A practical measure for determining if Diameter (D) and Height (H) should be combined into D^2H in allometric biomass models

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Abstract

Tree diameter at breast height (D) and tree height (H) are often used as predictors of individual tree biomass. Because D and H are correlated, the combined variable D^2H is frequently used in regression models instead of two separate independent variables, to avoid collinearity related issues. The justification for D^2H is that aboveground biomass is proportional to the volume of a cylinder of diameter, D, and height, H. However, the D^2H predictor constrains the model to produce parameter estimates for D and H that have a fixed ratio, in this case, 2.0. In this paper we investigate the degree to which the D^2H predictor reduces prediction accuracy relative to D and H separately and propose a practical measure, Q-ratio, to guide the decision as to whether D and H should or should not be combined into D^2H. Using five training biomass datasets and two fitting approaches, weighted nonlinear regression and linear regression following logarithmic transformations, we showed that the D^2H predictor becomes less efficient in predicting aboveground biomass as the Q-ratio deviates from 2.0. Because of the model constraint, the D^2H-based model performed less well than the separate variable model by as much as 12% with regard to mean absolute percentage residual and as much as

18% with regard to sum of squares of log accuracy ratios. For the analysed datasets, we observed a wide variation in Q-ratios, ranging from 2.5 to 5.1, and a large decrease in efficiency for the combined variable model. Therefore, we recommend using the Q-ratio as a measure to guide the decision as to whether D and H may be combined further into D^2H without the adverse effects of loss in biomass prediction accuracy.

Keywords: combined variable, diameter at breast height, tree height, biomass, allometric model, prediction

Introduction

Accurate and precise estimation of forest biomass is vital for successful implementation of climate change mitigation actions (Reilly et al., 2001; Brown, 2002; Ziegler et al., 2012; Intergovernmental Panel on Climate Change, 2014). Allometric biomass models are regression models that typically use tree diameter and/or tree height to predict biomass. Despite emerging new technologies such as remote sensing, empirical allometric models remain central when predicting forest biomass (Zianis and Radoglou, 2006; Vieilledent et al., 2012; McRoberts et al., 2015). Diameter at breast height (D, at 1.3 m above ground) is a basic forest inventory variable (Gschwantner et al., 2009) and is the most common predictor of tree volume or biomass (Zianis et al., 2005). Tree height (H) on the other hand is also an attractive predictor because of its practicality with, for example, airborne laser scanning auxiliary data (Jucker et al., 2017; Næsset, 1997; Næsset and Økland, 2002). Using both D and H to predict tree volume or biomass is common practice in forestry (Zianis et al., 2005). However, inclusion of H in the model would be of no value if D and H were perfectly correlated. Although D and H are always correlated to some degree, their relationship varies greatly (Feldpausch et al., 2010), being influenced by genotype, competition and environmental conditions (Egbäck et al., 2015; Hulshof et al., 2015; Dutcă et al., 2018b). As a result, including H in allometric models has been shown to improve biomass prediction accuracy (Chave et al., 2005, 2014; Feldpausch et al., 2012; Fayolle et al., 2013; Rutishauser et al., 2013; Dutcă et al., 2018a). Because D and H are correlated, the unique effect of each predictor (i.e., the main effect) is based on its unique information (i.e., disregarding shared information).

Collinearity increases standard errors and instability in parameter estimates (Dormann et al., 2013). Although collinearity between D and H does not necessarily have adverse effects on biomass prediction (Picard et al., 2015), it is often avoided by using a combined predictor of the form of D^2H (i.e., D^2 multiplied by H) based on the argument that aboveground biomass is proportional to the volume of a cylinder of diameter, D, and height, H. This combined predictor incorporates information from both D and H and, therefore, would be expected to produce more accurate biomass predictions than when using D alone.

The power-law function (Huxley, 1932) is widely accepted for describing the relationship between biomass and the predictor:

$$\mathrm{AGB} = \beta_0 \cdot (\mathrm{D}^2\mathrm{H})^{\beta_1} + \varepsilon \qquad (1)$$

where β_0 and β_1 are parameters to be estimated, D^2H is the predictor, AGB is aboveground individual tree biomass, and ε is a random residual term with mean 0. The analogous log-log transformed form of Eq. (1) is:

$$\ln(\mathrm{AGB}) = \ln(\beta_0) + \beta_1 \cdot \ln(\mathrm{D}^2\mathrm{H}) + \varepsilon \qquad (2)$$

where 'ln' is the natural logarithm. Furthermore, Eqs. (1) and (2) can be decomposed respectively into:

$$\mathrm{AGB} = \beta_0 \cdot \mathrm{D}^{2\beta_1} \cdot \mathrm{H}^{\beta_1} + \varepsilon \qquad (3)$$

and:

$$\ln(\mathrm{AGB}) = \ln(\beta_0) + 2\beta_1 \cdot \ln(\mathrm{D}) + \beta_1 \cdot \ln(\mathrm{H}) + \varepsilon \qquad (4)$$

Therefore, the parameter corresponding to D (i.e., $2\beta_1$) is constrained to take a value that is two times greater than the parameter corresponding to H (i.e., β_1). Differentiating Eq. (4), the parameters of D and H can be interpreted as measures of relative growth (Huxley, 1932). Consequently, D^2H as a predictor assumes that when D increases by 1% and H is held constant, the relative AGB growth is two times greater than the relative growth produced by a 1% increase in H with D held constant. However, in models for which D and H are used as separate predictor variables, the ratio of the parameter corresponding to D and the parameter corresponding to H is often greater than 2.0 (Nelson et al., 1999; Snorrason and Einarsson, 2006; Basuki et al., 2009; Moore, 2010; Mugasha et al., 2013). Despite the potential adverse consequences of this constraint, to our knowledge there are no guidelines in the literature indicating conditions for which use of D and H as a combined predictor, D^2H, is and is not justified. This study aims to develop a quantitative indicator that can be used to guide the decision as to whether separate predictors D and H can be combined into the single D^2H predictor without adverse consequences on prediction efficiencies.

Material and methods

Biomass data

To test the performance of the D^2H predictor, we used four publicly available biomass datasets, containing trees of different species, sampled from a wide range of conditions (Table 1). Together, the four datasets include data for 44,509 trees. However, because Chave et al. (2014) did not include small trees, for the sake of consistency among datasets, we removed all trees with D < 5 cm from the other datasets. We also removed all trees lacking one or more of the measurements for D, H and AGB from all datasets. Finally, we constructed a fifth dataset (S5) by merging the other four datasets (S1 to S4).

Approximate position of Table 1.

Fitting method

a) Nonlinear regression approach

For the nonlinear regression approach, we fit models using weighted nonlinear least squares methods (*nls* function in R). Because the variance is heteroscedastic on the original scale, increasing with increasing diameters, we weighted the observations using a 10-step procedure modified from McRoberts et al. (2015, 2016): i) fit a nonlinear model without weights; ii) calculate the heteroscedastic residuals (ε_i) and predicted biomass ($\widehat{\mathrm{AGB}}_\mathrm{i}$) for each tree; iii) sort the pairs $\widehat{\mathrm{AGB}}_\mathrm{i}$ and

ε_i in ascending order with respect to $\widehat{AGB}_i$; iv) group the pairs $\widehat{AGB}_i$ and ε_i into g groups of size 25; v) for each group, calculate the mean of $\widehat{AGB}_i$ ($\overline{\widehat{AGB}}_g$) and the variance of ε_i (${\sigma_g}^2$); vi) log-log transform the resulting group values; vii) fit a linear model to the log-log transformed data, predicting [$\ln({\sigma_g}^2)$] as a function of [$\ln(\overline{\widehat{AGB}}_g)$]; viii) back-transform the model, using a correction factor as in Eq. (5); ix) use the resulting model to predict variance for each tree (${\sigma_i}^2$), as a function of $\widehat{AGB}_i$; x) calculate weights for each tree, as the inverse of predicted variance for that tree ($w_i = 1/{\hat{\sigma}_i}^2$).

b) Log-linear model (linear model on log-log transformed data)

Logarithmic transformations are widely used when constructing allometric biomass models (Zianis et al., 2005; Dutcă et al., 2018c). However, whether logarithmic transformation or nonlinear methods are more appropriate has been greatly debated (see: Kerkhoff and Enquist 2009, Xiao et al. 2011, Packard 2013, Mascaro et al. 2014). For the purpose of the current study, we used ordinary least squares for a linear model on the log-log transformed scale. For back-transformation we used the bias correction (λ) (Goldberger, 1968; Baskerville, 1972):

$$\lambda = e^{\left(\frac{\hat{\sigma}^2}{2}\right)} \quad (5)$$

where $\hat{\sigma}^2$ is the estimated residual variance of the model on the transformed scale. The correction factor, as described in Eq. (5), was multiplied by the back-transformed biomass prediction.

The structure of tested allometric models

We tested the four model structures resulting from the two types of predictors (i.e., separate independent variables and combined predictor) and the two fitting approaches (i.e., weighted nonlinear regression and logarithmic transformation with ordinary least squares).

a) Separate predictors, D and H

- Nonlinear model:

$$AGB = \beta_0 \cdot D^{\beta_1} \cdot H^{\beta_2} + \varepsilon \quad (6)$$

- Linear model on log-log transformed data, with ordinary least squares:

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \cdot \ln(D) + \beta_2 \cdot \ln(H) + \varepsilon \quad (7)$$

b) Combined predictor, D^2H

- Nonlinear model (see Eq. 1);
- Linear model on log-log transformed data, with ordinary least squares (see Eq. 2).

Because Eqs. (1) and (2) are equivalent forms of the same model, apart from the residual term, the parameters have the same meaning; similarly for Eqs. (6) and (7). However, when comparing Eqs. (1) and (6) and Eqs. (2) and (7), which are different model forms, even though the same β_0 and β_1 notation is used for all model forms, the parameters should not be construed to have the same meaning.

Prediction accuracy

Assessing prediction accuracy in allometric models is challenging because of the inherent heteroscedastic nature of the residual variance (Kerkhoff and Enquist, 2009). The residuals, in absolute values, tend to be larger for large trees. Therefore, accuracy metrics based on absolute values such as RMSE (root mean squared error) are ineffective because the large residuals, when squared, disclose immense influence on resulting RMSE value. Nevertheless, the residuals resulting from back transformation of log-linear models show relative variation of observed AGB, relative to predicted AGB (Huxley, 1932; Cole, 2000; Kerkhoff and Enquist, 2009; Cole and Altman, 2017). Therefore, we assessed prediction accuracy using a series of metrics based on relative error in which error estimates are divided by predictions. For very small trees, because the denominator is small, the accuracy metrics based on relative errors may tend to take larger values. However, this was not an issue for our study because small trees (D < 5 cm) were not included for analysis.

a) Mean absolute percentage residual (MAPR):

$$\mathrm{MAPR} = \frac{1}{\mathrm{n}} \cdot \sum_{\mathrm{i}=1}^{\mathrm{n}} \left| \frac{\widehat{\mathrm{AGB}}_\mathrm{i} - \mathrm{AGB}_\mathrm{i}}{\widehat{\mathrm{AGB}}_\mathrm{i}} \right| \cdot 100 \qquad (8)$$

where $\widehat{\mathrm{AGB}}_\mathrm{i}$ and AGB_i represent the predicted and respectively observed aboveground biomass of tree *i*, and *n* is the total number of observations. MAPR is similar to mean absolute percentage error, however, it uses predicted biomass in the denominator, for several reasons. An important underlying assumption in modelling is that for each combination of values of the predictor variables, there is an entire distribution of possible values of the response variable. Furthermore, these response variable observations are assumed to be randomly distributed around their mean. This means, in regression problems, the prediction is actually a prediction of the mean of all the possible observations rather than a prediction for any particular observation. Therefore, MAPR shows an estimate of a constant value, rather than an estimate of a random value shown by the mean absolute percentage error.

b) The sum of squares of log accuracy ratios (SLAR)

$$\mathrm{SLAR} = \sum_{i=1}^{n} \left[\ln\left(\frac{\widehat{\mathrm{AGB}}_i}{\mathrm{AGB}_i}\right)\right]^2 \qquad (9)$$

SLAR is a symmetrical accuracy metric (i.e., interchanging between $\widehat{\mathrm{AGB}}_i$ and AGB_i, the SLAR value does not change) proposed by Tofallis (2015) which is very well-suited to models with heteroscedastic errors, such as allometric biomass models.

To compare models based on the two different types of predictors but adopting the same fitting approach, we used an additional metric, the Akaike Information Criterion (AIC):

$$\mathrm{AIC} = 2 \cdot \mathrm{k} - 2 \cdot \ln(\hat{\mathrm{L}}) \qquad (10)$$

where k is the number of parameters in the model and $\hat{\mathrm{L}}$ is maximum value of the likelihood function for the model (Akaike, 1987).

The efficiency of the D^2H predictor

Because Eq. (6) is equivalent to Eq. (1), and Eq. (7) is equivalent to Eq. (2), when the ratio between β_1 and β_2 equals 2.0, we assume that the efficiency of D^2H as predictor depends on the Q-ratio:

$$\mathrm{Q} = \frac{\hat{\beta}_1}{\hat{\beta}_2} \qquad (11)$$

where $\hat{\beta}_1$ and $\hat{\beta}_2$ are the parameter estimates from Eq. (6) and Eq. (7). For a ratio of Q = 2.0, the predictor D^2H is expected to have the same performance as the separate variable model. However, we hypothesize that the more Q deviates from 2.0, the less the accuracy of models that use D^2H as the sole predictor of AGB. The variance or standard error for the estimated Q-ratio can be estimated using the variances and covariances for the model parameter estimates (see Appendix 1).

a) MAPR efficiency

MAPR efficiency was defined as:

$$\mathrm{E}_1 = 1 - \frac{\mathrm{MAPR}_2 - \mathrm{MAPR}_1}{\mathrm{MAPR}_2} = \frac{\mathrm{MAPR}_1}{\mathrm{MAPR}_2} \quad (12)$$

where MAPR_1 is the MAPR from Eq. (8) calculated for models based on separate variables from Eqs. (6, 7); MAPR_2 is calculated for the combined predictor models from Eqs. (1, 2).

b) SLAR efficiency

SLAR efficiency was defined as:

$$\mathrm{E}_2 = 1 - \frac{\mathrm{SLAR}_2 - \mathrm{SLAR}_1}{\mathrm{SLAR}_2} = \frac{\mathrm{SLAR}_1}{\mathrm{SLAR}_2} \quad (13)$$

where SLAR_1 and SLAR_2 are the SLAR values from Eq. (9) for the separate variables model of Eqs. (6, 7) and combined predictor model of Eqs. (1, 2), respectively.

If the models based on the combined predictor produce less accurate predictions compared to separate variable models, then the efficiency metrics will take values less than 1.0. The difference between the efficiency metrics and 1.0 represent the loss in prediction accuracy due to combining the predictors.

Data processing

Statistical analysis was performed in R (R Core Team, 2017) with the RStudio interface (RStudio Team, 2016) and using the packages “nlme” (Pinheiro et al., 2018) and “car” (Fox and Weisberg, 2011).

Results

Firstly, it can be observed that regardless of fitting method, the Q-ratio was larger than 2.0 for all five datasets used for this study (Table 2). The smallest Q-ratio was 2.468 with SE = 0.061 for Dataset S1 when using the logarithmic transformation approach, and the largest was Q = 5.089 with SE = 0.212 for dataset S2 when using the nonlinear regression approach. The results of one-sample *t*-test (two-tailed) showed that, for each dataset and fitting approach, the Q-ratio was significantly different from 2.0 ($p < 0.001$). Compared to the logarithmic transformation approach, the nonlinear regression approach resulted in slightly larger Q-ratios in all cases. However, the nonlinear regression approach tended to produce very similar and, in some cases, slightly smaller values of both SLAR and MAPR. AIC (Eq. 10) was smaller for the separate variables model for all five datasets and all fitting approaches, except for dataset S1 with the nonlinear regression approach.

Approximate position of Table 2.

As expected, the accuracy metrics based on relative error, showed without exception, that the separate variable model produced more accurate predictions. MAPR from Eq. (8) varied between 0.3254 for dataset S1 for the combined predictor on nonlinear model and 0.1744 for dataset S4 for the separate variables on nonlinear model. The efficiency of the D^2H predictor decreased as the Q-ratio increased (Figure 1), confirming our hypothesis. The efficiency of D^2H models, with regard to both MAPR and SLAR showed a significant decline ($p < 0.001$) with increasing Q-ratio. There was a 3.9% loss in MAPR efficiency (E_1, Eq. 12) and a 6.2% loss in SLAR efficiency (E_2, Eq. 13), with every unit increase in Q-ratio, from 2.0 (Figure 1). Because of the model constraint, the D^2H-based model performed less well than the separate variable model by as much as 12% with regard to MAPR and as much as 18% with regard to SLAR. For Q = 2.0, the expected efficiency is 1.0, because the separate variables model and the combined predictor model are identical. However, assuming a linear loss in efficiency, the predicted values of $E_1 = 0.992$ and $E_2 = 1.005$ for Q = 2.0 were not significantly different from 1.0 (one sample *t*-test: $p = 0.665$ and $p = 0.886$ respectively).

Approximate position of Figure 1.

Discussion

Showing that the efficiency of models based on D^2H is smaller than for separate variable models, we proposed the Q-ratio as a metric to guide the decision as to whether D and H can be combined into D^2H without adverse effects on prediction efficiency. We showed that as the Q-ratio increased by one unit, the MAPR efficiency of the D^2H-based model decreased by 3.9% and the SLAR efficiency decreased by 6.2%. Although in this analysis we observed and presented the results only for Q-ratios larger than 2.0, the regression lines in Figure 1 would not be valid for Q-ratios smaller than 2.0. For Q-ratios smaller than 2.0, we would expect the efficiency of D^2H based model to also decrease, therefore, the peak efficiency of D^2H based model is obtained when Q = 2.0. When Q = 2.0 the model based on the D^2H predictor is identical to the separate variables model and shows isometry, i.e., the relative increase in predicted AGB is similar to that for the combined variable. However, although isometry of the D^2H-based model occurs only when Q = 2.0, the isometry of this model structure was commonly assumed in the past when predicting tree volume (Cunia, 1964; Meng and Tsai, 1986; Williams and Gregoire, 1993; Williams and Schreuder, 1996). A linear relationship between tree volume and D^2H was assumed, and a linear model with weighting to accommodate heteroscedasticity was fitted to the data. However, the relationship between tree volume (or biomass) and D^2H is linear only when isometric, therefore, only when Q = 2.0. Weighting to accommodate heteroscedasticity for this model structure has been extensively studied. Williams and Gregoire (1993) found that $D^{2.3}H^{0.7}$ more accurately approximated weights to accommodate heteroscedasticity for loblolly pine data. Because the heteroscedastic residual variance can be approximated as a function of predicted tree volume, it appears that the predicted volume itself may be more accurately predicted by a Q-ratio different from the constraining value of 2.0, in this case, Q = 3.3 which supports our findings.

The Q-ratio varied by dataset. For Dataset S5, the estimated Q-ratio was close to the average Q-ratios of component Datasets S1 to S4. The smallest Q-ratio in our study was for the Dataset S1 (Chave et al., 2014) which contains trees sampled from the tropical region, whereas Datasets S3 and S4 showed comparable Q-ratios while having common latitude from where the tree sample was acquired. Dataset S3 (Schepaschenko et al., 2017) contains trees sampled from Asia and Europe, from 32 to 70 degrees in latitude, and Dataset S4 (Ung et al., 2017) contains trees sampled from Canada, from 44 to 64 degrees in latitude (Table 1). Therefore, the Q-ratio apparently depends on latitude. This suggests that a 1% increase in H while D is constant may produce more biomass in tropical trees than in trees from higher latitudes.

The Q-ratio is influenced by the way trees allocate biomass to their components during development. A Q-ratio of 2.0 means that a 1% increase in D while H is constant produces twice as much AGB as a similar increase of H while D is constant. Q > 2.0 implies a larger difference between the main effect of D on AGB and the main effect of H on AGB. This difference can be caused by a stronger main effect of D on AGB (e.g., estimates of the parameter corresponding to D greater than 2.0), by a weaker main effect of H on AGB (e.g., estimates of the parameter corresponding to H lesser than 1.0), or both. The 'pipe theory' (Shinozaki et al., 1964) suggests that sapwood area is related to leaf area and, therefore, to leaf biomass. When D increases by 1% while H is constant, the sapwood area also increases, therefore, leaf biomass is expected to increase proportionally. However, a 1% increase in H while D is constant is expected to produce no increase in sapwood area and, therefore, in leaf biomass. Furthermore, Deng et al. (2014) showed that wood density along the stem decreased with tree height. Because a 1% increase in H while D is constant can be associated with accumulation of a wood layer towards the tree top, the AGB increase due to a 1% increase in H is likely to be affected also by less dense wood. Therefore, overall, the main effect of H on AGB is expected to be less than 1.0, suggesting that a larger Q-ratio may be more likely caused by a weaker main effect of H on AGB than by a stronger main effect of D on AGB. Q > 2.0 is frequently reported in the literature. The compiled database of allometric biomass models by Zianis et al. (2005) revealed that when predicting AGB, the Q-ratio varied between 2.06 and 14.09, with the most frequent values between 3 and 5. For small trees, and when diameter at collar height was used instead of diameter at breast height, Dutcă et al. (2018a) reported model parameter estimates with a ratio of 1.3, therefore smaller than 2.0. This small Q-ratio resulted however from parameter estimates of hierarchical linear models on log-log transformed data. Nevertheless, using ordinary least squares with a linear model and log-log transformed data (Dutcă, 2018), the resulting Q-ratio was larger than 2.0 (i.e., Q = 4.5).

Variations of the D^2H variable are often used to predict tree biomass. For example, wood density (ρ) is frequently incorporated in combined variables (e.g., ρD^2H) to account for the species effect in allometric biomass models (Brown et al., 1989; Chave et al., 2005, 2014; Vieilledent et al., 2012). The assumption of this model structure is that a 1% increase in H while D and ρ are constant produced an effect on AGB that is similar to a 1% increase in ρ while D and H are constant. Furthermore, the effect produced by 1% increase in D while H and ρ are constant is twice the effect produced by a 1% increase in either H or ρ. Instead of wood density, Dimobe et al. (2018) used crown diameter in a combined predictor. Jucker et al. (2017) used a combination of crown diameter and height, because this offers the possibility of predicting AGB from tree properties that can be remotely sensed. The assumption underlying this combined predictor is that height has similar effect on AGB as crown diameter.

Recommendations

The main reason to adopt a combined predictor is to overcome the adverse effects of collinearity between independent variables, in our study, between D and H. However, for the datasets used in this study, collinearity was not an issue. The variance inflation factor varied from 2.5 to 3.9. Hence, when collinearity is not a threat (e.g., variance inflation factor is less than 10), using the separate variable model should be always regarded as a better option. However, when a combined variable is preferred for various reasons, then D^2H can be used without adverse prediction consequences when the Q-ratio takes values between 1.5 and 2.5. For $Q < 1.5$ or $Q > 2.5$ we recommend not using D^2H so as to avoid the adverse effects of loss in biomass prediction accuracy. Nevertheless, a combined predictor can still be used (e.g., D^3H, $D^2H^{0.5}$) if the ratio between the parameter corresponding to D and the parameter corresponding to H in this new combined predictor equals or is very close to the Q-ratio.

Collinearity between D and H increases the standard errors of parameter estimates, producing less precise estimates of the Q-ratio. There are, however, circumstances when the Q-ratio cannot be computed such as when collinearity is so severe as to approach non-identifiability. In these conditions, a combined variable remains the only available solution.

The Q-ratio is intended to have practical utility, to determine if a combined predictor D^2H can be used without adverse prediction consequences. To calculate the Q-ratio, the user should first fit a model with D and H as separate predictor variables. Both, the logarithmic transformation and the weighted nonlinear approaches can be used to estimate parameters that are further used to calculate the Q-ratio. Because the parameters for D and H have the same meaning on both original and logarithmic scale, it is not important which fitting approach is used to estimate the Q-ratio. However, we recommend using the logarithmic transformation approach only when the heteroscedasticity is entirely removed by transformation, i.e., the residual variance is homogeneous on the logarithmic scale; otherwise, a weighted nonlinear regression approach is more versatile, being able to handle various patterns of heteroscedasticity and, therefore, we recommend weighted nonlinear regression approach for all situations.

Conclusions

Three conclusions can be drawn from the study. First, the Q-ratio, calculated as the ratio between the estimate of the parameter corresponding to D and the estimate of the parameter corresponding to H in the separate variable model, was a practical, informative and useful measure for assessing the relative effects on model prediction accuracy of using separate D and H predictor variables or a combined D^2H predictor variable. Second, prediction accuracies for models based on D^2H depend on the Q-ratio with accuracy decreasing as Q-ratio deviates more from 2.0. Third, the wide variation in Q-ratios observed in this study suggests that the Q-ratio should always be checked before combining D and H into D^2H.

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Appendix 1

Taylor series variance approximation for Q-ratio

For $Q = \beta_1 \cdot {\beta_2}^{-1}$, a first order Taylor series approximation is,

$$Q \approx \hat{Q} + \frac{\partial Q}{\partial \beta_1} \cdot \left(\beta_1 - \hat{\beta}_1\right) + \frac{\partial Q}{\partial \beta_2} \cdot \left(\beta_2 - \hat{\beta}_2\right) \tag{1}$$

Subtracting $\hat{Q}$ from both sides and squaring yields

$$\left(Q - \hat{Q}\right)^2 \approx \left[\frac{\partial Q}{\partial \beta_1} \cdot \left(\beta_1 - \hat{\beta}_1\right)\right]^2 + 2 \cdot \left[\frac{\partial Q}{\partial \beta_1} \cdot \left(\beta_1 - \hat{\beta}_1\right)\right] \cdot \left[\frac{\partial Q}{\partial \beta_2} \cdot \left(\beta_2 - \hat{\beta}_2\right)\right] + \left[\frac{\partial Q}{\partial \beta_2} \cdot \left(\beta_2 - \hat{\beta}_2\right)\right]^2$$

$$= \left(\frac{\partial Q}{\partial \beta_1}\right)^2 \cdot \left(\beta_1 - \hat{\beta}_1\right)^2 + 2 \cdot \frac{\partial Q}{\partial \beta_1} \cdot \frac{\partial Q}{\partial \beta_2} \cdot \left(\beta_1 - \hat{\beta}_1\right) \cdot \left(\beta_2 - \hat{\beta}_2\right) + \left(\frac{\partial Q}{\partial \beta_2}\right)^2 \cdot \left(\beta_2 - \hat{\beta}_2\right)^2 \tag{2}$$

Taking the statistical expectation of both sides and noting that $E\left(\beta_1 - \hat{\beta}_1\right)^2 = \mathrm{Var}\left(\hat{\beta}_1\right)$ and $E\left(\beta_2 - \hat{\beta}_2\right)^2 = \mathrm{Var}\left(\hat{\beta}_2\right)$ yields

$$\mathrm{Var}\left(\hat{Q}\right) \approx \left(\frac{\partial Q}{\partial \beta_1}\right)^2 \cdot \mathrm{Var}\left(\hat{\beta}_1\right) + 2 \cdot \frac{\partial Q}{\partial \beta_1} \cdot \frac{\partial Q}{\partial \beta_2} \cdot \mathrm{Cov}\left(\hat{\beta}_1, \hat{\beta}_2\right) + \left(\frac{\partial Q}{\partial \beta_2}\right)^2 \cdot \mathrm{Var}\left(\hat{\beta}_2\right) \tag{3}$$

Further noting that:

$$\frac{\partial Q}{\partial \beta_1} = {\beta_2}^{-1} \text{ and } \frac{\partial Q}{\partial \beta_2} = -\beta_1 \cdot {\beta_2}^{-2}$$

and substituting into (3) yields,

$$\mathrm{Var}\left(\hat{Q}\right) \approx {\beta_1}^{-2} \cdot \mathrm{Var}\left(\hat{\beta}_1\right) - 2 \cdot \beta_1 \cdot {\beta_2}^{-3} \cdot \mathrm{Cov}\left(\hat{\beta}_1, \hat{\beta}_2\right) + {\beta_1}^{2} \cdot {\beta_2}^{-4} \cdot \mathrm{Var}\left(\hat{\beta}_2\right) \tag{4}$$

Substituting $\hat{\beta}_1$ for β_1 and $\hat{\beta}_2$ for β_2 and factoring ${\hat{\beta}_1}^{2} \cdot {\hat{\beta}_2}^{-2}$ out of the right-side yields,

$$\widehat{\mathrm{Var}}\left(\hat{Q}\right) \approx {\hat{\beta}_1}^{2} \cdot {\hat{\beta}_2}^{-2} \cdot \left[{\hat{\beta}_1}^{-2} \cdot \mathrm{Var}\left(\hat{\beta}_1\right) - 2 \cdot {\hat{\beta}_1}^{-1} \cdot {\hat{\beta}_2}^{-1} \cdot \widehat{\mathrm{Cov}}\left(\hat{\beta}_1, \hat{\beta}_2\right) + {\hat{\beta}_2}^{-2} \cdot \widehat{\mathrm{Var}}\left(\hat{\beta}_2\right)\right]$$

$$\widehat{\mathrm{Var}}\left(\hat{Q}\right) \approx \hat{Q}^2 \cdot \left[\frac{\widehat{\mathrm{Var}}\left(\hat{\beta}_1\right)}{{\hat{\beta}_1}^{2}} - 2 \cdot \frac{\widehat{\mathrm{Cov}}\left(\hat{\beta}_1, \hat{\beta}_2\right)}{\hat{\beta}_1 \cdot \hat{\beta}_2} + \frac{\widehat{\mathrm{Var}}\left(\hat{\beta}_2\right)}{{\hat{\beta}_2}^{2}}\right] \tag{5}$$

Table 1 Datasets.

Dataset	Region	Sample size	Latitude range (Deg.)	D range (cm)	H range (m)	AGB range (kg)	Literature references
S1	Tropical	4004	-24.9, 25.0	5.0-212.0	1.2-70.7	1.2-76063.5	Chave et al. (2014)
S2	Global	3489	-51.6, 62.3	5.0-139.6	1.5-46.5	0.4-16418.4	Falster et al. (2015)
S3	Europe and Asia	5144	31.5, 69.9	5.0-72.9	2.3-42.8	0.6-4291.3	Schepaschenko et al. (2017)
S4	Canada	8659	43.9, 64.0	5.0-74.3	2.5-52.2	2.2-2951.4	Lambert et al. (2005); Ung et al. (2008, 2017)
S5	Global	21296	-51.6, 64.0	5.0-212.0	1.2-70.7	0.4-76063.5	S1-S4

Table 2 Accuracy metrics and Q-ratios.

Metric	**Fitting method**	**Predictor**	**Dataset:**				
			S1	**S2**	**S3**	**S4**	**S5**
MAPR	Nonlinear	Separate	0.3171	0.2625	0.1828	0.1744	0.2612
		Combined	0.3254	0.2984	0.1970	0.1899	0.2846
	Log-linear	Separate	0.3167	0.2623	0.1832	0.1747	0.2621
		Combined	0.3247	0.2982	0.1968	0.1900	0.2848
SLAR	Nonlinear	Separate	754.6	430.1	305.4	431.4	2372.9
		Combined	769.9	521.3	338.4	488.7	2645.4
	Log-linear	Separate	756.7	430.9	305.3	430.9	2362.5
		Combined	772.5	522.0	338.7	488.2	2633.6
AIC	Nonlinear	Separate	1.28e-08	7.50e-07	1.39e-08	4.43e-08	3.16e-09
		Combined	1.27e-08	7.77e-07	1.42e-08	4.52e-08	3.21e-09
	Log-linear	Separate	4522.9	2507.2	3.1	-1505.1	13047.7
		Combined	4599.8	3155.1	527.0	-440.9	15297.3
Q-ratio (SE)	Nonlinear	-	2.502 (0.060)	5.089 (0.212)	3.869 (0.126)	3.852 (0.089)	4.134 (0.066)
	Log-linear	-	2.468 (0.061)	4.638 (0.194)	3.622 (0.109)	3.634 (0.078)	3.691 (0.056)

List of figures:

Figure 1 Efficiency of the D^2H predictor as a function of Q-ratio. The grey-shaded area represents the 95% confidence interval.