

DOUGLAS-FIR SITE INDEX: FOUR STUDIES IN SEARCH OF PRODUCTIVITY

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ABSTRACT

Results are presented from several studies aimed at examining site productivity of stands containing inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Stem analysis was used to develop polymorphic site index and height growth curves that can be used in both even-aged and uneven-aged stands. Curve shape was found to differ among three major habitat type groupings. Comparison with other site index curves from the Northwest indicated that differences increased as geographic distance and ecological differences increased. Large differences between curves arising from the method of site curve construction were also found, with the underlying cause being the untenable assumptions needed to construct guide curves using inventory data. A soil-site study failed to uncover any important relationships between soil factors and site index. The two most likely explanations for these low correlations between edaphic factors and site index are (1) a large and complex study area where the number of important site factor interactions exceeded the sample size, and (2) failure of standard Soil Survey procedures to measure the true causes of site productivity. A genetics-site study found that a genetic index (3-year seedling height in a provenance test) was correlated higher with site index than any environmental factor. A path analysis revealed that genetic variation was about a third more important than environment in determining variation in dominant height growth. This means that site index is not solely determined by static environmental factors that we think of as "the site." Instead, more than half of the site index variation is determined by the genotypes present at the site, genotypes that are highly adapted to their local environment.

INTRODUCTION

Site index is the average height of selected dominant trees of a given species at an index age (e.g., 50 years). Because dominant height is relatively unaffected by stand density (except in the extremes), site index is more closely related to the capacity of a species to produce wood on a given site than any other single measure (Spurr and Barnes 1980). Site index thus attempts to capture the relationship between dominant height and age that is attributable to site rather than density effects.

When I moved to Idaho 15 years ago I was surprised to find myself working with the only team of forest growth modelers in the world that saw little if any utility in the concept of site index, which is best suited for pure, even-aged stands. Their

reasons were good: (1) the forests of the Northern Rockies are commonly irregular, almost always with a mixed species composition and quite often an uneven-aged structure; (2) because many of the species are intermediate to high in shade tolerance, we cannot be sure that alleged site trees were not suppressed in the past; (3) defoliators such as Douglas-fir tussock moth and western spruce budworm may have reduced height growth in the past; (4) good (and in some cases even bad) site curves are not available for several species; and (5) doubt existed as to the best species for indexing productivity in a mixed species stand. The net result was a strong and reasonable reluctance to base the Stand Prognosis Model (Stage 1973; Wykoff *et al.* 1982) on a construct as ill-behaved as site index appeared to be in the Northern Rockies.

My reaction was to go my separate way and see for myself just how far the concept of site index could be pushed and still be useful. I had just come from Wisconsin, where the northern hardwood forests are just as irregular as the conifer forests in the Rockies and where I built a stand simulator (FOREST; see Ek and Monserud 1974) for uneven-aged mixed-species stands; the basis of the height growth component was site index.

My goal was to build a system of height growth and site index curves that would be reliable regardless of the stand conditions where inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) was found, provided that suitable site trees could be found. None of this "only for pure even-aged stands" business.

Why Douglas-fir? Several reasons. Douglas-fir is the most important forest species in the Rockies, yet no one had built reliable site curves for the species. It has a wide ecological amplitude, occurring in almost every habitat type moister than the ponderosa pine series. This diversity of stand conditions made it an interesting species. And finally, I was being funded by the Douglas-fir Tussock Moth Research and Development Program, which was interested in having better growth and yield information for the substrate, Douglas-fir.

STEM ANALYSIS AND MODEL DEVELOPMENT

Stem analysis (the determination of age at several heights throughout the same tree) provides the most reliable data for developing site index curves. Because a real height growth series is measured, site index is actually observed. This eliminates the enormous bias that results when site index models must be developed from inventory data where only the current height and age are measured.

Monserud (1984a) established 135 stem analysis plots throughout the seven National Forests of northern Idaho and northwestern Montana. Plots were selected to cover a wide range of ages and habitat types. To assure that a wide range of ecological variation was considered, at least 20 plots were

located in each of the five major habitat series containing Douglas-fir: Douglas-fir (DF), grand fir (GF), western redcedar (WRC), western hemlock (WH), and subalpine fir (SAF). No requirements for species composition, uniform spacing, stand density, or age structure were used to constrain the selection of plots, although an effort was made to avoid clustering the plots geographically. These nonrestrictive procedures resulted in the selection of both even-aged and uneven-aged plots as well as both pure and mixed-species stands.

Suitable site trees were the three best growing (based on increment cores) dominants on an approximately 1/2-acre plot that was representative of the growing conditions in the stand. Site trees had healthy crowns with no sign of top damage, and had a history of radial growth that gave no indication of suppression or damage.

Using the stem analysis data from 349 dominant trees, Monserud (1984a) derived the following height growth and site index curves:

$$H = \frac{42.397 \cdot S^{(0.3197Z_1 + 0.3488Z_2 + 0.3656Z_3)}}{1 + e^{9.7278 - 1.2934 \ln A - (1.0232Z_1 + 0.9779Z_2 + 0.9527Z_3) \ln S}} \quad (1)$$

$$S = 38.787 - 2.805(\ln A)^2 + 0.0216A \cdot \ln A \quad (2)$$

$$+ (0.4948Z_1 = 0.4305Z_2 + 0.3964Z_3) \cdot H$$

$$+ (25.315Z_1 = 28.415Z_2 + 30.008Z_3) \cdot H/A$$

where **H** = total height - 4.5 feet, **S** = site index - 4.5 feet, **A** = age at breast height, *e* = the base of natural logarithms, $\ln \chi$ = the natural logarithm of argument χ , and

$$Z_1 = \begin{cases} 1 & \text{if habitat type is in the DF series, or} \\ 0 & \text{otherwise.} \end{cases}$$

$$Z_2 = \begin{cases} 1 & \text{if habitat type is in the GF or WRC series, or} \\ 1 & \text{if no habitat type information is available, or} \\ 0 & \text{otherwise.} \end{cases}$$

$$Z_3 = \begin{cases} 1 & \text{if habitat type is in the WH or SAF series, or} \\ 0 & \text{otherwise.} \end{cases}$$

Separate equations for predicting height growth and site index are needed because the parameters were derived from two different sum of squares surfaces (Draper and Smith 1981). Otherwise fitting height as a function of site index and age and then solving for site index will always result in a model that is both different and inferior to the model obtained from fitting site index as a function of height and age. When statistical variation is present (as it certainly is here), solving an equation such as 1 for another variable such as **S** produces a result that is seem-

ingly correct mathematically but is incorrect statistically. Separately estimated equations solve the problem. If you want to know the site index of a stand of known dominant height and age, then use equation 2. If you want to estimate the dominant height of a stand with a given age and site index, then use equation 1. And both equations 1 and 2 are needed to estimate the average dominant height development for a stand with site trees not at index age.

Note that age is measured at breast height. Although breast-high age is far more convenient to measure than total age, the real reason for using a breast-high age is to eliminate (or at least reduce) the influence of nonsite factors such as animal damage, snow damage, and local plant competition on the early development of the seedlings. By the time trees reach breast height it is more likely that the influence of such factors will be considerably reduced.

One of the most interesting aspects of the resulting height growth and site index curves is that habitat type affects curve shape (Figures 1 and 2). Monserud (1984a) found that three habitat series groupings were sufficient to explain variation related to habitat type. This means that there are three height growth and site index curves for a given site index. First of all, notice that differences among the three habitat series groupings are trivial before age 70; only when trees begin to reach maturity and fully occupy the site do differences become important. The lowest curve represents the driest habitat series: the Douglas-fir (DF) climax series. Reduced moisture availability is likely the cause of the large reduction in height growth once the site becomes fully occupied, which occurs at a younger age in stands of higher site index (Monserud 1985a).

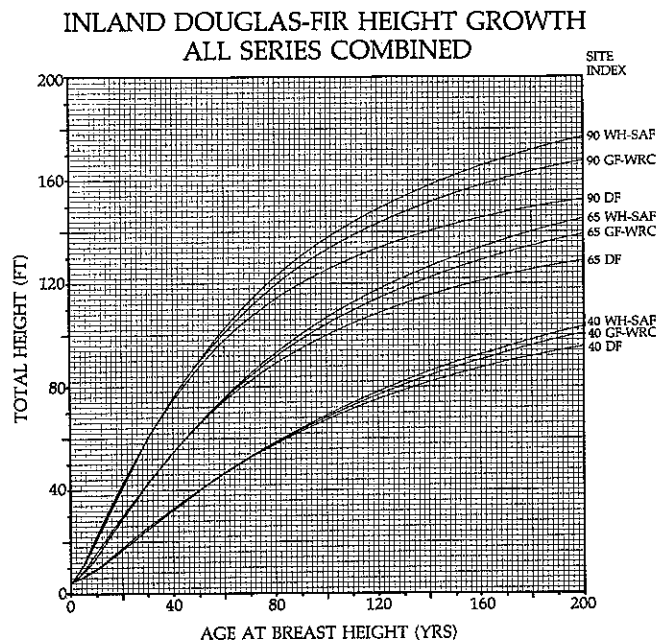


Figure 1. —Height growth model [1] vs. age, for each of three habitat series groups and for (approximately) the minimum (40), mean (65), and maximum (90) levels of site index sampled.

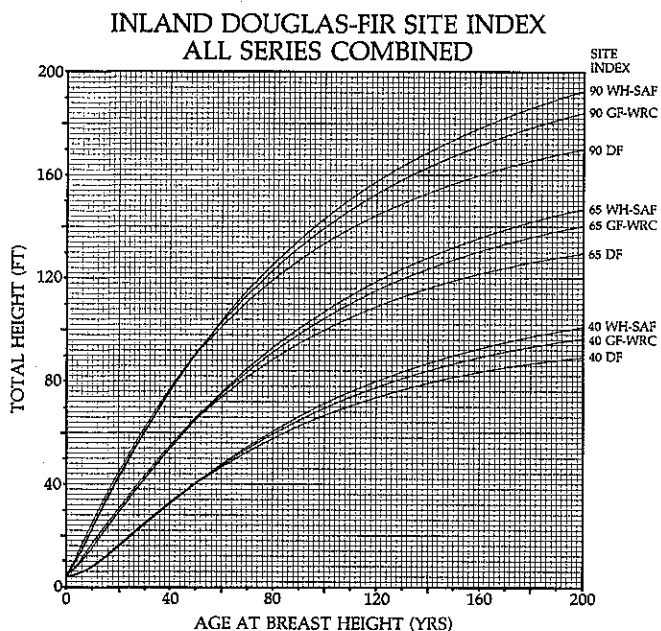


Figure 2. —Site index model [2] is plotted in conventional height vs. age format for each of the three habitat series groups and for (approximately) the minimum (40), mean (65), and maximum (90) levels of site index sampled.

The highest curve represents the moistest habitat series grouping: western hemlock and subalpine fir (WH-SAF) climax series. Good height growth continues longer on these WH-SAF habitats than on any of the others. Just because Douglas-fir growing on a western hemlock habitat has the same growth curve shape as on a subalpine fir habitat, it does not follow that the SAF series is as productive as the WH series. Quite the contrary, for plots in the SAF series had an average site index (53 feet) that was 13-feet lower than plots in the WH series. The SAF habitats are among the coldest, which has the effect of shortening the growing season and lengthening the time it takes for a tree to reach a given height.

The middle curve is the grand fir and western redcedar (GF-WRC) series grouping. These habitats are intermediate between the DF and WH-SAF habitats in both moisture availability and temperature regimes. In fact, the GF-WRC curves are so intermediate that they are not significantly different from the overall all-series combined curves. This result allowed Monserud (1984a) to incorporate the simplification found in both equations 1 and 2: the same equations can be used whether or not habitat type is known. Although the GF-WRC series plots are intermediate in curve shape, they are not intermediate in growth potential; their average site index (72 feet) is 8 feet higher than the plots on the other three habitat series (Monserud 1985a).

Monserud (1985a) discusses the application of these curves in detail, including sample size considerations and potential problems. The greatest problem, of course, is the failure to select suitable site trees. Because Douglas-fir commonly grows in irregular stands, care should be taken to examine increment cores

from potential site trees for indications of past suppression or damage.

Monserud's curves have passed several independent validation tests (Vander Ploeg 1987; Milner 1985 as cited on p. 675 of Monserud 1985b) and therefore should be applicable across the compositional range from pure even-aged stands to uneven-aged mixed-species stands, provided that suitable site trees are sampled.

COMPARISON WITH OTHER CURVES

Having created something new, it is natural to compare it with what already exists. Monserud (1985b) reports on the results of comparing equations 1 and 2 with all of the height growth and site index curves available for Douglas-fir in the Northwest. Results indicate that differences in the height growth pattern of Douglas-fir increase as both the geographic distance and the ecological differences between regions increase. This is certainly no surprise. Height growth differences were extremely small between the Northern Rockies and the east side of the Cascades and were rather large between the Rockies and the west side of the Cascades. The relatively small differences between the Northern Rockies and the Cascades crest fell between these two extremes. Small differences were found between northern Idaho and either Montana or central Idaho, except when the habitat types were much drier or colder than Monserud (1984a) was able to find.

A disturbing result was uncovered, however. By comparing curves based on stem analysis data with those constructed from inventory data (guide curves), Monserud (1985b) concluded that the type of data and the resulting methodology used to develop the site index curves are strongly related to the similarity of the resulting curves. Differences that are methodological rather than biological are clearly cause for concern. Curves derived from felled-tree stem analysis studies were quite similar to each other but differed substantially from curves derived by harmonized guide-curve methods. Furthermore, the inventory-based guide-curve systems produced curves that were surprisingly similar to each other, even though different varieties of Douglas-fir from different regions were being compared.

A controlled experiment was devised by constructing a guide curve using the same plots that Monserud (1984a) used to build the stem analysis curves. Differences were quite large and corresponded to differences detected between the other guide curve systems. The source of the problem is the untenable guide curve assumptions that are applied to inventory data from temporary plots. Before the average curve (the guide curve) can represent the true mean growth pattern, it is necessary for the distribution of site index across all age classes to be the same. There is no biological or ecological reason why the distribution of site index should be the same in both old growth and young growth stands. In fact, prior harvesting patterns in the age of the timber barons almost guaranteed that the more accessible and productive lower elevation sites would be logged far more intensively than the less productive and far more inaccessible high elevation sites. The result of such management practices would be an inventory with disproportionately fewer old growth stands with high rather than low site indices. The resulting guide curve would be quite biased, being too flat after index age because of a dearth of old high-site stands.

The real problem with the guide curve methodology as applied to inventory data is that site index is never actually observed. It is only inferred, and inferred from untenable assumptions (Monserud 1984b). Not all site index curves are created equal. A curve based on stem analysis data should always be more accurate.

SOIL-SITE RELATIONS

Obviously the best procedure for determining site index is to measure the heights and ages of appropriate site trees. Not all sites have suitable site trees, however, for the land may be cut over or burned over, or trees may have been seriously attacked by insects or diseases that adversely affect dominant height growth. These situations call for indirect methods of assessing site index, methods that rely on the relationships between environmental factors and site index. Such studies are traditionally called soil-site studies, even though the environmental factors considered often include climatic, physiographic, and vegetative indicators, as well as soil characteristics.

Given the need of foresters to accurately assess site productivity when suitable site trees are not available, a soil-site study was conducted (Monserud *et al.* 1990) using the same plots that were used to develop site curves. The goal was to use standard Soil Survey procedures (USDA Soil Survey Staff 1975) to find edaphic factors that could estimate site index in the absence of site trees.

Supporting this approach were hundreds of soil-site studies reporting varying degrees of success. Negative reviews (e.g., Stone 1978) warned of problems with the approach, but the expectation among field soil scientists and foresters in the region was that it should be fairly straight forward to find a set of soil factors that are strongly related to site index. In addition, this study had several advantages not shared by previous soil-site studies. First, a large and representative sample of plots with observed rather than predicted site index were available. Second, an ecologically based habitat type system was available (Daubenmire and Daubenmire 1968; Pfister *et al.* 1977) for stratifying the area into meaningful vegetation classes. And finally, the early results of Rehfeldt's (1989) genetics research had demonstrated that Douglas-fir was strongly adapted to its local environment. Surely there must be edaphic factors associated with this large variation in genotype. In short, I expected success.

Soil profile descriptions and physical analyses were determined on 133 plots by soil scientists from the respective National Forests. Several physiographic site descriptors were also measured. Chemical analyses were performed on soil samples from a third of these plots, and moisture availability was determined on 60% of the plots. All laboratory data were expressed on a volumetric basis (i.e., mass per soil volume) by multiplying by the rock-free proportion and bulk density. The thickness of each horizon was used in calculating a weighted average when combining horizon variables.

All soil properties were analyzed by classifying each profile five ways: (1) by A, B, and C horizons; (2) by position of the horizon in the profile (i.e., uppermost, second, third); (3) by four soil depth classes; (4) by plot average weighted by horizon

thickness; and (5) by plot average above a potentially limiting depth.

Elevation was the strongest predictor, accounting for a third of the variation in site index. The addition of habitat type information resulted in a significant improvement (as did longitude and an isohyetal estimate of precipitation) but still left over half the variation unexplained.

Several soil variables were statistically significant. Unfortunately, they were not very important. The best model using physical soil variables explained only one-sixth of the variation in site index. The best chemical variables explained less than one-tenth of the variation. After examining numerous physical and chemical soil properties, the standard error could only be reduced one foot, a disappointing result in light of the considerable time and expense necessary for soil sampling. Monserud *et al.* (1990) concluded that none of the models using soil descriptors was as good as models employing simple above ground descriptors such as elevation, habitat series, longitude, and annual precipitation (from isohyets).

The most striking aspect of this study is that the myriad of soil descriptors accounted for so little variation in site index (Monserud *et al.* 1990). Based on Stone's (1978) critique of soil-site studies, perhaps this result should have been expected. Based on the reaction of many land managers, foresters, and field soil scientists working in the forests of the Northern Rockies, however, this result has been quite surprising. The common expectation is that you can accurately predict site index if you measure the right edaphic factors. While this attitude is correct in the sense that soil surely is important to tree growth, it is far from trivial to both determine and measure the suite of edaphic factors that are indeed strongly related to growth in a given locality.

The causes of these low soil-site correlations could not be conclusively determined, but the most likely explanations are (1) the number of important site factor interactions occurring in this large and complex study area far exceeded the sample size, and (2) failure to measure the true causes of site productivity. The hypothesis that standard Soil Survey procedures would provide edaphic data that could reliably predict site index in the absence of site trees had to be rejected.

GENETIC AND ENVIRONMENTAL COMPONENTS OF VARIATION

When all else fails, try genetics. At Al Stage's (Project Leader, Intermountain Research Station) suggestion, I began to inquire about Rehfeldt's genetics results for inland Douglas-fir. What resulted was a full-blown study examining the genetic and environmental components of variation in site index (Monserud and Rehfeldt 1990).

The fields of forest mensuration and genetics have a common interest in phenotypic variation. Mensurationists attempt to predict site productivity from height growth, a phenotypic response of trees to the combined effects of environmental and genetic variation. Geneticists isolate the genetic components of phenotypic variation in order to breed fast-growing trees that retain adaptedness. However, mensurationists usually ignore this genetic component, even when trying to elucidate the factors affecting site productivity.

The fortuitous concurrence of two disparate and independent studies of variation in inland Douglas-fir (Rehfeldt 1979 *et seq.*; Monserud 1984 *et seq.*) provided the unusual opportunity for separating the genetic and environmental components of phenotypic variation in site index. Results from these studies were combined to answer the following questions. First, how much variation in site index is associated with genetic variation? Second, what is the relative importance of the genetic and environmental components of phenotypic variation in explaining differences in mean height among stands of mature trees? And third, what is the magnitude of the interaction?

Environmental heterogeneity is responsible for genetic differentiation of Douglas-fir populations, much of which is considered to be adaptive (Rehfeldt 1979, 1982, 1983, 1987). The species faces frost-free periods that differ by about 100 days across an elevational interval of 4,000 feet. (Baker 1944). Precipitation concomitantly varies from 20-60 inches annually. Orographic effects induced by the forested mountains produce a mosaic of topographic microclimates at a given locality (Daubenmire and Daubenmire 1968).

In a recent analysis, Rehfeldt (1989) summarizes previous studies of genetic variation among 228 populations from a portion of Idaho and Montana that encompasses the region sampled by Monserud (1984a). Based on provenance tests conducted on seedling populations growing in two environmentally contrasting gardens, Rehfeldt found that 3-year seedling height was a variable for which population differentiation was both pronounced and strongly intercorrelated with other traits. Adaptive variation could be summarized with a model (see Rehfeldt 1989) that predicted the standardized 3-year seedling height as a function of the elevation and geographic location (latitude, longitude and transformations thereof) of the seed source. This model, accounting for 80% of the variation among populations, included 19 independent variables that most likely are aliases for the average length of the frost-free period, a variable that is unobservable.

Variation in site index reflects phenotypic variation among stands. However, because progeny tests were not conducted on Monserud's 349 stem analysis trees, no genetic components can be estimated directly. For this reason, Rehfeldt's model of genetic variation (which predicts genetic variation among stands) was used to estimate a genetic component expected from progeny tests. Thus, Rehfeldt's (1989) genetic index (standardized deviates of 3-year seedling height) was calculated for each stand. Linear regression was then used to predict site index as a function of environmental variables, Rehfeldt's genetic index, and combinations of the two. Path analysis (Wright 1934; Li 1975) was then used to estimate the separate contributions of environmental and genetic effects on the phenotype, as well as the interaction.

Rehfeldt's genetic index (standardized 3-year height) alone accounted for 42% of the variation in site index. This is far more than any environmental factor, a rather surprising result. Combining the genetic index and simple environmental variables (elevation, habitat series, latitude, longitude) accounted for nearly half the variation in site index. Regardless of the set of variables used to describe the environmental components of phenotypic variation, the genetic index remained significant in

all regressions, even though it was constructed independently from a complex assortment of many of the same variables (namely elevation, latitude, and longitude).

Path analyses estimated a strong correlation (0.76) between genotype and environment: similar genotypes tend to recur in similar environments. This result reflects the steep adaptive clines that are well known for this species. The analysis also indicated that the genotype is about a third more important than the contemporary environment in determining phenotypic variation in dominant height of natural stands. The results from the path analysis seem sensible biologically. For both genotype and environment to strongly affect the phenotype is a result that is intuitively satisfying. However, it was somewhat surprising that genetic effects surpassed the environmental.

For long-lived forest trees growing in extremely heterogeneous natural environments, predicting phenotypic variation from genetic and environmental effects has not been demonstrated before. Monserud and Rehfeldt (1990) demonstrated that nearly half of the phenotypic variation in dominant height at breast high—ages 50 and 100 (site index) was attributable to the joint effects of genotype and environment. This is rather surprising, considering that (1) the effect of the contemporary environment was only that indirectly indexed by elevation and habitat series, and (2) the genetic effect was indexed by a model that used only elevation, latitude, and longitude to predict the relative height of seedlings growing in the same environments to the extremely young age of 3 years.

It is apparent that the genetic and environmental models used in this analysis incorporate several of the same geographic and physiographic variables that are serving as surrogates for environmental effects. It is important to realize that a particular geographic variable may be aliasing for different environmental effects in the two types of models. Elevation, for instance, may reflect the mean frost-free period for thousands of generations in the genetic model. In the environmental model, the same variable might represent growing season temperatures during only the past century or so. Thus, in the genetic model, the independent variables are surrogates for climate; in the environmental, the same variables are surrogates for weather. This distinction has been made quite well by Mayr (1983), who points out that all biological phenomena have a proximate cause and an evolutionary cause.

It is also important to emphasize that the two studies that produced the site index and the genetic index were completely independent of each other. Different trees were measured in the two studies; the trees were from different stands and were growing under different conditions on different sites.

A combination of genetic and mensurational models has a high potential for improving our understanding of basic biological relationships in forest populations, for improving stand management, and for implementing breeding programs. To geneticists, these results explain why making rigorous selections among wild phenotypes is an advantageous prelude to Douglas-fir breeding programs. Silviculturists might use models that combine genetic and environmental effects to select stands of superior productivity for collecting seeds. And mensurationists, as illustrated by Buford (1986) for artificial regeneration, could use such models for increasing the precision of estimating site

productivity. Perhaps more importantly, these results, their limitations notwithstanding, aptly illustrate that the forest resource is synergistic: more than the sum of soils, genotypes, or weather, the forest develops from a strongly intercorrelated network of genetic and environmental factors (Monserud and Rehfeldt 1990).

These results demonstrate that Douglas-fir site index is not just a static attribute of a physical piece of ground, for over half of the effect called site index is determined by the genotype of the trees growing on that site. It may seem unsettling, but site index is actually rather dynamic. That means that the productivity of the site can be altered by altering the mix of genotypes growing on that site (e.g., ignoring seed-transfer guidelines when planting). And global climatic change, if rapid and extreme enough, could likewise lower site productivity by rendering trees maladapted to the very site where they naturally regenerated.

The next step in this research (which has already begun) is to see if these results also hold within stands. If genetic variation within stands is strongly correlated with phenotypic variation of mature trees, then the potential utility of combined genetic/mensuration models would be great, especially in stand management (e.g., choosing crop trees in thinnings) and tree breeding (e.g., making selections from juvenile performance).

LITERATURE CITED

- Baker, F. S. 1944. Mountain climates of the Western United States. *Ecol. Mono.* 14:223-254.
- Buford, M. A. 1986. Height-diameter relationships at age 15 in loblolly pine seed sources. *For. Sci.* 32:812-818.
- Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. *Tech. Bull.* 60. Pullman, Washington Agricultural Exp. Sta. 104 pp.
- Draper, N. R., and H. Smith. 1981. *Applied regression analysis*, 2nd ed. New York, NY: John Wiley and Sons. 709 pp.
- Ek, A. R. and R. A. Monserud. 1974. FOREST: a computer model for simulating the growth and reproduction of mixed species forest stands. *Res. Rep.* R2635. Madison, Univ. of Wisconsin, College of Agriculture and Life Sciences. 90 pp.
- Li, C. C. 1975. *Path analysis primer*. Pacific Grove, CA: Boxwood Press. 347 pp.
- Mayr, E. 1983. *The growth of biological thought*. Cambridge, MA: Harvard Univ. Press. 974 pp.
- Monserud, R. A. 1984a. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.* 30:943-965.
- Monserud, R. A. 1984b. Problems with site index: an opinionated review. *In: J. Bockheim, ed., Forest land classification: experiences, problems, perspectives*. Madison: Univ. of Wisconsin Soil Science Dept. p. 167-180.
- Monserud, R. A. 1985a. Applying height growth and site index curves for inland Douglas-fir. Ogden, UT: USDA Forest Service, Intermountain Research Station. *Res. Pap.* INT-357. 22 pp.
- Monserud, R. A. 1985b. Comparison of Douglas-fir site index and height growth curves in the Northwest. *Can. J. For. Res.* 15(4): 673-679.
- Monserud, R. A., U. Moody and D. Breuer. 1990. Results of a soil-site study for inland Douglas-fir. *Can. J. For. Res.* 20:686-695.
- Monserud, R. A. and G. E. Rehfeldt. 1990. Genetic and environmental components of variation of site index in inland Douglas-fir. *For. Sci.* 36: 1-9.
- Pfister, R. D., B. L. Kovalchik, S. F. Arno and R. C. Presby. 1977. *Forest habitat types of Montana*. Ogden, UT: USDA Forest Service, Intermountain Research Station. *Gen. Tech. Rep.* INT-34. 174 pp.
- Rehfeldt, G. E. 1979. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. I. North Idaho and northeast Washington. *Heredity* 43:383-397.
- Rehfeldt, G. E. 1982. Ecological adaptations in Douglas-fir populations. II. Western Montana. *INT-295.* 8 pp.
- Rehfeldt, G. E. 1983. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho. *Can. J. For. Res.* 13:626-632.
- Rehfeldt, G. E. 1987. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). IV. Montana and Idaho near the Continental Divide. *W. J. Appl. For.* 3:101-105.
- Rehfeldt, G. E. 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. *For. Ecol. and Manage.* 28: 203-215.
- Spurr, S. H. and B. V. Barnes. 1980. *Forest ecology* (3d ed). New York, NY: John Wiley and Sons. 687 pp.
- Stage, A. R. 1973. *Prognosis Model for stand development*. Ogden, UT: USDA Forest Service, Intermountain Research Station. *Res. Pap.* INT-137. 32 pp.
- Stone, E. L. 1978. A critique of soil moisture-site productivity relationships. *In: W. E. Balmer, ed. Proceedings of the Symposium on Soil Moisture Site Productivity*. Atlanta, GA: USDA Forest Service, SE Area, State and Private Forestry. p. 377-387.
- Vander Ploeg, J. L. 1987. Comparison and development of height growth and site index curves for Douglas-fir in the Intermountain West. M.S. Thesis. Moscow, ID: Univ. of Idaho. 51 pp.
- Wright, S. 1934. The method of path coefficients. *Annals of Mathematical Statistics.* 5:177-180.
- Wykoff, W. R., N. L. Crookston and A. R. Stage. 1982. *User's guide to the Stand Prognosis Model*. Ogden, UT: USDA Forest Service, Intermountain Research Station. *Gen. Tech. Report* INT-133.
- USDA Soil Survey Staff. 1975. *Soil taxonomy. Handbook 436*. Washington D.C.: USDA Soil Conservation Service. Soil Survey Staff.

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