Development of allometric leaf area models for intensively managed black walnut (Juglans nigra L.)

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ORIGINAL PAPER

Development of allometric leaf area models for intensively managed black walnut (*Juglans nigra* L.)

Christopher E. Zellers · Michael R. Saunders · Robert C. Morrissey · Joshua M. Shields · Brian G. Bailey · Jacob Dyer · Jason Cook

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Abstract
• *Introduction* Intensive plantation management of high-value hardwoods, such as black walnut (*Juglans nigra* L.), is focused on maximizing both stem form and growth at the stand and tree level. While significant research has focused on genetic improvement in black walnut, little is known about the production ecology of this species in plantation settings.
• *Objectives* The aim of this study is to assess the applicability of nondestructive projected leaf area (PLA) estimation based on the pipe model theory in three single-aged *J. nigra* plantations representing discrete age classes ranging from 3 to 27 years of age.
• *Results* Branch-level PLA was modeled as a function of branch basal cross-sectional area (R^2=0.875). Six nondestructive tree-level PLA models were assessed, with four models yielding R^2>0.90. Tree-level models performed well across age classes, with model fits comparable to previous studies in coniferous species.
• *Conclusion* This study demonstrates that allometric approaches to modeling leaf area distribution in hardwoods are feasible, but future efforts may need to use different sampling approaches and/or quantify variables that have not been significant in conifers. This study represents an important first step into more quantitative analysis of production ecology of deciduous species in the CHFR of the USA.

Keywords Black walnut · Leaf area · Plantations · Central Hardwood Region · Hardwoods

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Contribution of the co-authors Zellers contributed with Majority of writing and analysis.
Saunders contributed with Supervised overall project and various subprojects.
Morrissey, Shields and Bailey contributed with Initial analysis of subproject concerning pole-sized walnut.
Dyer contributed with design and collection of data.
Cook contributed with Initial analysis of subproject concerning small sapling walnut.

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1 Introduction

The quantification of leaf area, at both the individual tree and stand levels, has been an important area of silvicultural research, as leaf area is the primary determinate of tree growth (Monserud and Marshall 1999). The intrinsic relationship between leaf area and growth is of particular concern, as most intermediate silvicultural treatments, such as thinning and green pruning, are manipulations of the amount and distribution of leaf area. The accurate estimation of leaf area permits greater insight into crown structure, allowing for more informed production silviculture (Kenefic and Seymour 1999; Meadows and Hodges 2002). Direct estimation of leaf area can be very costly and time-consuming; thus, research has focused on the development of allometric methods, many of which are based on the pipe model theory (Shinozaki et al. 1964; Waring et al. 1982). These methods relate leaf area to more easily measured attributes such as diameter, basal area, or sapwood area (Temesgen et al. 2011). Allometric leaf area estimation has gained widespread acceptance, and has been empirically validated in many coniferous species (Monserud and Marshall

1999) and some hardwood species (Vertessy et al. 1995; Meadows and Hodges 2002; Calvo-Alvarado et al. 2008).

Accuracy of allometric models, however, depends largely on the strength of the relationship between the dependent and independent variables (Temesgen et al. 2011). The strong apical dominance and epinastic control that is typical in conifer species lead to fairly regular growth patterns and therefore highly precise allometric relationships. Most hardwoods, on the other hand, exhibit weak apical dominance, and exhibit much less regular crown architecture, with highly variable branch angles and multiple leaders (Oliver and Larson 1990). The irregular morphology of hardwoods yields less precise allometric estimates of biomass, volume, and leaf area (Deusen and Roesch 2011). According to pipe model theory, sapwood-based leaf area estimation should still hold true in hardwoods with irregular crown structure, and has the benefit of usually being more accurate and/or less biased than diameter or basal area-based allometry (Snell and Brown 1978; Marshall and Waring 1986; Turner et al. 2000). For example, Meadows and Hodges (2002) found that total sapwood area was better related to both leaf area and foliar weight than current sapwood area (i.e., the outermost two growth rings sensu Rogers and Hinckley [1979]), diameter at breast height, or stem cross-sectional area (CSA).

However, in hardwoods, the relative improvement in precision of sapwood-based estimators over diameter-based estimators does not appear to be as pronounced as in conifers (Meadows and Hodges 2002), and in some species, diameter-based estimators perform better (Calvo-Alvarado et al. 2008). Further, measurement of sapwood area is commonly discouraged because it requires destructive sampling of tree stems (Nygren et al. 1993; Laubhann et al. 2010). Sapwood width at breast height can vary widely within a tree's cross-section depending on several factors, including branching and foliage distribution around the stem, uneven exposure of the stem (e.g., edge trees can have wider sapwood widths on exposed sides as opposed to sheltered sides; Assmann 1970), butt swell or buttressing on large trees (Vertessy et al. 1995), and healing of prior wounds. Single increment borings taken to estimate sapwood area cannot capture this variability and are, therefore, inherently unreliable unless several (four to six) are taken around the stem. This significantly reduces or even eliminates the economic value of the tree if it is being grown for veneer or high-quality sawtimber.

The purpose of this study was to determine the effectiveness of allometric modeling for leaf area estimation in intensively managed black walnut (*Juglans nigra* L.) plantations in Indiana. Our specific objectives were: (1) develop a suitable branch-level leaf area model using data from three distinct single-aged plantations ranging from 3 to 27 years in age; (2) assess the performance of several nondestructive, tree-level leaf area models; and (3) determine if tree-level allometry differs with age across three single-aged plantations with similar soils and silvicultural regimes.

2 Materials and methods

2.1 Study areas

This study was carried out in three distinct, intensively managed black walnut plantations in Tippecanoe County in Indiana, USA (~40.4° N, 87° W). Mean annual temperatures range from 10.0 to 12.8°C, with mean annual precipitation ranging from 88.9–101.6 cm (USDA NRCS 2011). Each plantation is single aged, with fill planting in the year following establishment to replace early mortality. All three plantations were chemically treated to control herbaceous competition during establishment, and in many years, the two older plantations were sprayed in late May with azoxystrobin for walnut anthracnose (caused by *Gnomonia leptostyla* [Fr] Ces. & De Not.) that, if left untreated, would lead to early leaf abscission (i.e., mid-August; Michler et al. 2007). Plantation ages are 3, 10, and 27 years, and are hereafter referred to as sapling, early-pole and late-pole stages, respectively. Early- and late-pole stage plantations have a history of corrective green pruning, and the sapling and early-pole plantations are subjected to fertigation. Sapling and early-pole plantations have deep, well-drained Elston loam and Elston sandy loam soils, respectively, while the late-pole plantation soils are somewhat poorly drained Ceresco loam (Soil Survey Staff 2011). Average site indices (m, base age 50) for the early- and late-pole stage plantations are 28.9±0.3 (standard error) and 22.7±0.5, respectively. The sapling stage plantation is too young to accurately estimate site index, but is likely similar to the early-pole stage plantation, given the similar soil types.

2.2 Field data collection

2.2.1 Sapling stage

Data were collected in late August 2010 from 13 trees (Table 1). Each tree was measured for total height (HT; in meters), height to live crown base (HCB; in meters), and diameter at 1.37 m (DBH; in centimeters). Within the crown, each branch was measured for branch collar diameter (BD; in centimeters) and branch height (BH; in meters). At least one branch from each sample tree (n=15) was stripped of all foliage, and leaves were promptly refrigerated at 2°C. To reduce processing time, subsamples of 25–50 leaves were randomly selected for branches that had excessive leaves (generally >50). Samples and subsamples were scanned at high resolution, and subsequently measured for projected leaf area (PLA) to the nearest 0.01 cm^2 using the

Table 1 Characteristics of 76 trees sampled to develop *J. nigra* L. leaf area prediction models

Attribute	Mean	Standard deviation	Minimum	Maximum
Sapling stage (n=13)				
DBH (cm)	2.3	0.6	1.2	3.2
HT (m)	2.3	0.3	1.7	2.9
HCB (m)	0.6	0.2	0.2	1.0
TLA (m^2)	6.3	3.4	1.4	15.2
Early-pole stage (n=51)				
DBH (cm)	14.1	1.8	9.8	17.8
HT (m)	9.2	0.8	7.2	11.2
HCB (m)	1.7	0.3	0.4	3.0
TLA (m^2)	104.0	25.9	57.4	167.1
Late-pole age (n=12)				
DBH (cm)	24.8	1.6	22.6	28.0
HT (m)	17.0	0.7	15.8	18.3
HCB (m)	5.9	1.6	3.9	8.2
TLA (m^2)	159.8	54.4	84.2	296.5

WinFolia™ 2009a software package (Régent Instruments, Québec, Canada). Subsamples and samples were then oven-dried at 65°C to a constant weight, and then massed to the nearest 0.01 g. Specific leaf area (SLA; in square centimeters per gram) for each subsample was determined by dividing the cumulative leaf area of the subsample by its entire dry mass, and then used to extrapolate PLA for each sample branch.

2.2.2 Early-pole stage

Data were collected in June to August 2010 from 51 trees (Table 1). Each tree was measured for HT, HCB, and DBH, as well as BD and BH for each branch within the crown. The current year growth of the most dominant stem was considered the terminal, and was treated as a branch. As these data are part of a multiyear pruning study, sample branches for foliage collection were only collected from trees included in one of the pruning treatments. Some trees had sample branches collected from the lower crown, as well as larger branches from the mid- or upper crown that exhibited strong branching angles (n=49). Determination of total PLA for each sample branch was performed as stated above.

2.2.3 Late-pole stage

Data were collected in July 2009 from 12 trees (Table 1). Each tree was in a dominant or co-dominant canopy position, and was scheduled to be felled in a planned thinning operation. After felling as gently as possible, each tree was measured for HT, HCB, and DBH, as well as BD and BH for each branch within the crown. Four sample branches, one from each vertical quadrant of crown length, were collected from each tree; subsequent preliminary analyses identified two outliers which upon visual inspected appeared to have either senesced early or been partially defoliated. Determination of total PLA for each the remaining 46 sample branches was performed as previously stated.

2.3 Data analysis

2.3.1 Branch-level equation

The branch-level equation was built using the sample branches from all three age classes (n=110). Evaluated model forms included branch leaf area (BLA; in square meters) as a function of branch CSA and, in order to account for differences in SLA throughout the crown, branch height relative to distance to the top of the tree crown (RELDEP; Kenefic and Seymour 1999). Since the relationship between BLA and BD has been previously shown to be nonlinear, the BLA model was formulated sensu Kenefic and Seymour (1999) as follows:

$$\mathrm{BLA} = \left(b_0 + b_1\mathrm{CSA}^{b_2} + b_3\mathrm{RELDEP}^{b_4}\right)^{b_5} \quad (1)$$

Covariates were assessed for significance (α=0.05), and models were assessed for heteroscedasticity. Branch-level analysis, as well as all subsequent analyses, was conducted using the statistical software R, version 2.12.0 (R Development Core Team 2010).

2.3.2 Tree-level equation

Tree-level leaf area (TLA; in square meters) was calculated for each sample tree via the "branch summation method," in which the branch-level model was applied to each branch, and summing the predicted BLA values (Monserud and Marshall 1999). Six published and unpublished model forms were evaluated (Table 2). Models were assessed for heteroscedasticity using plots of standardized residuals against predicted variables, and various weightings were tested when applicable. The preferred weighting for all models was a variance power function (Pinheiro and Bates 2000):

$$\mathrm{Var}(\varepsilon_i) = \sigma^2|v_i|^{2\delta} \quad (2)$$

where σ^2 is the residual sum of squares, v_i is the weighted covariate, and δ is the variance function coefficient to be estimated by the model. This weighting allows the model to find an optimal weight given the variance inherent in the data (Pinheiro and Bates 2000). Models were evaluated as both generalized nonlinear least squares and nonlinear mixed effects models (nlme) with a random effect for age class in the nlme library in R (Pinheiro et al. 2008). Models were evaluated for goodness of fit using a generalized R^2 and residual plots were compared. Additional evaluation of

Table 2 Model forms, model types, weighting factors, and original sources for nonlinear models tested for prediction of tree-level projected leaf area for intensively managed *J. nigra* L.

Model	Model form	Model type	Weighted covariate	Source[a]
1	$PLA = b_0 DBH^{b_1}$	nlme	DBH	Zellers (2010)
2	$PLA = b_0 CL^{b_1} \times \exp^{(b_2(DBH/HT))}$	gnls	CL	Maguire and Bennett (1996)
3	$PLA = CL^{b_0} \times \exp^{(DBH/HT)}$	gnls	CL	
4	$PLA = b_0 DBH^{b_1} CL^{b_2}$	gnls	CL	Guiterman (2009)
5	$PLA = b_0 DBH^{b_1} LCR^{b_2}$	gnls	LCR and DBH	
6	$PLA = b_0 (BA \times mLCR)^{b_1}$	gnls	BA	Valentine et al. (1994)

PLA projected leaf area (in square meters), *DBH* diameter at 1.3 m (in centimeters), *CL* crown length (in meters), *HT* tree height (in meters), *LCR* live crown ratio (CL/HT), *BA* basal area (in square centimeters), *mLCR* modified live crown ratio [CL/(HT−1.3)] (Valentine et al. 1994)

[a] Model forms, but not weighting factors are attributed to sources

model performance was performed by examination of Aikake information criteria, mean root squared error (RMSE, Eq. 3), log likelihood, and mean percentage of bias (MPB, Eq. 4). RMSE and MPB were calculated as follows:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(Y_i - \widehat{Y}_i\right)^2}{n}} \quad (3)$$

$$MPB = 100 \times \frac{\sum_{i=1}^{n}\left|Y_i - \widehat{Y}_i\right|}{\sum_{i=1}^{n} Y_i} \quad (4)$$

where Y_i and $\widehat{Y}_i$ are actual and predicted values for TLA for the *i*th observation, and n is the total number of observations.

3 Results

3.1 Branch-level projected leaf area

Specific leaf area varied considerably (28.9–247.9 $cm^2\ g^{-1}$) among branches and populations. Saplings had significantly lower SLA (105.4±1.5 $cm^2\ g^{-1}$, mean±standard error; $p<0.001$) than either early poles (162.0±6.4 $cm^2\ g^{-1}$) or late poles (151.9±6.8 $cm^2\ g^{-1}$), which did not differ ($p\gg0.1$). On the other hand, clear patterns between RELDEP and SLA were not evident ($p=0.157$), thus RELDEP was not included in the model for BLA. This reduced the model to simple power function of CSA (Eq. 5):

$$BLA = 0.280 \times CSA^{1.081} \quad (5)$$

Although the intercept, b_0, was not significant ($p=0.816$), the remaining parameter estimates were all highly significant ($p<0.001$). The final model had an RMSE of 2.418 and a generalized R^2 of 0.875. Even with the differences in SLA, this relationship was consistent across age classes ($p=0.230$; Fig. 1).

3.2 Tree-level projected leaf area

Tree PLA was best estimated using models 3 and 5, followed closely by model 2 (Table 3). The single parameter model 3 yielded a slightly improved generalized R^2 and RMSE over the three-parameter model 2 on which it was based. In both models 2 and 3, crown length (CL) is considered a surrogate for sapwood area, which has been shown to produce less biased estimates of tree PLA (Marshall and Waring 1986; Maguire and Bennett 1996), and both models were weighted by CL, as CL varied more in the older, larger trees in the late-pole stage plantation. Models 5 and 6 are similar in model form, but exhibited substantial differences in fit, likely due to more bias in the upper range of diameters

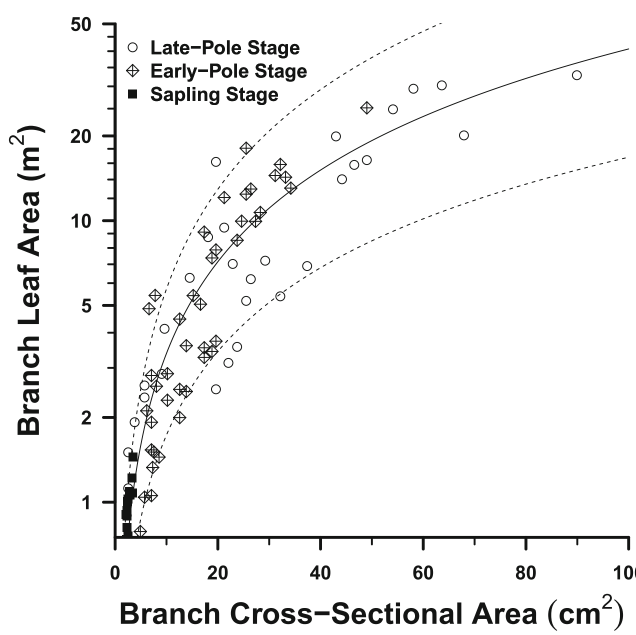

Fig. 1 Scatterplot of branch leaf area (in square meters) against branch cross-sectional area (in square centimeters) for sapling, early-pole, and late-pole stage plantations of *J. nigra* L. *Dotted lines* are the 95 % confidence interval for the relationship

Table 3 Significant parameter estimates ($p<0.001$) with SEs (in parentheses) and fit statistics for tree-level projected leaf area models for intensively managed *J. nigra* L.

Model	b_0	b_1	b_2	Generalized R^2	RMSE	AIC	Log likelihood	MPB
1	1.900 (0.254)	1.422 (0.077)	–	0.906	18.34	752.23	−371.12	15.62
2	0.938 (0.123)	1.548 (0.051)	1.023 (0.097)	0.916	17.19	732.58	−360.29	14.72
3	1.532 (0.009)	–	–	0.922	17.02	723.67	−358.84	14.68
4	1.998 (0.175)	1.081 (0.140)	0.515 (0.179)	0.800	26.96	763.34	−376.67	19.92
5	2.734 (0.305)	1.487 (0.036)	1.519 (0.264)	0.922	16.86	728.20	−359.40	14.58
6	1.163 (0.171)	0.897 (0.030)	–	0.824	25.41	777.85	−384.93	17.81

RMSE root mean squared error, *AIC* Akaike information criteria, *MPB* mean percent bias

in model 6 than model 5 exhibited. With the exception of model 1, generalized nonlinear least squares (gnls) regression was performed as well as nlme.

Surprisingly, model 1, which was the only model to include a random effect for age class, performed reasonably well considering DBH has been shown to be a biased estimator of PLA (Turner et al. 2000). Model 4, which includes DBH and CL as covariates, was the least desirable (R^2=0.800), also likely due to the variation in CL in the late-pole stage plantation. Because sapwood tapers below the base of the live crown (Maguire and Batista 1996), it has been suggested that the height to crown midpoint should be used as a predictor of PLA (Dean and Long 1986; Long and Smith 1989). This variable proved to be nonsignificant in any of the models and was therefore excluded from any further analysis.

Tree PLA appears to diverge with age (Fig. 2), suggesting that differentiation is slowly occurring, even in plantations of clonally propagated stock and growing conditions that are nearly homogeneous. This could be due to a combination of microsite variation and slight differences in pruning regimes.

4 Discussion

Our findings represent an important step in allometric leaf area modeling in hardwoods with irregular crowns and weak apical dominance. The branch-level model exhibited a similar fit to other published hardwood models (Nygren et al. 1993) but did not include RELDEP—a variable commonly significant in published conifer equations (Kenefic and Seymour 1999; DeRose and Seymour 2009)—likely because of the wide variation observed in SLA irrespective of tree height. We believe that the nonsignificance of RELDEP can be attributed to two factors, branch angle and differential treatment for walnut anthracnose among the plantations. With respect to anthracnose, leaves used for the determination of SLA would exhibit much lower values if significant numbers of leaflets have already been lost. Branch angle, which can be very variable in hardwood species, affects vertical foliar position, and therefore, irradiance is the major determinate of SLA. Future studies should include branch angle as a covariate in BLA models in hardwood species.

The model fits, in terms of generalized R^2, for tree PLA were comparable to those previously found in conifers (Gilmore et al. 1996; Monserud and Marshall 1999) and hardwoods (Meadows and Hodges 2002), despite the absence of sapwood area as a predictor variable. Model performance was undoubtedly enhanced by plantation management history. All of the *J. nigra* trees in the current study were genetically improved, with selections based on growth form rather than rate (Beineke 1989). They typically exhibit stronger apical dominance than unimproved *J. nigra* growing stock. Repeated green pruning of both the lower crown and stronger branches within the mid-crown also contributes to the regularity of crowns in the subject plantations. Interestingly, models were fit with the absence of a

Fig. 2 Beanplot of estimated tree leaf areas for *J. nigra* L. by age class. *Thin black lines* represent individual trees, *thick black lines* show mean leaf area for each age class, and the *dashed line* shows mean leaf area across age classes. *Outlined gray curves* are the estimated kernel density of observations

random effect for age class, despite older plantations having higher levels of previous green pruning histories that would reduce the amount of leaf area on a tree. This suggests that rapid crown expansion of plantation grown *J. nigra* compensates quickly for leaf area removal associated with green pruning; this pattern has been observed in much faster growing *Eucalyptus* spp. (Pinkard 2003; Alcorn et al. 2008).

The efficacy of the non-sapwood-based models in this study coincides with the findings of Meadows and Hodges (2002), who reported that cross-sectional area was only a slightly poorer predictor of leaf area and foliage weight than sapwood area in *Quercus falcata* var. *pagodifolia* (Ell.) and *Fraxinus pennsylvanica* (Marsh.). This allows for nondestructive estimation of leaf area, which is critically important in high-value hardwoods, such as *J. nigra*. The utility of such models could prove to be valuable to plantation managers, as they may permit more informed decisions on leaf area manipulations, such as thinning and green pruning. Specifically, commonly measured tree attributes can be employed to physiologically based decisions on which trees will likely respond better in a thinning operation, especially given the divergence in TLA values in older plantations (Fig. 2).

While allometry is undoubtedly influenced by the management practices outlined above, this study has shown that the fundamental relationships seen in conifers hold true in hardwoods lacking strong apical dominance. Extending this methodology to other hardwoods with less regular crown architecture will require careful consideration of the proportion of branch basal area that is conductive should one expect that the pipe model theory to be applicable. This is especially true in larger limbs that require greater support (Grote 2002). While adjustments to existing sampling methods will likely be necessary to permit estimation in forest-grown deciduous trees, this study represents another step extending allometric leaf area models beyond coniferous species.

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