL) behaves well under all types of thinnings (Wykoff 1990). The interaction terms: (RHD/100)/ln(DBH + 1) and (BAL/100)/ln(DBH + 1) instead of RHD and BAL, respectively, were included in the increment model to allow the effect of relative size to vary with changes in the distribution of diameters.

We were particularly interested in the effects of rock and habitat types on the pattern of within-stand distribution of fertilization growth response. Thus, we tested interaction terms of HAB × ROC × TRT with variables representing tree size or competitive effects in the model (eq. 2). We also tested lower order interactions of these variables. The interaction between (BAL/100)/ln(DBH + 1) and HAB × ROC × TRT was included in the increment model, because this term showed high statistical significance and weak collinearity (Belsley et al. 1980). Although other highest order interaction terms and some lower order interaction terms were also statistically significant, none of these terms was included in the increment model because their inclusion resulted in a substantial increase in collinearity statistics.

Fertilization response estimation

To quantify an individual tree's response to nitrogen fertilization, the response ratio (R) (Stage et al. 1990) for basal area increment is defined as

$$[6] \qquad R_p = \frac{\exp\{[\widehat{\ln(\mathrm{DDS})}]_p\}}{\exp\{[\widehat{\ln(\mathrm{DDS})}]_0\}}, \qquad p = 1 \text{ or } 2$$

where R_1 is the response ratio for the 224 kg N/ha treatment, R_2 is the response ratio for the 448 kg N/ha treatment, $[\widehat{\ln(\mathrm{DDS})}]_1$ is the predicted value from the growth model with the 224 kg N/ha treatment, $[\widehat{\ln(\mathrm{DDS})}]_2$ is the predicted value from the growth model with the 448 kg N/ha treatment, and $[\widehat{\ln(\mathrm{DDS})}]_0$ is the predicted value from the growth model with no treatment. Like a multiplier (Hamilton 1994), R measures relative basal area growth response to fertilization compared with a no-treatment alternative. When R is equal to 1, there is no growth response to fertilization; when R is greater than 1, there is positive growth response to fertilization; when R is less than 1, there is negative growth response to fertilization. However, it should be noted that higher relative response does not necessarily translate into higher absolute basal area growth. Absolute basal area growth depends on R and basal area growth under the no-treatment alternative as well.

Because the dependent variable in the growth model was the logarithmic transformation of DDS, predicted values of DDS based on the model were corrected using a correction factor suggested by Flewelling and Pienaar (1981) and employed by Hökkä and Groot (1999). The estimate of the logarithmic transformation of response to fertilization in eq. 6 was expressed as the ratio between the estimate of basal area increment for a fertilized tree and the estimate for an unfertilized tree. When this ratio is computed, variables in the increment model that do not interact with treatment sum to zero. The only remaining variable that interacted with the fertilization treatment is the (BAL/100)/ln(DBH + 1) term. The resultant response model is therefore given by

$$[7] \qquad \ln(R_p) = c_{0p} + \frac{c_{1p}(\mathrm{BAL}/100)}{\ln(\mathrm{DBH}+1)}, \qquad p = 1 \text{ or } 2$$

where p = 1 for the 224 kg N/ha treatment or 2 for the 448 kg N/ha treatment, R_1 and R_2 are as described in eq. 6, BAL and DBH are as previously defined, and the values of c_{01} and c_{02} are the estimates of the parameters b_{31} and b_{32} in eq. 2, and the value of c_{1p} is the difference between the estimates of the parameters d_{1rt} in the growth model (eq. 2) for treatment p and control by rock type on moist sites.

Results

The maximum-likelihood (ML) estimates of the parameters, standard errors, and p values of the parameters, from the SAS PROC MIXED procedure using METHOD = ML, for the basal area increment model (eq. 2) with the compound-symmetry covariance structure are listed in Table 4. With the exception of the coefficients associated with (SL/100)(sin(ASP)) and (BAL/100)/ln(DBH + 1) × D_{hrt} for sedimentary rocks with the 224 and 448 kg N/ha treatments, all other coefficients associated with continuous variables were statistically significant at α = 0.01 and have appropriate signs in the context of a theoretical biological model (Wykoff 1990). For two covariance parameter estimates, both asymptotic Wald tests indicate a significant difference from 0. The "null model likelihood ratio test chi-square" value,

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Table 3. The dummy variables for the 18 combinations D_{hri} or D_{hrti} of habitat type, rock type, and fertilizer treatment for stand i in eq. 5.

			Group[a]																	
Habitat	Rock	Treatment	11	120	121	122	130	131	132	140	141	142	150	151	152	21	22	23	24	25
Moist[b]	Granite		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Basalt	Control	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		224 kg N/ha	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		448 kg N/ha	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Metasediment	Control	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
		224 kg N/ha	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
		448 kg N/ha	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	Sediment	Control	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
		224 kg N/ha	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
		448 kg N/ha	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	Mixed	Control	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
		224 kg N/ha	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
		448 kg N/ha	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Dry[c]	Granite		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Basalt		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Metasediment		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	Sediment		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	Mixed		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

[a]Coding for the groups is as follows: the first number is the habitat ((1) moist; (2) dry), the second is the rock type ((1) granite; (2) basalt; (3) metasediment; (4) sediment; (5) mixed), and the third is the treatment ((0) control; (1) 224 kg N/ha; (2) 448 kg N/ha).
[b]Includes grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.
[c]Includes dry Douglas-fir habitat types.

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Table 4. Parameter estimates for fixed (A) and random effects (B) for the increment model (eq. 2) using the maximum likelihood estimation method.

(A) Fixed effects.

Variable	Estimate	SE	df	$P > \|t\|$
Constant	0.831 78	0.128 95	245	0.0001
HB	0.289 20	0.032 69	245	0.0001
RC_1	0.165 70	0.056 33	245	0.0036
RC_2	0.038 61	0.040 59	245	0.3424
RC_3	0.118 94	0.052 88	245	0.0254
RC_4	–0.320 57	0.056 99	245	0.0001
TT_1	0.099 20	0.034 32	245	0.0042
TT_2	0.159 04	0.034 08	245	0.0001
SL/100(sin(ASP))	–0.052 98	0.066 22	245	0.4245
SL/100(cos(ASP))	–0.217 34	0.075 32	245	0.0043
$(EL/10000)^2$	–1.751 73	0.238 52	245	0.0001
ln(DBH)	1.300 59	0.039 86	4787	0.0001
ln(CR/100)	0.795 34	0.023 53	4787	0.0001
ln(TPA/100)	–0.188 14	0.035 16	245	0.0001
RHD/ln(DBH + 1)	0.687 65	0.135 75	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{11}	–0.951 87	0.083 02	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{120}	–0.964 25	0.091 43	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{121}	–0.729 61	0.088 88	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{122}	–0.806 92	0.102 49	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{130}	–0.777 71	0.087 21	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{131}	–0.822 04	0.085 82	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{132}	–0.497 27	0.097 11	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{140}	–0.334 57	0.107 38	4787	0.0018
(BAL/100)/ln(DBH + 1) × D_{141}	0.128 27	0.195 76	4787	0.5124
(BAL/100)/ln(DBH + 1) × D_{142}	–0.119 83	0.145 70	4787	0.4109
(BAL/100)/ln(DBH + 1) × D_{150}	–0.724 58	0.101 49	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{151}	–0.588 81	0.109 29	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{152}	–0.353 63	0.129 04	4787	0.0062
(BAL/100)/ln(DBH + 1) × D_{21}	–0.569 11	0.084 19	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{22}	–0.396 27	0.068 73	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{23}	–0.697 91	0.139 84	4787	0.0001
(BAL/100)/ln(DBH + 1) × D_{24}	–0.336 34	0.105 23	4787	0.0014
(BAL/100)/ln(DBH + 1) × D_{25}	–0.624 38	0.074 06	4787	0.0001

(B) Random effects.

Variance component	Estimate	SE	$P > \|z\|$
Stand	0.039 054 07	0.004 288 24	0.0001
Error	0.107 723 43	0.002 205 49	0.0001

–2 times the log likelihood from the null model (i.e., the model with only the fixed effects and the random error) minus –2 times the log likelihood from the fitted model, is 781.4567. Comparing this value with χ^2 distribution with one degree of freedom yields a p value less than 0.0001. This indicates that modeling the random stand effect is superior to fitting the model with only the fixed effects and the random error. The residual plots from the increment model (eq. 2) using the maximum-likelihood estimates did not show any objectional trends and did not suggest any problems with the assumptions made in fitting the model. Coefficients c_{01} and c_{02} are 0.099 20 and 0.159 04, respectively, and coefficients,

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Table 5. Coefficients for the response model (eq. 7) by rock type and treatment on moist sites.

	224 kg N/ha		448 kg N/ha	
Rock type	c_{11}	P	c_{12}	P
Basalt	0.234 64	0.0340	0.157 33	0.1906
Metasediment	–0.044 33	0.6777	0.280 44	0.0142
Sediment	0.462 83	0.0267	0.214 74	0.1844
Mixed	0.135 77	0.2863	0.370 95	0.0094

Note: Moist sites include grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.

Table 6. Average plot response ratios for basal area increment by rock type and treatment on moist sites based on the increment model (eq. 2).

	224 kg N/ha		448 kg N/ha	
Rock type	Mean R	P^a	Mean R	P^a
Basalt	1.173 32	<0.0001	1.220 72	<0.0001
Metasediment	1.090 52	<0.0001	1.272 24	<0.0001
Sediment	1.268 54	<0.0001	1.248 83	<0.0001
Mixed	1.139 56	<0.0001	1.279 40	<0.0001

Note: Moist sites include grand fir, moist Douglas-fir, western redcedar, and western hemlock habitat types.

[a]Probability of obtaining a larger $|t|$ under the null hypothesis H_0: parameter $R = 1$. The hypothesis test was conducted based on the number of plots involved in each combination.

c_{1p}, by rock type and fertilizer treatment on moist sites for the response model in eq. 7 are given in Table 5.

The average Douglas-fir plot fertilization response ratios for 10-year basal area increment analysis by rock type and treatment on moist sites based on the increment model (eq. 2) and data used in the model development are provided in Table 6. With the exception of the sedimentary rock type, 448 kg/ha of nitrogen produced greater relative response than the 224 kg N/ha treatment. All responses were significantly different than the null hypothesis that $R = 1$. On dry sites or on granite rocks, the average response ratios for the 224 and 448 kg N /ha treatments are 1.104 29 and 1.172 39, respectively.

Discussion

The results of this study are directly useful for quantifying nitrogen fertilizer response of individual Douglas-fir trees in the region. Equation 2 is compatible with individual tree growth simulation models, such as FVS (Wykoff et al. 1982), commonly used to forecast growth and yield in the Inland Northwest. In fact, our study substantially expands the work of Stage et al. (1990) by providing fertilization response estimates for various habitat type and rock type combinations. Alternatively, the parameters provided in Table 6 could be used as crude individual tree N fertilization response growth multipliers by those who do not use individual tree simulation models formulated similar to the FVS model.

Perhaps the most interesting results of our study are the quantitative insights into individual tree competitive relationships across a variety of moisture (i.e., habitat types) and mineral nutrient (i.e., rock types) environments. These insights were developed by evaluating the tree growth (eq. 2) and the response ratio (eq. 7) for three nitrogen treatment levels (control, 224 kg N/ha, and 448 kg N/ha), two habitat types (moist and dry), and five rock types (granite, basalt, metasedimentary, sedimentary, and mixed) across a range of tree diameters from 3 to 30 inches (7.62–76.20 cm) and BAL from 0 to 300 ft^2/ac (0–68.87 m^2/ha) with the values of other independent variables being held constant at their means. In the interest of brevity, only selected combinations are shown in Figs. 1 and 2.

As expected, large dominant trees (i.e., those with low BAL) growing on moist sites show the greatest absolute growth over a 10-year period (Fig. 1). However, the effect of nitrogen fertilization on stand dynamics, i.e., within-stand distribution of fertilizer response, for different rock and treatment types on moist sites is better demonstrated by relative growth (Fig. 2).

Moist habitats produced relatively greater response than dry habitats across all rock types except granite rocks and metasedimentary rocks with the 224 kg N/ha treatment. In addition, the shape of response surfaces, i.e., the relative distribution of response between individual trees within stands, differs between moist and dry habitats. On moist sites the response surface is upward sweeping; trees of small diameter with high BAL produced higher relative fertilization response than large diameter trees with low BAL. The only exception to this response pattern for moist sites occurred for stands growing on granite rocks and metasedimentary rocks with the 224 kg N/ha treatment. The shape of the response surface for metasedimentary rocks was slightly downward sloping. Small trees with high BAL produced relatively less fertilization response than large trees with low BAL growing in the same stand (Fig. 2). Although not shown, response surfaces for the 448 kg N/ha treatment were flat and similar to those for the 224 kg N/ha treatment, with somewhat higher relative response on granite rocks or on dry sites. Soils derived from granite rocks can be somewhat infertile with respect to nutrients other than N. Perhaps more importantly, soils derived from granite rocks have a sandy texture with low moisture holding capacity and low cation exchange capacity. Thus, Douglas-fir growing on granite sites behave similarly to dry sites with respect to N fertilization response.

On moist sites, trees growing in subordinate crown positions, those of small diameter with high BAL (i.e., suppressed), produced larger relative response to N fertilization than did large diameter trees with low BAL (i.e., dominants). This suggests that competition for N was particularly acute for the suppressed trees, since they exhibited the greatest relative response when additional N was supplied by fertilization. However, this response pattern was only evident on moist sites (Fig. 2). After N deficiency was alleviated by fertilization, suppressed trees on moist sites apparently had sufficient moisture available to allow these trees to increase their growth rate in response to increased N availability. On drier sites, lack of moisture likely inhibited fertilization growth response by the suppressed trees. These response patterns suggest that N fertilization would have

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Fig. 1. Ten-year basal area increment on moist sites (eq. 2) depends on tree diameter (DBH (cm)), basal area in trees larger than the subject tree (BAL (m^2/ha)), treatment, and rock type: (*a*) control–basalt, (*b*) 224 kg N – basalt, (*c*) 448 kg N – basalt, (*d*) control–metasediment, (*e*) 224 kg N – metasediment, (*f*) 448 kg N – metasediment, (*g*) control–sediment, (*h*) 224 kg N – sediment, (*i*) 448 kg N – sediment, (*j*) control–mixed, (*k*) 224 kg N – mixed, (*l*) 448 kg N – mixed.

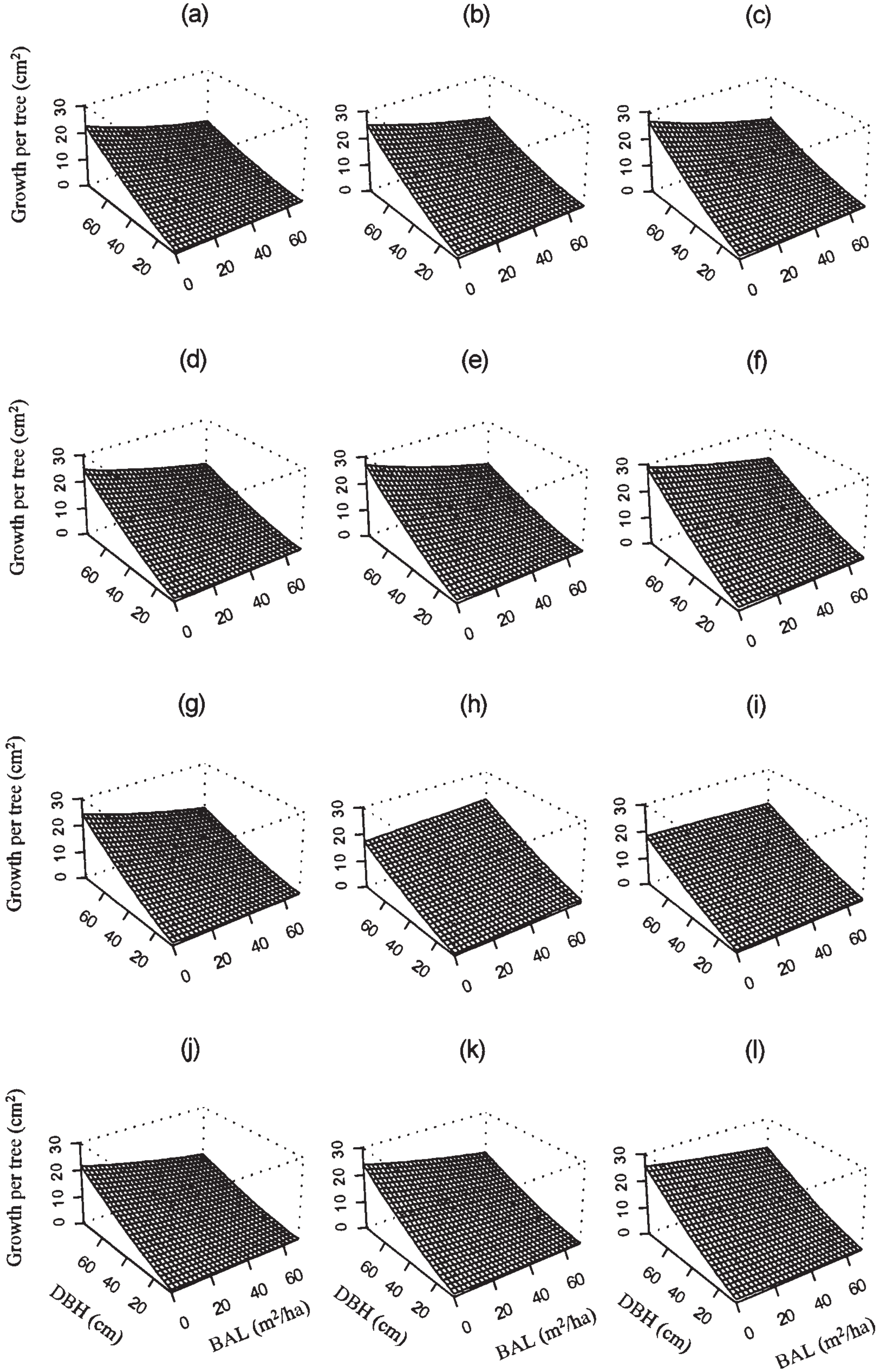

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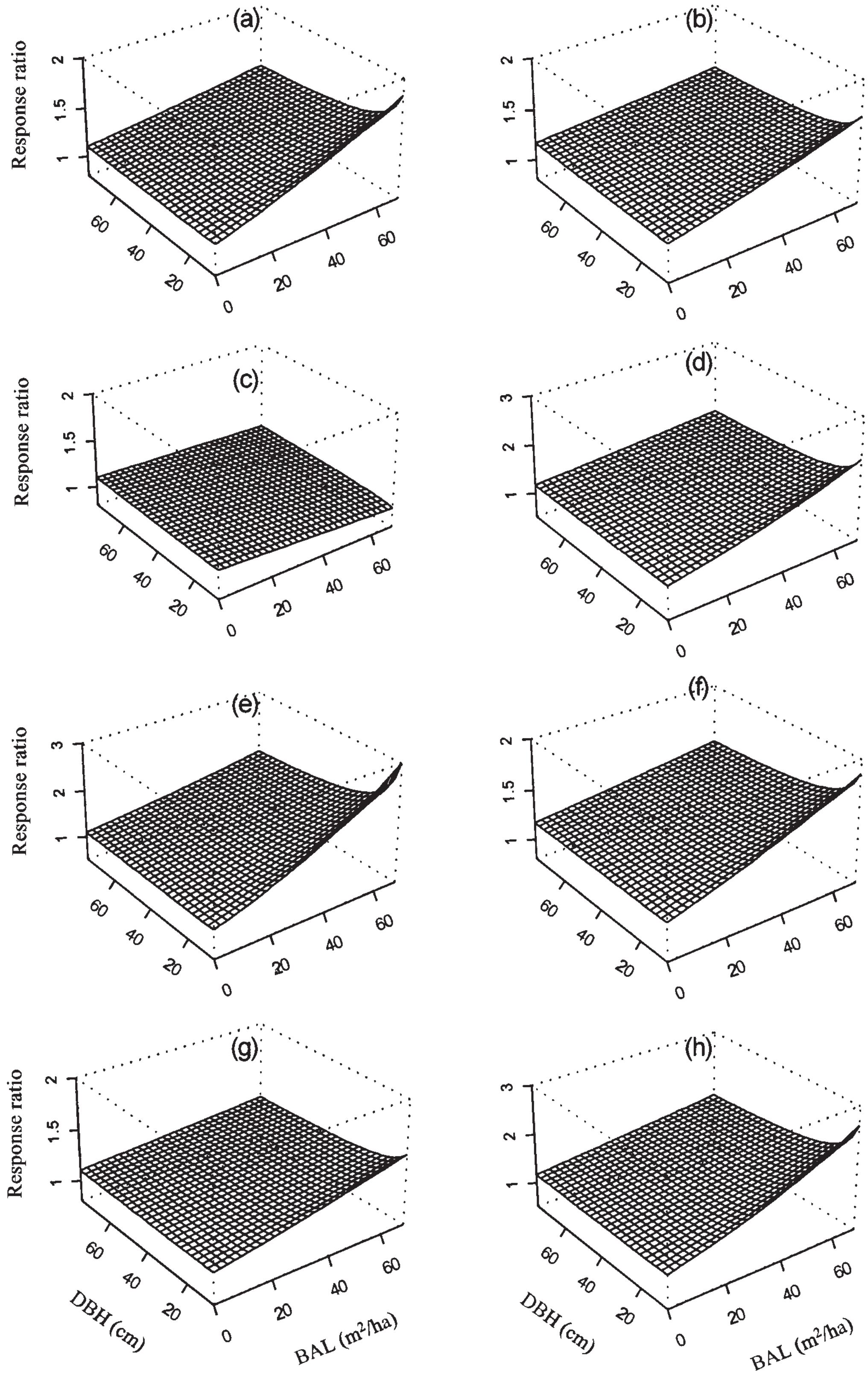
Fig. 2. Response ratio for 10-year basal area increment on moist sites (eq. 7) depends on tree diameter (DBH (cm)), basal area in trees larger than the subject tree (BAL (m^2/ha)), treatment, and rock type: (*a*) 224 kg N – basalt, (*b*) 448 kg N – basalt, (*c*) 224 kg N – metasediment, (*d*) 448 kg N – metasediment, (*e*) 224 kg N – sediment, (*f*) 448 kg N – sediment, (*g*) 224 kg N – mixed, (*h*) 448 kg N – mixed.



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different long-term effect on stand structure depending on rock and habitat type combinations.

The shape of the response surface for metasedimentary rocks associated with moist habitats is downward sloping similar to those for drier sites but unlike any other moist habitat – rock type combination. We feel the absence of response to N fertilization by suppressed trees growing on metasedimentary rocks results from a lack of mineral nutrients such as potassium, phosphorus, and some micronutrients rather than moisture limitations as previously discussed for drier sites. We feel this explanation is plausible for two reasons: (*i*) soils occurring on the moist–metasedimentary sites have good physical properties with high moisture holding capacity (Mital 1995); (*ii*) soils developed from metasedimentary rocks in this region are infertile, particularly with respect to potassium (Moore et al. 1998). Metasedimentary rocks are composed primarily of SiO_2 (~90% by weight), with very low content of essential mineral nutrients. Sites with low potassium status showed significantly lower stand level response to N fertilization than those with good K status (Mika and Moore 1990). The only exception to the general N response pattern for 224 versus 448 kg/ha treatment occurred on metasedimentary rocks associated with moist habitats (Table 6). The relatively high average individual tree response is counter to what we expected. The high N fertilization rate produced significantly higher mortality rates for the moist habitat type and metasedimentary rock type category than for any other strata in our study (G. Shen, C. Hatch, and J. Moore, unpublished data[3]). The higher mortality likely resulted from N fertilization induced nutrient imbalances (Mika and Moore 1990; Moore et al. 1998). Therefore, since our analysis is based only on trees alive at the end of the period, we feel that the apparent high relative response to the 448 kg N treatment is at least partially due to a thinning effect from trees that died during the period.

We suggest that rock type represents broad differences in the nutrient environment in which trees grow. Using rock type in an individual tree growth model is analogous to including habitat type as a variable to represent differences in moisture and temperature growing regimes. We feel that rock type, or a conceptually similar variable, should be useful for explaining variation in tree growth response to silvicultural treatments, such as fertilization, in other geographic regions.

Essentially all Douglas-fir stands in the Inland Northwest are deficient in nitrogen (Moore et al. 1991), but, as demonstrated in our study, the within-stand distribution of fertilization growth response among individual trees is influenced by the availability of other growth limiting resources. Our results suggest that site moisture and availability of other nutrients are the factors that affect the different patterns of individual tree response among stands. Suppressed trees show the greatest relative differences in growth response to N fertilization, reflecting acute intertree competitive interactions for moisture, nitrogen, and other nutrients. This finding leads to the following speculation: currently dominant trees are sampled for foliage analysis to assay a stand's nutrient status (Everard 1973); perhaps, sampling suppressed trees for foliar analysis would be more diagnostic.

Conclusions

This study quantifies the interactions of tree size, stand density, habitat type, and rock type to predict individual tree basal area growth response to N fertilization. Suppressed trees growing on moist sites and soils derived from granite, basalt, sedimentary, and mixed (glacial) rock types showed relatively greater response to N fertilization than dominant trees in the same stand. However, suppressed trees growing on drier sites or on soils derived from granite rocks did not exhibited different relative fertilization response than dominants. Thus, our study quantitatively demonstrates differences in individual tree competitive relationships across broad differences in the nutrient environment represented by different rock types. The basal area increment 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 allow better representation of N fertilization effects on stand development dynamics.

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