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| The effect of thinning and stand density on temporal patterns of white pine growth efficiency |
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| The purpose of this project is to examine the effects of initial density and thinning on temporal patterns of white pine growth efficiency in a long-term silvicultural experiment. This report documents data preparation, model fitting procedures in R and JAGS, and preliminary results, and is submitted in fulfillment of final project requirements for the courses Hierarchical Models and Advanced Biometry at the University of Maine. Periodic height and diameter measurements from a permanent plot network were used with increment core data in linear-mixed effects models to predict annual height and diameter increment for all trees. Individual tree volume increments were computed from taper equations and summed to generate plot-level estimates of volume increment. Plot volume increments were combined with data from litter traps to calculate annual plot-level foliar growth efficiencies. Temporal patterns of plot-level growth efficiency were computed, and estimates of foliar and size growth efficiencies were compared to examine possible differences in trends between growth efficiency metrics. |

# Introduction

Growth efficiency (GE) defined as net production per unit of occupied growing space is a frequently used comparative measure of tree and stand vigor (Assmann 1970, Waring et al. 1980, Waring 1983, O’Hara 1988, Webster and Lorimer 2002). Though growing space is best understood as the availability of all resources needed to exist on a given site (Oliver and Larson 1996), direct or surrogate measures of tree size and leaf area including basal area increment (BAINC), volume increment (VINC), crown projection area (CPA), sapwood basal area (SBA) are frequently used indices of growing space occupancy in calculating growth efficiency. Measuring GE in terms of leaf area is attractive because of the direct physiological link between leaf area and productivity, but size-based measurements of GE may be more stable as they are not subject to the variability of leaf area dynamics over time and space. Because forest managers have typically been interested in optimizing stemwood volume production, the ratio of volume increment per unit of leaf area and per unit basal area are therefore both useful measures of growth efficiency at the tree and stand scale.

Many studies have shown that GE is determined by complex interactions between tree- and site-level factors. At the tree level, crown characteristics and social position have a significant impact on GE. Because stemwood production is a relatively weak carbon sink suppressed trees have been shown to exhibit low GE as most of their carbon production is allocated for maintenance respiration and other costs (Assmann 1970). In general, GE has been shown to increase with increasing competitive status as trees higher in the canopy are able to allocate a higher proportion of photosynthate to stemwood production (Roberts and Long 1992). Within a given social position within the canopy, however, GE has been shown to decrease with crown size, probably because smaller trees within a given crown class have relatively lower leaf areas but a higher proportion of their leaves in the more photosynthetically active outer foliar shells (Assmann 1970, Sterba and Amateis 1998, Roberts and Long 1992). Likewise dominant and open-grown trees have been shown to have comparatively low GEs, probably because large amounts of carbon must be allocated to maintain the extensive branch architecture needed to support high leaf areas, only a portion of which is optimally photosynthetically active (Long and Smith 1990).

Site quality is known to have an impact on measures of growth efficiency (DeRose and Seymour 2009). Fertilization has been shown to increase GE (Binkley and Reid1984), and trees that are limited by nutrient uptake are predicted to have lower GEs because of biochemical bottlenecks in carbon synthesis and solute transport. Tree water relations under water stress maintain relatively lower stomatal conductance, limiting photosynthetic activity, and stands that are frequently under water stress also support lower LAIs than other stands (Vose et al. 1994). Stem density and thinning are thought to impact stand-level growth efficiency similarly to the way that foliar density and display characteristics do for individual trees. In scaling up, the most growth efficient stands should be composed of tightly packed stems with relatively small, compact crowns whose leaf area is displayed optimally for light interception. Given the known effects of individual tree and stand characteristics on GE, we should observe predictable patterns in stand growth efficiency over time throughout forest development. Stand dynamics theory suggests that GE should start low during stand initiation and reach a peak shortly after crown closure and just prior to the onset of self-thinning. During the period of stem exclusion, GE is expected to decline slowly, declining faster as the stand reaches understory re-initiation, approaching a hypothetical asymptote. Based on a similar theoretical foundation, thinning is expected to result in temporary increases in growth efficiency, followed by declines as leaf area increases.

Despite these assumptions, relatively little research has been done directly measuring the long-term temporal patterns of growth efficiency of stands of different densities, ages, and thinning treatments, however. The purpose of the present study is to use annual litterfall data, periodic growth measurements, and increment cores to examine patterns of white pine growth efficiency over time, investigating patterns of GE over time in a variety of stand conditions. This draft is a limited report detailing the use of increment cores, periodic permanent plot measurements, and annual litterfall data to calculate annual plot-level foliar- and size-based measures GE in stands of varying densities and thinning treatments over periods of 1 to 20 years. In particular, this draft details the use of multilevel models to interpolate individual tree heights and diameters in the calculation of annual VINC and GE. The report also presents preliminary results of growth efficiency over time in plots of a variety of densities and thinning treatments.

# Methods

Study sites are located within the Dwight D. Demeritt Forest of the University of Maine. Growth efficiency over time was calculated using litterfall collection data from thirteen fully-stocked even-aged white pine plots representing a variety of stand development stages and thinning treatments. Plot level GE was defined both according leaf area (GE-L) and size metrics (GE-S). GE-L was defined as the ratio of total plot volume increment to plot leaf area index (LAI). GE-S was defined as the ratio of plot volume increment to total plot volume.

Table 1: Plot characteristics reprinted from Bland 2012

## LAI Estimation

For each plot, annual LAI (Figure 2) was calculated by scaling up leaf area measurements from individual traps as described by Bland (2012). Because plots contained a varying number of traps, the average of scaled trap LAIs in a given year was used in calculating plot-level GE-L. Figure 1 shows annual patterns of leaf area over time for all measured plots.

## Increment Cores

1-3 Increment cores were taken from each tree on permanent plots. Cores used for calculating annual increment were taken through the center of the tree, from bark to bark through the pith, in an effort to obtain accurate measurements of inside-bark diameter (DIB). All cores were analyzed using WinDENDRO tree ring image analysis software (Regent Instruments, Inc. 2012). Ring increments for a given year were averaged within each tree to compute an annual mean radial increment, and the cumulative sum of all prior mean radial increments was used as an estimate of DIB for that year.

## Growth Plot Measurements

Permanent growth plots were measured periodically from 1993 to 2011. In inventory years, height, diameter, and crown characteristics were recorded for each tree on each plot.

## Height and Diameter Models

Data files and R scripts detailing data combining and cleaning are included as .txt files within the parent directory of this report. In order to calculate annual plot VINC I developed height and diameter estimates for each tree in non-measured years using linear mixed-effects models fit by two methods. First, varying-slope, varying-intercept models were fit using the lme4 package (Bates et al. 2013, Bates 2010) within R 3.0.0 (R Core Team 2013) to obtain parameter estimates predicting known height and diameter measurements for each tree from tree core height, DIB, and age. Three separate models for each dependent variable were fit with different combinations of predictors, but all six models followed the basic varying slope and varying intercept linear model form in which all predictor coefficients were fit individually to each of *j* trees through assigning random effects to each individual. This model is expressed formally as:

where **β** is the J by K matrix of K data level regression coefficients for each of the *j* = 540trees, **X** is the n by K data matrix of predictors, **U** is the K length vector of the means of the distribution of the j slopes and intercepts, and **Σ** is the covariance matrix of the slopes and intercepts. Following model fitting, distributions of residuals and plots of predicted versus fitted values were examined for each model as an assessment of model performance. Model performance was also assessed and compared numerically using Akaike’s Information Criterion (AIC), Bayesian Information Criterion (BIC) (Table 2, Figure 5), as well as root mean squared error (RMSE), and mean absolute bias (MAB) (Table 2, Figure 6). Figures depicting model fits and comparisons can be found as separate .pdf files within the parent directory of this report.

Table 2: Model performance according to four measures of fit.

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|  | Measure of Fit | | | |
| Model | AIC | BIC | RMSE | MAB |
| Ht = β0 + β1\*age | 6157.02 | 6190.115 | 0.4986 | 0.3531 |
| Ht = β0 + β1\*DIB | 6918.559 | 6951.654 | 0.4942 | 0.3338 |
| Ht = β0 + β1\*age + β2\*DIB | 5923.393 | 5978.551 | 0.4691 | 0.3353 |
| DBH = β0 + β1\*DIB | 6556.735 | 6589.83 | 0.2245 | 0.1507 |
| Ht = β0 + β1\*DIB + β2\*age | 6322.529 | 6377.688 | 0.184 | 0.1187 |
| Ht = β0 + β1\*DIB + β2\*Ht + β2\*age | 5679.264 | 5762.002 | 0.1383 | 0.084 |

Following fitting using lme4, a relatively simple varying slope-varying intercept model predicting diameter from DIB was fit using JAGS 3.3.0 as called from R using R2jags (Su and Yajima 2012) in order to gain experience in Bayesian estimation and to compare fitting techniques. The Gibbs sampler initially failed to converge on a model form, as defined by an R-hat threshold of 1.1 on all parameter estimates. Ultimately, in order to achieve convergence the variance-covariance matrix of the slope and intercept parameters was modeled using the scaled inverse Wishart distribution in order to more easily meet restrictions of positive-definiteness. Model convergence was then achieved after 500 iterations following a burnin period of 250 iterations, with a maximum R-hat value among all parameters of 1.05. Following successful fitting of this simple JAGS model, I attempted to fit a more complex diameter model incorporating additional predictors, but failed to specify the model properly, so could not proceed. Parameter estimates from lmer() models selected for predication and for the successfully fit JAGS model are presented in table 3.

Table 3: Parameter estimates of models selected for prediction, and from fitting a simple JAGS model.

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## Plot Volume Increment and Growth Efficiency

Individual tree parameter estimates from lme4 models with best performance according to an evaluation of AIC, BIC, RMSE, and MAB were used to predict height and diameter of each tree in every year throughout the study period. Volume for individual trees was then computed from these predicted height and diameter values using the regional white pine stem-taper equation described by Li et al. (2012). Size-based and leaf area based metrics of growth efficiency were then calculated. GE-L was defined as the ratio of annual volume increment to LAI, and GE-S was defined as the ration of annual volume increment to total volume.

# Results

Mean parameter estimates for the two models selected for prediction are presented in Table 3. Model fitting details and results of growth efficiency analysis are presented in .pdf files that can be found in the parent directory of this report.

# Discussion

I will not venture too far into interpretation here because of time constraints and the as yet provisional nature of the results. Though the predictive models used in this analysis perform relatively well, adjustments incorporating site index (SI) and possibly plot-level random effects may show continued improvement over the model forms presented here. Additionally, I plan on conducting extensive Bayesian model fitting for the model forms chosen in this analysis to see if they show improvements over lmer() , but achieving that level of nuance and sophistication was beyond the scope of my skill and timeframe for the current project.

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