

RESEARCH ARTICLE

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Linking individual-tree and whole-stand models for forest growth and yield prediction

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Abstract

Background: Different types of growth and yield models provide essential information for making informed decisions on how to manage forests. Whole-stand models often provide well-behaved outputs at the stand level, but lack information on stand structures. Detailed information from individual-tree models and size-class models typically suffers from accumulation of errors. The disaggregation method, in assuming that predictions from a whole-stand model are reliable, partitions these outputs to individual trees. On the other hand, the combination method seeks to improve stand-level predictions from both whole-stand and individual-tree models by combining them.

Methods: Data from 100 plots randomly selected from the Southwide Seed Source Study of loblolly pine (*Pinus taeda* L.) were used to evaluate the unadjusted individual-tree model against the disaggregation and combination methods.

Results: Compared to the whole-stand model, the combination method did not show improvements in predicting stand attributes in this study. The combination method also did not perform as well as the disaggregation method in tree-level predictions. The disaggregation method provided the best predictions of tree- and stand-level survival and growth.

Conclusions: The disaggregation approach provides a link between individual-tree models and whole-stand models, and should be considered as a better alternative to the unadjusted tree model.

Keywords: Disaggregation; Combination method; Loblolly pine; *Pinus taeda*

Background

Information provided by growth and yield models is essential for forest managers to make informed decisions on how to manage their forests. Munro (1974) classified growth and yield models into whole-stand models and individual tree models. He further separated individual-tree models into distance-independent and distance-dependent models. The whole-stand models (low resolution) and individual-tree models (high resolution) represent two extremes. In the middle are medium-resolution models such as diameter-distribution models and stand-table projection models, which provide information for each diameter class (Figure 1).

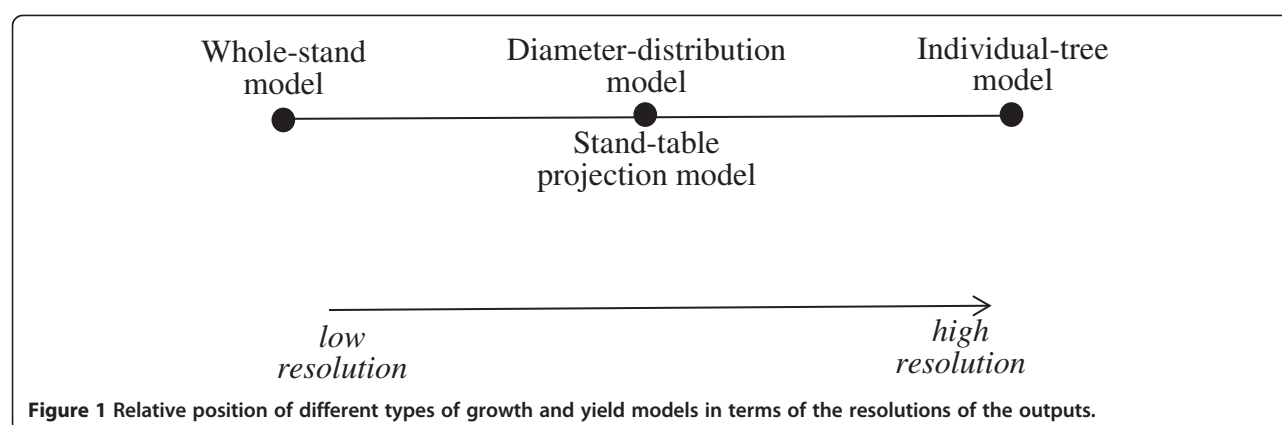
Each type of model has its own benefits and drawbacks. Whole-stand models often provide well-behaved

outputs at the stand level, but these outputs lack information on stand structures. Detailed information from individual-tree models and size-class models, on the other hand, typically results in stand-level outputs that are not as accurate or precise because they suffer from accumulation of errors (Garcia 2001, Qin and Cao 2006).

Daniels and Burkhart (1988) attempted to link different types of growth and yield models by developing a framework for an integrated system in which models of different resolutions are related in a unified mathematical structure. The functions used in these models can therefore be considered invariant at different levels of dimensionality.

Zhang et al. (1997) used the multi-response parameter estimation developed by Bates and Watts (1987, 1988) to constrain an individual-tree model by optimizing for both tree and diameter-class levels. This approach was later modified by Cao (2006) to produce a constrained

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tree model that was optimized for both tree and stand levels.

Disaggregation method is a method that has been used by many researchers for linking an individual-tree model and a whole-stand model (Ritchie and Hann 1997). In this method, outputs from the individual-tree model are adjusted such that the resulting stand summary matches prediction from a whole-stand model.

The disaggregation method above assumes that outputs from whole-stand models are more reliable than those from individual-tree models. Yue et al. (2008) found that stand-level outputs from whole-stand and individual-tree models could be combined to improve predictions. The weighted average approach was extended by Zhang et al. (2010) to include stand-level outputs from a diameter distribution model.

In this paper, the disaggregation method and combination method were evaluated against the unadjusted individual-tree model by use of data from unthinned loblolly pine (*Pinus taeda* L.) plantations.

Review of methods for linking individual-tree models and whole-stand models

Stand-level summary is obtained by aggregating (or summing) tree-level outputs from individual-tree models. Because this summary is often believed to be not as accurate and precise as direct prediction from a whole-stand model, the individual-tree model can be adjusted such that the resulting stand-level output matches that from a whole-stand model. In other words, output from the whole-stand model is disaggregated to tree level by use of some disaggregating function.

Ritchie and Hann (1997) provided an excellent review on disaggregation methods, classifying the disaggregating functions into additive and proportional. In the **additive growth method**, the basal area growth of each tree is equal to the average tree basal area growth plus an adjustment based on tree basal area (Harrison and

Daniels 1988) or tree diameter (Dhote 1994). Another category of disaggregation methods involves proportional allocations that can be applied to either growth or yield. In the **proportional yield method**, predicted tree basal area is adjusted to match predicted stand basal area (Clutter and Allison 1974, Clutter and Jones 1980, Pienaar and Harrison 1988, Nepal and Somers 1992, McTague and Stansfield 1994, 1995). The **proportional growth method** involves adjusting predicted tree basal area growth to match predicted stand basal area growth (Campbell et al. 1979, Moore et al. 1994), tree volume growth to match stand volume growth (Dahms 1983, Zhang et al. 1993), or tree diameter growth to match stand diameter growth (Leary et al. 1979).

Qin and Cao (2006) evaluated four methods to link an individual-tree model and a whole-stand model by use of disaggregation. In the **proportional yield method**, the predicted tree survival probability, diameter, and total height were multiplied by adjustment factors (equations 1–3 of Table 1). Tree diameter and height growth were adjusted in the **proportional growth method**, while tree survival probability was adjusted based on the ratio of dead and alive probabilities (equations 4–6 of Table 1). The **constrained least squares method** (Matney et al. 1990, Cao and Baldwin 1999) was used to adjust tree attributes (tree survival probability, squared diameter, or total height) by minimizing the sums of squared differences between the predicted and adjusted attributes, subject to the constraints that the aggregations had to match predictions from a whole-stand model (equations 7–8 of Table 1). Finally, in the **coefficient adjustment method**, adjusting coefficients were added to modify the coefficients of the original individual-tree model to yield stand attributes identical to those produced by the whole-stand model (equations 10–12 of Table 1). The four methods evaluated produced similar results, with the coefficient adjustment selected as the method to disaggregate predicted stand growth among trees in the tree list. The adjusted tree model combined the

Table 1 List of adjustment functions used in recent methods to link models of different resolutions

Citation	Method	Eq. no.	Adjustment function ^{1'}
Qin and Cao (2006)	Proportional yield	1	$\tilde{p}_{2,i} = \hat{p}_{2i} \left(\frac{s\hat{N}_2}{\sum_j \hat{p}_{2j}} \right)$
		2	$\tilde{d}_{2,i}^2 = \hat{d}_{2i}^2 \left(\frac{s\hat{B}_2/K}{\sum_j \hat{p}_{2j} \hat{d}_{2j}^2} \right)$
		3	$\tilde{h}_{2,i} = \hat{h}_{2i} \left(\frac{s(\hat{V}_2 - a\hat{N}_2)}{b \sum_j \hat{p}_{2j} \hat{d}_{2j}^2 \hat{h}_{2j}} \right)$
	Proportional growth	4	$\tilde{p}_{2i} = \frac{\hat{p}_{2i}}{\hat{p}_{2i} + m_p(1 - \hat{p}_{2i})}$
		5	$\tilde{d}_{2,i}^2 = d_{1i}^2 + \left(\frac{s\hat{B}_2/K - \sum_j \tilde{p}_{2j} d_{1j}^2}{\sum_j \tilde{p}_{2j} (\hat{d}_{2j}^2 - d_{1j}^2)} \right) (\hat{d}_{2i}^2 - d_{1i}^2)$
		6	$\tilde{h}_{2,i} = h_{1i} + \left(\frac{s(\hat{V}_2 - a\hat{N}_2) - b \sum_j \tilde{p}_{2j} \hat{d}_{2j}^2 h_{1j}}{b \sum_j \tilde{p}_{2j} \hat{d}_{2j}^2 (\hat{h}_{2j} - h_{1j})} \right) (\hat{h}_{2i} - h_{1i})$
	Constrained least squares	7	$\tilde{p}_{2i} = (\hat{p}_{2i} + s\hat{N}_2 - \sum \hat{p}_{2j})/n$
		8	$\tilde{d}_{2,i}^2 = \hat{d}_{2i}^2 - \tilde{p}_{2i} \left(\frac{\sum_j \tilde{p}_{2j} \hat{d}_{2j}^2 - s\hat{B}_2/K}{\sum_j \tilde{p}_{2j}^2} \right)$
		9	$\tilde{h}_{2,i} = \hat{h}_{2i} - \tilde{p}_{2i} \tilde{d}_{2,i}^2 \left(\frac{\sum_j \tilde{p}_{2j} \tilde{d}_{2j}^2 \hat{h}_{2j} + s(a\hat{N}_2 - \hat{V}_2)/b}{\sum_j \tilde{p}_{2j}^2 \tilde{d}_{2j}^2} \right)$
	Coefficient adjustment	10	$\tilde{p}_{2i} = p_{1i} / (1 + \exp[a_0 + a_1 H_1 + a_2 m_p(d_{1i}/Dq_1)])$
		11	$\tilde{d}_{2i} = d_{1i} \left\{ 1 + \exp[\beta_0 + \beta_1 \ln B_1 + \beta_2 A_1 + \beta_3 \ln H_1 + \beta_4 m_d \left(\frac{d_{1i}}{Dq_1} \right) + \beta_5 \ln h_{1i}] \right\}$
		12	$\tilde{h}_{2i} = h_{1i} \left\{ 1 + \exp[\gamma_0 + \gamma_1 \ln B_1 + \gamma_2 A_1 + \gamma_3 \ln H_1 + \gamma_4 m_h \left(\frac{d_{1i}}{Dq_1} \right) + \gamma_5 \left(\frac{h_{1i}}{H_1} \right) + \gamma_6 \ln d_{1i}] \right\}$
Cao (2006)	Disaggregation	13	$\tilde{p}_{2i} = \hat{p}_{2i}^{m_p}$
		14	$\tilde{d}_{2,i}^2 = d_{1i}^2 + \left(\frac{s\hat{B}_2/K - \sum_j \tilde{p}_{2j} d_{1j}^2}{\sum_j \tilde{p}_{2j} (\hat{d}_{2j}^2 - d_{1j}^2)} \right) (\hat{d}_{2i}^2 - d_{1i}^2)$
	Constraining individual-tree model with diameter-class attributes	15	$\begin{cases} \hat{p}_{2i} = 1/(1 + \exp[a_0 + a_1 N_1 + a_2 B_1 + a_3 d_{1i}]) \\ \hat{h}_{2,k} = \sum_{i=1}^{n_{1,k}} \hat{p}_{2i} \end{cases}$
		16	$\begin{cases} \hat{d}_{2i} = d_{1i} + \beta_1 \left(\frac{A_2}{A_1} \right)^{\beta_2} H_1^{\beta_3} B_1^{\beta_4} d_{1i}^{\beta_5} \\ \hat{h}_{2,k} = k \sum_{i=1}^{n_{1,k}} \hat{p}_{2i} \hat{d}_{2i}^2 \end{cases}$
	Constraining individual-tree model with stand attributes	17	$\begin{cases} \hat{p}_{2i} = 1/(1 + \exp[a_0 + a_1 N_1 + a_2 B_1 + a_3 d_{1i}]) \\ \hat{N}_2 = \sum \hat{p}_{2i}/s \end{cases}$
		18	$\begin{cases} \hat{d}_{2i} = d_{1i} + \beta_1 \left(\frac{A_2}{A_1} \right)^{\beta_2} H_1^{\beta_3} B_1^{\beta_4} d_{1i}^{\beta_5} \\ \hat{B}_2 = \left(\frac{K}{s} \right) \sum \hat{p}_{2i} \hat{d}_{2i}^2 \end{cases}$

Table 1 List of adjustment functions used in recent methods to link models of different resolutions (Continued)

Yue et al. (2008)	Combined estimator	19	$\tilde{B}_2 = w\hat{B}_{2T} + (1 - w)\hat{B}_{2S}$, where w is selected to minimize the variance of \tilde{B}_2 .
Zhang et al. (2010)	Combined estimator	20	$\tilde{B}_2 = w_1\hat{B}_{2T} + w_2\hat{B}_{2S} + w_3\hat{B}_{2D}$, where w_k is selected to minimize $\sum (B_2 - \tilde{B}_2)^2$, and $\sum_k w_k = 1$.
Cao (2010)	1	21	$\tilde{p}_{2i} = \hat{p}_{2i}^m$
Tree survival	2	22	$\tilde{p}_{2i} = \frac{\hat{p}_{2i}}{\hat{p}_{2i} + m_p(1 - \hat{p}_{2i})}$
	3	23	$\tilde{p}_{2i} = 1 / (1 + \exp[m_p a_0 + a_3 d_{1i}])$
	4	24	$\tilde{p}_{2i} = 1 / (1 + \exp[a_0 + a_1 N_1 + a_2 B_1 + m_p d_{1i}])$
	5	25	$\tilde{p}_{2i} = \hat{p}_{2i} + \left(\frac{s\hat{N}_2 - \sum_j \hat{p}_{2j}}{sN_1 - \sum_j \hat{p}_{2j}} \right) (1 - \hat{p}_{2i})$
Cao (2010)	1	26	$\hat{d}_{2i} = d_{1i} + m_d d_1^{\beta_5}$
Tree diameter growth	2	27	$\hat{d}_{2i} = d_{1i} + \beta_1 \left(\frac{A_2}{A_1} \right)^{\beta_2} H_1^{\beta_3} B_1^{\beta_4} d_1^{m_d}$
	3	28	$\tilde{d}_{2i}^2 = d_{1i}^2 + \left(\frac{s\hat{B}_2/K - \sum_j \tilde{p}_{2j} d_{1j}^2}{\sum_j \tilde{p}_{2j} (d_{2j}^2 - d_{1j}^2)} \right) (\hat{d}_{2i}^2 - d_{1i}^2)$

^{1/} Notation:

A_1 = stand age at the beginning of the growth period.

A_2 = stand age at the end of the growth period.

H_1 = dominant height at age A_1 .

N_1 = number of trees per ha at age A_1 .

\hat{N}_2 = predicted number of trees per ha at age A_2 .

B_1 = stand basal area at age A_1 .

\hat{B}_2 = predicted stand basal area at age A_2 .

\hat{B}_{2D} = predicted stand basal area at age A_2 from a diameter distribution model.

\hat{B}_{2S} = predicted stand basal area at age A_2 from a whole-stand model.

\hat{B}_{2T} = predicted stand basal area at age A_2 from an individual-tree model.

\tilde{B}_2 = combined estimator for stand basal area at age A_2 .

\hat{V}_2 = predicted volume per ha at age A_2 , Dq_1 = quadratic mean diameter at age A_1 .

a and b = parameters of the individual tree volume equation, $v_i = a + b d_i^2 h_i$.

v_i , d_i , and h_i = tree volume, dbh, and total height of tree i , respectively.

s = plot size in ha.

$K = \pi/40\,000$ = constant to convert diameter in cm to area in m^2 .

n = number of trees in the plot.

d_{1i} or d_{1j} = dbh of tree i or j at age A_1 .

\hat{d}_{2i} or \hat{d}_{2j} = predicted dbh of tree i or j at the end of the growth period.

\tilde{d}_{2i} = adjusted dbh of tree i at the end of the growth period.

h_{1i} = total height of tree i at age A_1 .

\hat{h}_{2i} or \hat{h}_{2j} = predicted total height of tree i or j at the end of the growth period.

\tilde{h}_{2i} = adjusted total height of tree i at the end of the growth period.

p_{1i} = survival probability of tree i at age A_1 .

\hat{p}_{2i} or \hat{p}_{2j} = predicted survival probability of tree i or j at the end of the growth period.

\tilde{p}_{2i} or \tilde{p}_{2j} = adjusted survival probability of tree i or j at the end of the growth period.

$a_0 \dots a_3$ = parameters of the tree survival equation.

$\beta_0 \dots \beta_5$ = parameters of the tree diameter growth equation.

$\gamma_0 \dots \gamma_6$ = parameters of the tree height growth equation.

$n_{1,k}$ = number of trees of the k^{th} diameter class at age A_1 .

$\hat{n}_{2,k}$ = predicted number of trees of the k^{th} diameter class at age A_2 .

$\hat{b}_{2,k}$ = predicted basal area of the k^{th} diameter class at age A_2 , and m_p , m_d , and m_h = adjustment coefficients to be iteratively solved to ensure that the resulting number of trees per ha, stand basal area, and stand volume, respectively, match those produced by the whole-stand model.

best features of whole-stand and individual-tree models. Compared to the unadjusted tree model, the adjusted model performed better in predicting stand attributes in terms of stand density, basal area, and volume, especially for long projection periods. The adjusted model also

provided comparable predictions of tree diameter, height, and survival probability.

Cao (2006) evaluated a disaggregation method against two approaches to constrain an individual-tree model. In the **disaggregation method**, the predicted tree survival

probability was adjusted with a simple power function, in which the power was iteratively solved such that the adjusted survival probability summed up to the predicted stand density (equation 13 of Table 1). The proportional growth formula was used in adjusting diameter growth (equation 14 of Table 1). The individual-tree model was constrained by **diameter-class attributes** (equations 15–16 of Table 1) by use of the multi-response parameter estimation method (Zhang et al. 1997, Bates and Watts 1987, 1988). Also included in the evaluation was a similar approach to constrain the individual-tree model by **stand attributes** (equations 17–18 of Table 1). Cao (2006) found that while the two constrained models performed slightly better than the unconstrained tree model in predicting tree and stand attributes, the disaggregation method provided the best predictions of tree- and stand-level survival and growth.

Cao (2010) listed different disaggregation methods for predicting tree survival and diameter growth. These include five disaggregation methods for adjusting tree survival probability (equations 21–25 of Table 1) and three methods for diameter growth adjustment (equations 26–28 of Table 1). His results showed that the different methods produced similar results. Cao (2010) also found that use of observed rather than predicted stand attributes for disaggregation led to improved predictions for tree survival and diameter growth, i.e. the quality of the tree-level predictions in disaggregation depended on the reliability of the stand predictions.

Yue et al. (2008) used the method introduced by Bates and Granger (1969) and Newbold and Granger (1974) to combine stand-level outputs from whole-stand and individual-tree models. The combined estimator is a weighted average of outputs from both models (equation 19 of Table 1). The optimum weights were selected to minimize the variance of the combined estimator. Zhang et al. (2010) extended this approach to also include stand-level outputs from a diameter distribution model (equation 20 of Table 1). The least-squares estimate of the weights was computed according to Tang (1992, 1994).

Methods

Stand- and tree-level growth models developed by Cao (2006) were used in this study. The whole-stand model consisted of equations for predicting stand density in terms of number of trees and basal area per hectare as follows:

$$\hat{N}_{2,i} = N_{1,i} / [1 + \exp(16.3197 - 42.4204 RS_{1,i} - 0.7466 H_{1,i} - 0.0269 N_{1,i}/A_1 + 50.2622/A_1)], \quad (1)$$

$$\hat{B}_{2,i} = B_{1,i} / [1 + \exp(-3.3259 - 0.7800 B_{1,i}/A_1 + 41.0393/A_1)] \quad (2)$$

where:

$N_{1,i}$ = number of trees per ha in plot i at age A_1 ,

$\hat{N}_{2,i}$ = predicted number of trees per ha in plot i at age A_2 ,

$H_{1,i}$ = average dominant and codominant height (m) of plot i at age A_1 ,

$RS_{1,i} = (10,000/N_{1,i})^{0.5} / H_{1,i}$ = relative spacing of plot i at age A_1 ,

$B_{1,i}$ = stand basal area (m^2/ha) of plot i at age A_1 , and

$\hat{B}_{2,i}$ = predicted stand basal area (m^2/ha) of plot i at age A_2 .

The individual-tree model included equations for predicting tree survival probability and diameter growth as follows:

$$\hat{p}_{ij} = [1 + \exp(1.3586 - 0.0010 N_{1,i} + 0.1042 B_{1,i} - 0.2902 d_{1,ij})]^{-1} \quad (3)$$

$$\hat{d}_{2,ij} = d_{1,ij} + 0.7168 \left(\frac{A_2}{A_1} \right)^{2.0192} H_{1,i}^{-1.0111} B_{1,i}^{-0.3166} d_{1,ij}^{1.5117} \quad (4)$$

where:

\hat{p}_{ij} = predicted probability that tree j in plot i is alive at age A_2 , given that it was alive at age A_1 ,

$d_{1,ij}$ = diameters (cm) of tree j in plot i at age A_1 , and

$\hat{d}_{2,ij}$ = predicted diameters (cm) of tree j in plot i at age A_2 .

Data

Equations (1, 2, 3 and 4) above were derived from 100 plots from loblolly pine (*Pinus taeda* L.) plantations in the Southwide Seed Source Study, which include 15 seed sources planted at 13 locations across 10 southern states (Wells and Wakeley 1966).

Data used in this study were from another 100 plots, also randomly selected from the Southwide Seed Source Study. Each 0.0164 ha plot consisted of 49 trees, planted at a 1.8 m × 1.8 m spacing. Tree diameters and survival were recorded at ages 10, 15, 20, and 25 years, resulting in a total of 300 growth periods (Table 2).

Methods evaluated

In addition to the individual-tree model (equations 3 and 4), the disaggregation and combination methods were evaluated in this study.

Disaggregation method

The tree survival probability (\hat{p}_{ij}) predicted from equation (3) was adjusted by use of Cao's (2010) method as follows:

Table 2 Means (and standard deviations) of stand and tree attributes, by age

Attribute	Stand age (years)			
	10	15	20	25
Dominant height (m)	9.1 (1.3)	13.4 (1.6)	16.9 (1.9)	19.9 (2.2)
Number of trees/ha	1696 (627)	1448 (548)	1143 (350)	1013 (334)
Basal area (m ² /ha)	19.2 (5.6)	28.8 (5.9)	33.2 (8.1)	37.4 (9.4)
Tree diameter (cm)	11.6 (3.1)	15.4 (4.1)	18.7 (4.6)	21.0 (5.2)

$$\tilde{p}_{ij} = \hat{p}_{ij}^{\alpha} \quad (5)$$

where α is the adjustment coefficient used to match the sum of adjusted tree survival probabilities (\tilde{p}_{ij}) to predictions from the stand survival model (equation 1).

From equation (4), the projected tree diameter ($\hat{d}_{2,ij}$) was adjusted (Cao 2010) so that the resulting stand basal area matches the prediction from the whole-stand model (equation 2):

$$\hat{d}_{2,ij}^2 = d_{1,ij}^2 + \beta(\hat{d}_{2,ij}^2 - d_{1,ij}^2) \quad (6)$$

where:

$$\beta = \frac{s\hat{B}_{2,i}/K - \sum \tilde{p}_{ij} d_{1,ij}^2}{\sum [\tilde{p}_{ij}(\hat{d}_{2,ij}^2 - d_{1,ij}^2)]}, \text{ and:}$$

$$K = \pi/40\,000.$$

Combination method

The combined estimator of stand survival was the weighted average of stand-level predictions from the whole-stand model (equation 1) and the individual-tree model (equation 3). The weights were computed according to a method described by Tang (1992, 1994) and applied by Zhang et al. (2010). A similar procedure was applied to compute the combined estimator for stand basal area.

Predictions from the individual-tree model were then adjusted from the combined estimators for stand survival and basal area, using the disaggregation method described earlier.

Evaluation criteria

The performance of the unadjusted, disaggregation, and combination methods was evaluated at both stand and tree levels, based on the following statistics.

Mean difference:

$$MD = \sum (y_i - \hat{y}_i) / n \quad (7)$$

Mean absolute difference:

$$MAD = \sum |y_i - \hat{y}_i| / n \quad (8)$$

Fit index:

$$FI = \sum (y_i - \hat{y}_i)^2 / (y_i - \bar{y})^2 \quad (9)$$

Log-likelihood:

$$-2\ln(L) = -2 \left[\sum p_i \ln(p_i) + \sum (1-p_i) \ln(1-p_i) \right] \quad (10)$$

where:

y_i and \hat{y}_i = observed and predicted values at the end of the growth period of stand variables (stand survival and basal area) or tree variables (tree diameter and survival probability),

\bar{y} = average of y_i ,

n = number of observations, and

p_i = predicted survival probability of tree i .

Results and discussion

Table 3 shows that the whole-stand model (disaggregation method) produced the best MD and MAD values for stand density while the combination method yielded the best FI value. For stand basal area, all of the best evaluation statistics came from the whole-stand model (Table 3). At tree level, the disaggregation method returned the best evaluation statistics for both tree survival probability and tree diameter (Table 3).

Disaggregation method

From Table 3, it is clear that the whole-stand model was more accurate (lower MD) and precise (lower MAD and higher FI) in predicting stand density and basal area than the individual-tree model. The differences were substantial. Compared to the individual-tree model, the whole-stand model decreased MD by 88 and 97%, decreased MAD by 15 and 46%, and increased FI by 8 and 28% for stand density and stand basal area, respectively. Predicted stand attributes from the tree-level model were not as reliable because they were obtained through summation of individual-tree predictions, resulting in accumulation of error.

Qin and Cao (2006) showed that a tree-level model, after being adjusted from observed stand attributes through disaggregation, outperformed the unadjusted tree model. They inferred that the performance of disaggregation models depended largely on how close the stand predictions were to the observed values. The whole-stand model seemed a good candidate in this case, yielding FI values of 0.825 and 0.862 in predicting stand density and basal area, respectively. The tree-level statistics support this hypothesis: the disaggregation model reduced MD by 26 and 19%, and MAD by 14 and 11% for tree survival probability and tree diameter, respectively, as compared to the unadjusted tree model. It

Table 3 Stand-level and tree-level evaluation statistics for three methods

Statistic ^{1/}	Unadjusted tree model	Disaggregation method	Combination method
Stand level			
Stand density (trees/ha)			
MD	28.1	-3.5 ^{2/}	4.1
MAD	176.1	148.8	149.4
FI	0.765	0.825	0.830
Stand basal area (m ² /ha)			
MD	2.05	0.06	1.89
MAD	3.99	2.17	3.87
FI	0.676	0.862	0.699
Tree level			
Tree survival probability			
MD	0.019	-0.014	0.019
MAD	0.239	0.206	0.239
-2ln(L)	5167	4615	4976
Tree diameter (cm)			
MD	0.16	-0.13	0.27
MAD	0.94	0.84	1.03
FI	0.939	0.952	0.927

^{1/} Notations:
 $MD = \sum (y_i - \hat{y}_i) / n$; $MAD = \sum |y_i - \hat{y}_i| / n$; $FI = \sum (y_i - \hat{y}_i)^2 / (\sum (y_i - \bar{y})^2)$; $-2 \ln(L) = -2[\sum p_i \ln(p_i) + \sum (1 - p_i) \ln(1 - p_i)]$, where y_i and \hat{y}_i = observed and predicted values at the end of the growth period of stand variables (stand survival and basal area) or tree variables (tree diameter and survival probability); \bar{y} = average of y_i ; n = number of observations, and p_i = predicted survival probability of tree i .

^{2/} For each evaluation statistic, the bold italic number denotes the best among three methods.

also decreased $-2\ln(L)$ for tree survival by 11% and increase FI for tree diameter by 1%.

Combination method

In this study, combining stand predictions from the whole-stand and individual-tree models resulted in predictions of stand density and basal area that were better than those from the individual-tree model, but not as good as those from the whole-stand model. Among six evaluation statistics considered, the combination method only edged the whole-stand model in fit index (0.830 versus 0.825), while came in second for the remaining statistics. This was contrary to past reports of superior performance by the combination method (Yue et al. 2008, Zhang et al. 2010). In a study by Zhang et al. (2010), similar fit index values, ranging from 0.9466 to 0.9494, were obtained for predicted stand basal area from three different types of models for the validation data set. In this study, a considerable difference in fit index of stand basal area prediction between the individual-tree model (0.676) and the whole-stand model (0.862) might

result in mediocre performance of the combination method ($FI = 0.699$ for stand basal area).

The tree survival model that was disaggregated from the combined estimator gave similar evaluation statistics as did the unadjusted tree survival equation (Table 3). On the other hand, the tree diameter model from the combination method performed worse than the unadjusted tree diameter growth equation (Table 3).

Tree-level predictions were disaggregated from the whole-stand model for the disaggregation method and from the combined estimator for the combination method. Based on the data from this study, the disaggregation method was better for predicting both tree survival and diameter in terms of all evaluation statistics.

Conclusions

The disaggregation method involves adjusting outputs from the individual-tree model to match predictions from the whole-stand model. It was shown in previous findings and also in this study that this method provided better predictions of tree survival and diameter growth. Compared to the whole-stand model, the combination method did not show improvements in predicting stand attributes in this study. The combination method also did not perform as well as the disaggregation method in tree-level predictions.

Competing interest

The author declares that he has no competing interests.

Acknowledgement

Funding for this project was provided in part by the McIntire-Stennis funds.

Received: 25 July 2014 Accepted: 4 September 2014

Published online: 14 October 2014

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doi:10.1186/s40663-014-0018-z

Cite this article as: Cao: Linking individual-tree and whole-stand models for forest growth and yield prediction. *Forest Ecosystems* 2014 1:18.

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