ECOLOGICALLY STRATIFIED HEIGHT-DIAMETER MODELS FOR HARDWOOD SPECIES IN NORTWESTERN LOWER MICHIGAN

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ABSTRACT.—Ecological classification systems (ECS) have been developed for northwestern Lower Michigan to stratify the landscape into areas of similar ecological potential. ECS are useful only to the extent that they capture quantifiable differences in tree form and function between defined strata and provide valuable, ecologically-referenced information for forest managers. Ecologically referenced height-diameter functions were developed here to demonstrate the utility of an ECS as a stratification tool for modeling stem form for northern hardwoods.

Ecological classification systems (ECS) have been developed and mapped to different scales across the United States (McNab and Avers 1994). The usefulness of an ECS hinges upon observable differences in variability in ecosystem structure and process between ECS map units. In other words, ECS are basically spatial stratification systems that assume that the variability within ECS units is less than the variability between them. If forest managers are to use ECS they need to see how they can be applied in an operational context. Here, height-diameter (H-D) functions, which are useful in forest inventory, were fitted to individual tree measurement data to determine if variation in tree morphology was effectively captured by Ecological Land Types (ELT), a type of ECS, defined for the Huron-Manistee National Forest in Michigan. Huang et al. (2000) undertook a similar study for white spruce in boreal forests, but ecologically referenced H-D functions have not been developed yet for northern hardwoods.

Methods

The goals for this study were to utilize variability in individual tree measurements across the landscape to see if differences in height-diameter relationships for different species were substantially affected by a site potential defined by an ECS.

Study area and data

The area of study was the Manistee portion of the Huron-Manistee National Forest, in northern Lower Michigan. The study area was large (~290,000 ha) covering a diverse array of glacial landforms and forest ecosystems (Host et al. 1988). Ecological land types (ELT), a type of ECS, were developed and mapped for much of this area. ELTs were based on regional differences in glacial parent material for soil formation and field estimates of soil properties and ground flora composition (Host and Pregitzer 1991) and are described by Cleland et al. (1993).

ELT units included are: Outwash Plains (OWP), described as *red oak-white oak-heath (Vaccinum spp.)* communities occurring on excessively-drained sand plains; Dry Ice-contact and Sand Hills (DSH), described as *mixed oak-red maple-Trientalis* communities occurring on excessively-drained over-washed moraines, kame terraces and glacial spillways; Mesic Ice-contact Sand Hills (MSH), described as *northern red oak-red maple-Viburnum spp*. communities occurring on well-drained sand hills; Herb-Poor Moraines (HPM), described as *sugar maple-American beech-Maianthemum* communities occurring on well-drained morainal sands; and Herb-Rich Moraines (HRM) described as *sugar maple-white ash-Osmorhiza* communities occurring on nutrient-enriched morainal sands.

Individual tree measurements data were available from 74 experimental reference stands used for developing ELTs for the Huron-Manistee National Forest (detailed methods are presented in Host et al. 1988). Only well-stocked (Basal area > 7 m^2 ha^{-1}), even-aged stands of at least 1 ha. in area, with minimal evidence of

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Table 1.—Summary statistics for individual tree data for trees measured in 1983 and 2003, broken down by ecological land type (ELT). Mean values are followed by [std; min, max]

ELT	n	height (m)	dbh (cm)	age (years)[†]
OWP	795	17.9 [4.5; 2.7, 30.4]	27.0 [11.6; 6.3, 106.7]	76.7 [19.9; 32, 138]
DSH	797	20.5 [5.0; 3.5, 34.4]	28.2 [11.0; 3.8, 65.0]	82.0 [14.7; 37, 127]
HPM	923	24.7 [6.0; 4.6, 43.8]	30.4 [14.1; 4.8, 97.8]	66.0 [10.5; 42, 93]
HRM	531	25.4 [5.7; 3.0, 41.7]	32.1 [14.3; 6.0, 106.6]	66.7 [12.0; 21, 102]
MSH	1242	27.4 [5.5; 6.0, 42.9]	34.8 [12.6; 5.8, 100.6]	76.0 [12.7; 47, 116]

[†]age was measured from a smaller number of trees than n.

disturbance, were selected (these stands originated from heavy logging at the turn of the last century). Study plots were established in each stand, in 1983. Four permanent point plots were randomly located to assess variability within the stand. An iron rod or piece of PVC pipe was placed at the center of each point plot and a BAF 10 cruising prism was used to estimate the number of trees in the plot (i.e., basal area in 1983). A metal tag, embossed with a tree identification number, was affixed to the base of each tree with a nail. Stem diameter at breast height (D) and total tree height (H) were measured for each tree. Age (A) was estimated in 1983 from an extracted core, on a subset of dominant or co-dominant trees, designated to estimate site index for common trees. Point plots were relocated in 2003 and dbh and height were measured again. Age for trees measured in 2003 was computed by adding 20 to the age measured in 1983. Measurement data are summarized by ELT in Table 1.

Analysis

The exponential Michelis-Menten model was used to model H-D relationships (Pacala et al. 1994):

$$H = \mu\left(1 - e^{-(\beta/\mu)D}\right) \qquad (1)$$

where H is the height (m) of a tree and D is its diameter (cm) at breast height (at 130 cm above ground). The parameter μ is asymptotic height and β is the initial slope of the H-D relationship.

Equation 1 was chosen because μ and • should have an interpretable ecological meaning and because μ, in particular, should relate to site quality. An estimate of the parameter • for a group of trees growing in the same ELT should roughly correspond to the effect of ecological conditions on the average taper of smaller (dbh), suppressed and intermediate trees. However, it should be difficult to separate an "ELT" effect on β from other factors that influence H-D ratios, namely differences in stand density (Wang 1998). The parameter μ, in the scenario described, corresponds to the average upper limits of height for the larger (dbh), dominant and co-dominant trees within a particular ecological land type (ELT). Given the well-established influence of water and nutrient availability on the upper limits of height growth (Ryan and Yoder 1997), μ should reflect major differences in site quality, for trees large or old enough that they are approaching their height limit. Differences in μ should also be much less sensitive to stand density because the largest trees were likely much less influenced by competitive effects on height and diameter growth. Since the ELTs for the Huron-Manistee N.F. were defined (through multivariate statistical methods) by differences in soil texture and herbaceous plant composition (which have been shown to be correlated with available soil water and nutrients, Host and Pregitzer 1991), significant differences the parameter μ, between ELTs, should reflect that meaningful differences in site quality on stem form.

Individual trees measured in both 1983 and 2003 were pooled into two groups for analysis: (1) all trees pooled by ELT, and (2) all trees pooled of a species by ELT, to assure that trees covering a wide range of sizes and ages (Table 1) from a range of stand conditions were represented within each ELT. Species examined were: northern red oak (RO, *Quercus rubra*), white oak (WO, *Q. alba*), black oak (BO, *Q. velutina*), northern pin oak (PO, *Q. ellipsoidalis*), red maple (RM, *Acer rubrum*), sugar maple (SM, *A. saccharum*), American beech (AB, *Fagus grandifolia*) and white ash (WA, *Fraxinus americana*). BO and PO were grouped together as in the OWP because field crews did not separate them there. Equation 1 was fitted for ELT and species-ELT combinations and parameters μ and β were estimated using non-linear regression analysis. Some species were not present in sample plots within a particular ELT or were present in insufficient numbers to obtain a statistically valid estimate of parameters μ and β, however, so an exploration of all possible species-ELT combinations was not possible.

The precision of each model was estimated with the coefficient of determination (r^2). To determine how much additional variation in height was explained by adding species level information, r^2 estimated for each ELT model were compared to that estimated for species-ELT models. Average residual error of prediction (= observed-predicted height) was used to detect for bias in each model, i.e., systematic over- or under-prediction of height. A two-tailed t-test for differences in means was used to test for significant (α = 0.05) differences in model parameters. Differences in model parameters between ELTs were assumed to represent the effects of an ELT on the H-D relationship of *any* tree in the total population of trees, regardless of its species. Differences in model parameters between species within an ELT were assumed to represent the combined effect of species and ELT on H-D relationships. Although other factors, including local differences in stand basal area, past disturbance and stand age should also influence H-D relationships, I assumed that pooling trees from a wide diversity of locations, stand types and ages would allow for site (ECS) and species effects on H-D relationships for individual trees to be assessed, while accounting for these other influential variables. To test for this, residuals were analyzed to determine if significant residual error could be attributed to differences in stand basal area or tree age.

Results

H-D functions for ELTs and species-ELT combinations are presented in Table 2. Values for μ and β result in essentially anamorphic H-D functions (fig. 1) with significant differences in H-D functions between 4 of the 5 ELT examined. There was no statistically significant difference between the two types of moraines (HPM and HRM). Thus, the original 5 ELTs could be effectively collapsed to represent 4 strata which meaningfully separate out differences in H-D relationships as a function of ELT.

Although tree stem diameter within ELTs was fairly well correlated (r^2 ranged from 0.63 to 0.68) with tree height, about one third of the variability in height remained unexplained by dbh. At least part of this unexplained error is likely due to the difficulty in accurately estimated the total height of hardwood species in mature, closed-canopy stands. Despite the unexplained error, average error of prediction for the ELT models was very small, ranging from 0.03 to 0.10 m (table 3). However, all models systematically under-predicted height for the tallest trees (fig. 2) due to the fact the μ represents the *average* asymptotic height (i.e., dominant canopy height) rather than a true maximum height. This is likely a problem when fitting any H-D functions with an asymptotic model, although authors more typically plot residual error as a function of predicted height (Huang et al. 2000) or dbh (Peng et al. 2001), which does not reveal this pattern. Analysis of residuals revealed no significant residual error explained by either tree age or stand basal area, thus, these factors were effectively scaled out of these H-D functions.

When species were used as an additional stratification tool along with ELT (table 2), there was very little differentiation between species on either DSHs or HRMs, except for AB, which differed substantially from other species on HRMs, due to the fact that smaller (dbh) AB were shorter than other species at the same dbh (β lower). On OWPs, H-D functions were different for all three species (and groups, i.e., BOPO) with significant differences in μ for WO and in β for RO. H-D functions for RO and RM were essentially the same on MSHs, but asymptotic height for WO was about 5.5 m below them. H-D functions on the HPM were essentially the same for two groups of species, [RO and RM] and [SM and AB], with an estimated 10 m greater asymptotic height between them.

To determine if ELT models were enhanced with species information, ELT models (table 2) were used to predict height for trees in species-ELT combinations. When individual trees were grouped by species and ELT, the fit of the H-D functions improved dramatically for a few species (as indicated by differences in r^2 vs. r^2 (ELT) (table 2), but in many cases resulted in only a small improvement in fit. Average error of prediction, on the other hand, was significantly improved when species information was used (table 3). However, as this error was generally less than 1 m for the ELT-only models (table 3), the magnitude of

Table 2.—Height diameter functions for different species within ecological land types (ELT). μ and β are the asymptotic height (m) and the H-D ratio for very small trees, respectively, estimated by least squares non-linear regression from eq. 1. Model parameters which are not significantly different (α = 0.05) between ELTs or species within an ELT are assigned the same lower case letter (w, x, y, z,) or (a, b, c), respectively. r^2 is the fit of the model and r^2(ELT) is the fit when the ELT model (Table 1) is used to predict height for species-ELT combinations.

	n	μ	95%CI for μ	β	95%CI for μ	r^2	r^2(ELT)
OWP	795	24.84 w	[24.05, 25.63]	1.31a	[1.25, 1.36]	0.65	-
WO	295	22.77 a	[21.33, 24.21]	1.29a	[1.19, 1.40]	0.60	0.56
RO	105	24.46 b	[22.88, 26.05]	1.68b	[1.51, 1.86]	0.67	0.40
BOPO	339	25.65 b	[24.52, 26.77]	1.27a	[1.18, 1.36]	0.59	0.58
DSH	797	27.57 x	[26.75, 28.40]	1.49b	[1.42, 1.56]	0.67	-
RO	297	26.97 a	[25.91, 28.03]	1.61a	[1.49, 1.73]	0.61	0.59
WO	225	28.69 ab	[26.60, 30.79]	1.45a	[1.32, 1.57]	0.60	0.60
RM	81	28.76 ab	[23.24, 34.29]	1.56a	[1.37, 1.75]	0.72	0.70
BO	177	31.25 b	[27.68, 34.82]	1.18b	[1.03, 1.32]	0.49	0.44
HRM	531	33.12 y	[32.12, 34.13]	1.73c	[1.64, 1.81]	0.63	-
SM	239	32.53 a	[30.99, 34.07]	1.84a	[1.72, 1.96]	0.70	0.70
WA	62	33.18 a	[30.64, 39.03]	1.77a	[1.38, 2.08]	0.49	0.49
AB	15	34.20 a	[26.23, 42.16]	1.18a	[0.83, 1.53]	0.81	0.61
RO	65	35.08 a	[33.05, 37.11]	1.58a	[1.34, 1.82]	0.53	0.49
HPM	923	34.08 y	[33.25, 34.92]	1.66c	[1.60, 1.72]	0.67	-
AB	111	28.10 a	[26.29, 29.90]	2.04a	[1.77, 2.31]	0.66	0.58
SM	344	28.38 a	[27.16, 29.61]	2.06a	[1.91, 2.20]	0.61	0.55
RO	290	37.14 b	[35.66, 38.61]	1.47a	[1.37, 1.57]	0.61	0.58
RM	61	37.19 b	[27.42, 46.96]	1.51a	[1.20, 1.81]	0.50	0.50
MSH	1242	35.20 z	[34.51, 35.88]	1.69c	[1.64, 1.75]	0.68	-
WO	114	30.05 a	[28.12, 31.98]	1.86a	[1.58, 2.13]	0.59	0.14
RO	846	35.30 b	[34.47, 36.12]	1.73a	[1.65, 1.80]	0.56	0.56
RM	199	36.56 b	[34.56, 38.56]	1.64a	[1.54, 1.74]	0.83	0.82

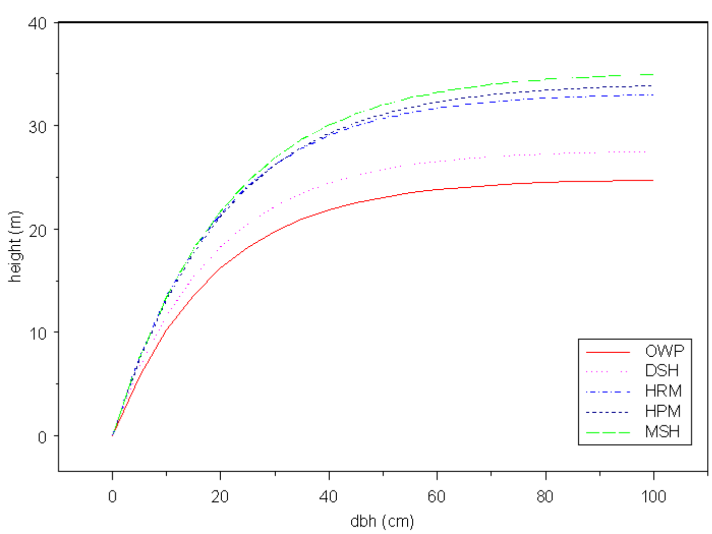

Figure 1.—Height-diameter functions for any tree species growing within an ecological land type (ELT). Curves for HRM and HPM are not statistically different.

Table 3. —Average error in height prediction (= observed – predicted height) for height-diameter functions (table 2). error(SPELT) refers to species-ELT models and error(ELT) refers to the error in the ELT model, or the error when the ELT model is used to predict height for a species within that ELT.

ELT	SPP	n	error(SPELT)	error(ELT)
OWP		795	-	0.03
	WO	295	0.01	-0.84
	RO	105	0.01	1.84
	BOPO	339	0.05	0.20
DSH		797	-	0.10
	RO	297	-0.05	0.25
	WO	225	-0.02	0.15
	RM	81	-0.07	0.56
	BO	177	0.00	-0.62
HRM		531	-	0.04
	SM	239	0.04	0.44
	WA	60	0.01	0.23
	AB	15	0.11	-3.12
	RO	65	0.01	0.64
HPM		923	-	0.10
	AB	111	0.00	-0.68
	SM	344	0.01	0.06
	RO	290	0.05	0.44
	RM	61	0.06	-0.23
MSH		1242	-	0.05
	WO	114	0.00	-1.82
	RO	846	0.01	0.30
	RM	199	0.02	0.10

improvement was small relative to the probable accuracy of the height measurements. Thus, while knowledge of species improved the power of H-D functions in most cases, these results suggest that the effect of ecological conditions (as indicated by soil-site conditions) was far more influential than the effect of species (i.e., genetics) on stem form. Hence, in this case, H-D functions developed for ELTs alone would be more robust than those developed for individual species.

Conclusion

Ecological Land Types (ELT) developed for the Huron-Manistee National Forest appear to be useful stratification tools for partitioning variability in H-D functions (i.e., stem form) across the varied glacial landscape of northwestern lower Michigan. Consistent with other studies (e.g., Host and Pregitzer 1991, Wang et al. 2000), these results suggest that effectively stratifying sites through the use of Ecological Classification Systems (ECS) can provide useful, ecologically-referenced information for managing forested ecosystems.

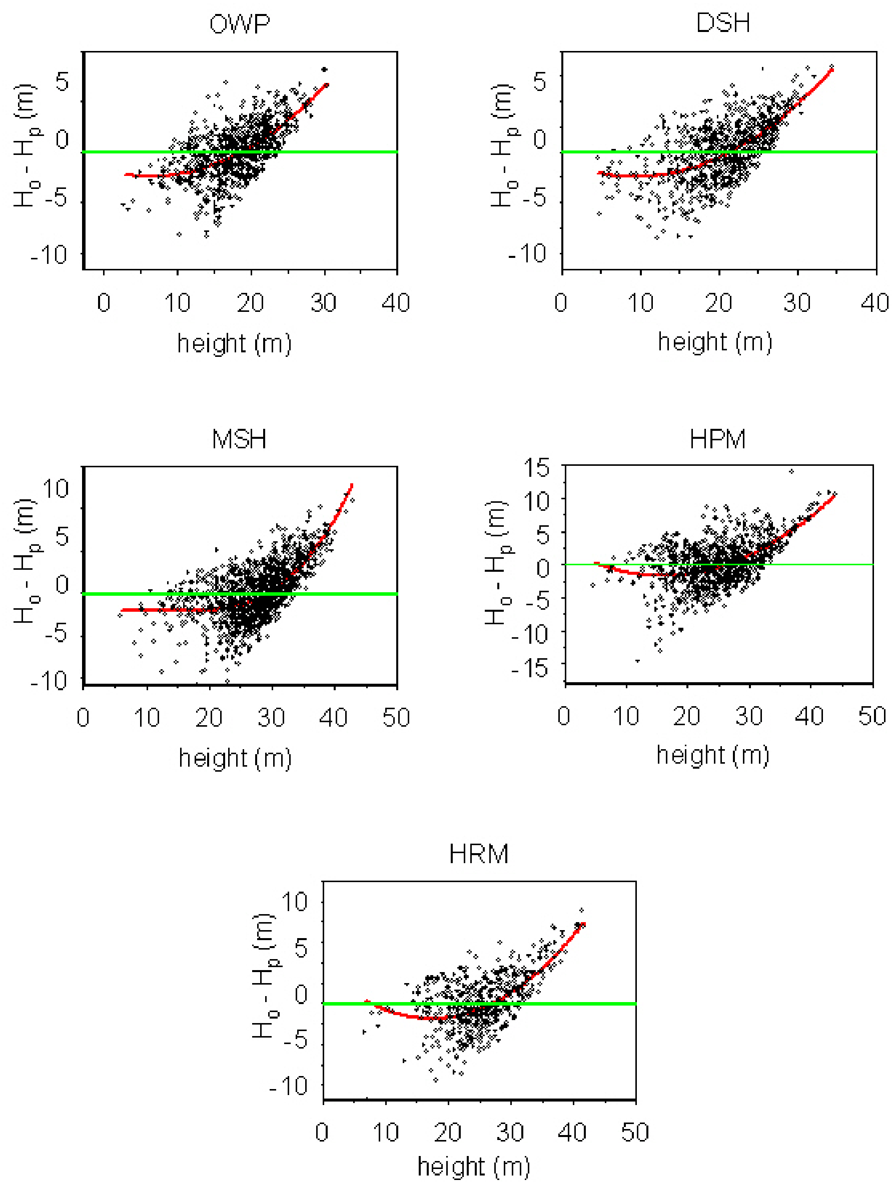

Figure 2.—Residual error of prediction (= observed height – predicted height = H_o – H_p) from height-diameter functions for ELTs (Table 2) plotted against observed tree height. The curved line through each scatter plot represents the best fit line for the data, using a second order polynomial model, and the horizontal line represents the zero error line.

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