

Interactions of Elevation, Aspect, and Slope in Models of Forest Species Composition and Productivity

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Abstract: We present a linear model for the interacting effects of elevation, aspect, and slope for use in predicting forest productivity or species composition. The model formulation we propose integrates interactions of these three factors in a mathematical expression representing their combined effect in terms of a cosine function of aspect with a phase shift and amplitude that change with slope and elevation. This model allows the data to determine how the aspect effect changes with elevation and slope. Earlier articles concerning the interactions of slope, aspect, and elevation have been incomplete by either treating elevation as fixed or ignoring the possibility that aspect effect must also involve slope. The proposed set of variables is illustrated in four applications: (1) a hypothetical data set for probability of stocking by “species” having different adaptations to elevation, (2) in a discriminant function for forest/nonforest classification of data from Utah, (3) estimating mean annual increment of Utah forests, and (4) estimating the height asymptote in a mixed-model differential equation predicting Douglas-fir height growth. *FOR. SCI.* 53(4):486–492.

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ASPECT, SLOPE, AND ELEVATION have been demonstrated to be useful surrogates for the spatial and temporal distribution of factors such as radiation, precipitation, and temperature that influence species composition and productivity. Predictive models using slope, aspect, and elevation can be useful for extrapolating present or historical effects to areas where observations of species composition or productivity are not available. These predictive models can also be used to assess whether more complex models of direct effects of radiation, precipitation, and temperature adequately estimate historical integration of effects of these factors. Thus, they can serve as a reality check before predicting effects of changing climate using the more detailed models. Our references to the effect of aspect are phrased for the northern hemisphere; in the southern hemisphere, of course, the roles of north and south are reversed. However, to retain the appropriate roles of east and west, aspect is here defined as the azimuth measured clockwise from north by an observer facing downslope.

Earlier proposals of how to represent interactions of aspect, slope, and elevation in models of species composition and productivity have been incomplete. Beers et al. (1966) observed that southwest aspects are often the most severe sites for forest regeneration and growth. Accordingly, they recommended using cosine of aspect with a predetermined phase shift of 45° to create a variable ($\cos[\alpha - 45^\circ]$) that would have its maximum of unity at northeast and its minimum of minus unity at southwest. Then the amplitude of the contrast between these extremes is estimated by the regression coefficient of $\cos[\alpha - 45^\circ]$. Stage (1976) demonstrated a transformation that permitted the phase shift of the cosine to an optimum aspect and an amplitude that is a function of slope to be estimated directly from the coefficients of a linear model. Roise and Betters

(1981) extended the discussion to relations with elevation, but omitted slope interactions. Their observation that the optimum aspect at high elevations could be in the opposite quadrant to the optimum at the lower elevations was an important contribution. However, by representing the phase shift as $\arccos[(a - E)/b]$ of elevation (E) scaled symmetrically about the middle elevation (a) between the lowest elevation of $a - b$ and the highest of $a + b$, their expression switches the optimum from south at high elevation to north at low elevation by passing the optimum aspect through east or west at a mid-elevation. We argue that, instead, it should be the amplitude of the cosine of aspect that passes through zero as the phase shift to optimality reverses quadrants at some mid-elevation. Effects of aspect, furthermore, should be greatest at the extremes of elevation for the species being represented. At the lower elevation limit for a species, the absolute value of the magnitude of the interaction with the trigonometric aspect factors should increase at an increasing rate as elevation decreases. Conversely, at the upper elevation range for a species, the rate of change of the absolute magnitude should increase, either because of the physiological limits of the species or as a complement (through competitive exclusion) to the behavior of species better adapted to the higher elevation. Furthermore, the amplitude should be able to change with elevation and slope, particularly because aspect is undefined on flat ground.

If the amplitude of $\cos(\alpha - \beta)$ passes through zero at some mid-elevation, then this behavior explains insignificant effects of slope/aspect variables in analyses of some data sets. If the range of elevations in a particular study is nearly centered on the elevation at which the switch occurs, then fitting a model having only a single transformation of aspect will have opposing aspect effects above and below the transition. Analysis would show no net effect of aspect.

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The set of variables advocated by Stage (1976) included slope percentage (s), slope percentage times cosine of aspect ($s \cdot \cos(\alpha)$), and slope percentage times sine of aspect ($s \cdot \sin(\alpha)$). Then a linear regression of a growth response including these three variables

$$y = b_0 + b_1s + b_2s \cos(\alpha) + b_3s \sin(\alpha) \quad (1)$$

is trigonometrically identical to

$$y = b_0 + b_1s \pm \sqrt{b_2^2 + b_3^2} s \cos(\alpha - \beta), \quad (2)$$

where $\pm \sqrt{b_2^2 + b_3^2} s$ is the amplitude of the cosine function and $\beta = \arctan(b_3/b_2)$ is the phase shift. For $b_2 > 0$ use the positive root for the amplitude. If $b_2 = 0$ the cosine term of (1) is omitted, leaving only the sine term in Equation 1. If $b_2 < 0$ use Equation 2 with the negative root. Thus, this formulation is identical to that of Beers et al. (1966), but permits the data to determine the phase shift rather than specifying it arbitrarily in advance. Further note that the extremes of the cosine function must occur at diametrically opposite azimuths, whatever the phase shift—a limitation that can be relaxed by adding additional terms for sine and cosine of twice the aspect (Stage 1976). The separate slope term allows the reference value for level ground to be positioned independently of the range of the aspect term(s). Although this formulation has been effective in many analyses of species growth, it does not include aspect/elevation interactions and thus could not capture the switch in optimum aspect discussed by Roise and Betters (1981)—an omission that may be particularly serious for predictions of species distributions.

Our formulation for adding an elevation effect continues the philosophy of deriving the parameters from the data set being analyzed, and preferably in the context of multivariate linear regression. We replace the set of three variables representing the effects of slope and aspect with two sets of three derived from the original set by multiplying each set of three by one or the other of two “opposing” functions of elevation. By “opposing” we mean that one of the functions is sensitive to effects of variation at low elevations, and the other is sensitive to elevation effects at high elevations. Main effects of elevation capable of describing an optimum (or minimum) should also be included in the expression to represent elevation effects on flat ground. For example, using elevation (el) and elevation-squared as main effects, by permitting a maximum with respect to elevation, will serve, although other pairs may be even better. Then, the formulation becomes

$$\begin{aligned} y = & b_0 + f_1(el) \cdot s[b_1 + b_2\cos(\alpha) + b_3\sin(\alpha)] \\ & + f_2(el) \cdot s[b_4 + b_5 \cos(\alpha) + b_6 \sin(\alpha)] \\ & + b_7el + b_8 el^2. \end{aligned} \quad (3)$$

Choice of $f_1(el)$, $f_2(el)$

Naive empiricism would suggest using elevation and elevation-squared for the pair of elevation interactions. However, this choice does not have the desired behavior because the amplitude would approach zero as elevation

approaches sea-level. A pair that does meet the behavior specifications is $f_1(el) = \ln(el + 1)$ and $f_2(el) = el^2$. The sensitivity (derivative with respect to elevation) of $f_1(el)$ is $1/(el + 1)$ and of $f_2(el)$ is proportional to elevation. Unfortunately, the goodness-of-fit for the interaction with $\ln(el + 1)$ is not invariant with scale; that is, the standard error of estimate would be different for elevation measured in hundreds of feet from the fit for elevation measured in meters. Therefore, we recommend $f_1(el) = \ln[(el + 1) \cdot k] = [\ln(el + 1) + \ln(k)]$. Strictly, the value added (here taken as unity) to make the argument of the logarithmic function always positive should also depend on scale of the elevation variable and the possibility of sites below sea-level. However, the coefficients of the triplet without elevation include $\ln(k)$, which is just a constant, define the optimum scaling of elevation in the logarithmic function and also define the aspect effect for an elevation of zero [1]. Then

$$\begin{aligned} y = & b_0 + s[b_1 + b_2\cos(\alpha) + b_3\sin(\alpha)] \\ & + \ln(el + 1) \cdot s[b_4 + b_5\cos(\alpha) + b_6\sin(\alpha)] \\ & + (el^2) \cdot s[b_7 + b_8\cos(\alpha) + b_9\sin(\alpha)] + b_{10}el + b_{11}el^2. \end{aligned} \quad (4)$$

The switch of optimum aspect occurs at the elevation at which the amplitude of the aspect effect equals zero:

$$\sqrt{[b_2 + b_5\ln(el + 1) + b_8el^2]^2 + [b_3 + b_6\ln(el + 1) + b_9el^2]^2} = 0. \quad (5)$$

Unfortunately, Equation 5 must be solved by iterative methods.

The phase shift also changes with elevation. Whereas the usual assumption (in the northern hemisphere) is that southwest is the most adverse at lower elevations (Beers et al. 1966), at high elevations the optimum may be at the southeast, where morning sun enhances the more favorable warmth of southern aspects.

The emphasis in this article is on the aspect/elevation interactions in topography where temperature follows typical lapse rates with elevation. An elevation effect not being captured is the effect of drainage configurations that create so-called “thermal belts” and frost pockets caused by the nighttime descent of colder air from higher elevations.

Concerning Tests of Significance

The model formulation we propose represents interactions of three factors of environment: aspect, slope, and elevation. These factors are integrated into a mathematical expression that represents the combined effect in terms of a cosine function of aspect with a phase shift and amplitude that change with slope and elevation. The overall structure of the model is derived from qualitative knowledge of the processes involved. Although the quantitative values of the parameters are derived from the data set being analyzed, they are not independent. Parameters close to zero do not indicate that a variable is not significant because the same variable in a different part of the expression may be needed. Near-zero coefficients are

legitimate in the calculations of phase shift, etc. Therefore, independent tests for zero parameters are not appropriate. The collection of nine variables should be considered as a set—take it or leave it. Their combined contribution to the precision of the prediction can be evaluated by an F-test on the difference in the regression sum-of-squares between regressions with and without the set, with 9 and $n - 9 - p$ degrees of freedom, where n is the number of data and p is the number of coefficients estimated for other variables in the expression.

Model Behavior

We illustrate the behavior of our proposed formulation with three data sets: a synthetic data set that was constructed to represent the hypothesized behavior, and two real data sets. One real data set comes from the systematic sample of the Uinta National Forest in Utah measured by the Intermountain West Forest Inventory and Analysis project of the US Forest Service, Rocky Mountain Experiment Station (Moisen and Frescino 2002). The Utah dataset should contain the extremes of the elevation range of the tree species and would, therefore, correspond to the requirements of the approach of Roise and Betters (1981). The second real data set is from a study of the effects of competition on height increment of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) in the interior northwest of the United States. The Douglas-fir data were from a designed study spanning the distribution of site index for the species and principal habitat types in which it grows (Monserud 1984).

Synthetic Data Set

This data set represents two hypothetical species adapted to different elevations. The data represent the probability that the species would occur on either a northern or a southern aspect (Figure 1). Each species is more likely to occur on northern aspects at lower elevations, and on southern aspects at higher elevations. To simplify the example, slope is assumed a constant, say 25%. To explore effects of asymmetry of the high/low representation, one species is almost a mirror image of the other.

Each “species” in the hypothetical data was modeled independently with a logistic transformation of the dependent variable. The sine aspect term and slope have been omitted because only northern and southern aspects on a constant slope are represented:

$$\ln\left[\frac{1-p}{p}\right] = b_1 + b_2(el) + b_3(el^2) + \cos(\alpha)[b_4 + b_5\ln(el + 1) + b_6(el^2)]. \quad (6)$$

In this equation, the effect on flat ground is parabolic in elevation. The term k is represented implicitly by the coefficient b_4 in the interaction to overcome the effects of different units of measure of elevation in the logarithmic transformation. Omitting the logarithmic term for species B resulted in less sensitivity to aspect at the lower elevations.

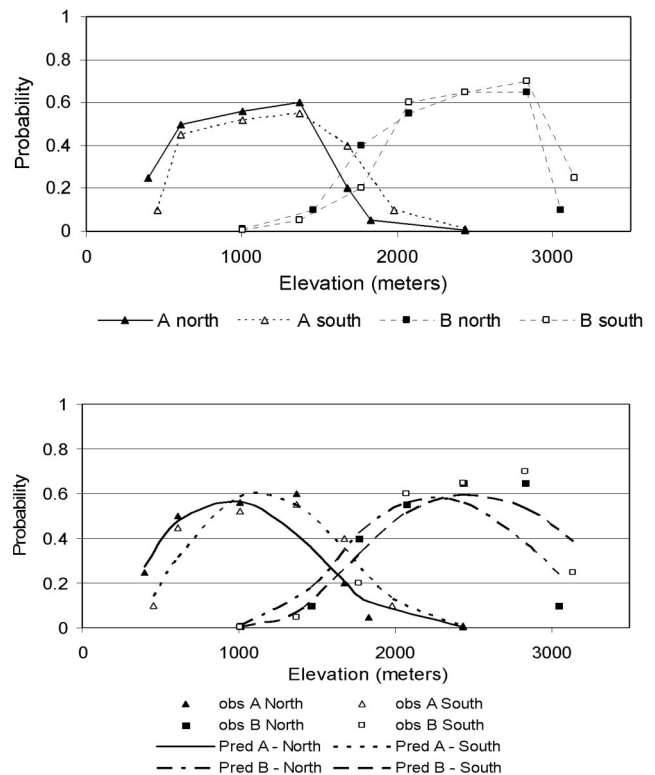


Figure 1. Hypothetical data for two species (A, B) adapted to differing elevations, each species on two opposing aspects (top panel). Fit of Equation 6 to each species separately (bottom panel).

Graphs of the solutions for Equation 6 for each of the two species are shown in Figure 1. Although the switch in optimum aspects is well represented at the elevation extremes, the mid-elevations are biased even though the logistic is supposed to have a flatter peak than would the Gaussian with $\ln(p)$ as the dependent variable.

Utah Data Set

Moisen and Frescino (2002) analyzed this data set using several alternative models. They concluded that for estimating forest parameters, it was first necessary to mask the nonforest observations rather than entering their attributes as zeroes. Following their suggestion, we illustrate the behavior of our representation of the aspect/elevation relation in two analyses. The first is a simple linear discriminant function (Fisher 1946, p. 285) using all 1,075 data points to classify locations as forest or nonforest. The second analysis predicts the mean annual increment ($m^3/ha/yr$) of only the 822 forested plot locations.

The discriminant function was calibrated as a linear regression (Equation 7) with y equal to proportion of forested plots as the dependent variable for the forested plots and the negative of proportion of nonforested plots as the dependent variable for the nonforested plots (Fisher 1946, p. 286). In addition to the elevation/aspect variables from Equation 4, latitude and longitude scaled as Univ. Trans.

Merc. coordinates (Albrx, Albry) were used to localize the slope/aspect/elevation effects:

$$y = b_0 + s[b_1 + b_2\cos(\alpha) + b_3\sin(\alpha)] \\ + \ln(el + 1) \cdot s[b_4 + b_5\cos(\alpha) + b_6\sin(\alpha)] \\ + (el^2) \cdot s[b_7 + b_8\cos(\alpha) + b_9\sin(\alpha)] \\ + b_{10}el + b_{11}el^2 + b_{12}Albrx + b_{13}Albry. \quad (7)$$

With this function, a positive prediction of y would be classed as forested, and a negative prediction would be classed as nonforest. Figure 2 shows the effect of varying elevation in the discriminant function for northern and southern aspects at the average UTM location and for slopes of 20% and 5%. The actual range in elevations was from 1,280 to 3,900 meters.

The discriminant shows the switch in classification of forest/nonforest at elevation extremes between northerly and southerly aspect and the reduced amplitude of the aspect effect at flatter slopes. An unexpected outcome of this analysis is that level ground would be more likely classified as forested at higher elevations than sloping ground on either aspect.

Values of the discriminant with varying aspect are shown for two extremes of elevation, at 20% slope and the average UTM coordinates in Figure 3. At the low elevation, the optimum value for classifying as forest is about NE. At the high elevation, the optimum is almost due south, illustrating that the phase shift is not limited to just a 180° difference between high and low elevations.

Analysis of mean annual increment (MAI) was limited to the 822 locations classified as forest from direct examination. The model was

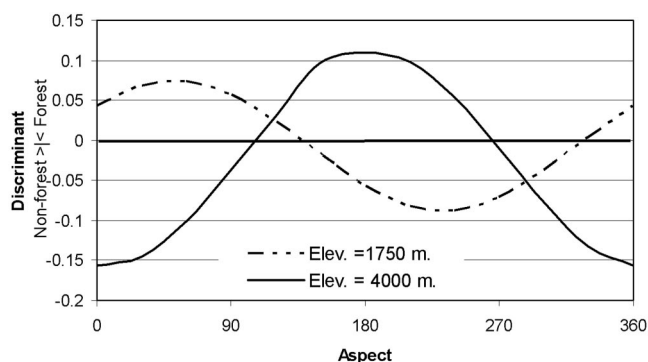


Figure 3. Varying aspect in forest/nonforest discriminant function for the Utah data set for 25% slope, at two elevations. Aspect in degrees from north.

$$\ln(\text{MAI}) = b_0 + s[b_1 + b_2\cos(\alpha) + b_3\sin(\alpha)] \\ + \ln(el + 1) \cdot s[b_4 + b_5\cos(\alpha) + b_6\sin(\alpha)] \\ + (el^2) \cdot s[b_7 + b_8\cos(\alpha) + b_9\sin(\alpha)] \\ + b_{10}el + b_{11}el^2 + b_{12}Albrx + b_{13}Albry. \quad (8)$$

Figure 4 shows the expected switch of optimum aspects between high and low elevations. Productivity of level ground falls between the northern and southern aspects at low elevations, but is less than either northern or southern aspects at high elevations. The data apparently indicate that level ground at high elevations is more likely to be forested, but with forests of lower productivity. Does this result suggest effects of frost pockets at the higher elevations?

At lower elevations, the optimum aspect is NNE, switching to SSW at the higher elevations (Figure 5) as hypothesized.

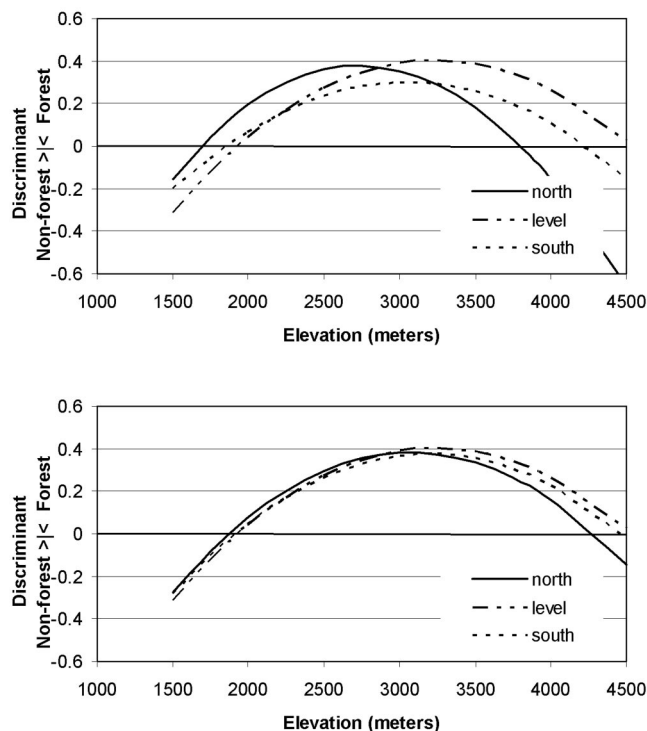


Figure 2. Varying elevation in forest/nonforest discriminant function for the Utah data set (top panel slope = 20%, bottom panel slope = 5%).

Douglas-Fir Height Asymptote

Data for this analysis are from an intermediate step in the development of a differential equation for height increment as a function of height and vegetative competition, including both overstory and shrubs and forbs. As part of this study, Salas (2006) estimated parameters of a mixed-effects model of height increment (Equation 9) using the restricted maximum likelihood (REML) fitting method,

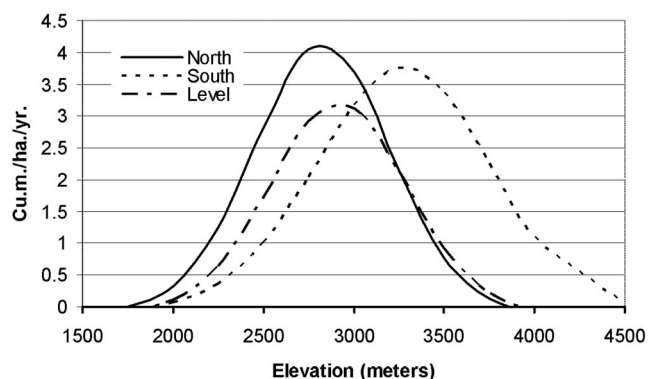


Figure 4. Mean annual stand volume increment (Equation 8) for the Utah data set varying elevation for level ground and two aspects, slope = 25%; geographic coordinates at their mean.

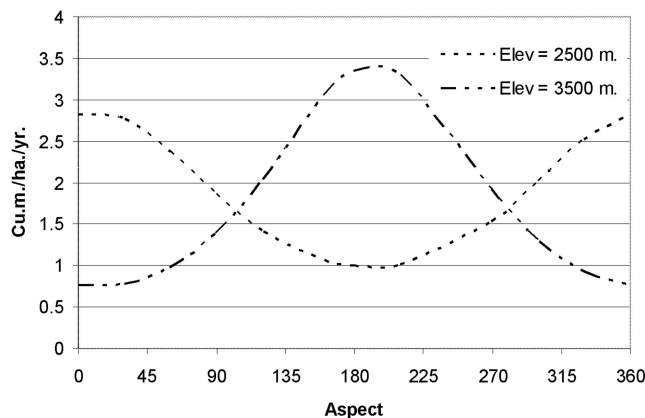


Figure 5. Mean annual stand volume increment (Equation 8) varying aspect for high and low elevations for the Utah data set, slope = 25%; geographic coordinates at their mean. Aspect in degrees from north.

$$h_1 = a \{ 1 - [1 - (h_0/a)^c] e^{-b(t_1 - t_0)} \}^{1/c}, \quad (9)$$

where h_1 , t_1 and h_0 , t_0 are the tree height and year-date for the top and bottom of the periodic increment—usually for periods of 10 years. The asymptote a was the random parameter for each plot, to be considered as representing the site factors affecting the cluster of trees and other unexplained variations common to the trees in each plot.

Our current analysis uses a portion of the data obtained from stem analyses by Monserud for estimating site index of Douglas-fir in the northern Rocky Mountains (Monserud 1984). His sample trees were clustered in plots for which stand and site parameters were also measured. His plots were subjectively located to span the range of habitat types (*sensu* Daubenmire (1952) and geographic range of the species in Idaho, Montana, and northeast Washington. Site factors extracted from his data included aspect, slope, elevation, and habitat type. Habitat types were grouped in the same set of six classes used by Wykoff et al. (1982) and listed in Table 1. We used only the height increment for the period just before the tree was felled for stem analysis because that was the period for which the stand data were most relevant.

We used the 121 plot estimates of a from a total of 383 trees as the variable to be predicted from site factors. The variables in the linear site factor model (Equation 4) were augmented by indicator (0–1) variables for each of five of the six groups of habitat types,

$$\begin{aligned} a = & b_0 + s[b_1 + b_2\cos(\alpha) + b_3\sin(\alpha)] \\ & + \ln(el + 1) \cdot s[b_4 + b_5\cos(\alpha) + b_6\sin(\alpha)] \\ & + (el^2) \cdot s[b_7 + b_8\cos(\alpha) + b_9\sin(\alpha)] \\ & + b_{10}el + b_{11}el^2 + b_{11+i}\text{Hab}_i. \end{aligned} \quad (10)$$

where $\text{Hab}_i = 1$ if the plot is classed as the i th habitat group ($i = 1, \dots, 5$) and 0 otherwise. The intercept term includes the effect of the *Pseudotsuga menziesii* habitats.

Three ordinary least-squares solutions for subsets of variables in Equation 10 were calculated: (1) including only elevation and its square, (2) adding the five variables for habitat type, and (3) adding the nine variables for the interactions of slope and aspect with elevation to the previous seven variables. Analysis of variance (ANOVA) of the marginal increments in regression sum-of-squares are shown in Table 2. Habitat types are the result of environmental factors related to elevation, aspect, and slope. Thus, their contribution added to the elevation regression sum-of-squares is already partly the effect of aspect and slope. However, the explicit terms adding the aspect-slope-elevation interactions still improve the fit of the model by removing 10.3% of the remaining, unexplained, sum-of-squares. The F-statistic, however, for the marginal interaction sum-of-squares of 1.33 is less than the $\alpha = 0.01$ F of 4.55. Comparing the first line of each sequence in Table 2 shows that adding the interaction terms to just elevation and its square increases the AIC Akaike (1973) index from 371.69 to 378.20. By these criteria, the model is overparameterized for these data.

Figure 6 (top panel) shows that without considering habitat types our model shows a general decline in the height asymptote with increasing elevation, but the amplitude of the aspect effect is virtually zero at the middle

Table 1. Grouping of habitat types following Wykoff et al. (1982)

Habitat type groups and Series	Understory type	Number of trees	Number of plots in group
Intercept			
<i>Pseudotsuga menziesii</i>	<i>Vaccinium caespitosum</i>	2	25
<i>Pseudotsuga menziesii</i>	<i>Physocarpus malvaceus</i>	68	
<i>Pseudotsuga menziesii</i>	<i>Calamagrostis rubescens</i>	6	
Hab. variable 1			
<i>Abies lasiocarpa</i>	<i>Linnaea borealis</i>	12	10
<i>Abies lasiocarpa</i>	<i>Xerophyllum tenax</i>	18	
Hab. variable 2			
<i>Abies grandis</i>	<i>Xerophyllum tenax</i>	3	12
<i>Abies lasiocarpa</i>	<i>Clintonia uniflora</i>	38	
Hab. variable 3			
<i>Abies grandis</i>	<i>Clintonia uniflora</i>	94	29
Hab. variable 4			
<i>Thuja plicata</i>	<i>Clintonia uniflora</i>	93	29
Hab. variable 5			
<i>Tsuga heterophylla</i>	<i>Clintonia uniflora</i>	49	16
Total		383	121

Habitat type is a binomial consisting of the overstory series name concatenated with understory type name.

Table 2. Analysis of variance of height asymptote in Douglas-fir height growth model predicted by Equation 10

	df	Ssq	Msq	F	-2ln(likelihood)	AIC
Sequence starting with elevation terms, adding aspect interactions last:						
Elevation-squared	2	397.59	198.80	12.93	367.69	371.69
Adding habitat types	5	703.31	140.66	9.15	327.44	341.44
Adding aspect, slope, and elevation interactions	9	183.86	20.43	1.33	314.26	346.26
Error	104	1,597.96	15.37			
Total	120	2,882.71	24.02			
Sequence starting with elevation and aspect terms first, adding habitat types last:						
Slope, aspect elevation	11	622.73	56.61	3.68	356.20	378.20
Adding habitat types	5	662.02	132.40	8.61	314.26	346.26
Error	104	1,597.96	15.37			
Total	120	2,882.71	24.02			

Marginal contributions of groups of explanatory variables to explained sum-of-squares (in addition to contributions from all variables in the lines above) are shown when entered in two different sequences. Likelihood and AIC (Akaike 1973) values are for the cumulative model including all variables in this line and the lines above. Units are meters.

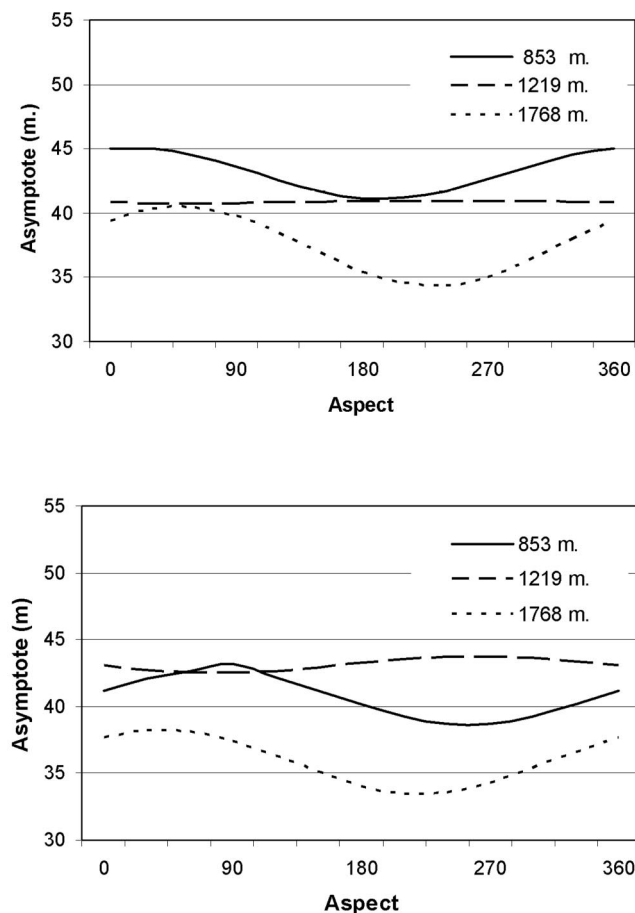


Figure 6. Douglas-fir asymptote data fit with Equation 10. Slope = 25% (top panel without habitat type, SE = ± 4.6 m). Lower panel with habitat type, *Abies lasiocarpa* group shown for upper, *Abies grandis/Clintonia uniflora* for middle, and *Pseudotsuga menziesii* for the low elevations. SE = ± 3.9 m. Aspect in degrees from north.

elevations. The surprise is that the optimum aspects indicated by these data do not reverse: northeast is still the optimum, with southerly aspects being more adverse at both higher and lower elevations.

Adding an intercept for habitat type groups changes the regression coefficients somewhat. The bottom portion of Table 2 shows that given all the elevation, aspect, and slope variables, adding habitat types almost doubles the variation explained.

The overall pattern is similar to the trends without habitat, but using a specific habitat type for each elevation changes their relative levels (Figure 6, bottom). The mid-elevation curve still has a reduced amplitude.

Although the equation form would permit the optimum to switch aspects between extremes of elevation, our model calibrated to these data indicates otherwise. One might wonder if the behavior of the model is an artifact of the model, or a real property of the data. Therefore, we divided the data into three elevation ranges and fit the model of Equation 10 without elevation to each of the three subsets independently. The resulting coefficients reproduced the behavior of the combined analysis, with the mid-elevation curve having little amplitude (Figure 7) and a different intercept for the specific habitat (*Abies grandis/Clintonia uniflora*). The consistency of the model behaviors illustrated by Figures 6 and 7 suggest that the unexpected aspect of the optimum is a property of the data, not an artifact of the model.

The contrasts with behavior shown in the Utah data illustrate the flexibility of the model to capture a wide range of behaviors inherent in the data. However, our interpretation of the specifics of the Douglas-fir data is limited by the lack of randomization from a defined population. Lacking a defined probability sample, we cannot say whether the unexpected elevation effects truly express the elevation

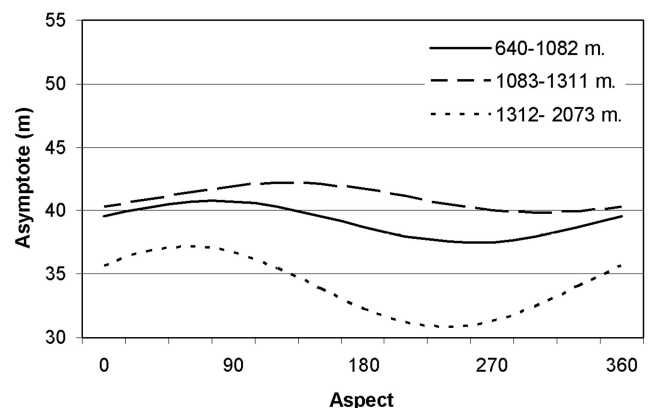


Figure 7. Douglas-fir asymptote data divided by elevation into three subsets of equal numbers. Habitat types for elevation classes are the same as in Figure 6; the model omitted all terms involving elevation from Equation 10. Aspect in degrees from north.

effects conditional on the correlated effect of a specific habitat type or are just an artifact of the data distribution.

Conclusion

Models of combined, interacting effects of elevation, aspect, and slope on species distribution and productivity are presented that are more general than previously published formulations. When fitted to data that are probability samples from a defined population, as in the Utah data, the curves generated by coefficients of the model are in accord with prior, qualitative expectations. When the data are from nonrandom samples and the factors are not independent of other factors in the model, as in the Douglas-fir height asymptote data, interpretation of the importance and functional form of the fitted model is more complicated. For example, the AIC index for the Douglas-fir height asymptote penalizes the full model for using nine parameters compared to a simpler version.

We recommend this formulation as a way to represent interacting effects of aspect, elevation, and slope with behavior consistent with current hypotheses about species presence and productivity. Its use in prediction equations and as variables in systems for imputing these attributes to mapping units where species presence and productivity are not universally represented should improve the accuracy of the end product.

Endnote

- [1] Users may be concerned with the effect of correlations among the eleven variables in Equation 4 induced by terms involving functions of elevation. These correlations can be reduced, improving the matrix

condition, by the mathematically identical formulation in which elevation-squared in each variable in which it appears is replaced by elevation centered by subtracting an approximate mean or median before squaring.

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