

MODELING THE REGENERATION AND EARLY STAND DYNAMICS OF
MISSOURI OZARK FORESTS

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MISSOURI OZARK FORESTS

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To Scarlett and Autumn, who have served as inspiration throughout.

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MODELING REGENERATION AND EARLY STAND DYNAMICS OF MISSOURI OZARK FORESTS

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ABSTRACT

Projecting the effects of silvicultural choices on forest regeneration has traditionally been difficult. In an effort to improve upon this, a collection of empirical models based on leading hypotheses and theories of tree and stand development were constructed to simulate regeneration and early stand dynamics in Missouri Ozark forests. The stochastic models of establishment across a gradient of residual overstory density (Chapter 2) are consistent with the variable nature of the regeneration process. Linking establishment outcomes with models of annual height growth based on residual overstory density (Chapter 3) and size (Chapter 4) provides a powerful tool for both applied and empirical objectives.

Quantitative interpretation of the regeneration process is as important as simulation of it. Developmental milestones for successful canopy recruitment were identified to improve evaluations of individual trees in even-aged stands during the regeneration process (Chapter 4). The reference chart methodology presented in Chapter 5 increases the inference obtainable from a single measurement by providing interpretation of individual tree development in the context of a variety of peer groups. Though imperfect, the combination of these models and tools should increase our understanding and ability to recreate the regeneration process, and as a result, the efficacy of our efforts to manipulate it.

Chapter 1: Introduction

Forest regeneration can generally be described as the process through which individual or collections of trees are replaced or augmented with a new generation of trees. The term reproduction has been reserved for the trees that comprise the new generation (Johnson *et al.* 2009). Forest regeneration is a complex and dynamic process involving establishment, growth, and mortality. Establishment is the culmination of a series of events involving production, dispersal, and germination of seeds and their initial survival. Once successfully established, reproduction must continue to survive and grow to recruit into the canopy (Dey 2014).

In many ways, the composition of future forests is a function of the composition and structure of previous forests (Egler 1954). However, the impact of previous generations on future composition is not thought to be strictly deterministic. Rather, the regeneration process often exhibits a high degree of variance and stochastic influences (Gleason 1917). The influence of variance and stochasticity does not refute that certain developmental pathways are more likely than others (Gould and others 2005), but the ultimate identity of the regenerating stand will likely be reflective of the magnitude and timing of disturbances and their biological impacts on stand development (Oliver & Larson 1996).

Foresters have long understood that species differ in their abilities to flourish following disturbances of varying magnitudes and frequencies (Assmann 1970, Büsgen and Münch 1929, Puetmann *et al.* 2008). Grubb (1977) described the suite of conditions required for a high chance of replacing one mature individual with a new individual of the next generation as the “regeneration niche” of a

species. Harper and others (1961) coined the term “safe site” to describe a physical location where the regeneration requirements of an individual were provided along with some degree of insulation from hazard. The culmination of events that must transpire to ensure successful establishment occurs only sporadically, often resulting in the creation of ephemeral cohorts of reproduction (Johnson 1993). However successful regeneration requires more than establishment of a new cohort (Loftis 1983, Dey 2014), and the suite of conditions required for continued survival and recruitment into the canopy may differ from those required for establishment (Crow 1988, Poorter *et al.* 2005).

Successfully securing regeneration is important for both ecological and economic reasons. Given the complexity and variability associated with this vital process, regeneration objectives beyond simply replacing one group of trees with another are often difficult to achieve. Indeed, volumes have been written and multiple symposia held to address regeneration concerns, even for those species that are seemingly ubiquitous, both in abundance and breadth of range as adults (*e.g.*, Kabrick *et al.* 2007, Loftis and McGee 1993). These difficulties can be multifaceted and arise from failures to provide and/or maintain the suite of conditions required for establishment and recruitment. Furthermore, due to the extended timeframe encompassed by the regeneration period, which can range from a few years, to decades, to essentially being continuous depending on management objectives (Johnson *et al.* 2009, Smith *et al.* 1996), and the dynamic nature of the regeneration process, regeneration failures may not be recognized until late in the regeneration period, when options for amelioration are

limited. For these reasons, the ability to forecast regeneration outcomes via models and simulators is appealing. Unfortunately, most existing models focus on the dynamics of other phases of forest development and only have rudimentary regeneration capabilities (*e.g.*, Crookston and Dixon 2005) if regeneration is incorporated at all. Consequently, most existing regeneration models and simulators were developed as standalone programs.

Though many regeneration models have been developed, most were designed to operate within a specific silvicultural system in a specific region and only provide output at the end of the regeneration period. However, there have been dramatic shifts in management objectives in recent decades in favor of more structurally and compositionally diverse forests (Puetmann *et al.* 2008). Therefore, more robust regeneration modeling strategies are required. In an effort to address this need and improve the capacity to model regeneration under a variety of residual overstory conditions in the Missouri Ozarks a collaborative research program was established between the USDA Forest Service, the Missouri Department of Conservation, and the University of Missouri. The chapters that follow describe the progress that has been made to date.

Chapter 2 describes a strategy for simulating reproduction establishment under a variety of residual overstory conditions consistent with leading hypotheses and theories of forest regeneration and early stand development. Empirical models of reproduction establishment and allometry are presented for a variety of species native to the forests of the Missouri Ozarks. Chapter 3 describes empirical models of the impact of residual overstory density on the height development of

reproduction during canopy recruitment. Chapter 4 describes empirical models of the impact of increasing height on the annual height growth of reproduction. In addition, developmental milestones of height development are identified using the growth patterns of trees that successfully recruited in to the upper canopy by the end of the regeneration period following clearcutting in naturally regenerated mixed species stands. Chapter 5 describes a reference chart method for assessing juvenile height development. These reference charts are similar to those used by physicians to assess juvenile development in humans. When applied to tree development, reference charts provide opportunities to gain greater inference from evaluations and monitoring of the canopy recruitment process. Finally, Chapter 6 provides a summary of the findings from the preceding chapters and identifies areas in need of additional research.

References

- Assmann, E. 1970. *The Principles of Forest Yield Study*. Pergamon Press. 506p.
- Büsgen, M., Münch, E. 1929. *The Structure and Life of Forest Trees*. Chapman & Hall.
- Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: a review of its structure, content, and applications. *Computers and Electronics in Agriculture*. 49: 60-80.
- Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. *For. Sci.* 34(1): 19-40.
- Dey, D.C. 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* *in press*.
- Egler, F.E., 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412-417.
- Gleason, H.A. 1917. The structure and development of the plant association. *Bull. Torr. Bot. Club*. 43: 463-481.
- Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2005. Developmental pathways following the harvest of oak-dominated stands. *For. Sci.* 51(1): 76-90.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*. 52: 107-145.
- Harper, J.L., Clatworthy, J.N., McNaughton, I.H., Sagar, G.R. 1961. The evolution and ecology of closely related species living in the same area. *Evolution*. 209-227.
- Johnson, P.S. 1993. Perspectives on the Ecology and Silviculture of Oak-Dominated Forests in the Central and Eastern States. USDA For. Serv. Gen. Tech. Rep. NC-153.
- Johnson, P.S., Shifley, S.R., Rogers, R. 2009. *The Ecology and Silviculture of Oaks*. CABI. 600p.
- Kabrick, J.M., Dey, D.C., Gwaze, D. 2007. Shortleaf pine restoration and ecology in the Ozarks.: proceedings of a symposium . USDA For. Serv. Gen. Tech. Rep.
- Loftis, D.L. 1983. Regenerating Red Oak on Productive Sites in the Southern Appalachians: A Research Approach. In: Jones, E.P. Jr. Ed. Proceedings: 2nd Biennial Southern Silvicultural Research Conference. 1982 November 4-5. Atlanta, GA. USDA For. Serv. Gen. Tech. Rep. SE-24. Pgs. 144-150.

- Loftis, D.L., McGee, C.E. eds. 1993. Oak regeneration: serious problems, practical recommendations. Symposium Proceedings. USDA For. Serv. Gen. Tech. Rep. SE-84.
- Oliver, C.D., Larson, B.C. 1996. *Forest Stand Dynamics*. 2nd ed. John Wiley & Sons, Inc. New York. 520p.
- Poorter, L., Bongers, F., Sterck, F.J., Woll, H. 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *J. Ecol.* 93: 256-267.
- Puettmann, K.J., Coates, K.D., Messier, C.C. 2008. *A Critique of Silviculture: Managing for Complexity*. Island Press. 206p.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S. 1996. *The Practice of Silviculture: Applied Forest Ecology*. 9th Ed. John Wiley & Sons, New York.

Chapter 2:

A STRATEGY FOR SIMULATING REGENERATION ESTABLISHMENT –
STAND DEVELOPMENT HYPOTHESES AND EMPIRICAL MODELS

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Abstract

Predicting the effects of silvicultural choices on tree regeneration has traditionally been difficult with the tools currently available to foresters. To improve this, we have developed a collection of empirical establishment models based on hypotheses of stand dynamics for several species found in the Missouri Ozarks. This collection of empirical models was developed for use in an establishment module of a regeneration simulator. The reproduction establishment models estimate distribution parameters for stochastic number generators to simulate regeneration following a variety of harvest-based silvicultural manipulations. Estimates of total height, crown dimensions, diameter at breast height, and spatial pattern are provided for each new stem as a function of residual overstory density, species, and various other covariates and allometric relationships. A pre-disturbance inventory is used to account for existing conditions and published sprouting parameters define the potential contributions of stump-sprouts to regeneration. Separate simulator modules are planned for growth and mortality, with output provided as a tree-list to facilitate connection with other forest growth models. The development of empirical establishment models and their role in the simulation strategy of the establishment module will be discussed.

Introduction

Forest regeneration is a dynamic process involving the establishment, growth, and mortality of trees. Sometimes the regeneration process is delineated into two stages: regeneration (establishment) and recruitment (growth and mortality) (Dey 2014), but the basic components remain the same. Complex interactions between these three components continually shape the regeneration process, yet their outcomes may not manifest until years or decades have passed (Quero *et al.* 2011). Given this timeframe and the crucial role of regeneration to sustainable forestry, the need for computer simulated projections of regeneration to expedite silvicultural diagnoses and improve the likelihood of achieving desired outcomes at the end of regeneration is clear.

Several approaches have been used to model forest regeneration. Philosophical, ecological, and technical differences have resulted in models with different function and form. The scope varies from projections of annual seed production (*e.g.*, Rogers and Johnson 1998) to gap and/or stand composition (*e.g.*, Loftis 1989, Millington *et al.* 2013). Weiskittel and others (2011) make a distinction between models that incorporate aspects of seed production, dispersal, and germination and those that begin with established reproduction and model their subsequent development.

Several models have been designed to evaluate the regeneration potential of a single species or species group and provide management guidelines for regeneration success. Sander and others (1984) were among the first to develop

probabilistic models to evaluate regeneration potential in oak dominated forests of the central United States. The probabilities of oak reproduction of various sizes being alive and \geq a predetermined height threshold (which was related to the expected height of a codominant oak) at a specified stand age was derived empirically for the Missouri Ozarks. Regeneration was assumed adequate if it provided 30% stocking of dominant or codominant oaks at the end of the regeneration period. This success criteria and simulation strategy has been termed the “dominance probability” approach (Johnson *et al.* 2009) and variations of this approach have been applied with success to project oak regeneration success in other settings. Loftis (1990) used dominance probabilities to model regeneration in the Southern Appalachians. Spetich and others (2002) adapted the approach for the Boston Mountains of Arkansas by relating the threshold height for success to the composition of neighboring trees on a plot. Weigel and Peng (2002) developed dominance probabilities for sprout origin reproduction in Indiana. Dey and others (2009) examined differences in dominance probabilities among sites in Arkansas, Missouri, and Indiana. Preharvest basal diameter and/or height, tree age, and site productivity are common covariates used to model the dominance probability of oak stumps sprouts and advance reproduction.

Similar approaches have been employed to evaluate reproduction in other oak dominated forests of the United States (*e.g.*, McWilliams *et al.* 1995, Belli *et al.* 1999, Steiner *et al.* 2008). Some models further delineate between the various origins of reproduction (Gould *et al.* 2006 Gould *et al.* 2007, McQuilkin 1975).

The fundamental research required to build these models and guidelines has been instrumental to the development and synthesis of forest regeneration theory. Unfortunately, the dominance probability approach may have limited application in multi-cohort stands where both crown classes and their ability to denote recruitment success are more ambiguous. In addition, the combining of growth and survival, though biologically sound for the intended application, may limit the capacity to model variations in factors known to drive hardwood regeneration such as initial floristics (Egler 1954) and residual overstory density through their influence on tree establishment, growth, and survival throughout the regeneration period. Furthermore, regeneration evaluations and guidelines that follow the dominance probability or related approaches are specific to a particular species or species group. The data required to adapt these tools to other species is extensive and require long-term commitment.

Bugmann (2001) provides a review of many gap models and some of the various ways regeneration and recruitment are incorporated. Gap models have been developed for several areas. Waldrop and others (1986) developed FORCAT, an adaptation of FORET (Shugart and West 1977) to model stand development on the Cumberland Plateau (Waldrop *et al.* 1986). Solomon and Leak (2002) developed FOREGEN to simulate species composition three years post-harvest for openings of various sizes in the northern hardwood forests of New England. The SORTIE model (Pacala *et al.* 1993) incorporates models of seed dispersal (Ribbens *et al.* 1994, Clark *et al.* 1999), juvenile growth (Pacala *et al.* 1994, Wright *et al.* 2000, Finzi and Canham 2000) and mortality (Kobe *et al.* 1995) for a

variety of forest types, including those in the northeast United States and British Columbia, Canada.

Many models are based on theory and statistical analysis, while others are based on various combinations of theory, empirical data, and expert experience. Loftis (1989) developed a model that estimated future species composition in the Southern Appalachians that was primarily parameterized using expert experience. Vickers and others (2011) extended this approach to additional regions using empirically informed parameterization to complement expert opinion. Marquis and Ernst (1992) developed SILVAH to provide prescription and management guidelines to forest managers in the Alleghenies based on empirical data and expert experience. The SILVAH-OAK program (Stout *et al.* 2007, Brose *et al.* 2008) is an extension of the SILVAH framework that incorporates additional empirical analyses and experiences from oak dominated forests of the Mid-Atlantic states.

For mixed hardwood forests in the central hardwood region of the eastern United States, perhaps the three most applicable and readily available multi-species regeneration simulators are FVS (Crookston and Dixon 2005), ACORn (Dey 1991), and REGEN (Loftis 1989). The regeneration simulator in the southern and central states variants of FVS has been described as a partial establishment model as opposed to the full establishment model which was calibrated for parts of Montana, Idaho, and Alaska (Dixon 2002). The partial establishment model simulates regeneration only from stump sprouting of inventoried trees, leaving the inclusion of other regeneration sources to user discretion. In order to input

non-sprout regeneration, users can simulate a “planting” by entering the number of new stems by species along with other stem attributes. While the convenience of regenerating a stand directly within a powerful growth simulator such as FVS is appealing, the inadequacies of the partial establishment model, particularly the lack of stochastic seed origin reproduction establishment, are limiting.

Dey (1991) developed ACORn, a regeneration simulator for stands in the Missouri Ozarks following clearcut or classic shelterwood harvests. ACORn projects height and diameter growth as well as survival of inventoried reproduction to create diameter distributions by species, stocking values, density measures for the stand at the end of the regeneration period. The target projection for ACORn is 21 years following harvest and includes most of the common woody species found in the Missouri Ozarks. Required inputs for ACORn are an inventory of stems for stump sprouting and an inventory of advance reproduction. Stump sprouting, survival of advance reproduction, and growth of individual stems are projected using empirically derived models.

Loftis (1989) developed the REGEN model to estimate the species composition of stems in the codominant or dominant crown classes at canopy closure in developing mixed species forests following a clearcut harvest using combinations of expert experience and empirical data when available. REGEN requires an inventory of all sprouting species with a dbh and an advance reproduction survey of all species in predefined size classes. REGEN uses competitive rankings of regeneration sources including stump sprouts, root sprouts, new seedlings, and various sizes of advance reproduction. The competitive rankings range from 1-8,

with lower numbers indicating stronger competitors. For each simulated plot, REGEN will select a predetermined number of stems to establish based on a forest inventory. The inventoried regeneration sources with the strongest competitive ranks are established on the simulated plot. Vickers and others (2011) found the REGEN model produced reasonable results when the competitive rankings were informed with local empirical data from the Central Appalachians. Clatterbuck (2015) found reasonable performance of the REGEN model parameters in the Ridge and Valley province of Tennessee, but noted that local parameterization was needed to improve estimates.

Statistical estimation of REGEN competitive rankings using local empirical data may be possible (Radtke 2015). However, the relative nature of competitive rankings among species creates difficulties and the development of competitive rankings for REGEN can be daunting in diverse forests. When fully parameterized, REGEN can consider seven or more competitive rankings per species to account for initial size and source of reproduction (*e.g.*, new seedlings, germinants, small advance, medium advance, large advance, stump sprouts, root sprouts), and also to consider competitive differences that vary considerably across site classes and regions (Vickers *et al.* 2011, Clatterbuck 2015). Keyser and others (2013) found that the point estimate of species composition for stems in the codominant and dominant crown classes provided by REGEN required major assumptions to provide input for existing growth and yield simulators, but Keyser and Keyser (2013) successfully input results from REGEN into FVS

(Crookston and Dixon 2005) to examine the impact of various regeneration techniques on species composition in the Southern Appalachians.

Many of the previously described strategies for regeneration simulation were developed to operate within a specific silvicultural system in a specific region and often combine the outcomes of regeneration and recruitment into a single point estimate of certain attributes (density, composition, structure). Combining regeneration and recruitment is biologically sound and likely has little impact for most applied objectives. However, non-process based modeling approaches incur an opportunity cost in limited ability to simulate novel floristic and management scenarios. Non-process based models are typically incapable of generating output in incremental time steps throughout the regeneration period. Consequently, they lack the ability to support adaptive management.

There have been dramatic shifts in management objectives in recent decades in favor of more structurally and compositionally diverse forests with continuous canopy cover (Puetmann *et al.* 2008). Foresters have long recognized differences in life history traits among species and the influence of overstory density and crown cover on regeneration dynamics. Indeed, the history of silvicultural terminology (Puetmann *et al.* 2008) suggests that a foundational hypothesis of scientific forest management is that overstory density, and disturbance thereof, are the primary drivers of regeneration dynamics. Despite this longstanding hypothesis, foresters have made little progress to quantitatively simulate the impact of varied overstory conditions on the development of reproduction, particularly in naturally regenerated mixed species stands.

Accordingly, many of the previously described strategies for simulating regeneration are not readily adaptable to the more structurally diverse forest conditions embodied by current management objectives.

In an effort to improve upon the current capacity of foresters to simulate regeneration in more structurally diverse conditions, a research project was initiated to quantify and model the impact of overstory density on the establishment, growth, and mortality of reproduction in the Missouri Ozarks. The objectives are to 1) develop a framework of models that simulate regeneration as a dynamic process and that 2) can be used in diverse forests for a range of structural objectives, 3) produce output that is compatible with existing growth models, and 4) permits regional calibration, if necessary.

This framework considers regeneration a series of events and interactions in response to management practices that alter stand composition and structure (Fig. 2.1). This framework allows for predictions in incremental time steps, which contrasts to models that produce point estimates of structure, stocking and composition at the end of regeneration. In addition, this framework permits evaluating the impact of varying residual overstory density resulting from differing regeneration methods on regeneration and thus, is a more robust modeling approach. In this approach, various silvicultural regeneration methods are viewed simply as manipulations that result in varying overstory density that is retained long enough to effect regeneration, and whose affect can vary spatially throughout the stand. The framework largely follows the “established seedling”

approach described by Weiskittel and others (2011, p157), by requiring an inventory of advance reproduction and sprouting sources.

The focus of the remainder of this chapter is to describe the development of empirical models of reproduction establishment and other parameters designed an establishment module within the framework of a regeneration simulator. For the purposes of this project, establishment is defined as: presence of reproduction (trees $\leq 5\text{cm dbh}$) three years following disturbance. Fig. 2.2 provides a visual representation of the structure and order of the establishment simulation module. Probabilistic sprouting of inventoried trees and stochastic establishment of small advance reproduction and post-disturbance reproduction are also incorporated. Because tree form has a strong influence on function (Assmann 1970, Oliver and Larson 1996, Horn 1971), many growth models require various stem attributes to project future conditions. By including the attributes described above for each tree this design promotes compatibility with existing growth simulators and has predictive robustness. Additionally, each stem is stochastically assigned a spatial coordinate to facilitate the use of neighborhood density metrics later in the growth and mortality modules

Methods

The data used in this project were collected from the Missouri Ozark Forest Ecosystem Project (MOFEP), which encompasses more than 3700 hectares within the Current River watershed in Carter, Reynolds, and Shannon Counties

of southeastern Missouri. The study region is an unglaciated, deeply dissected plateau primarily comprising Ordovician and Cambrian dolomites and sandstones (Kabrick *et al.* 2000). Average annual precipitation is 115 cm and average annual temperature is 13.5° C (Kabrick *et al.* 2008b). Slope aspect and slope position are important characteristics used for site classification in the region (Nigh *et al.* 2000). The sites used in this study were on exposed (aspect: 136 - 315°) and protected (aspect: 316 - 135°) backslopes with an average site index (*Quercus velutina* Lam., base age 50) of 21.0 ± 1.3m and 22.0 ± 1.1m, respectively (McQuilkin 1974). Overstory species composition on both sites classes are heavily dominated (>70% basal area) by oak species (primarily *Q. velutina* Lam., *Q. alba* L., *Q. coccinea* Münchh., *Q. stellata* Wangenh.) and compositional differences between the two site classes are subtle (Kabrick *et al.* 2004). Protected backslopes usually have a slightly higher *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* Mill. are more common on exposed backslopes (Kabrick *et al.* 2004). Shifley and Brookshire (2000) provided a detailed documentation of the abundance and diversity of species found on MOFEP.

MOFEP is a long-term, landscape-scale experiment initiated in 1989 by the Missouri Department of Conservation (MDC) to evaluate the effects of forest management on ecosystem composition, structure, and function within the Missouri Ozark Highlands (Brookshire and Shifley 1997). The forest management systems under evaluation at MOFEP include even-aged, uneven-aged, and no-harvest management. The even-aged treatments included

clearcutting with reserves ($\sim 5\text{m}^2 \text{ha}^{-1}$) for stands to be regenerated and intermediate thinning elsewhere, as prescribed by Roach and Gingrich (1968). In the clearcut stands, all live trees $> 3\text{m}$ in total height or $> 4\text{cm}$ dbh were felled, with the exception of trees left as reserves (Missouri Department of Conservation 1986). The uneven-aged regime consisted of single-tree selection on a 15-year harvest cycle with group-openings that ranged from one to two tree heights (0.03-0.15ha) interspersed throughout and summed to 5% of the harvested land area, as prescribed by Law and Lorimer (1989). Areas designated for a no-harvest management regime were maintained as experimental controls. In 1996, stands were harvested following MDC Forest Land Management Guidelines (1986). For additional information on MOFEP, including study rationale, experimental design, site conditions, inventory methods, and early findings, see Brookshire and Shifley (1997), Shifley and Brookshire (2000), Shifley and Kabrick (2002), and Knapp and others (2014).

Woody overstory vegetation on MOFEP was sampled via 648 circular 0.2-ha permanent plots that were randomly located throughout the study area with the constraint that each stand must have at least one plot. Within these 0.2-ha plots, the dbh and species of trees $\geq 11\text{cm}$ dbh were recorded. The dbh and species of woody midstory vegetation 4 - 11cm dbh was sampled on four 0.02-ha subplots nested within each 0.2-ha plot. The dbh and species of saplings (height $\geq 100\text{cm}$ and a dbh $< 4\text{cm}$) were recorded from 0.004-ha understory plots nested inside each 0.02-ha subplot. Stem counts by species for seedlings (height $< 100\text{cm}$) were recorded from 4 quadrats (m^2) nested within each 0.02-ha subplots.

Data from a stratified random sample of ninety MOFEP plots were used for analyses in this project (18 that were clearcut, 24 that were thinned, 16 harvested with single-tree selection, 8 in group-openings, 24 in stands that were not harvested). These plots were equally allocated to exposed and protected backslopes. Due to the random determination of plot locations, the proportion of a subplot occupied by a group opening or single-tree gap varied. On a single 0.02-ha understory subplot within each overstory plot, all woody stems with a height $\geq 100\text{cm}$ were mapped and the species, dbh (1.37m), total height, crown width, crown length, apparent stem origin (seed or sprout), and other categorical variables were recorded for each stem in 1995 (1 yr pre-treatment), 1999 (3 yrs post-treatment) and again in 2004 (8 yrs post-treatment). Crown width was measured in perpendicular directions (NS & EW). Unfortunately, the additional pretreatment (1995) measurements were not completed on the 18 0.02-ha subplots for the clearcut treatment.

Given the number of species included in this dataset, some species were grouped for analyses at the genera or sub-genera level. All woody species inventoried were included in one of the following thirteen species groups: 1) ashes (*Fraxinus americana* L., *F. pennsylvanica* Marsh.), 2) blackgum (*Nyssa sylvatica* Marsh.), 3) black cherry (*Prunus serotina* Ehrh.), 4) dogwood (*Cornus florida* L.), 5) elms (*Ulmus alata* Michx., *U. rubra* Muhl., *U. americana* L.), 6) hickories (*Carya tomentosa* Sarg., *C. glabra* Mill., *C. ovata* (Mill.) K. Koch., *C. texana* Buckley, *C. cordiformis* (Wangenh.) K. Koch.), 7) red maple (*Acer rubrum* L.), 8) red oaks (*Q. rubra* L., *Q. velutina*, *Q. coccinea*, *Q. marilandica* Münchh.),

9) sassafras (*Sassafras albidum* J. Presl.), 10) shortleaf pine (*Pinus echinata* Mill.), 11) sugar maple (*Acer saccharum* Marsh.), 12) white oaks (*Q. alba*, *Q. stellata*, *Q. muehlenbergii* Engelm.), and 13) other species (Appendix 2.1).

The variability in post-treatment overstory densities of the MOFEP study plots offered a gradient to estimate the effects of residual overstory density on reproduction establishment and allometry. All characteristics of reproduction (height, crown length, etc.) were modeled from the mapped 0.02-ha understory subplots; whereas, characteristics of the residual overstory (seed source presence, basal area per hectare of stems ≥ 11.43 cm dbh) was calculated from the 0.2-ha overstory plot that each understory subplot was nested within.

Residual basal area was estimated from ninety 0.2-ha overstory plots two years following treatment.

Although overstory basal area is an imperfect descriptor of stand density, it is widely used in silvicultural prescriptions because it is simple to measure.

Overstory basal area is strongly correlated with canopy openness in the Missouri Ozarks (Blizzard *et al.* 2013), and has proven a useful indicator of the competitive pressure exerted by overstory trees in other locales (Biging and Dobbertin 1995, Lorimer 1983). Because regeneration simulation plots are typically relatively small, it is assumed that the establishment environment (resource availability, site suitability) on a plot is reasonably uniform and adequately captured by common overstory metrics such as basal area. However, the growing environment is likely to be more spatially diverse when there is residual overstory, both horizontally and vertically; therefore, more thorough

descriptions of site occupancy may be required to simulate longer term growth and mortality of regeneration.

All statistical analysis and random number generation was completed in R statistical software version 3.0.3 (R Development Core Team 2014). The packages and functions used are mentioned in capital letters throughout the document. Prior to model fitting, the data was inspected for implausible datapoints that may have resulted from typographical or other data management errors. Implausible datapoints without obvious remedies were removed.

The post-disturbance establishment of reproduction ($\text{dbh} \leq 5\text{cm}$) not originating from obvious sprout origin but possibly from small advance reproduction (height $< 100\text{cm}$), or seed disseminated immediately following disturbance for a given species group was hypothesized to be a function of residual overstory density ($\text{basal area} \cdot \text{ha}^{-1}$; $\text{dbh} \geq 11.43\text{cm}$), advance reproduction presence ($\text{dbh} \leq 3.8\text{cm}$), residual seed source presence ($\text{dbh} \geq 11.43\text{cm}$) and their potential interactions. However, all possible models that could be developed from the various combinations of these three main effects and their interactions were not considered candidate models. It was hypothesized that residual overstory density was the primary influence on seedling establishment. This hypothesis is fundamental to the regeneration simulation strategy used herein. Although prior presence and residual seed sources can inform the probability that new seedlings of a species can disperse and germinate, the probability of establishment (as defined herein) is strongly influenced by residual overstory density and its impact on resource availability (Reineke 1933, Yoda *et al.* 1963,

Gingrich 1967, Assmann 1970, Oliver and Larson 1996). Therefore, all candidate models for seedling establishment included residual overstory density as an effect (Table 2.1).

Because we defined establishment as the number of stems present 3 years following disturbance, *i.e.*, a count per specified unit of time, it was expected to be well-represented by a Poisson distribution (Faraway 2005). The Poisson distribution is a discrete distribution that assumes the expected value (mean) is equal to the variance and, therefore, both can be estimated by the single parameter λ . Preliminary Poisson parameter estimates for regeneration establishment were obtained via the generalized linear models function (GLM) with a log link. Preliminary model diagnostics suggested that the assumption of equal mean and variance was violated for most species groups due to overdispersion, *i.e.*, for a candidate model the variance estimate was considerably greater than the mean. The negative binomial distribution has been recommended as an alternative to the Poisson distribution for overdispersed count data (Hilbe 2011). The negative binomial distribution is a discrete distribution with two parameters, which are often the mean (μ) and a dispersion parameter (k [or θ in R statistical software]) for ecological data (Bolker 2008). The parameters for all candidate models of seedling establishment were estimated with negative binomial regression with a log link using the negative binomial regression function (GLM.NB) within the MASS package (Venables and Ripley 2002) for those species with sufficient data. However, the parameters for intercept-only Poisson models were estimated for those species groups

(shortleaf pine and sugar maple) with insufficient data (due to rarity) for negative binomial regression and the inclusion of covariates.

The candidate models were compared using Akaike's Information Criterion (AICc) corrected for small sample sizes (Burnham and Anderson 1998). For a species group, the most parsimonious model within 2 units of the model with the lowest AICc value was selected as the "best" among those considered (Burnham and Anderson 1998) provided that it produced estimates within the range of the data for all covariate scenarios. If a candidate model met the AICc criteria to be selected as "best", but produced estimates outside the range of the data, the candidate model with the next lowest AICc that also produced reasonable estimates was selected as "best". Scattergraphs with fitted model curves for all species groups are provided in the Appendix. Candidate models for a species group that failed to converge after 10,000 iterations of the negative binomial function were considered to be over-parameterized or otherwise misspecified and were not included in further model comparisons.

Due to the complexity of combining the various inventory timings, protocols, and plot designs of the ordinary MOFEP plots and the supplemental subplots, data preparation for reproduction establishment model parameterization was convoluted. A summary follows. Presence data for residual seed sources was obtained from the 0.2-ha overstory plots. Presence data for large advance reproduction (height $\geq 100\text{cm}$; dbh $\leq 3.8\text{cm}$) were obtained from the 0.004-ha understory plot that was nested within the mapped 0.02-ha subplots. Presence data for small advance reproduction (height $< 100\text{cm}$) were obtained from the

four quadrats (m^2) nested within the mapped 0.02-ha subplots. Presence data for large and small advance reproduction were combined into a single advance reproduction presence variable.

Because the fate of large advance reproduction is handled elsewhere in the establishment module, the objective for these models of post-disturbance reproduction establishment was to estimate the net contribution of small advance reproduction and disturbance triggered germination. Therefore, large advance reproduction that was tagged prior to disturbance were not included in the post-disturbance abundance data used as the response variable in these models. The post-disturbance abundance used as the response variable in the reproduction establishment models were obtained from the 0.02-ha mapped subplots dataset, but only those stems that were within the boundaries of the nested 0.004-ha understory plot were tallied. This was for three reasons: 1) to facilitate later model validation on the larger population of MOFEP plots, 2) to strengthen the assumption of plot-level homogeneity in establishment conditions, and 3) to allow the pre-disturbance inventory of stems on the 0.004-ha understory plot in the MOFEP dataset to serve as a substitute for the pre-disturbance data in the 0.02-ha mapped subplot dataset for the 18 clearcut plots that were not inventoried prior to disturbance. On these 18 plots, the pre-disturbance counts of large advance reproduction were subtracted from the post-disturbance abundance of reproduction that was not from obvious sprout origin.

For each species, all previously untagged reproduction 100cm and taller were tagged and measured three and eight years post-disturbance on the 0.02-ha

mapped subplots. It was assumed that all reproduction that could establish was present three years post-disturbance and that any new reproduction tagged eight years post-disturbance was present but shorter than the 100cm inventory threshold three years post-disturbance. It is possible that additional reproduction were present post-disturbance but died without reaching the 100cm height threshold or before the first post-disturbance inventory. This ephemeral population is ignored.

After the fate of residual stems and large advance reproduction are determined and new reproduction has been estimated, each new or sprouted stem must be assigned various attributes, including total height, crown dimensions, diameter at breast height (137.5cm), and spatial coordinates. Species-specific parameters are used to stochastically assign each tree a value for these attributes. Because all measurements must be assigned artificially to new stems, it is important to follow a biologically plausible process. The underlying hypothesis of tree development used to determine the order in which tree attributes are assigned via allometric relationships follows. Primary growth (extension) is a function of individual traits and environment. In most cases, primary growth serves to increase (or maintain) resource acquisition. Increases in resource acquisition beyond that required for basic functions can be allocated to secondary growth and/or storage (thickening). Therefore, height development impacts crown development which, in turn, impacts stem development. Similar approaches to modeling tree development have been used with success in the TASS model (Mitchell 1975) and the SYLVAN model (Larsen 1991, 1994).

Because the data used to develop allometric relationships were structured as repeated measurements (trees) in space (subplot), it was likely that trees on the same subplot had correlated errors. Subplot-specific random effects on the attributes of an individual stem were not of interest. Rather, the average effect of proposed covariates on stem attributes was desired. Thus, the possible correlation among trees on an individual subplot was considered a nuisance rather than a research interest and generalized estimating equations were used to obtain estimates of the effect of proposed covariates on stem attributes.

Generalized estimating equations fit a marginal (population averaged) distribution to provide estimates in the presence of possible error correlation as opposed to the conditional (subject-specific) distribution provided by generalized mixed effects models (Liang and Zeger 1986, Zeger and Liang 1986, Hardin and Hilbe 2012). Generalized estimating equations are often more robust to misspecification of the within-subject covariance structure than generalized mixed effects models (Liang and Zeger 1986, Zeger and Liang 1986). An exchangeable (compound symmetric) covariance structure was incorporated in all allometric models to account for within-subplot error correlation (Zuur *et al.* 2009).

Because generalized estimating equations utilize *quasi*-likelihood estimators, likelihood based methods of model comparison and fit testing are not available. Model comparison for candidate models parameterized via generalized estimating equations was accomplished using Pan's Quasi-likelihood under the Independence model Criterion (QICc) corrected for small sample sizes (Pan

2001, Ekstrom 2014). For a species group, the most parsimonious model within 2 units of the model with the lowest QICc value was selected as the “best” among those considered provided that it produced estimates within the range of the data for all covariate scenarios. If a candidate model met the QICc criteria to be selected as “best” but produced estimates outside the range of the data, the candidate model with the next lowest QICc that also produced reasonable estimates was selected as “best”. Scattergraphs with fitted model curves for all species groups are provided in the Appendix.

Counts were available for reproduction of all sizes, but heights were only measured on reproduction $\geq 100\text{cm}$. In order to assign heights to all new stems, a multi-step approach was required to accommodate this shortcoming of the dataset. First, probabilistic models were developed to estimate the proportion of new stems on a plot that would attain an initial height $\geq 100\text{cm}$ three years post-disturbance. The stems that will not attain an initial height $\geq 100\text{cm}$ are assigned a height in the range of 1-99.9cm using a random uniform distribution. Stems that do attain an initial height $\geq 100\text{cm}$ three years after harvest are assigned a height ($\geq 100\text{cm}$) based on draws from an empirically parameterized distribution.

It was hypothesized that the proportion of stems that would attain an initial height $\geq 100\text{cm}$ three years post-disturbance was a function of residual overstory density (basal area per hectare $\geq 11.43\text{cm dbh}$), stem origin (obvious sprout or not), and site class (exposed or protected backslopes). Preliminary analyses revealed that stem origin was highly deterministic. Within the dataset analyzed, all stems of obvious sprout origin were $\geq 100\text{cm}$ three years post-disturbance, regardless of

species, residual overstory density, or site class. Thus, all new sprouts in the simulator should be assigned an initial height $\geq 100\text{cm}$. In order to assign initial heights to the remaining stems (not obvious sprouts or advance reproduction), probabilistic models of having an initial height $\geq 100\text{cm}$ were developed for each species group using residual overstory density and site class as covariates.

Four candidate models for the probability that a seedling (non-sprout origin) would have an initial height $\geq 100\text{cm}$ three years post-disturbance were compared for each species group (Table 2.2). It was hypothesized that residual overstory density was the primary influence on regeneration outcomes, including reproduction height. Therefore, except for a null model (intercept-only), all candidate models for the probability of initial height $\geq 100\text{cm}$ included residual overstory density as an effect (Table 2.2). Because the response variable was binary (1 if initial height $\geq 100\text{cm}$, 0 otherwise), logistic regression was appropriate (Hosmer *et al.* 2013). Logistic regression within the generalized estimating equations framework was accomplished using the generalized estimating equations function (GEEGLM) within the GEEPACK package (Højsgaard *et al.* 2006, Yan and Fine 2004, Yan 2002), using a binomial error distribution with a logit link (Faraway 2005, Zuur *et al.* 2009).

It was hypothesized that the assigned height of a stem (stump-sprout, top-killed large advance reproduction, new reproduction) with an initial height $\geq 100\text{cm}$ three years post-disturbance was a function of residual overstory density (basal area per hectare $\geq 11.43\text{cm dbh}$), stem origin (obvious sprout or not) and site class (exposed or protected backslopes). Thus, several candidate models that

included combinations of these factors and their interactions were compared for each species group (Table 2.3). It was hypothesized that residual overstory density was the primary influence on regeneration outcomes, including reproduction height. Therefore, all possible models that could be developed from combinations of these three factors and their interactions were not considered candidate models. Except for a null model (intercept-only), all candidate models for initial height assignment included residual overstory density as an effect.

Because there was a sampling threshold of 100cm in the dataset, 100cm was subtracted from the height of each stem to ensure that estimates were bounded by a more convenient lower limit for regression analyses. Consequently, 100cm must be added to estimates of mean height from models fitted in this manner.

Because tree heights cannot be negative, a fitted model used to assign heights must also be constrained so that negative values are not possible. A generalized linear model with errors modeled as a Gamma distribution accomplishes this (Faraway 2005) without requiring transformations of the original data. Parameter estimates for initial (3rd year) height were obtained via the generalized estimating equations function (GEEGLM) within the GEEPACK package (Højsgaard *et al.* 2006, Yan and Fine 2004, Yan 2002), using a Gamma error distribution with an inverse link.

The Gamma distribution is a continuous distribution, and variance is a proportion of the expected value (constant coefficient of variation). Within R, a Gamma distribution can be defined by shape and scale parameters or shape and rate parameters (R Development Core Team 2014). A generalized linear model with a

Gamma error distribution and the canonical (reciprocal) link yields estimates for the expected value (μ^{-1}) and dispersion (ϕ) within R statistical software (R Development Core Team 2014) which can be converted to shape, scale, and rate parameters as follows: Shape = ϕ^{-1} , Rate = Shape $\cdot \mu^{-1}$, and Scale = ϕ/μ^{-1} .

For reproduction taller than 100cm, crown length was assigned via models of live crown ratio (total height/live crown height). It was hypothesized that live crown ratio was a function of stem height and residual overstory density. Three candidate models were compared for each species group (Table 2.4). Because values of live crown ratio lie exclusively within the standard interval (0,1) beta regression has been suggested as an appropriate method of analysis (Ferrari and Cribari-Neto 2004). Previous applications of beta regression in forestry include percent canopy cover (Korhonen *et al.* 2007) and percent shrub cover (Ekleston *et al.* 2011). Unfortunately, the current beta regression package (BETAREG, Cribari-Neto and Zeileis 2010) for R does not yet accommodate correlated errors. Generalized mixed models or generalized estimating equations that accommodate correlated errors can be used as alternatives to beta regression if the expected values are unlikely to fall outside the standard interval (P. Speckman Ph.D. [statistics], personal communication, March 13, 2015). Therefore, parameter estimates were obtained via the generalized estimating equations function (GEEGLM) within the GEEPACK package (Højsgaard *et al.* 2006, Yan and Fine 2004, Yan 2002), using a Gaussian error distribution with an identity link. Caution was exercised during stochastic assignment of live crown ratio to ensure values were within the standard interval.

The ability to predict crown radius via crown length or other covariates is essential. Shape ratios are convenient representations of these relationships. In this case, a shape ratio defined as crown radius/crown length was used to determine crown radius from crown length and tree height. In this context, a shape ratio of 1 would indicate that crown radius is the same as crown length. A shape ratio >1 would indicate that the radius of the crown exceeds the length of the crown; whereas, a shape ratio <1 would indicate the radius is less than the length of the crown. It was also hypothesized that live crown ratio and residual overstory density could impact crown shape ratio. For each species group the candidate models in Table 2.5 were compared. There are several examples of existing models of crown allometry using dbh as a covariate (Weiskittel *et al.* 2011, Burkhart and Tomé 2012). However, covariate selection is constrained in a reproduction establishment scenario, and modeling crown dimensions as a function of dbh would be inconsistent with the allometric strategy previously outlined.

Because the shape ratio cannot be negative in this context, a fitted model used to assign heights must also be constrained so that negative values are not possible. Parameter estimates for shape ratios were obtained via the generalized estimating equations function (GEEGLM) within the GEEPACK package (Højsgaard *et al.* 2006, Yan and Fine 2004, Yan 2002), using a Gamma error distribution with a log link. Preliminary data analysis suggested that the relationship between shape ratio and live crown ratio was consistent across all tree sizes (reproduction and mature trees). Therefore, this relationship was

modeled for trees of all sizes (height $\geq 100\text{cm}$) within each species group.

Therefore, the relationship was across for all trees $\geq 100\text{cm}$ in total height that were present 3 years after harvesting.

For each species group, diameter at breast height was modeled as a function of crown surface area (m^2) and site class. Crown surface area was calculated as the lateral surface area of a paraboloid (excluding its base) as follows:

$$\bullet \text{ CSA} = \frac{\pi}{6} \cdot \frac{R}{L^2} \cdot [(R^2 + 4 \cdot L^2)^{3/2} - R^3]$$

where: CSA = lateral crown surface area (m^2), R = crown radius (m) and L = crown length (m). Crown radius was obtained by halving mean crown width measurements for each tree.

Candidate models for each species groups included either crown surface area alone, crown surface area together with site class, or crown surface area and site class together with their interaction (Table 2.6). Because dbh cannot be negative, generalized linear model with errors modeled as a Gamma distribution avoids the need to transform the original data (Faraway 2005). Parameter estimates for dbh were obtained via the generalized estimating equations function (GEEGLM) within the GEEPACK package (Højsgaard *et al.* 2006, Yan and Fine 2004, Yan 2002), using a Gamma error distribution with a log link. Preliminary data analysis suggested that the relationship between dbh and crown surface area was consistent across all tree sizes (reproduction and mature trees). Therefore, this relationship was modeled for trees of all sizes (height $\geq 137.5\text{cm}$) within each species group.

Spatial pattern can have important impacts on regeneration and early stand dynamics. However, inventory plots are seldom mapped. Thus, a routine to assign spatial coordinates from a random uniform distribution to unmapped inventories was established. Because Cartesian coordinates are desired, center clustering in circular plots is avoided by converting random polar coordinates (distance and azimuth) as follows:

- $X = \sqrt{D} \cdot \cos(A) \cdot (R)$; $Y = \sqrt{D} \cdot \sin(A) \cdot (R)$

where: X and Y are cartesian coordinates, D is polar distance, A is polar angle, and R is plot radius.

Empirical investigation of species-specific spatial patterns (clumping, avoidance, *etc.*) and the influence of interspecific interactions may produce more realistic simulations than the current null hypothesis of random uniform spatial distribution will allow. Moreover, spatial heterogeneity at a scale finer than the plot may influence reproduction establishment. Although such work is warranted, it was beyond the scope of the current effort. Therefore, the assumption of a uniform establishment plot is made, suggesting that regardless of the arrangement of the residual trees on a plot, the probability of a seedling becoming established is uniform across the entire plot; with the exception of the portions physically occupied by the stems or stumps of inventoried trees. A minimum distance of 1cm (outside bark) is required between all trees. It is assumed that each stem is a circle that is centered on the assigned spatial coordinate.

Regenerated stems that establish from stump sprouting retain a spatial coordinate near that of the parent stem. Stump sprouts are assigned random coordinates within an arbitrary “sprouting zone” that is established along the circumference of the stump of the parent stem. The “sprouting zone” has an arbitrary width of 4cm, and is centered on the perimeter of the stump, *i.e.*, 2cm inside bark and 2cm outside bark. Note that for tree with a stump diameter $\leq 4\text{cm}$ the “sprouting zone” is effectively stump diameter + 2cm. To create this “sprouting zone” for all species groups, the dbh of the parent stem is converted to stump diameter using the following allometric equation developed by Dey (1991) for oaks in the Missouri Ozarks:

- $$\text{DSH} = 2.54 \cdot \{1.3322 \cdot (0.3937 \cdot \text{DBH})^{0.9955}\}$$

where: DSH = stump diameter (cm), DBH = diameter at breast height (cm).

A minimum distance of 1cm (between sprout centers) is required between all sprouts arising from a single stump. In cases where there is more than one sprout to be established per stump, the routine for randomly assigning spatial coordinates within the “sprouting zone” is repeated until this condition is met or 1000 failed attempts have passed. If this attempt limit is reached, fewer sprouts than estimated by the clumping parameter will be established on the stump.

Newly established reproduction are required to have a minimum distance of 1cm (center to center) between one another and at least 1cm (outside bark) away from inventoried trees. The 1000 attempt limit described for stump clumps is also employed here.

Vegetative reproduction via stump sprouting is an important component of regeneration establishment for several species in the Missouri Ozarks (Johnson *et al.* 2009). However, sprouting species do not always produce sprouts. Thus, probabilistic models of stump sprouting have been developed and the details of their use in the establishment module are described below. However, in order for these equations to be utilized, individual stems with the *potential* to sprout must first be identified from a provided inventory. For the purposes of the establishment module, the parent stem (all stems for multi-stemmed parents) must be identified as a tree to be removed in the pre-disturbance inventory. For multi-stemmed parents, attributes (dbh, spatial coordinates, *etc.*) of the largest stem are used for sprouting probabilities and spatial assignment.

Although some species can produce basal sprouts under an intact parent stem, this regeneration source was not included. Root sprouts (suckers) are not directly accounted. Rather, it is assumed that root sprouts are indirectly accounted for in the establishment estimates for reproduction not from obvious sprout origin.

Existing models for estimating the probability of establishment via stump sprouting were utilized for the species groups included in the establishment module. The models used for estimating stump-sprouting, along with their origin, are provided in Table 2.7. The parameters designated for the other species group were used for any sprouting species not included in the remaining groups. These probabilities are used in a binomial random number generator to stochastically determine the sprouting outcome (success or failure) of each inventoried stem that is a potential stump sprout. Accommodations will be

necessary to distinguish stem death from total tree death in the mortality module so that the stump sprouting models can be applied in cases of competition induced dieback. The sprouting equations developed by Dey (1991) were originally fit using stump diameter (dsh) rather than dbh (X_1). dsh is not commonly inventoried, thus, these equations were modified to include the dbh to dsh conversions also developed by Dey (1991) into a single equation.

Because an ecological classification system was used to delineate site differences in the simulation model, it was assumed that site index (X_2) will usually be unknown. For sprouting equations that require site index (black oak, northern red oak, white oak), empirically derived mean and standard deviation site index values for each site class (exposed backslopes: $21.0 \pm 1.3\text{m}$, protected backslopes: $22.0 \pm 1.1\text{m}$; black oak, base age 50) are used in to stochastically assign a site index value for a plot.

Some sprouting equations require tree age, but tree age is not included in forest inventories. Thus, it was assumed that tree age (X_3) will be unknown and published equations for converting diameter at breast height to tree age (Lowenstein *et al.* 2000) were used when required (northern red oak, white oak). Due to a positive interaction between tree age and diameter in the sprouting equation used for white oak, increasing tree age substantially improved sprouting probability with increasing diameter. However this interaction produced biologically spurious estimates when age exceeded 165, e.g., a 300 year old tree with a 75cm diameter has a sprouting probability of 0.9994. In contrast, Johnson and others (2009) suggest that it is unlikely that large diameter oaks will sprout if

harvested. Thus, the age estimates for white oak were not allowed to exceed 165 yrs.

Because a stump that successfully sprouts often produces more than one stem, existing models of stems per sprouted stump were used to account for multi-stemmed stump-clumps. The models used for estimating the number of stems per sprouted stump, along with their origin, are provided in Table 2.8.

Results and Application

Parameter estimates for the models of regeneration establishment are provided in Table 2.9. All models were statistically significant per the X^2 goodness of fit test ($\alpha = 0.05$). Parameters for the shortleaf pine and sugar maple species groups were obtained using only an intercept due to sparse data for those groups. For all remaining species groups, residual overstory density was a statistically significant ($\alpha = 0.05$) covariate (except ash, *p-value*: 0.0859) and included in the “best” models of reproduction establishment. Modeled reproduction establishment declined precipitously with increasing residual overstory density for all species that included it as a covariate regardless of other covariates (Figure 2.3).

The “best” model for blackgum and red maple reproduction establishment was model 5 (Table 2.9), which, for both species groups, was not the most parsimonious model within 2 AICc units of the lowest AICc. For both of these species groups, there were candidate models with lower AICc than model 5 that produced estimates outside the range of observed data and thus were

eliminated. For all species groups except shortleaf pine, sugar maple, and dogwood, the presence of advance reproduction was included in the “best” models of post-disturbance reproduction establishment and was a statistically significant predictor (except for hickories, which included a statistically significant interaction between residual overstory density and presence of advance reproduction). The modeled effect of advance reproduction presence on reproduction establishment was positive for all species groups that included it as a covariate except for hickories which was negative below $3 \text{ m}^2\text{ha}^{-1}$ due to the interaction with residual overstory density.

Only blackgum, red maple, and the other species groups included presence of a residual seed source in their “best” model of reproduction establishment. The effect of residual seed source presence on the other species group was statistically significant and positive. Due to interactions between advance reproduction presence and presence of a residual seed source, as well as interactions between residual seed source presence and residual overstory density for blackgum and red maple, the effects of advance reproduction presence and residual seed source presence were too complex for simple interpretation. The presence of a residual seed source and its interactions with covariates were statistically significant for red maple, but not for blackgum.

Without advance reproduction or a residual seed source total reproduction establishment across all species groups tended to be lower than with either alone or both together (Fig. 2.3). At low residual overstory densities, dogwood, sassafras, hickories, and the other species groups tended to have greater

reproduction establishment in the absence of both advance reproduction and residual seed sources. In this case, differences in reproduction establishment were minimal between species groups once residual overstory density exceeded $\approx 15 \text{ m}^2\text{ha}^{-1}$. For all species groups, average reproduction establishment beyond $\approx 20\text{m}^2\text{ha}^{-1}$ was limited. The presence of a residual seed source alone increased the reproduction establishment for the other species group and red maple across the entire gradient of residual overstory density.

Elms, red maple, and sassafras tended to have much higher reproduction establishment, on average, than all other species groups when residual overstory density $\leq 10 \text{ m}^2\text{ha}^{-1}$ (elms) - $15 \text{ m}^2\text{ha}^{-1}$ (red maple and sassafras) in the presence of advance reproduction alone. Once residual overstory density exceeded $\approx 15 \text{ m}^2\text{ha}^{-1}$, differences in reproduction establishment were minimal between species groups. For all species groups, average reproduction establishment beyond $\approx 20\text{m}^2\text{ha}^{-1}$ was limited.

With both advance reproduction and a residual seed source elms tended to have greater reproduction establishment at low residual overstory densities ($\leq 5 \text{ m}^2\text{ha}^{-1}$) than all species groups. Apart from elms, sassafras established more reproduction, on average, when residual overstory density was less than $\approx 15 \text{ m}^2\text{ha}^{-1}$ and was greater than elms beyond $\approx 5 \text{ m}^2\text{ha}^{-1}$. The other species group also established considerably more reproduction than the remaining species groups at residual overstory densities \leq about $10 \text{ m}^2\text{ha}^{-1}$. With both advance reproduction and a residual seed source, differences in reproduction establishment were minimal between species groups when residual overstory

density exceeded $\approx 15 \text{ m}^2\text{ha}^{-1}$, and reproduction establishment beyond $\approx 20\text{m}^2\text{ha}^{-1}$ was limited.

The parameterized models of reproduction establishment (Table 2.9) were used to add new seedling records in the establishment simulator. Rather than adding new seedlings deterministically using the expected value (μ) from the parameterized models, stochastic establishment of new seedlings was preferred. This was accomplished by entering the expected value (μ) for a given covariate scenario and dispersion parameter (k) provided in Table 2.9 into the RNBINOM function as the “mu” and “size” arguments respectively to produce negative binomial distributed random deviates. An example of the stochastic establishment procedure is provided in Figure 2.4. In this example, red oaks were established in a simulation plot with a residual overstory density of $5\text{m}^2\text{ha}^{-1}$. Red oak advance reproduction was present, but a residual seed source was not. Using the fitted parameters for red oak (Table 2.9) in this scenario, the expected value (μ) was $2.2 \text{ stems} \cdot 0.004\text{ha}^{-1}$ and the dispersion parameter was 0.5835. Those values were entered as the “mu” and “size” arguments respectively of the RNBINOM function and 1000 random deviates were produced. The 1000 random deviates were multiplied by 250 to obtain a sample distribution of reproduction establishment per hectare in that scenario (Figure 2.4). Although mean reproduction establishment in this scenario was $550 \text{ stems} \cdot \text{ha}^{-1}$ ($2.2 \cdot 250$), 84% of the 1000 random deviates were 0 suggesting that red oak reproduction was rarely established in this scenario. Approximately 10% of the 1000 random deviates were less than $1000 \text{ stems} \cdot \text{ha}^{-1}$, suggesting that when red oak

reproduction was successfully established in this scenario, few seedlings were added to the simulation plot. This procedure can be repeated for each species group to stochastically establish reproduction originating from small advance reproduction or post-disturbance germination.

Reproduction establishment estimation models were developed for species groups, which may contain several species. It is assumed that the within group composition of the new cohort will reflect the inventoried predisturbance within group composition. Accordingly, during the stochastic reproduction establishment routine each new stem within a species group is assigned a species code with a probability proportional to the predisturbance within group composition.

The parameter estimates for the “best” models of the probability that reproduction originating from small advance reproduction or post-disturbance germination would have a height $\geq 100\text{cm}$ three years post-disturbance are provided in Table 2.10. Due to rarity, shortleaf pine was modeled using an intercept only. In addition to shortleaf pine, the “best” models for ashes, hickories, and sugar maple included only an intercept. Although an intercept only model produced the lowest QICc for white oak, the model produced estimates that appeared too low at low residual overstory densities and too high at high residual overstory densities. A Wald test confirmed that including residual overstory density for white oaks was significantly different than an intercept only model. Therefore, model 3, which included residual overstory density as a covariate was selected as the “best” model for white oaks.

Residual overstory density was included in the “best” models for all remaining species groups. The effect of residual overstory density on the probability of a stem attaining a height $\geq 100\text{cm}$ by three years post-disturbance was negative when included indicating that the probability declined with increasing residual overstory density (Figure 2.5). Site class was included in “best” models for blackgum, dogwood, elms, other species, and sassafras species groups. The effect of protected vs exposed backslopes on the probability of a stem attaining a height $\geq 100\text{cm}$ by three years post-disturbance was positive for blackgum. An interaction between residual overstory density and site class was included in “best” models for dogwood, elms, and sassafras species groups, which made interpretation more complex. The effect of protected vs exposed backslopes on dogwood tended to be positive, particularly when residual basal area was $<$ about $20\text{m}^2\text{ha}^{-1}$ (Fig. 2.5). For elms, attaining a height $\geq 100\text{cm}$ by three years post-disturbance declined much more rapidly with increasing residual overstory density on protected backslopes compared to exposed backslopes. Sassafras also exhibited a steeper decline in probability of attaining a height $\geq 100\text{cm}$ by three years post-disturbance with increasing residual overstory density on protected backslopes compared to exposed backslopes, but probabilities for sassafras were considerably greater on protected backslopes than exposed backslopes when residual basal area was $<$ about $10\text{m}^2\text{ha}^{-1}$.

The parameter estimates for the “best” models of three years post-disturbance height for stems $\geq 100\text{cm}$ in height are provided in Table 2.11. For all species groups except shortleaf pine, which was modeled with an intercept only due to

rarity, residual overstory density was included as a covariate in the “best” models of height three years post-disturbance. Increasing residual overstory density decreased the mean height of stems with a height $\geq 100\text{cm}$ three years post-disturbance when included as a covariate for all species groups (Fig. 2.6).

Stem origin was included in “best” models of height for stems with a height $\geq 100\text{cm}$ three years post-disturbance for black cherry, red maple, red oaks, and white oaks. The effect sprout origin on height was positive for red maple, red oaks, and white oaks (Table 2.11), though interactions between stem origin and site class for black cherry made interpretation of the effect more complex. The effect of sprout origin tended to reduce the mean height of black cherry across both site classes, with the effect more pronounced on protected backslopes than on exposed backslopes (Fig. 2.6). In addition to black cherry, site class was also included in “best” models for blackgum, dogwood, and red oaks. The effect of protected vs exposed backslopes on height was positive for blackgum and dogwood (Table 2.11), but an interaction between site class and residual overstory density made interpretation of the effect more complex for red oaks (Figure 2.6). On exposed backslopes, red oaks tended to be somewhat taller than on protected backslopes when residual overstory density was low ($< 5\text{m}^2\text{ha}^{-1}$), but at higher residual overstory densities red oaks tended to be shorter on exposed backslopes than on protected backslopes.

The parameterized models of the probability of a stem being $\geq 100\text{cm}$ three years post-harvest (Table 2.10) and the mean height of stems $\geq 100\text{cm}$ three years post-harvest (Table 2.11) were combined to assign each new seedling,

top-damaged advanced reproduction, or stump sprout a height in the establishment simulator. In order to assign a height to an individual stem, the probability estimate for a given covariate scenario from Table 2.10 was entered as the “prob” argument in the RBINOM function. An outcome of 0 indicated the individual has a height < 100cm, whereas an outcome of 1 indicated the individual has a height ≥ 100cm. Because empirical data on the height distribution below 100cm was not available, individuals that were probabilistically determined to have a height < 100cm were assigned a height from 1-99.9cm using the random uniform distribution function (RUNIF). For individuals that were probabilistically determined to have a height ≥ 100cm, the assigned height was obtained from a gamma distribution with parameter estimates obtained from the fitted models in Table 2.11. This was accomplished by converting the expected value (μ) for a given covariate scenario and dispersion parameter (ϕ) into the shape and scale arguments as follows: Shape = ϕ^{-1} , Scale = ϕ/μ^{-1} for the RGAMMA function to produce gamma distributed random deviates.

An example of the stochastic height assignment procedure is provided in Figure 2.7. In this example, height distributions were developed for 1250 sprout origin and 1250 non-sprout origin red oaks on exposed backslopes with a residual overstory density of $5\text{m}^2\text{ha}^{-1}$. The expected values (μ) for red oaks in this scenario was 42.02cm for non-sprouts and 56.5cm for sprouts (Table 2.11), which produced a Scale parameter of 24.5 for non-sprouts ($0.583/42.02^{-1}$) and 32.94 for sprouts ($0.583/42.02^{-1}$). The Shape parameter for both sprouts and non-sprouts was 1.71 (0.583^{-1}). Because 100cm was subtracted during the

model fitting process to obtain the expected values (μ) in Table 2.11, 100cm was added to each random deviate produced by the Gamma distribution. This procedure can be repeated for each species group to stochastically assign third years post-disturbance heights to new seedlings, top-damaged advance reproduction, and stump sprouts on each simulation plot.

The parameter estimates for the “best” models of live crown ratio three years post-disturbance are provided in Table 2.12. Although distance to nearest neighbor was suspected to impact live crown ratio, preliminary analysis suggested that there was no meaningful relationship at three years post-disturbance. The natural log of total height was included in the “best” models for all species groups except shortleaf pine and sugar maple which were modeled using only an intercept due to rarity. When included, the effect of increasing tree height was slightly positive on live crown ratio (Fig. 2.8). Residual overstory density was included in the “best” model for dogwood and the effect of increasing residual overstory density was to decrease live crown ratio.

Stochastic assignment of live crown ratio to individual stems with an initial height $\geq 100\text{cm}$ was accomplished in a similar manner to that described for height.

However for live crown ratio, gaussian random deviates were obtained using the RNORM function. The estimates of expected values (μ) and square root of the variance (s^2) from the models in Table 2.12 were entered into the RNORM function as the “mean” and “sd” arguments, respectively. Caution was exercised during stochastic assignment to ensure that deviates were within the standard interval (0,1). In cases where an invalid value was produced, an additional

deviate was produced until a valid value was obtained. For stems with a height < 100cm, a live crown ratio between 0.01 and 1 was assigned using the random uniform distribution function, RUNIF, in R statistical software (R Development Core Team 2014).

Crown radius was obtained via crown shape ratios (crown radius/crown length). The parameter estimates for the “best” models of crown shape ratio are provided in Table 2.13. Except for shortleaf pine and sugar maple, live crown ratio was included in the “best” models of crown shape ratio. The effect of increasing live crown ratio was negative on crown shape ratio, with crown shape ratio decreasing with increasing live crown ratio (Fig. 2.9).

Residual overstory density was included in the “best” models of crown shape ratio for all species groups except ashes, elms, shortleaf pine, and sugar maple. The effect of residual overstory density on crown shape ratio tended to be positive when included (Table 2.13), resulting in an increase in crown shape ratio with increasing residual overstory density (Fig. 2.9). Although the coefficient for residual overstory density in the “best” model for white oaks was negative, an interaction between live crown ratio and residual overstory density complicated interpretation of the effect of residual overstory density alone on crown shape ratio (Table 2.13). The “best” models for blackgum, dogwood, red maple, and the other species group also included an interaction term between live crown ratio and residual overstory density. Though increasing residual overstory density tended to increase crown shape ratio for these species, the interaction between residual overstory density and live crown ratio indicated that the magnitude of the

effect of residual overstory density was not constant across all values of live crown ratio (Fig. 2.9). Crown shape ratio, and thus, crown radius was stochastically assigned using a similar protocol to that described for heights.

The parameter estimates for the “best” models of diameter at breast height are provided in Table 2.14. Crown surface area was included in the “best” models for all species groups. The effect of crown surface area on diameter at breast height was positive for all species groups. Site class was included in the “best” models for dogwood, elms, red maple, other species, and sassafras. The effect of protected vs exposed backslopes on diameter at breast height was positive for red maple and sassafras (Table 2.14). However an interaction between crown surface area and site class was included in the “best” models for dogwood, elms, and other species, indicating that interpretation of the effect of crown surface area and site class on diameter at breast height was more complex for those species groups (Fig. 2.10). For dogwood, elms, and the other species groups, the net effect of protected vs exposed backslopes tended to be increasingly negative with increasing crown surface area. Diameter at breast height was stochastically assigned using a similar protocol to that described for heights and crown radius.

Discussion

Ecological classification systems have been suggested for regeneration research (Dey *et al.* 2009, Kabrick *et al.* 2008). Accordingly, an ecological classification system was used to delineate site differences in establishment simulation. It has

been well documented that site conditions exhibit a strong influence on regeneration dynamics, particularly in oak dominated forests (Johnson *et al.* 2009). It has been shown that variables such as soil acidity, available water capacity, slope-aspect, and others can impact the density of advance reproduction (Bigelow and Canham, 2002, Fei and Steiner 2008, Kabrick *et al.* 2014). The regeneration simulator described herein has been designed to utilize an inventory of pre-harvest conditions, thus, it is hypothesized that the net impact of site differences in the Missouri Ozarks on regeneration establishment has been manifested primarily as the presence and density of a species group. This, in turn, influences regeneration dynamics through the composition and abundance of advance reproduction, sprout sources, and residual seed sources. Though micro-site variables can impact establishment via other mechanisms (seed production rates, germination rates, safe site availability, *etc.*), a more macro approach with a hypothesis that the impact of site on regeneration dynamics is primarily manifested during the recruitment process in the Missouri Ozarks was taken in the development of the reproduction establishment models. Forest regeneration is a defining example of secondary succession (Horn 1974). A fundamental concept of secondary succession is the development of and reliance upon regeneration sources disseminated prior to or immediately following disturbance. Therefore, the composition of future forests is largely a function of the composition of previous forests (Egler 1954), but the ultimate identity of the regenerating stand will likely be more reflective of the magnitude

and timing of disturbances and their biological impacts on stand development along with other stochastic influences (Gleason 1917).

A common feature of most regeneration models is the requirement of some metric of advance reproduction as input data. The models of reproduction establishment presented herein were developed as a complement to an inventory rather than as a substitute. The occurrence of advance reproduction has been modeled (e.g., Larsen *et al.* 1997) and mapped (e.g., Kabrick *et al.* 2014) as a function of biotic and abiotic factors, but the data are often highly variable. The abundance and composition of advance reproduction, particularly large advance reproduction, is often the product of a complex series of disturbances and stochastic events over the course of several years to decades that are often unknown and/or not readily captured in the limited number of covariates used in regression models. For example, oak silviculturists have empirically shown that *intentional* development of large advance reproduction often requires a series of disturbances over the course of years to decades in some scenarios (Loftis and McGee 1993). It was in recognition of the complexity of this dynamic process and inability to readily capture disturbance history that an inventory of advance reproduction and potential stump sprout contributors was required as a starting point for the regeneration establishment simulator. While models of advance reproduction occurrence without an inventory could certainly be useful tools in developing a more autonomous regeneration simulator, their development will likely be challenging.

Most existing regeneration models only provide regeneration estimates for complete overstory removal. In contrast, the models presented herein provide estimates of reproduction establishment across a gradient of residual overstory density. The increased generalization offered by these models greatly increases the breadth of harvest and natural gap-based disturbance scenarios that can be examined for their impact on regeneration. However, the of reproduction establishment models (Table 2.9) are currently “cohort based”, *i.e.*, establishment of new seedlings was largely modeled as an addition of propagules triggered by a single, known disturbance event. The strong reliance on disturbance to initiate the regeneration process is consistent with leading hypotheses of forest stand development (Oliver and Larson 1996). “Ambient” establishment (*i.e.*, establishment without discernable disturbance), though rare and not a reliable source of canopy recruitment, may nonetheless influence regeneration by altering the abundance and composition of advance reproduction prior to a recruitment triggering disturbance. At the highest levels of residual overstory densities included in our models, the estimates of establishment provided were universally low and essentially were three-year “ambient” establishment rates because those plots were not harvested and had not experienced major disturbance in the recent past.

Compositional outcomes of regeneration events are affected at both the establishment and the recruitment stages. Our results are consistent with the report of Larsen and others (1997) that reproduction occurrence decreases with increasing residual overstory density. There was evidence of interspecific

differentiation in reproduction establishment, particularly at low residual overstory densities (Fig. 2.3). In most scenarios, interspecific differentiation in reproduction establishment was progressively muted with increasing residual overstory density. Vickers and others (2014) found a similar trend of reduced interspecific differentiation in growth rates of saplings with increasing residual overstory on the same plots. Species groups such as elms, dogwood, and red maple that tended to be ranked relatively high in reproduction establishment rates tended to be relatively low or intermediate in reported rates of sapling growth across a gradient of overstory density (Vickers *et al.* 2014). Oaks and hickories tended to have relatively low rates of establishment, but relatively high reported rates of sapling growth. Establishment rates of sassafras reproduction tended to be relatively high in all scenarios. Vickers and others (2014) reported that the effect of increased residual overstory density impacted the growth of sassafras the least. In addition the growth rates of sassafras were highly dependent on site class, with sassafras exhibiting relatively intermediate growth rates on exposed backslopes but relatively high on protected backslopes. Although site was not a covariate included in models of reproduction establishment, the establishment rates of sassafras tended to be considerably higher when present as advance reproduction. The reproduction establishment rates of sassafras also tended to be high, relative to the remaining species groups across the entire gradient of residual overstory density.

Another scenario that requires additional research is the role of repeated disturbance, particularly the interaction of disturbance scale and disturbance

frequency, on reproduction establishment. It is unlikely that the models of reproduction establishment presented herein will provide reasonable estimates in a frequent disturbance scenario, especially for intermediate to large scale disturbances, because a controlling mechanism for seedling accumulation was not incorporated. In this scenario, application of the establishment models are likely to provide overestimates of establishment arising from subsequent disturbances due to a failure to account for existing reproduction that established as a result of recent disturbance.

The solution to this problem is not straightforward. Most metrics of stand density and/or occupancy are not applied at the seedling level (Gingrich 1967, Reineke 1933), and adaptations to these metrics for multi-cohort stands with complex structure (e.g., Ducey and Knapp 2010) are not widespread. While the laws of site occupancy and self-thinning (e.g., Yoda *et al.* 1963) theoretically apply at the seedling level, occupancy measures at this scale are rare. Fei and others (2006) described a measure of occupancy (aggregate height) for seedling populations that combined size (height) and abundance into a species-specific metric of site occupancy for even-aged stands similar to basal area for larger trees. Describing a previously established seedling cohort with an aggregate height metric may provide a useful covariate in the development of reproduction establishment models for multiple disturbances. However, it is not yet clear how this methodology applies to multi-cohort stands or how various size and abundance attributes of a previous cohort impact reproduction establishment (*i.e.*, abundance) of a new cohort following a subsequent disturbance.

An alternative way to account for the existence of previously established seedlings in estimates of reproduction establishment following a subsequent disturbance may be through spatial partitioning, or “digital” density controlling metrics. A rudimentary application of this approach is currently implemented during the stochastic spatial coordinate assignment procedure in the establishment module to adjust overestimates of reproduction establishment. In its current state, new stems are not allowed to establish within an arbitrary, predetermined distance (1cm) of one another or inventoried trees/stumps. When each additional stem is added to the treelist, up to 1000 random spatial coordinates are generated. If all of the generated coordinates fail to satisfy the minimum distance requirement, the stem is not added to the plot. A more sophisticated version of this “digital” density approach that is empirically informed and more theoretically robust may be a pragmatic approach to determining probabilities of reproduction establishment while accounting for a previous cohort.

For example, given an existing cohort abundance, size distribution, spatial clustering coefficient, and a predefined distance criteria, the probability of drawing random coordinates from a sufficiently large number of attempts would effectively describe the probability of a new propagule finding a suitable site to establish. This probability could then be combined with a dispersal parameter (likely from a Poisson or negative binomial distribution) to derive a joint probability of reproduction establishment. Additional covariates such as species, competition indices, etc. may prove important. This approach has appeal for the

most complex scenarios and for large plots where homogeneity of the establishment environment is a questionable assumption. However, this approach would likely require finer-scale parameter estimation (e.g., viable seed production and dispersal) than used in the establishment models presented in Table 2.9.

Most of the available models of stump sprouting probabilities were developed from data following clearcut harvesting. Evidence of reductions in stump sprouting probabilities with increasing residual density in oak-dominated forests has been reported 9-11 years after harvesting (Atwood *et al.* 2009), but a separate study conducted 1-3 years after harvesting did not report reductions in stump sprouting probabilities with increasing residual density (Keyser and Zarnoch 2014). Keyser and Zarnoch (2014) suggested that this discrepancy could be due to accumulated mortality in the older stands analyzed by Atwood and others (2009). This suggestion is supported by the report of Dey and others (2008), that increasing residual density lowered survival and growth of oak stump-sprouts 10 years after harvesting, but the proportion of sprouting stumps in the first year after harvest was not significantly affected (Dey and Jensen 2002). Keyser and Zarnoch (2014) also found that the heights of sprouts were reduced with increasing residual density. In light of these reports, it is apparent that residual density influences stump sprouting dynamics in oak dominated forests. However, this influence appears to be primarily a reduction in growth rates which, in turn, reduces stump-sprout survival during stem exclusion. This hypothesis is followed in the regeneration simulator. Dey and Jensen (2002) also

reported that the number of oak sprouts per stump was significantly affected by stump diameter, but not by residual density. Consequently, models of stump sprouting probabilities following clearcutting may provide reasonable estimates of third-year regeneration establishment following a variety of harvest-based silvicultural manipulations. However, the prolonged influence of residual overstory density on sapling survival which, in turn, influences the abundance of potential sprouting sources should be considered in simulations of partial harvesting systems. Additional research into the influence of residual density on stump sprouting dynamics is warranted but beyond the scope of this effort.

The size of advance reproduction has long been identified as an important covariate for predicting post-disturbance growth in oak-dominated forests (Sander 1971). This is thought to be due to a more established root system and possibly greater root reserves of total nonstructural carbohydrates (Johnson *et al.* 2009, Kobe *et al.* 2010). This predisturbance size-growth hypothesis has been incorporated into existing regeneration models and evaluations in various ways, ranging from descriptions of pre-disturbance size via continuous metrics (*e.g.*, Loftis 1990, Dey 1991) to categorical tallies (*e.g.*, Belli *et al.* 1999, Loftis 1989). The regeneration simulator described herein also incorporates this hypothesis. Advance reproduction is segregated into two categories: large (height \geq 100cm) and small (height < 100cm). Large advance reproduction is inventoried so that size-dependent differences in height growth can be projected for several species groups (Vickers *et al.* 2014) in the growth module of the regeneration simulator. The probability of large advance reproduction being damaged or top-killed during

a disturbance has not been accounted for empirically. Until more comprehensive empirical models can be developed for this phenomenon, a simple probabilistic model was assumed (Fig. 2.11). It was assumed that the probability of damage/top-kill for large advance reproduction was a logistic function that increased with increasing overstory disturbance to an asymptote of 85%. The same function was applied to all species groups. Additional research to provide empirical parameters for the probability of damage/topkill and subsequent sprouting probabilities to large advance reproduction is warranted. Many studies suggest that the sprouting probability of small diameter trees is high after harvesting, but the minimum diameter included in sprouting models vary (e.g., Johnson *et al.* 2009). For simplicity, it was assumed that all large advance reproduction of sprouting species that was damaged in a disturbance would sprout, but this parameter should be amended as additional empirical insight becomes available.

To maintain consistency with the predisturbance size-growth hypothesis, large advance reproduction that is top-killed during disturbance should probably be assigned height as a sprout origin stem using the height assignment equations in Table 2.11 in the Missouri Ozarks to reflect the likely contributions of a more established root system than that of small advance reproduction.

It may be possible to improve the height assignment of large advance reproduction with an additional size covariate such as ground-line or root-collar diameter to capture differences, which have been reported to impact post-disturbance height growth of seedling-sprouts (Johnson *et al.* 2009). However,

the inclusion of a ground-line or root-collar diameter covariate would require greater, perhaps considerably greater, inventory effort. Moreover, despite the clear empirical trend and biologically sound basis in predisturbance size-growth hypothesis, these relationships typically exhibit substantial variance (Dey 1991, Loftis 1990, McQuilkin 1975, Sander 1971). For this reason, the benefit from including these covariates may largely be interpretive power rather than statistical improvement over the stochastic assignment from an empirical distribution approach used herein.

Due to data limitations, the post-disturbance height assignment protocol for small advance reproduction and disturbance triggered reproduction, the height assignment procedure was modeled both probabilistically and stochastically. Conceptually, this height assignment protocol resembles a hurdle model (e.g., Mullahy 1986), *i.e.*, binary function that a “hurdle” is achieved at which point an estimate of a continuous outcome is provided. In this application, the “hurdle” was the probability of attaining a height $\geq 100\text{cm}$, in which case the actual height ($\geq 100\text{cm}$) was assigned as a random deviate from an empirical distribution rather than an uninformed random uniform distribution (1-99.9cm) if the “hurdle” was not achieved. An entire post-disturbance empirical height distribution would likely be an improvement over the probabilistic mixing of a truncated empirical distribution (height $\geq 100\text{cm}$) and a random uniform distribution (height $< 100\text{cm}$) that was imposed by data limitations. The predisturbance size-growth relationships described earlier theoretically apply to small advance reproduction, but minimal differences in growth and survival probabilities have been reported

among various sizes of small advance reproduction (Dey 1991). In addition, McQuilkin (1975) reported that both direct seeded white oaks and 1-0 nursery stock exhibited considerably lower growth than that of larger advance reproduction.

Several models have been developed to estimate crown length, or live crown ratio, for existing trees with incomplete measurements. These models typically include diameter, height, stand density metrics, and/or age (Burkhart and Tomé 2012). The natural log of height and residual overstory density were used to model live crown ratio of reproduction. Because this was a reproduction establishment scenario, opportunities to utilize other stem attributes were limited. While height was an important predictor for all species groups with sufficient data to include covariates, residual overstory density was only included in the “best” model for one species group. Moreover, preliminary analysis did not reveal any trends with distance to nearest neighbor. The lack of importance for these density metrics, which are often used as surrogates for competition, suggest that the live crown ratio of recently established reproduction, while extremely variable, is invariant of competition. This might readily be explained for reproduction in large openings that have not yet reached canopy closure, but not for reproduction established in an understory. It has been suggested that juveniles are often more tolerant of stress than adults of the same species (Givnish 1988). This may be due to ontogenetic differences in carbohydrate storage (Myers and Kitajima 2007), photosynthetic adjustment (Walters and Reich 2000), and resource partitioning/allocation (Kobe *et al.* 2010, Messier *et al.* 1999). It is also

possible that any limitation in light availability among the reproduction layer was captured by the height covariate.

Though live crown ratio was highly variable it was an important covariate for crown shape ratio. The results of the shape ratio models (Fig. 2.9) are consistent with several hypotheses of tree growth and stand development and their impact on tree form (Oliver and Larson 1996). Forest grown trees with deep crowns typically have developed in relatively open conditions that have allowed retention of apical dominance, minimal crown recession, and stronger epinastic control. Examples of this may include young saplings in openings prior to canopy closure. Temesgen and others (2005) found that live crown ratio decreased with increasing height and competition. Trees in relatively open forest conditions are often developing among several neighbors and the environment changes rapidly as canopy closure is reached. As reported by Temesgen and others (2005) crown recession is hastened with the onset of canopy closure which may cause dramatic shifts in live crown ratio and thus crown shape ratio, particularly for trees with decurrent growth forms.

That residual overstory density was included in the “best” models for the majority of species groups was expected. While the effect of residual overstory density likely had minimal impact on the shape ratio of large trees after only three years of post-disturbance development, the effect on reproduction that established as a result of the disturbance was likely more pronounced. There was a reduced rate of crown shape ratio increase with decreasing live crown ratio depicted by the models in Fig. 2.9 for low residual overstory density vs high residual overstory

density. This is consistent with the descriptions of the impact of high shade vs low or side shade on tree form by Oliver and Larson (1996, p52-60). Saplings that have developed under a dense overstory often experienced height growth reduction, crown recession, loss of apical dominance, and reduced epinastic control. This environment leads to a flat-topped or umbrella appearance (Oliver and Larson 1996) due to shallow, wide crowns. In contrast, saplings that have developed in close competition within a dense cohort are often physically constrained such that crown radius cannot readily expand, thus the shape ratio in this scenario would not increase as rapidly with decreasing live crown ratio as was found for understory saplings.

It was expected that the “best” models of diameter at breast height would include a positive relationship with crown surface area (Burkhart and Tomé 2012). Crown surface area has been used with success in other models (Larsen 1991) of diameter due to a high correlation with sapwood area (Gould and Harrington 2008, Margolis *et al.* 1995, Maguire and Hann 1989). This relationship has also been used in allometric models designed to predict crown dimensions for a given diameter (Waring *et al.* 1982, Gholz *et al.* 1979). These findings are consistent with fundamental theories of tree development that highlight the role of the crown in light acquisition and resource production (Assmann 1970, Horn 1971, Kozlowski and Pallardy 1997). While crown surface area has also shown to be a good predictor of leaf area in hardwood forests (Larsen, D.R. *unpublished data*), it is imperfect surrogate due to an inability to capture differences in leaf surface area per unit crown surface area due to varying crown patchiness/transparency

(Canham *et al.* 1994, Larsen and Kershaw 1996). Indeed, some of the unexplained variation in the models of diameter at breast height is likely due to differences in leaf area among trees with similar crown surface areas (Vose and Allen 1988, Albaugh *et al.* 1998, Fox *et al.* 2007). It is also possible that shapes other than or in addition to a paraboloid to describe crown dimensions as well as estimates of the proportion of crown receiving direct sunlight could improve predictions (Hann 1999).

It was hypothesized that as site class improved from exposed backslopes to protected backslopes diameters would be greater per unit crown surface area, largely due to an expected increase in water availability. While the models support that hypothesis for red maple and sassafras, site class was not an important predictor of diameter for most other species groups. The effect of improving site class on modeled diameters was unexpected for dogwood, elms, and the other species group and provided stronger evidence to reject that hypothesis. For these species groups, the effect of improved site class on diameter tended to be increasingly negative as crown surface area increased. This suggests that on protected backslopes there was an increasing loss of efficiency compared to exposed backslopes as crown surface area increased for these three species groups. However, the results are inconclusive because overstory composition, structural arrangement, and other potentially confounding differences among plots were not accounted for. Vickers and others (2014) found that the height growth of dogwood saplings was lower on protected backslopes than exposed backslopes on the same plots. Because these species groups

primarily inhabit the understory of Missouri Ozark forests, it is plausible that increased solar radiation and/or differences in canopy composition on exposed backslopes compared to protected backslopes may benefit these species groups, or increased competition on protected backslopes is detrimental. Differences in density, structure, and composition of the overstory has been shown to influence the quantity and quality of light reaching the forest floor (Canham *et al.* 1994, Larsen and Kershaw 1996), and the availability of water and nutrients (Coomes and Grubb 2000).

Conclusion

Regeneration is a dynamic process involving the establishment, growth, and mortality of individual trees and their neighbors. The capability to stochastically simulate reproduction establishment across a gradient of residual overstory density as outlined above is consistent with this process (Objective 1). Linking the residual overstory density based reproduction establishment simulations with size and residual overstory density based models of annual growth (*e.g.*, Vickers *et al.* 2014) and mortality simulations will provide powerful tools not only for applied objectives but empirical ones as well. The combination of these models, while imperfect, should increase our ability to recreate the regeneration process, and as a result, our understanding of it. Areas in need of additional work have been suggested and use of the combined models as a simulation system will

undoubtedly highlight other weaknesses in the individual models and in our current ability to quantify the regeneration process.

The covariates chosen for the empirical models of reproduction establishment and the structure of the simulation module itself were strongly influenced by leading hypotheses and theories of tree and stand development. Therefore, the output should be sufficiently general to describe the establishment of a variety of species under a variety of scenarios (Objective 2). The output is provided as a treelist enumerated from inventoried and empirical parameters and individual tree attributes derived from allometrically derived relationships. This should foster compatibility within the different modules of the regeneration simulator itself as well as existing growth and yield models (Objective 3).

The empirically derived parameters for reproduction establishment are separate files from the structure of the simulator. This accommodates the possibility for future improvement and/or modification for other regions and scenarios (Objective 4). Parameterization for the Missouri Ozarks was accomplished using a combination existing data sources from tagged and untagged plots monitored before and after disturbance. Parameterization of reproduction establishment could be accomplished by establishing several tagged plots prior to planned disturbance and tracking their development for a short period following disturbance. Simultaneous collection of a combination of stem analysis data and additional tagged plots on stands/cohorts in different stages of development would likely expedite parameterization of growth and mortality functions as

opposed to only following the reproduction establishment plots for decades to collect parameters for growth and mortality.

“Essentially, all models are wrong, but some are useful. Since all models are wrong, the scientist cannot obtain a “correct” one by excessive elaboration.”

– *George E.P. Box*

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References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S. 1998. Leaf-area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* 44: 317-328.
- Assmann, E. 1970. *The Principles of Forest Yield Study*. New York. Pergamon Press. 506p.
- Atwood, C.J., Fox, T.R., Loftis, D.L. 2009. Effects of alternative silviculture on stump sprouting in the southern Appalachians. *For. Ecol. Mgmt.* 257: 1305-1313.
- Belli, K.L., Hart, C.P., Hodges, J.D., Stanturf, J.A. 1999. Assessment of the regeneration potential of red oaks and ash on minor bottoms of Mississippi. *South. J. Appl. For.* 23(3): 133-138.
- Bigelow, S.W., Canham, C.D. 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. *J. Ecol.* 90: 188-200.
- Biging, G.S., Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41(2): 360-377.
- Blizzard, E.M., Kabrick, J.M., Dey, D.C., Larsen, D.R., Pallardy, S.G., Gwaze, D.P. 2013. Light, canopy closure, and overstory retention in upland Ozark forests. p.73-79 *in*: Guldin, J.M. (ed). 2013. Proceedings of the 15th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SRS-GTR-175.
- Bolker, B.M. 2008. *Ecological Models and Data in R*. Princeton University Press. 408p.
- Brookshire, B.L., Shifley, S.R. (Eds.) 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium.: An experimental approach to landscape research. St. Louis, MO, June 3-5, 1997. USDA For. Serv. Gen. Tech. Rep. NC-193.
- Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L. 2008. Prescribing regeneration treatments for mixed oak forests in the Mid-Atlantic Region. USDA For. Serv. Gen. Tech. Rep. NRS-33.
- Bugmann, H. 2001. A review of forest gap models. *Climate Change* 51: 259-305.
- Burkhart, H.E., Tomé, M. 2012. *Modeling Forest Trees and Stands*. Springer. 457p.
- Burnham, K.P., Anderson, D.R. 1998. *Model Selection and Inference. A Practical Information-Theoretic Approach*. Springer. 353p.

- Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24: 337-349.
- Clabo, D.C. 2014. Shortleaf pine sprout production capability in response to disturbances. M.S. Thesis, University of Tennessee, Knoxville, Tennessee.
- Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*. 80: 1475-1494.
- Clatterbuck, W.K. 2015. An evaluation of the hardwood regeneration model (REGEN) 16 years post-harvest of a regenerated stand in East Tennessee. *In: Holley, G.A., Conner, K.F. eds. Proceedings of the 17th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SRS-203. 352-257.*
- Coomes, D.A., Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Mon.* 70(2): 171-207.
- Cribari-Neto, F., Zeileis, A. 2010. Beta regression in R. *J. Stat. Soft.* 34(2): 1-24.
- Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: a review of its structure, content, and applications. *Computers and Electronics in Agriculture*. 49: 60-80.
- Dey, D.C. 1991. A comprehensive Ozark regenerator. Ph.D. Dissertation, University of Missouri, Columbia, Missouri. 283p.
- Dey, D.C., Jensen, R.G. 2002. Stump sprouting potential of oaks in Missouri Ozark forests managed by even- and uneven-aged silviculture. *USDA For. Serv. Gen. Tech. Rep. NC-227: 102-113.*
- Dey, D.C., Jensen, R.G., Wallendorf, M.J. 2008. Single-tree harvesting reduces survival and growth of oak stump sprouts in the Missouri Ozark Highlands. P. 26-37 in *Proc. 16th Central Hardwood Forest Conf.* Jacobs, D.F., and C.H. Michler (eds.). *USDA For. Serv. Gen. Tech. Rep. NRS-P-24.*
- Dey, D.C., Spetich, M.A., Weigel, D.R., Johnson, P.S., Graney, D.L., Kabrick, J.M. 2009. A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. *New. For.* 37: 123-135.
- Dixon, G.E. 2002. Essential FVS: a user's guide to the Forest Vegetation Simulator. Revised: January 2014. *USDA For. Serv. Forest Management Service Center.*

- Ducey, M.J., Knapp, R.A. 2010. A stand density index for complex mixed species forests in the northeastern United States. *For. Ecol. Mgmt.* 260: 1613-1622.
- Egler, F.E., 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412-417.
- Ekleston, N.I., Madsen, L., Hagar, J.C., Temesgen, H. 2011. Estimating riparian understory vegetation cover with beta regression and copula models. *For. Sci.* 57: 212-221.
- Ekstrom, C. 2014. MESS: Miscellaneous esoteric statistical scripts. R package version 0.2-1. <http://CRAN.R-project.org/package=MESS>.
- Faraway, J.J. 2005. *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Taylor & Francis. 312p.
- Fei, S., Gould, P.J., Steiner, K.C., Finley, J.C. 2006. Aggregate height – a composite measure of stand density for tree seedling populations. *For. Ecol. Mgmt.* 223: 336-341.
- Fei, S., Steiner, K.C., 2008. Relationships between advance oak regeneration and biotic and abiotic factors. *Tree Physiol.* 28: 1111-1119.
- Ferrari, S.L.P., Cribari-Neto, F. 2004. Beta regression for modeling rates and proportions. *J. Applied Statistics.* 31(7): 799-815.
- Finzi, A.C., Canham, C.D. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. *For. Ecol. Mgmt.* 131: 153-165.
- Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A. 2007. Tree nutrition and forest fertilization of pine plantations in the Southern United States. *South. J. Appl. For.* 31(1): 5-11.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Oregon State University, Forest Research Laboratory. Research Paper 41. 39p.
- Gingrich, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. *For. Sci.* 13(1): 38-53.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant. Phys.* 15: 63-92.
- Gleason, H.A. 1917. The structure and development of the plant association. *Bull. Torr. Bot. Club.* 43: 463-481.

- Gould, P.J., Fei, S., Steiner, K.C. 2007. Modeling sprout-origin oak regeneration in the Central Appalachians. *Can. J. For. Res.* 37: 170-177.
- Gould, P.J., Harrington, C.A. 2008. Extending sapwood-leaf area relationships from stems to roots in coast Douglas-fir. *Ann. For. Sci.* 65: 802.
- Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2005. Developmental Pathways Following the Harvest of Oak-Dominated Stands. *For. Sci.* 51(1): 76-90.
- Gould, P.J., Steiner, K.C., McDill, M.E., Finley, J.C. 2006. Modeling seed-origin oak regeneration in the central Appalachians. *Can. J. For. Res.* 36: 833-844.
- Hann, D.W. An adjustable predictor of crown profile for stand grown Douglas-fir trees, *For. Sci.* 45: 217-225.
- Hardin, J.W., Hilbe, J.M. 2012. *Generalized Estimating Equations, 2nd ed.* Chapman and Hall/CRC. 277p.
- Hilbe, J.M. 2011. *Negative Binomial Regression 2nd ed.* Cambridge University Press. 553p.
- Højsgaard, S., Halekoh, U., Yan, J. 2006. The R package geepack for generalized estimating equations. *J. Statistical Software.* 15(2): 1-11.
- Horn, H.S. 1974. The ecology of secondary succession. *Ann. Rev. Eco. Syst.* 5: 25-37.
- Hosmer, D.W. Jr., Lemeshow, S., Sturdivant, R.X. 2013. *Applied Logistic Regression 3rd ed.* Wiley. 528p.
- Johnson, P.S. 1975. Growth and structural development of red oak sprout clumps. *For. Sci.* 21: 413-418.
- Johnson, P.S., Shifley, S.R., Rogers, R. 2009. *The Ecology and Silviculture of Oaks.* CABI. 600p.
- Kabrick, J.M., Villwock, J.L., Dey, D.C., Keyser, T.L., Larsen, D.R. 2014. Modeling and mapping oak advance reproduction density using soil and site variables. *For. Sci.* 60(6): 1107-1117.
- Kabrick, J.M., Zenner, E.K., Dey, D.C., Gwaze, D., Jensen, R.G. 2008. Using ecological land types to examine landscape-scale oak regeneration dynamics. *For. Ecol. Mgmt.* 255: 3051-3062.
- Kays, J.S., Canham, C.D. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. *For. Sci.* 37: 524-539.

- Keyser, T.L., Keyser, C.E. 2013. Modeling the long-term effects of oak shelterwood regeneration treatments on species diversity and oak abundance in Southern Appalachian forests of North Carolina. *In*: Guldin, J.M. ed. 2013. Proceedings of the 15th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SRS-GTR-175. 281-288.
- Keyser, T.L., Keyser, C.E., Loftis, D., Boucugnani, D. 2013. Linking the REGEN model to the southern variant of the Forest Vegetation Simulator. Oral Presentation. 17th biennial southern silvicultural research conference. March 4-7, 2013. Shreveport, LA.
- Keyser, T.L., Zarnoch, S.J. 2014. Stump sprout dynamics in response to reductions in stand density for nine upland hardwood species in the southern Appalachian Mountains. *For. Ecol. Mgmt.* 319: 29-35.
- Knapp, B.O., Olson, M.G., Larsen, D.R., Kabrick, J.M., Jensen, R.G. 2014. Missouri Ozark Forest Ecosystem Project: a long-term landscape-scale, collaborative forest management research project. *J. For.* 112(5): 513-524.
- Kobe, R.K., Iyer, M., Walters, M.B. 2010. Optimal partitioning theory revisited: nonstructural carbohydrates dominate root mass responses to nitrogen. *Ecology.* 91(1): 166-179.
- Kobe, R.K., Pacala, S.W., Silander, J.A. Jr., Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5: 517-532.
- Korhonen, L., Korhonen, K.T., Stenberg, P., Matamo, M., Rautianen, M. 2007. Local models for forest canopy cover with beta regression. *Silva Fennica.* 41: 671-685.
- Kozlowski, T.T., Pallardy, S.G. 1997. *Physiology of Woody Plants 2nd ed.* Elsevier Inc. 411p.
- Larsen, D.R. 1991. An adaptive stand dynamics model. Ph.D. Dissertation. University of Washington. 232p.
- Larsen, D.R. 1994. Adaptable stand dynamics model integrating site-specific growth for innovative silvicultural prescriptions. *For. Ecol. Mgmt.* 69: 245-257.
- Larsen, D.R., Kershaw, J.A. 1996. Influence of canopy structure assumptions on predictions from Beer's law. A comparison of deterministic and stochastic simulations. *Agr. Forest Meteorol.* 81: 61-77.
- Larsen, D.R., Metzger, M.A., Johnson, P.S. 1997. Oak regeneration and overstory density in the Missouri Ozarks. *Can. J. For. Res.* 27(6): 869-875.

- Liang, K-Y., Zeger, S.L. 1986. Longitudinal data analysis using generalized linear models. *Biometrika*. 73(1): 13-22.
- Loewenstein, E.F., Johnson, P.S., Garrett, H.E. 2000. Age and diameter structure of a managed uneven-aged oak forest. *Can. J. For. Res.* 30: 1060-1070.
- Loftis, D.L. 1989. Species composition of regeneration after clearcutting Southern Appalachian hardwoods. *In: Miller, J.H. ed. Proceedings of the 5th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SO-74. 253-257.*
- Loftis, D.L. 1989. Species composition of regeneration after clearcutting Southern Appalachian hardwoods. *In: Miller, J.H. ed. Proceedings of the 5th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SO-74. 253-257.*
- Loftis, D.L. 1990. Predicting post-harvest performance of advance red oak reproduction in the Southern Appalachians. *For. Sci.* 36(4): 908-916.
- Loftis, D.L., McGee, C.E. eds. 1993. Oak regeneration: serious problems, practical recommendations. *Symposium Proceedings. USDA For. Serv. Gen. Tech. Rep. SE-84.*
- Lorimer, C.D. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Mgmt.* 6: 343-360.
- MacDonald, J.E., Powell, G.R. 1983. Relationships between stump sprouting and parent-tree diameter in sugar maple in the 1st year following clear-cutting. *Can. J. For. Res.* 13: 390-394.
- Maguire, D.A., Hann, D.W. 1989. The relationship between gross crown dimensions and sapwood area at crown base in Douglas-fir. *Can. J. For. Res.* 19: 557-565.
- Margolis, H.A., Oren, R., Whitehead, D., Kaufmann, M. 1995. Leaf area dynamics of conifer forests. *in: Smith, W.K., Hinkley, T.M. eds. Ecophysiology of Coniferous Forests. Academic Press.*
- Marquis, D.A., Ernst, R.L., Stout, S.L. 1992. Prescribing Silvicultural Treatments in Hardwood Stands of the Alleghenies (Revised). *USDA For. Serv. Gen. Tech. Rep. NE-96.*
- McQuilkin, R.A. 1975. Growth of four types of white oak reproduction after clearcutting in the Missouri Ozarks. *USDA For. Serv. Res. Pap. NC-116.*
- McWilliams, W.H., Stout, S.L., Bowersox, T.W., McCormick, L.H. 1995. Adequacy of advance tree-seedling regeneration in Pennsylvania's forests. *North. J. Appl. For.* 12(4): 187-191.

- Messier, C., Doucet, R., Ruel, J., Claveau, Y., Kelly, C., Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* 29: 812-823.
- Millington, J.D.A., Walters, M.B., Matonis, M.S., Liu, J. 2013. Filling the gap: a compositional gap regeneration model for managed northern hardwood forests. *Ecological Modelling.* 253: 17-27.
- Missouri Department of Conservation 1986. *Forest Land Management Guidelines.* Missouri Department of Conservation, Jefferson City, Missouri. 81p.
- Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. *For. Sci. Mon.* 17: 1-39.
- Mullahy, J. 1986. Specification and testing of some modified count data models. *J. Econometrics.* 3: 341-365.
- Myers, J.A., Kitajima, K. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. *J. Ecol.* 95: 383-395.
- Oliver, C.D., Larson, B.C. 1996. *Forest Stand Dynamics.* 2nd ed. John Wiley & Sons, Inc. New York. 520p.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr. 1993. Forest models defined by field measurements: I. The design of a northeast forest simulator. *Can. J. for. Res.* 23: 1980-1988.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr., Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. for. Res.* 24: 2172-2183.
- Pan, W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics,* 57: 120-125.
- Petrice, T.R., Haack, R.A. 2011. Effects of cutting time, stump height, and herbicide application on ash (*Fraxinus* spp.) stump sprouting and colonization by emerald ash borer (*Agrilus planipennis*). *North. J. Appl. For.* 28(2): 79-83.
- Pinheiro, J.C., Bates, D.M. 2000. *Mixed-Effects Models in S and S-PLUS.* Springer-Verlag New York, Inc. 528p.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., R Development Core Team. 2013. *nlme: Linear and nonlinear mixed effects models.* R package version 3.1-113.
- Puettmann, K.J., Coates, K.D., Messier, C.C. 2008. *A Critique of Silviculture: Managing for Complexity.* Island Press. 206p.

- Quero, J.L., Herrero, A., Zamora, R. 2011. Linking stochasticity to determinism of woody plant recruitment in a mosaic landscape: a spatially explicit approach. *Basic and Applied Ecology*. 12: 161-171.
- R Development Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Radtke, P. 2015. Calibrating the REGEN model for regeneration success using permanent plot measurements in a maximum likelihood framework. Oral presentation. 18th biennial southern silvicultural research conference. March 2-5, 2015. Knoxville TN.
- Reineke, L.H. 1933. Perfecting a stand density index for even-aged forests. *J. Agric. Res.* 46(7): 627-638.
- Ribbens, E., Silander, J.A. Jr., Pacala, S.W. 1994. Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology*. 75: 1794-1806.
- Roach, B.A., Gingrich, S.F. 1968. Even-aged silviculture for upland central hardwoods. USDA For. Serv. Agriculture Handbook 355.
- Rogers, R., Johnson, P.S. 1998. Approaches to modeling natural regeneration in oak-dominated forests. *For. Ecol. Mgmt.* 106. 45-54.
- Sander, I.L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. *J. For.* 69: 809-811.
- Sander, I.L., Johnson, P.S., Rogers, R. 1984. Evaluating oak advance reproduction in the Missouri Ozarks .USDA For. Serv. Res. Pap. NC-251.
- Shifley, S.R., Kabrick, J.M. (Eds.) 2002. Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium. St. Louis, MO, October 17-18, 2000. USDA For. Serv. Gen. Tech. Rep. NC-227.
- Shugart, H.H., West, D.C. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Environ. Manage.*, 5: 161-179.
- Solomon, D.S., Leak, W.B. 2002. Modeling the regeneration of northern hardwoods with FOREGEN. USDA For. Serv. Res. Pap. NE-719. 9p.
- Spetitch, M.A., Dey, D.C., Johnson, P.S., Graney, D.L. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. *For. Sci.* 48(3): 504-517.
- Steiner, K.C., Finley, J.C., Gould, P.J., Fei, S., McDill, M. 2008. Oak regeneration guidelines for the Central Appalachians. *North. J. Appl. For.* 25(1): 5-16.

- Stout, S.L., Brose, P., Gottschalk, K., Miller, G., Knopp, P., Rutherford, G., Deibler, M., Frank, G., Gilmore, G. 2007. SILVAH-OAK: ensuring adoption by engaging users in the full cycle of forest research. In: Miner, C., Jacobs, R., Dykstra, D., Bittner, B. eds. Proceedings: international conference on transfer of forest service knowledge and technology. USDA For. Serv. Gen. Tech. Rep. PNW-726. 229-238.
- Temesgen, H., Lemay, V., Mitchell, S.J. 2005. Tree crown ratio models for multi-species and multi-layered stands of southeastern British Columbia. *For. Chron.* 81: 133-141.
- Veneables, W.N., Ripley, B.D. 2002. *Modern Applied Statistics with S. 4th ed.* Springer. 498p.
- Vickers, L.A., Fox, T.R., Loftis, D.L., Boucugnani, D.A 2011. Predicting forest regeneration in the Central Appalachians using the REGEN expert system. *J. Sust. For.* 30(8): 790-822.
- Vickers, L.A., Larsen, D.R., Knapp, B.O., Kabrick, J.M., Dey, D.C. 2014. The impact of overstory density on sapling height growth in the Missouri Ozarks – implications for interspecific differentiation during canopy recruitment. *Can. J. For. Res.* 44(11): 1320-1330.
- Vose, J.M., Allen, H.L. 1988. Leaf area, stemwood growth, and nutrient relationships in loblolly pine. *For. Sci.* 34: 547-563.
- Waldop, T.A., Buckner, E.R., Shugart, H.H.Jr., McGee, C.E. 1986. FORCAT: A Single Tree Model of Stand Development Following Clearcutting on the Cumberland Plateau. *For. Sci.* 32(2): 297-317.
- Walters, M.B., Reich, P.B. 2000. Trade-offs in low-light CO₂ exchange: a component of variation in shade tolerance among cold temperate tree seedlings. *Func. Ecol.* 14: 155-165.
- Waring, R.H., Schroeder, P.E., Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12: 556-560.
- Weigel, D.R., Peng, C.-Y.J. 2002. Predicting stump sprouting and competitive success of five oak species in southern Indiana. *Can. J. For. Res.* 32: 703-712.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A. Jr., Vanclay, J.K. 2011. *Forest Growth and Yield Modeling.* Wiley-Blackwell. 415p.
- Wendel, G.W. 1975. Stump sprout growth and quality of several Appalachian hardwood species after clearcutting. USDA For. Serv. Res. Pap. NE-329.

- Wright, E.F., Canham, C.D., Coates, C.D. 2000. Effects of suppression and release on sapling growth for eleven tree species of northern, interior British Columbia. *Can. J. For. Res.* 30: 1571-1580.
- Yan., J. 2002. Geepack: Yet another package for generalized estimating equations. *R-news.* 2/3: 12-14.
- Yan., J., Fine, J.P. 2004. Estimating equations for association structures. *Statistics in Medicine.* 23: 859-880.
- Yoda, K., Kira, T., Ogawa, H., Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol. Osaka City Univ.* 14:107-129.
- Zeger, S.L., Liang, K-Y. 1986. Longitudinal data analysis for discrete and continuous outcomes. *Biometrics.* 42(1): 121-130.
- Zuur, A. Ieno, E.N., Walker, N., Saveliev A.A., Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R.* Springer. 574p.

Tables

Table 2.1. Reproduction establishment candidate models.

Candidate	Generalized Linear Model Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3 + \beta_6 X_2 X_3 + \beta_7 X_1 X_2 X_3$	8
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3 + \beta_6 X_2 X_3$	7
3	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3$	6
4	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_2 X_3$	6
5	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_3 + \beta_5 X_2 X_3$	6
6	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2$	5
7	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_3$	5
8	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_2 X_3$	5
9	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$	4
10	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_3$	4
11	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$	4
12	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
13	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_3$	3
14	$y = \beta_0 + \beta_1 X_1$	2
15	$y = \beta_0$	1

Where: y = number of established stems per 0.004ha, X_1 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$), X_2 = presence of advance reproduction (1 if present, 0 if absent; $\text{dbh} \geq 3.81\text{cm}$), X_3 = presence of residual seed source (1 if present, 0 if absent; $\text{dbh} \geq 11.43\text{cm}$).

Table 2.2. Candidate models for probability of new reproduction with an initial height $\geq 100\text{cm}$.

Candidate	Generalized Linear Model Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$	4
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
3	$y = \beta_0 + \beta_1 X_1$	2
4	$y = \beta_0$	1

Where: y = logit of probability of reproduction having an initial height (year 3) $\geq 100\text{cm}$, X_1 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$), and X_2 = site class (1 if protected backslopes, 0 if exposed backslopes).

Table 2.3. Candidate models for initial height assignment.

Candidate	Generalized Estimating Equation Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3 + \beta_6 X_2 X_3$	7
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2$	5
3	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_3$	5
4	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_2 X_3$	5
5	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$	4
6	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
7	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_3$	3
8	$y = \beta_0 + \beta_1 X_1$	2
9	$y = \beta_0$	1

Where: y = mean initial height (year 3), X_1 = residual overstory basal area ($\text{m}^2 \text{ha}^{-1}$; $\text{dbh} \geq 11.43\text{cm}$), X_2 = stem origin (1 if obvious sprout, 0 if not), X_3 = site class (1 if protected backslopes, 0 if exposed backslopes).

Table 2.4. Candidate models for initial live crown ratio assignment.

Candidate	Generalized Estimating Equation Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$	4
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
3	$y = \beta_0 + \beta_1 X_1$	2

Where: y = mean initial height (year 3), X_1 = natural log of seedling height ($\geq 100\text{cm}$), X_2 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$).

Table 2.5. Candidate models for crown shape ratio and crown width assignment.

Candidate	Generalized Least Squares Equation Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$	4
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
3	$y = \beta_0 + \beta_1 X_1$	2
4	$y = \beta_0$	1

Where: y = crown shape ratio (radius/length), X_1 = natural log of live crown ratio, X_2 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$).

Table 2.6. Candidate models for diameter at breast height assignment for stems with a height ≥ 137.5 cm.

Candidate	Generalized Least Squares Equation Form	df
1	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$	4
2	$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$	3
3	$y = \beta_0 + \beta_1 X_1$	2

Where: y = diameter at breast height (cm), X_1 = natural log of crown surface area, X_2 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$).

Table 2.7. Available stump sprouting parameters.

Species Group		Sprouting probability	Source
	ashes	0.96	Petrice & Haack 2011
	blackgum	$\{1+e^{-(5.5798-0.2011 \cdot X_1)}\}^{-1}$	Keyser & Zarnoch 2014
	black cherry	0.98	Wendel 1975
	dogwood	0.88	Keyser & Zarnoch 2014
	elms	$\{1+e^{-(1.6323-0.0608 \cdot X_1)}\}^{-1}$	Olson. M.G. unpublished
	hickories	0.77	Keyser & Zarnoch 2014
	other species	0.89	Keyser & Zarnoch 2014
	red maple	0.95	Keyser & Zarnoch 2014
	black oak	$\{1+e^{-(0.7523-0.2691[1.2703(0.3937 \cdot X_1)^{1.0105}]+0.0615[3.2808 \cdot X_2])}\}^{-1}$	Dey 1991
red oaks	scarlet oak	$\{1+e^{-(5.7710-0.3513[1.2154(0.3937 \cdot X_1)^{0.9798}])}\}^{-1}$	Dey 1991
	blackjack oak	$\{1+e^{-(2.6481-0.3005[1.3322(0.3937 \cdot X_1)^{0.9955}])}\}^{-1}$	Dey 1991
	northern red oak	$\{1+e^{-(7.4793-0.0005[(0.3937 \cdot X_1)X_3]+3.1679 \cdot \ln X_2)}\}^{-1}$	Weigel & Peng 2002
	sassafras	0.91	Keyser & Zarnoch 2014
	shortleaf pine	0.667	Clabo 2014
	sugar maple	0.81	MacDonald & Powell 1983
white oaks	white oak	$\{1+e^{-(1.7378-0.5476[1.5443(0.3937 \cdot X_1)^{0.9532}]-0.0546 \cdot X_3+0.0033[X_3(1.5443(0.3937 \cdot X_1)^{0.9532}])]+0.0705[3.2808 \cdot X_2])}\}^{-1}$	Dey 1991
	post oak	$\{1+e^{-(2.6481-0.3005[1.3322(0.3937 \cdot X_1)^{0.9955}])}\}^{-1}$	Dey 1991

Where: X_1 = diameter at breast height (cm), X_2 = site index (m), X_3 = tree age (yrs). These probabilities are used in binomial random number generator to stochastically determine the sprouting outcome (success or failure) of each inventoried stem that is a potential stump sprout. Values for black cherry were modified slightly from those reported (100%). Sprouting probabilities for shortleaf pine were derived from clipped seedlings, and therefore were not used for dbh > 5cm. An ecological classification system is used to delineate site differences in the simulation model, thus site index (X_2) is assumed unknown. For sprouting equations that require site index (black oak, northern red oak, white oak), empirically mean and standard deviation site index values for each site class (exposed backslopes: 21.0 ± 1.3 m, protected backslopes: 22.0 ± 1.1 m; black oak, base age 50) are used in a Gaussian random number generator to stochastically assign a site index value for a plot. Tree age (X_3) is also assumed unknown. For sprouting equations that require tree age (northern red oak, white oak), published diameter at breast height to tree age conversions (Lowenstein *et al.* 2000) are used. However, the age for white oak is not allowed to exceed 165 yrs due to biologically implausible interactions with the sprouting equation used (age substantially increased probability with increasing diameter trees). The sprouting equations developed by Dey (1991) were originally fit using stump diameter rather than diameter at breast height. These equations were modified to include separate diameter at breast height to stump diameter conversions (Dey 1991) into a single equation.

Table 2.8. Available stump-clump parameters.

Species Group		Stems per stump (λ)	Source
ashes		5.2	Kays & Canham 1991
blackgum		4.3	Atwood <i>et al.</i> 2009
black cherry		4.3	Kays & Canham 1991
dogwood		4.3	Atwood <i>et al.</i> 2009
elms		7.3	Olson, M.G. unpublished
hickories		3.2	Atwood <i>et al.</i> 2009
other species		4.3	Atwood <i>et al.</i> 2009
red maple		6.2	Kays & Canham 1991
	black oak	$21.028+(-0.0310[1.2703(0.3937 \cdot X_1)^{1.0105}] + (-0.1537 \cdot X_2))$	Dey & Jensen 2002
red	scarlet oak	$20.9773+(-0.0310[1.2154(0.3937 \cdot X_1)^{0.9798}] + (-0.1537 \cdot X_2))$	Dey & Jensen 2002
oaks	blackjack oak	$21.028+(-0.0310[1.3322(0.3937 \cdot X_1)^{0.9955}] + (-0.1537 \cdot X_2))$	Dey & Jensen 2002
	northern red oak	$3.7+8.82([0.3937 \cdot X_1]/X_3^2)$	Johnson 1975
sassafras		4.3	Atwood <i>et al.</i> 2009
shortleaf pine		2.1	Clabo 2014
sugar maple		10	MacDonald & Powell 1983
white	white oak	$17.0967+(-0.0310[1.5443(0.3937 \cdot X_1)^{0.9532}] + (-0.1537 \cdot X_2))$	Dey & Jensen 2002
oaks	post oak	$17.0967+(-0.0310[1.3322(0.3937 \cdot X_1)^{0.9955}] + (-0.1537 \cdot X_2))$	Dey & Jensen 2002

Where: X_1 = diameter at breast height (cm), X_2 = tree age (yrs), and X_3 = stand age (yrs). A stand age of 3 is used for stem establishment in the simulator. For equations that required tree age (oaks), published diameter at breast height to tree age conversions (Lowenstein *et al.* 2000) are used. An algorithm was required to ensure that the equations that required tree age did not produce spurious (negative) estimates outside the range of the original dataset. These parameter estimates are used in a Poisson random number generator to stochastically determine the number of new stems to be established per sprouted stump following a harvest-based silvicultural manipulation. The equations developed by Dey and Jensen (2002) were originally fit using stump diameter rather than diameter at breast height. These equations were modified to include separate diameter at breast height to stump diameter conversions (Dey 1991) into a single equation.

Table 2.9 Parameter estimates for “best” models of mean reproduction establishment.

Species Group	“Best” Model	Expected Value (μ)	Dispersion (k)
ashes	12	$e^{-1.3965+(-0.0761 \cdot X_1)+(2.4934 \cdot X_2)}$	0.3777
blackgum	05 [†]	$e^{0.9791+(-0.1522 \cdot X_1)+(1.1785 \cdot X_2)+(-1.0621 \cdot X_3)+(0.0840 \cdot X_1 X_3)+(1.0055 \cdot X_2 X_3)}$	1.0708
black cherry	14	$e^{0.344+(-0.1377 \cdot X_1)}$	0.6814
dogwood	14	$e^{2.1610+(-0.1404 \cdot X_1)}$	0.5487
elms	12	$e^{0.4034+(-0.2580 \cdot X_1)+(3.1708 \cdot X_2)}$	0.1497
hickories	09	$e^{1.9595+(-0.1855 \cdot X_1)+(-0.2857 \cdot X_2)+(0.1096 \cdot X_1 X_2)}$	0.7365
other species	13	$e^{1.5508+(-0.1135 \cdot X_1)+(1.0136 \cdot X_3)}$	0.4284
red maple	05 [†]	$e^{0.8669+(-0.1873 \cdot X_1)+(2.6784 \cdot X_2)+(1.3941 \cdot X_3)+(0.1122 \cdot X_1 X_3)+(-2.8237 \cdot X_2 X_3)}$	0.6051
red oaks	12	$e^{0.3334+(-0.1153 \cdot X_1)+(1.0313 \cdot X_2)}$	0.5835
sassafras	12	$e^{2.1403+(-0.1293 \cdot X_1)+(0.8838 \cdot X_2)}$	0.7266
shortleaf pine*	15	$e^{-2.8904}$	-
sugar maple*	15	$e^{-3.1135}$	-
white oaks	12	$e^{0.9538+(-0.1754 \cdot X_1)+(0.9978 \cdot X_2)}$	0.7201

Where: X_1 = residual overstory basal area ($m^2 \cdot ha^{-1}$; $dbh \geq 11.43cm$), X_2 = presence of advance reproduction (1 if present, 0 if absent; $dbh \geq 3.81cm$), X_3 = presence of residual seed source (1 if present, 0 if absent; $dbh \geq 11.43cm$). Parameter estimates were obtained via negative binomial regression with a log-link. The most parsimonious candidate model within two units of the model with the lowest AICc (Akaike’s Information Criterion corrected for small samples) was selected as “Best”, provided that it produced reasonable estimates within the range of the data. Negative binomial regression yields estimates for the two parameters (μ, k) of the negative binomial distribution. These parameter estimates are used in a negative binomial (or Poisson) random number generator to stochastically determine the number of new reproduction to be established following a harvest-based silvicultural manipulation. Expected values are for 0.004-ha plots; therefore, randomly generated numbers must be multiplied by 250 to obtain stems $\cdot ha^{-1}$. [†]This model was not the most parsimonious candidate within two units of the model with the lowest AICc, but was the model with the lowest AICc that also produced reasonable estimates within the range of the data. * Intercept-only Poisson regression with a log-link was used to estimate the single parameter (λ) of the Poisson distribution for the shortleaf pine and sugar maple species groups due to data limitations (rarity).

Table 2.10. Parameter estimates for “best” models of mean probability of new reproduction with a height $\geq 100\text{cm}$ (non-sprout stem origin).

Species Group	“Best” Model	Expected Value (μ)
ashes	4	$\{1+e^{-[0.244]}\}^{-1}$
blackgum	2	$\{1+e^{-[-0.1309+(-0.0766 \cdot X_1)+(0.2862 \cdot X_2)]}\}^{-1}$
black cherry	3	$\{1+e^{-[0.0394+(-0.0622 \cdot X_1)]}\}^{-1}$
dogwood	1	$\{1+e^{-[-1.4127+(-0.0150 \cdot X_1)+(1.2166 \cdot X_2)+(-0.0588 \cdot X_1 X_2)]}\}^{-1}$
elms	1	$\{1+e^{-[-0.1849+(-0.0075 \cdot X_1)+(-0.0533 \cdot X_2)+(-0.0787 \cdot X_1 X_2)]}\}^{-1}$
hickories	4	$\{1+e^{-[-1.89]}\}^{-1}$
other species	2 [†]	$\{1+e^{-[-1.1345+(-0.0158 \cdot X_1)+(0.4197 \cdot X_2)]}\}^{-1}$
red maple	3	$\{1+e^{-[-0.7503+(-0.0422 \cdot X_1)]}\}^{-1}$
red oaks	3	$\{1+e^{-[-0.6562+(-0.0786 \cdot X_1)]}\}^{-1}$
sassafras	1	$\{1+e^{-[-0.4978+(-0.0903 \cdot X_1)+(1.1541 \cdot X_2)+(-0.1256 \cdot X_1 X_2)]}\}^{-1}$
shortleaf pine*	4	$\{1+e^{-[-0.246]}\}^{-1}$
sugar maple	4	$\{1+e^{-[-0.936]}\}^{-1}$
white oaks	3 [†]	$\{1+e^{-[-1.3034+(-0.0581 \cdot X_1)]}\}^{-1}$

Where: y = probability of reproduction (non-sprout origin) to have an initial height (year 3) $\geq 100\text{cm}$, X_1 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$), and X_2 = site class (1 if protected backslopes, 0 if exposed backslopes).

Parameter estimates were obtained via generalized estimating equations using a binomial error family and logit link (logistic regression). The most parsimonious candidate model within two units of the model with the lowest QICc (Quasi-likelihood under the Independence model Criterion corrected for small samples) was selected as “Best”, provided that it produced reasonable estimates within the range of the data. Logistic regression provides estimates for the expected value or probability that reproduction will have an initial height (year 3) $\geq 100\text{cm}$ (μ).

These parameter estimates are used in a binomial random number generator to stochastically determine which stems will be assigned heights between 1-99.9cm at random and which stems will be assigned a height $\geq 100\text{cm}$ based on empirically estimated parameters of a height distribution. [†]This model was not the most parsimonious candidate within two units of the model with the lowest QICc, but was the model with the lowest QICc that also produced reasonable estimates within the range of the data. *Intercept-only logistic regression was used for the shortleaf pine group due to data limitations (rarity). All sprout origin stems in the dataset were $\geq 100\text{cm}$.

Table 2.11. Parameter estimates for “best” models of mean initial height for stems with a height $\geq 100\text{cm}$.

Species Group	“Best” Model	Expected Value (μ)	Dispersion (ϕ)
ashes	8 [†]	$\{0.0156+(0.0007 \cdot X_1)\}^{-1}$	0.7
blackgum	7	$\{0.0179+(0.0007 \cdot X_1)+(-0.0055 \cdot X_3)\}^{-1}$	0.59
black cherry	4	$\{0.0138+(0.0009 \cdot X_1)+(0.0133 \cdot X_2)+(-0.0059 \cdot X_3)+(-0.0225 \cdot X_2 X_3)\}^{-1}$	0.577
dogwood	7	$\{0.0243+(0.0002 \cdot X_1)+(-0.0025 \cdot X_3)\}^{-1}$	0.57
elms	8	$\{0.0112+(0.0009 \cdot X_1)\}^{-1}$	0.589
hickories	8 [†]	$\{0.0228+(0.0007 \cdot X_1)\}^{-1}$	0.637
other species	8	$\{0.0148+(0.0006 \cdot X_1)\}^{-1}$	0.725
red maple	6	$\{0.0207+(0.0005 \cdot X_1)+(-0.0112 \cdot X_2)\}^{-1}$	0.811
red oaks	3	$\{0.0148+(0.0018 \cdot X_1)+(-0.0061 \cdot X_2)+(0.0024 \cdot X_3)+(-0.0010 \cdot X_1 X_3)\}^{-1}$	0.583
sassafras	8	$\{0.0206+(0.0006 \cdot X_1)\}^{-1}$	0.592
shortleaf pine	9	$\{0.0266\}^{-1}$	2.11
sugar maple	8	$\{0.0103+(0.0013 \cdot X_1)\}^{-1}$	0.725
white oaks	6	$\{0.0175+(0.0007 \cdot X_1)+(-0.0060 \cdot X_2)\}^{-1}$	0.666

Where: y = mean initial height (year 3) -100cm, X_1 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$), X_2 = stem origin (1 if obvious sprout, 0 if not), X_3 = site class (1 if protected backslopes, 0 if exposed backslopes). Parameter estimates were obtained via generalized estimating equations. The most parsimonious candidate model within two units of the model with the lowest QICc (Quasi-likelihood under the Independence model Criterion corrected for small samples) was selected as “Best”, provided that it produced reasonable estimates within the range of the data. Gamma regression yields estimates for the expected value (μ) and dispersion which can be converted to shape, scale, and rate parameters of the Gamma distribution by the following formulae: Shape = ϕ^{-1} , Rate = $\text{shape} \cdot \mu^{-1}$, and Scale = ϕ/μ^{-1} . These parameter estimates are used in a Gamma random number generator to stochastically determine the number of new seedlings to be established following a harvest-based silvicultural manipulation. Expected values are for trees $\geq 100\text{cm}$; therefore 100cm must be added to interpret the mean or to randomly generated numbers. [†]This model was not the most parsimonious candidate within two units of the model with the lowest QICc, but was the model with the lowest QICc that also produced reasonable estimates within the range of the data. *Intercept-only Gamma regression was used for the shortleaf pine group due to data limitations (rarity).

Table 2.12. Parameter estimates for “best” models of mean initial live crown ratio for stems with a height ≥ 100 cm.

Species Group	“Best” Model	Expected Value (μ)	Variance (s^2)
ashes	3	$-0.3444+(0.1531 \cdot X_1)$	0.0233
blackgum	3	$-0.870+(0.286 \cdot X_1)$	0.0312
black cherry	3	$-0.7637+(0.2662 \cdot X_1)$	0.027
dogwood	2	$-0.3534+(0.1864 \cdot X_1)+(-0.0111 \cdot X_2)$	0.0332
elms	3	$-0.0671+(0.1165 \cdot X_1)$	0.0282
hickories	3	$-0.6405+(0.2260 \cdot X_1)$	0.0295
other species	3	$-0.6622+(0.2253 \cdot X_1)$	0.0302
red maple	3	$-0.3315+(0.153 \cdot X_1)$	0.0279
red oaks	3	$-0.7192+(0.2446 \cdot X_1)$	0.0249
sassafras	3	$-1.0621+(0.2911 \cdot X_1)$	0.0346
shortleaf pine*	-	-0.4397	0.0219
sugar maple	-	-0.4463	0.0248
white oaks	3	$-0.6472+(0.2258 \cdot X_1)$	0.028

Where: y = mean initial live crown ratio (year 3), X_1 = natural log of seedling height (cm ; height ≥ 100 cm), X_2 = residual overstory basal area (m^2ha^{-1} ; dbh ≥ 11.43 cm). Parameter estimates were obtained via generalized estimating equations. The most parsimonious candidate model within two units of the model with the lowest QICc (Quasi-likelihood under the Independence model Criterion corrected for small samples) was selected as “Best”, provided that it produced reasonable estimates within the range of the data. Generalized estimating equations with a Gaussian error distribution and identity link yields estimates for the expected value (μ) and variance of the Gaussian distribution. These parameter estimates are used in a Gaussian random number generator to stochastically determine the number of new seedlings to be established following a harvest-based silvicultural manipulation. An intercept only was used for the shortleaf pine and sugar maple groups due to data limitations (rarity).

Table 2.13. Parameter estimates for “best” models of crown shape ratio for stems with a height $\geq 100\text{cm}$.

Species Group	“Best” Model	Expected Value (μ)	Dispersion (ϕ)
ashes	3 [†]	$e^{-1.4501+(-0.641 \cdot X_1)}$	0.248
blackgum	1	$e^{-1.5937+(-0.7062 \cdot X_1)+(0.03 \cdot X_2)+(-0.0144 \cdot X_1 X_2)}$	0.264
black cherry	2	$e^{-1.6349+(-0.091772 \cdot X_1)+(0.024 \cdot X_2)}$	0.13
dogwood	1	$e^{-1.702+(-0.6287 \cdot X_1)+(0.0467 \cdot X_2)+(-0.0087 \cdot X_1 X_2)}$	0.356
elms	2 [†]	$e^{-1.219+(-0.723 \cdot X_1)}$	0.486
hickories	2	$e^{-1.8817+(-0.7497 \cdot X_1)+(0.0263 \cdot X_2)}$	0.427
other species	1	$e^{-1.5914+(-0.5338 \cdot X_1)+(0.0248 \cdot X_2)+(-0.0179 \cdot X_1 X_2)}$	0.235
red maple	1	$e^{-1.7227+(-0.4777 \cdot X_1)+(0.026 \cdot X_2)+(-0.0264 \cdot X_1 X_2)}$	0.349
red oaks	2	$e^{-2.0194+(-0.8353 \cdot X_1)+(0.0228 \cdot X_2)}$	0.197
sassafras	2	$e^{-1.7017+(-0.8772 \cdot X_1)+(0.0268 \cdot X_2)}$	0.136
shortleaf pine	4	$e^{-0.9454}$	0.264
sugar maple	4	$e^{-0.995}$	0.31
white oaks	1	$e^{-1.6214+(-0.5814 \cdot X_1)+(-0.0025 \cdot X_2)+(-0.0244 \cdot X_1 X_2)}$	0.198

Where: y = crown shape ratio (radius/length) X_1 = natural log of live crown ratio, X_2 = residual overstory basal area (m^2ha^{-1} ; $\text{dbh} \geq 11.43\text{cm}$). Parameter estimates were obtained via generalized estimating equations with a gamma error distribution. The most parsimonious candidate model within two units of the model with the lowest QICc was selected as “Best”, provided that it produced reasonable estimates within the range of the data. [†]This model was not the most parsimonious candidate within two units of the model with the lowest QICc, but was the model with the lowest QICc that also produced reasonable estimates within the range of the data.

Table 2.14. Parameter estimates for “best” models of diameter at breast height for stems ≥ 137.5 cm.

Species Group	“Best” Model	Expected Value (μ)	Dispersion (ϕ)
ashes	1	$e^{0.3080+(0.3760 \cdot X_1)}$	0.222
blackgum	3 [†]	$e^{0.0742+(0.4848 \cdot X_1)}$	0.531
black cherry	3	$e^{-0.1934+(0.5570 \cdot X_1)}$	0.274
dogwood	1	$e^{-0.1955+(0.6521 \cdot X_1)+(0.2803 \cdot X_2)+(-0.1190 \cdot X_1 X_2)}$	0.357
elms	1	$e^{-0.3739+(0.6543 \cdot X_1)+(0.4573 \cdot X_2)+(-0.2488 \cdot X_1 X_2)}$	0.386
hickories	3	$e^{0.7788+(0.4359 \cdot X_1)}$	0.263
other species	1 [†]	$e^{-0.1537+(0.5821 \cdot X_1)+(0.2783 \cdot X_2)+(-0.2433 \cdot X_1 X_2)}$	0.389
red maple	2	$e^{-0.1083+(0.4067 \cdot X_1)+(0.2314 \cdot X_2)}$	0.557
red oaks	3	$e^{0.5179+(0.5571 \cdot X_1)}$	0.276
sassafras	2	$e^{0.1121+(0.4248 \cdot X_1)+(0.1010 \cdot X_2)}$	0.611
shortleaf pine	3	$e^{1.1258+(0.5355 \cdot X_1)}$	0.119
sugar maple	3 [†]	$e^{0.246+(0.419 \cdot X_1)}$	0.212
white oaks	3	$e^{0.3803+(0.5590 \cdot X_1)}$	0.177

Where: y = diameter at breast height (cm) X_1 = natural log of crown surface area (m^2), X_2 = site class (1 if protected backslopes, 0 if exposed backslopes).

Parameter estimates were obtained via generalized estimating equations with a gamma error distribution. The most parsimonious candidate model within two units of the model with the lowest QICc was selected as “Best”, provided that it produced reasonable estimates within the range of the data. [†]Some candidate models would not converge, in these cases the selected model was at least two QICc units better than converged models or an intercept only model.

Figures

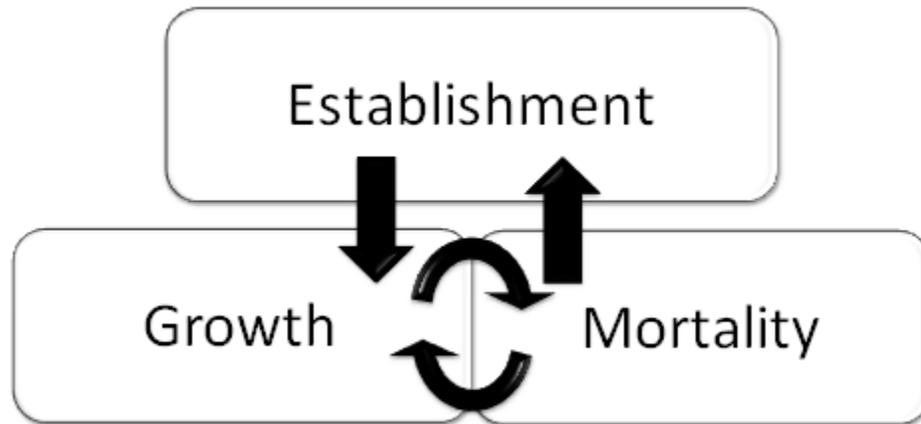


Figure 2.1. Regeneration as a dynamic process. This conceptual model suggests that there are three main components of regeneration: establishment, growth, and mortality. Regeneration simulations based on this concept must aim to reproduce the series of events within each of these main components and the interactions among them.

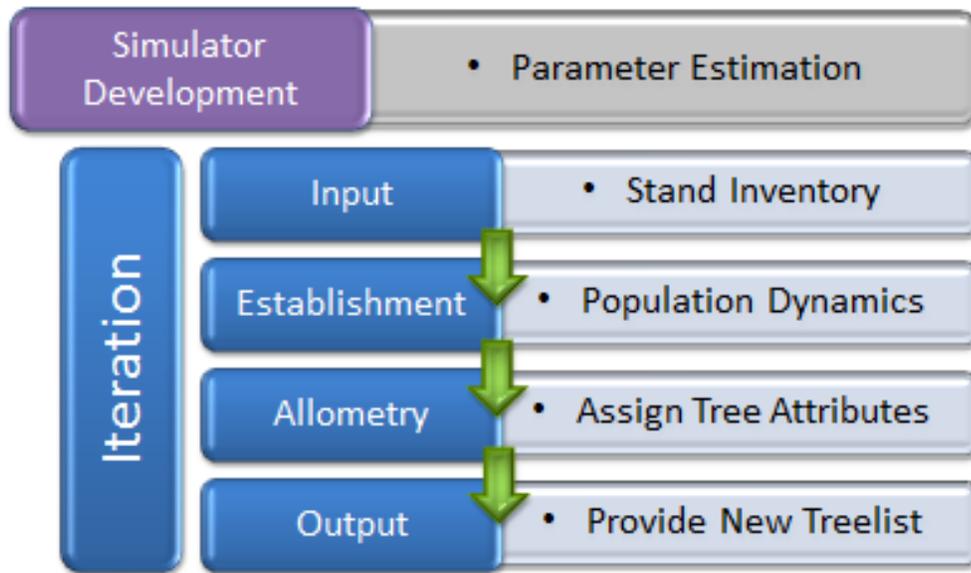


Figure 2.2. Visual representation of the structure of the establishment module of the regeneration simulator. Establishment is defined as the reproduction (woody plants) that is present three years post-disturbance. Although the parameter estimation during the simulator development step is technically part of the simulation process, it is a one-time event that not required again for each iteration of the simulation model. The establishment module requires a stand inventory with silvicultural prescriptions for each tree (remove or not) along with an inventory of large advance reproduction and a presence/absence survey of small advance reproduction as input. During the establishment step the population dynamics that occur as a result of the proposed disturbance are emulated. This step includes determining the post-disturbance sprouting of removed trees, fate of large advance reproduction, and the collective contribution of small advance reproduction and new seedlings to the reproduction pool. Once the post-disturbance reproduction pool has been enumerated each sprout, top-damaged large advance reproduction, and seedlings are stochastically assigned third year attributes during the allometry step. These attributes include height, crown length, crown radius, diameter at breast height (if applicable), and spatial coordinates. Finally, a treelist that includes each surviving inventoried tree and large advance reproduction (or sprout) along with the reproduction that was established as a result of the disturbance is output for stand-alone use or as input to the growth and mortality modules of the regeneration simulator.

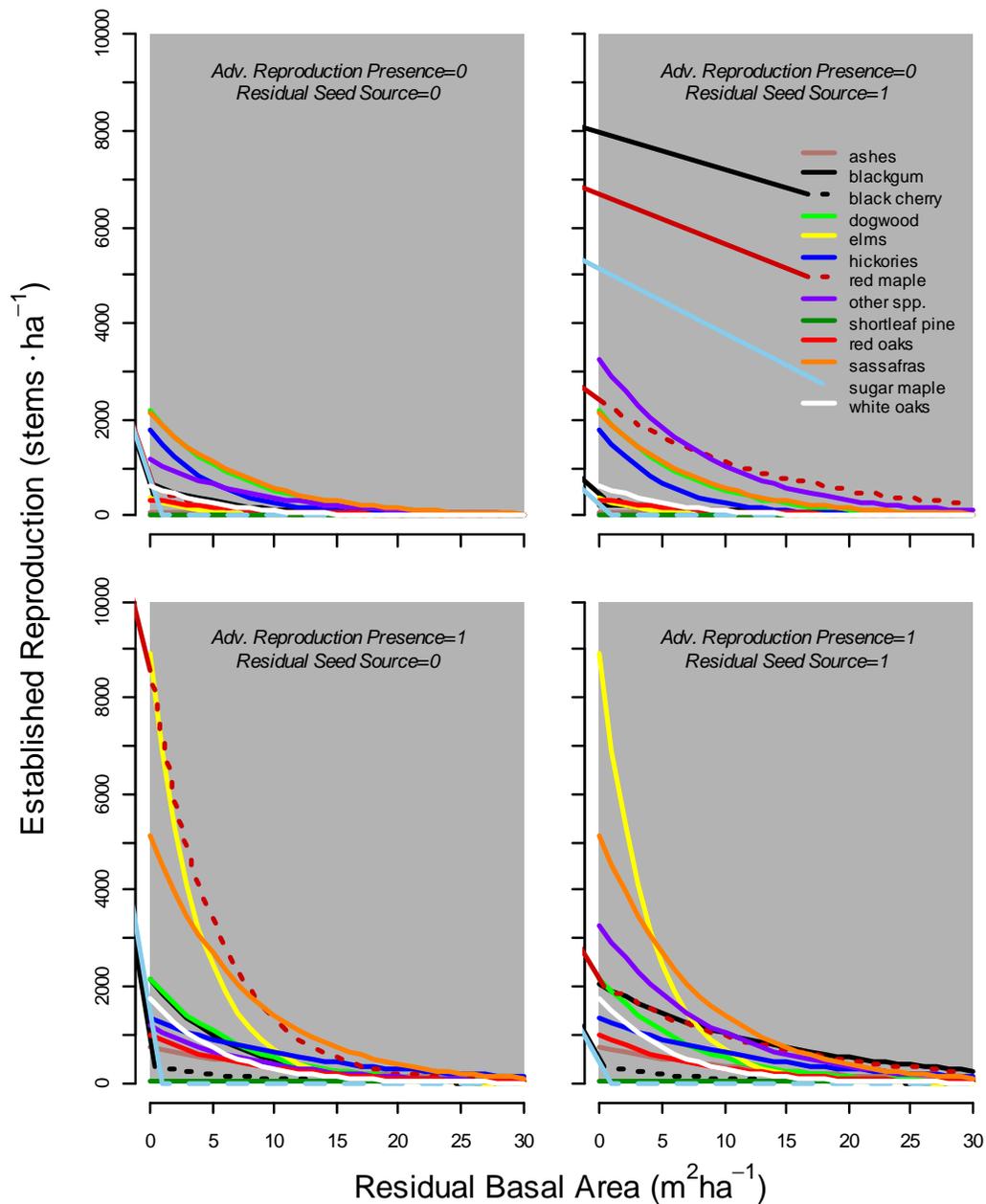


Figure 2.3. Mean reproduction establishment for thirteen species groups in the Missouri Ozarks as a function of residual overstory density, presence of advance reproduction, and presence of a residual seed source. Curves are drawn using the establishment models and parameters from Table 2.9 multiplied by 250 to obtain stems·ha⁻¹. Top row depicts average reproduction establishment when advance reproduction is absent ($X_2 = 0$), bottom row depicts average reproduction establishment when advance reproduction is present ($X_2 = 1$). Left column depicts average reproduction establishment when a residual seed source is absent ($X_3 = 0$), right column depicts average reproduction establishment when a residual seed source is present ($X_3 = 1$).

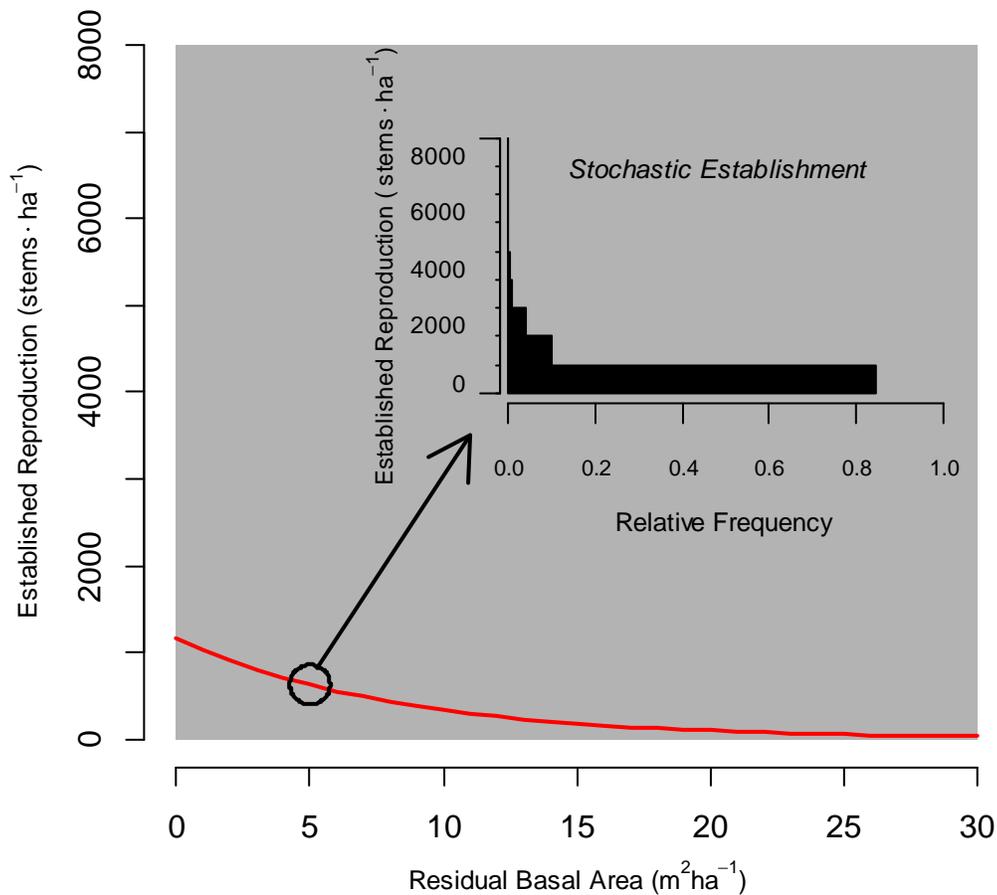


Figure 2.4. Stochastic reproduction establishment example for red oaks in the Missouri Ozarks. The reproduction establishment curve for red oaks (red line) was drawn using the establishment models and parameters from Table 2.9 ($\mu = e^{0.3334+(-0.1153 \cdot X_1)+(1.0313 \cdot X_2)}$) multiplied by 250 to obtain stems·ha⁻¹. Curve depicts mean reproduction establishment when advance reproduction is present ($X_2 = 1$) but a residual seed source is not present ($X_3 = 0$). When residual overstory basal area is held constant at 5m²·ha⁻¹ ($X_1 = 5$), $\mu = 550$. This value, along with the dispersion parameter ($k = 0.5835$) from Table 2.9 are estimates for the two parameters of a negative binomial distribution. These parameter estimates are used in a negative binomial random number generator to stochastically determine the number of new reproduction to be established following a harvest-based silvicultural manipulation. Using these parameters, 1000 random numbers were generated for this example (inset). Under these conditions, there will not be any red oak reproduction added to the plot in a vast majority of simulations (84%). in those simulations in which reproduction added (16%) the number will usually be less than 1000 stems·ha⁻¹ (10% of all simulations).

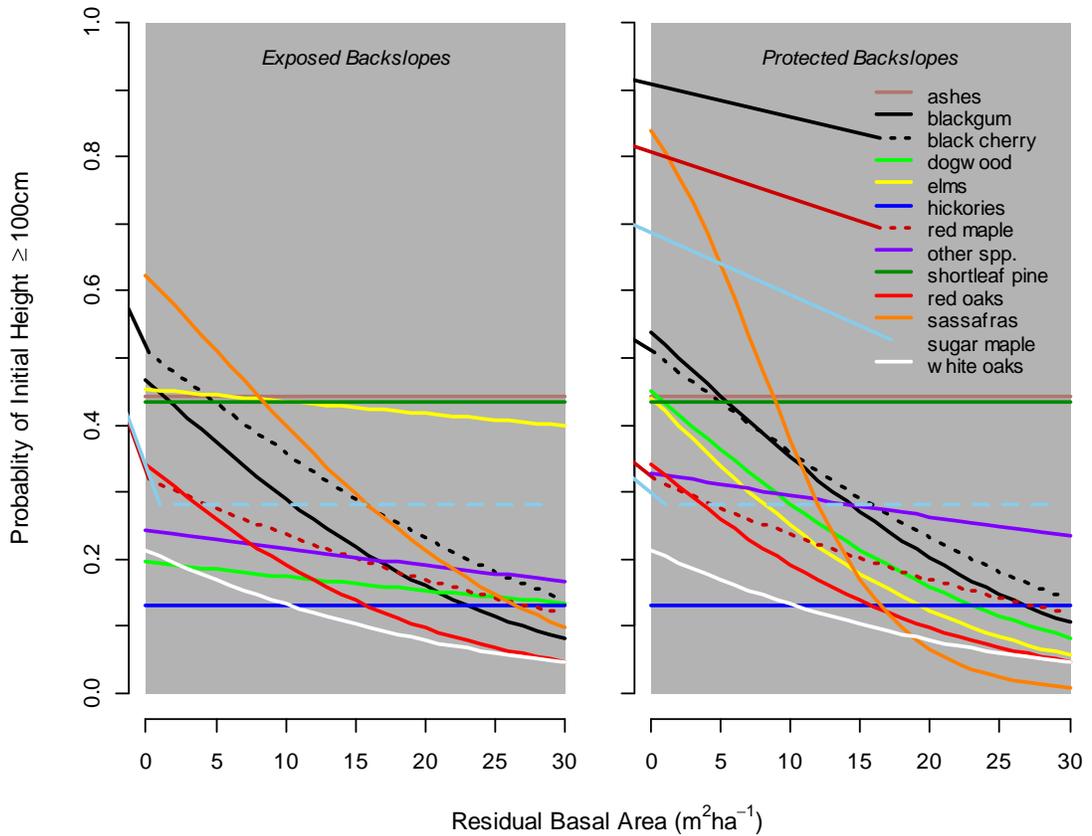


Figure 2.5. Probability of initial height $\geq 100\text{cm}$ for new reproduction (non-sprout origin) as a function of residual overstory density and site class in the Missouri Ozarks for reproduction. Curves are drawn using the probabilistic models and parameters from Table 2.10. Curves on the left column depict probabilities for initial height $\geq 100\text{cm}$ on exposed backslopes ($X_2 = 0$); whereas, curves on the right column depict probabilities for initial height $\geq 100\text{cm}$ on protected backslopes ($X_2 = 1$). All sprout-origin stems in the dataset were $\geq 100\text{cm}$ at year 3.

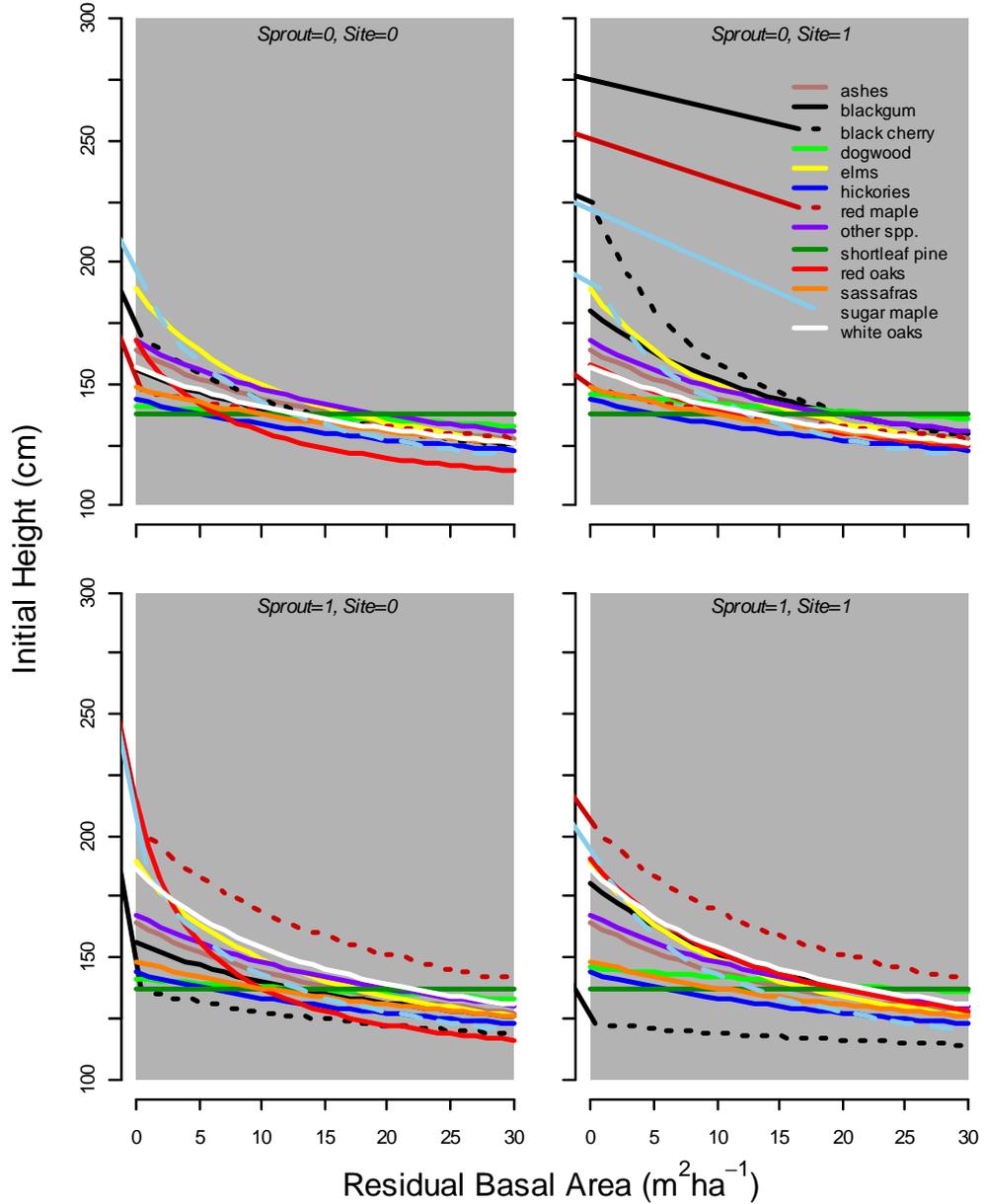


Figure 2.6. Mean initial height for new reproduction (height ≥ 100 cm) as a function of residual overstory density, stem origin, and site class in the Missouri Ozarks. Curves are drawn using the initial height models and parameters from Table 2.11. Because those models were fit with 100cm subtracted from the initial height, 100cm was added to the estimates here. Curves on the top row depict mean initial height for non-sprout origin stems ($X_2 = 0$); whereas, curves on the bottom row depict mean initial height for sprout origin stems ($X_2 = 1$). Curves on the left column depict mean initial height on exposed backslopes ($X_3 = 0$); whereas, curves on the right column depict mean initial height on protected backslopes ($X_3 = 1$).

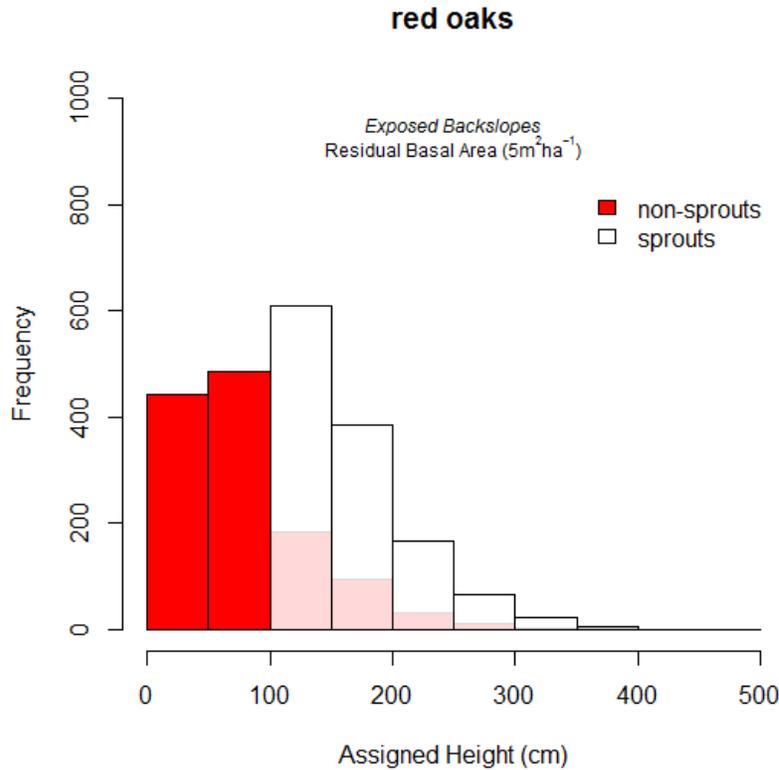


Figure 2.7. Stochastic height assignment example for red oaks in the Missouri Ozarks at three years post-disturbance. The example height distributions are 1250 sprout origin and 1250 non-sprout origin red oaks on exposed backslopes with a residual overstory density of $5\text{m}^2\text{ha}^{-1}$. All sprouts were $\geq 100\text{cm}$. The probability that an individual non-sprout origin red oak was $\geq 100\text{cm}$ three years post-disturbance was obtained from the parameters in Table 2.10. For individuals probabilistically determined to have a height $< 100\text{cm}$, a height between 1 and 99.9cm was assigned using a random uniform distribution. For individuals probabilistically determined to have a height $\geq 100\text{cm}$, a random deviate was drawn from a Gamma distribution by converting the estimates of μ and ϕ from the height models in Table 2.11 to the shape and scale parameters of the Gamma distribution as follows: Shape = ϕ^{-1} , Scale = ϕ/μ^{-1} . The expected values (μ) for red oaks in this scenario was 42.02cm for non-sprouts and 56.5cm for sprouts, which produced a Scale parameter of 24.5 for non-sprouts ($0.583/42.02^{-1}$) and 32.94 for sprouts ($0.583/56.5^{-1}$). The Shape parameter for both sprouts and non-sprouts was 1.71 (0.583^{-1}). Because 100cm was subtracted during the model fitting process to obtain the expected values (μ) in Table 2.11, 100cm was added to each random deviate produced by the Gamma distribution.

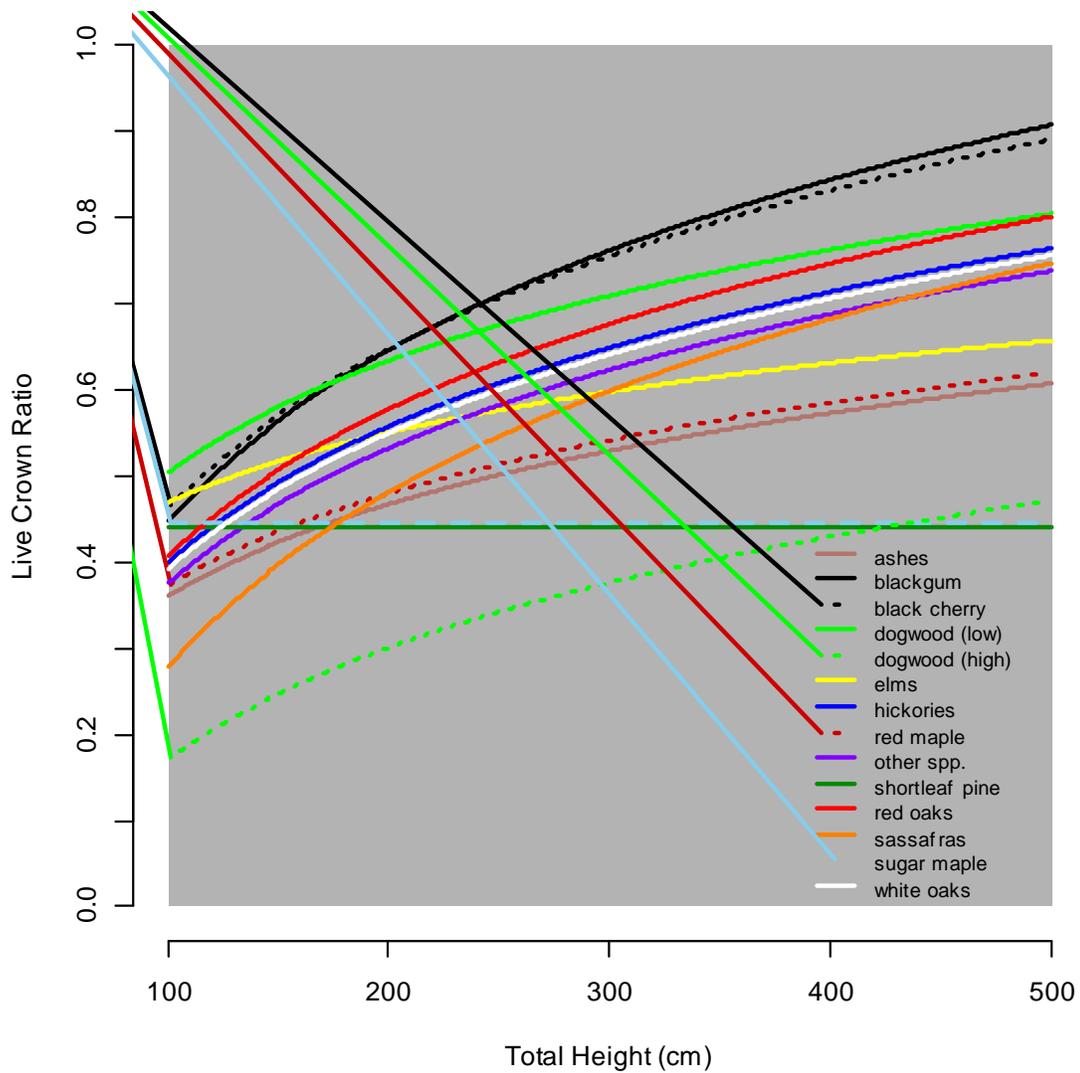


Figure 2.8. Mean initial live crown ratio for new stems (height ≥ 100 cm) as a function of total height and residual overstory density in the Missouri Ozarks. Curves are drawn using the initial live crown ratio models and parameters from Table 2.12. There are two curves for dogwood, one depicting live crown ratio for low residual overstory density ($X_2 = 0\text{m}^2\text{ha}^{-1}$, solid line) and one depicting live crown ratio for high residual overstory density ($X_2 = 30\text{m}^2\text{ha}^{-1}$, broken line). Residual overstory density was only included in the “best” model for dogwood.

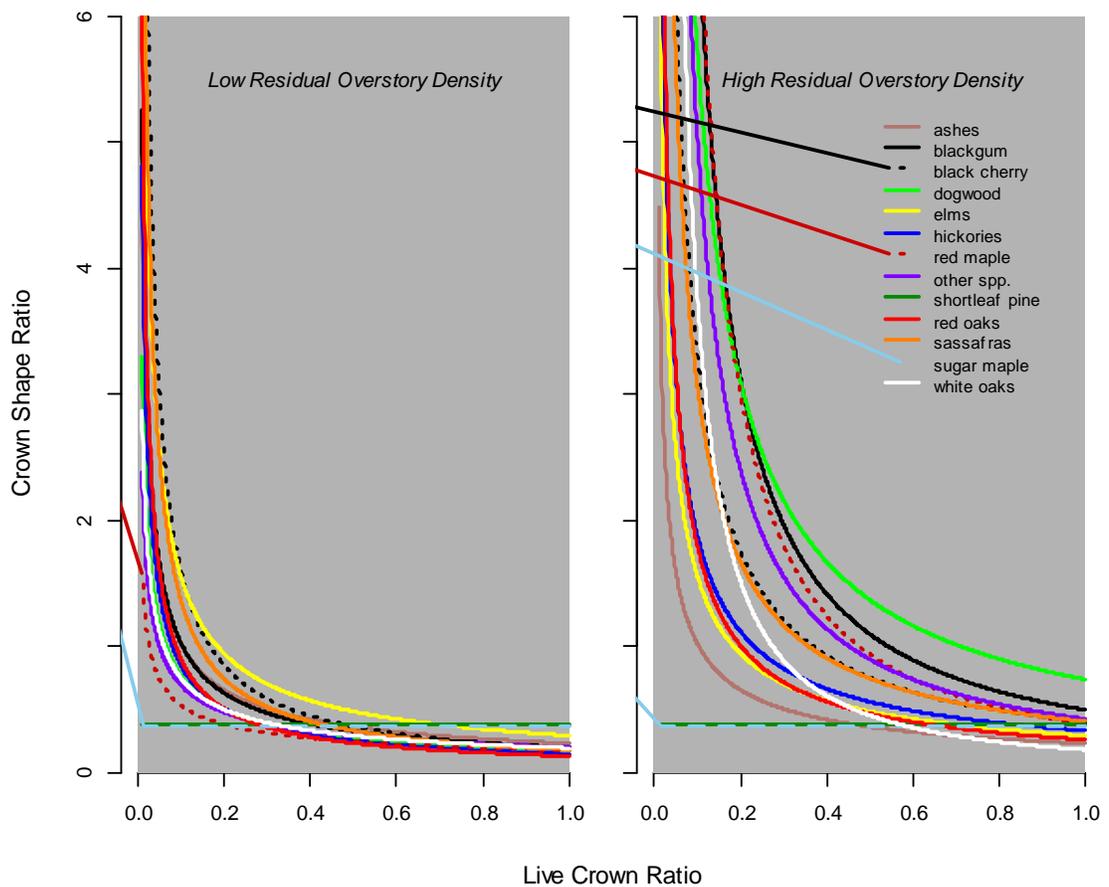


Figure 2.9. Mean crown shape ratio (crown radius/crown length) for trees of all sizes (height $\geq 100\text{cm}$) as a function of live crown ratio and residual overstory density in the Missouri Ozarks. Curves are drawn using the crown shape ratio models and parameters from Table 2.13. All species groups except shortleaf pine and sugar maple included live crown ratio (X_1) as a covariate. Only shortleaf pine, sugar maple, ashes, and elms did not include residual overstory density (X_2) as a covariate. The graph on the left depicts crown shape ratio for low residual overstory density ($X_2 = 0\text{m}^2\text{ha}^{-1}$), the graph on the right depicts crown shape ratio for high residual overstory density ($X_2 = 30\text{m}^2\text{ha}^{-1}$). Residual overstory density was included as a continuous covariate.

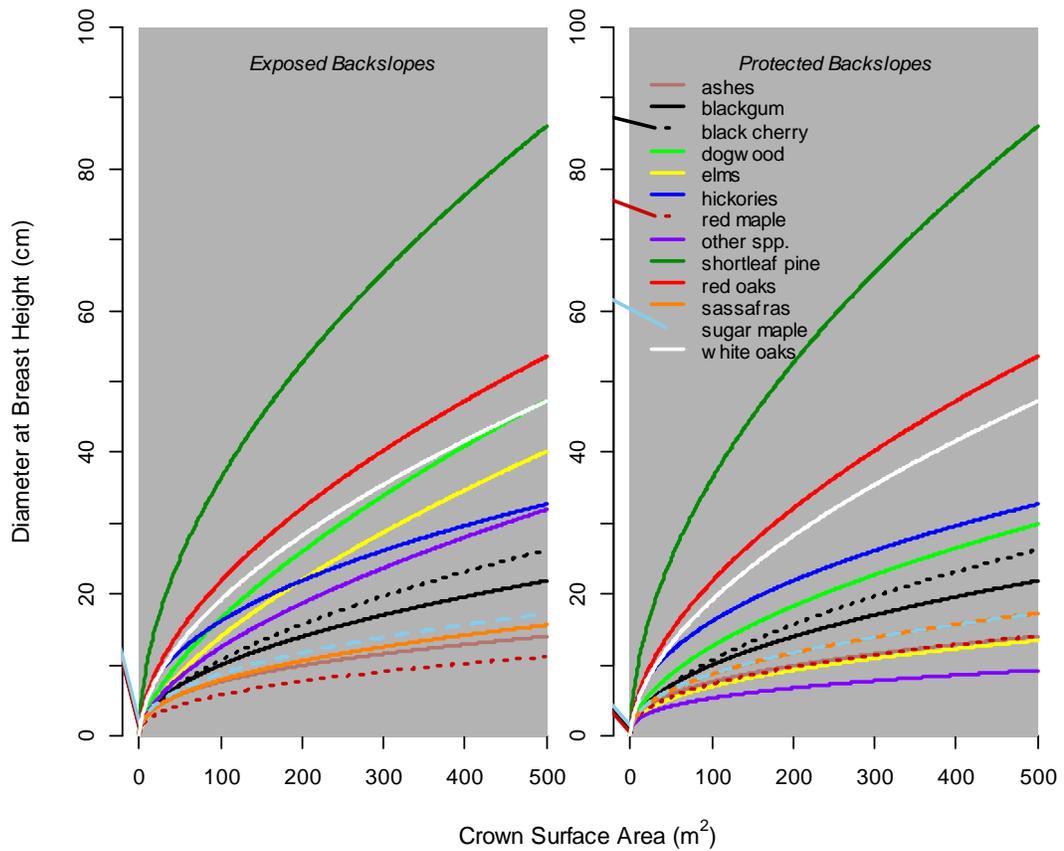


Figure 2.10. Mean diameter at breast height for trees of all sizes (height $\geq 137.5\text{cm}$) as a function of crown surface area and site class in the Missouri Ozarks. Curves are drawn using the models and parameters from Table 2.14. All species groups included crown surface area (X_1) as a covariate. Crown surface area was calculated as the lateral surface area of a paraboloid with radius and length equal to crown radius and crown length respectively. Only dogwood, elms, red maple, other species, and sassafras included site class (X_2) as a covariate. The graph on the left depicts diameter at breast height for exposed backslopes ($X_2 = 0$), the graph on the right depicts diameter at breast height for protected backslopes ($X_2 = 1$).

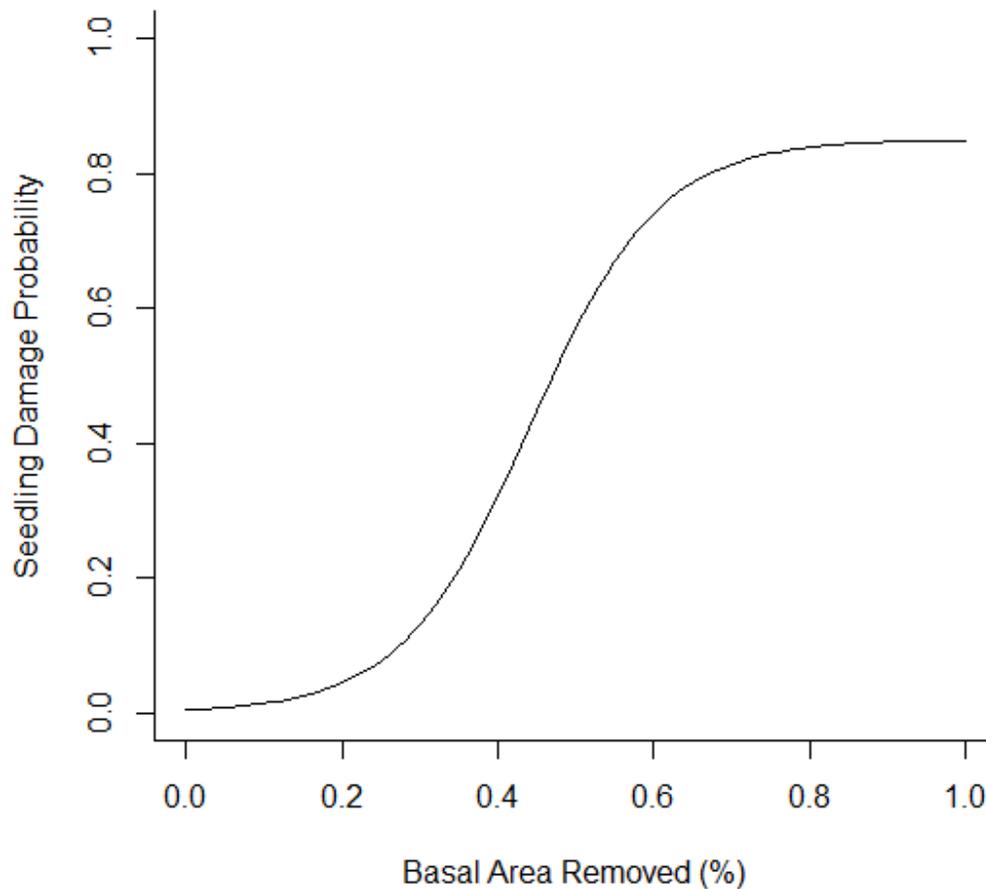
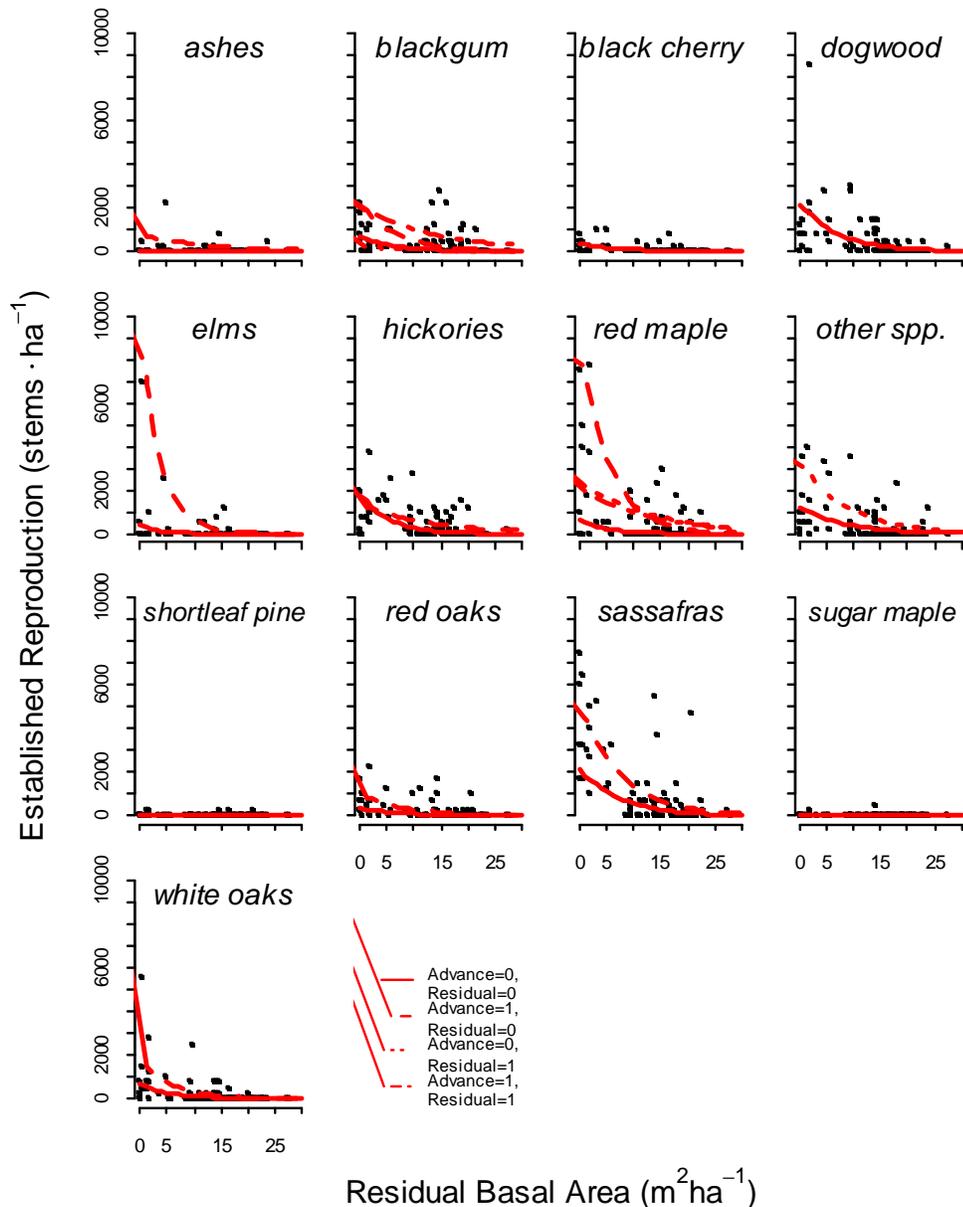


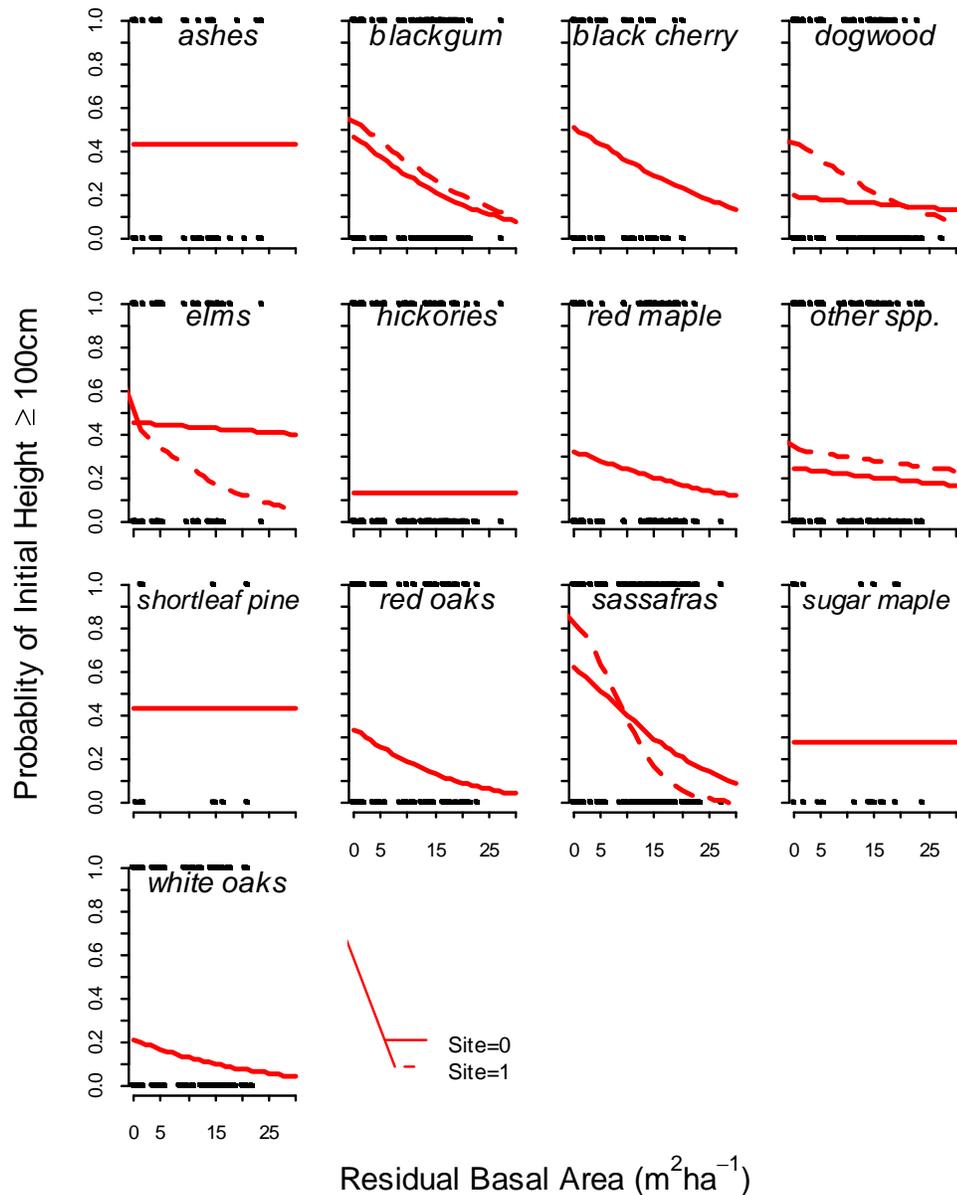
Figure 2.11. Assumption based function for determining the probability that an individual stem of large advance reproduction will be top-damaged in a disturbance in the Missouri Ozarks. The probability of top-damage is assumed to be a logistic function that increases with the proportion of overstory removed in the disturbance to an asymptote of 85%. This function is used to determine if an inventoried stem of advance reproduction will require new stem allometrically derived attributes (height, dbh, etc.) as a result of resprouting from top-damage experienced during the disturbance. This function is not based on empirical or published data and should be replaced when such information is available.

Appendix 2.1. Species included in the “other species” species group for models of reproduction establishment and allometric models.

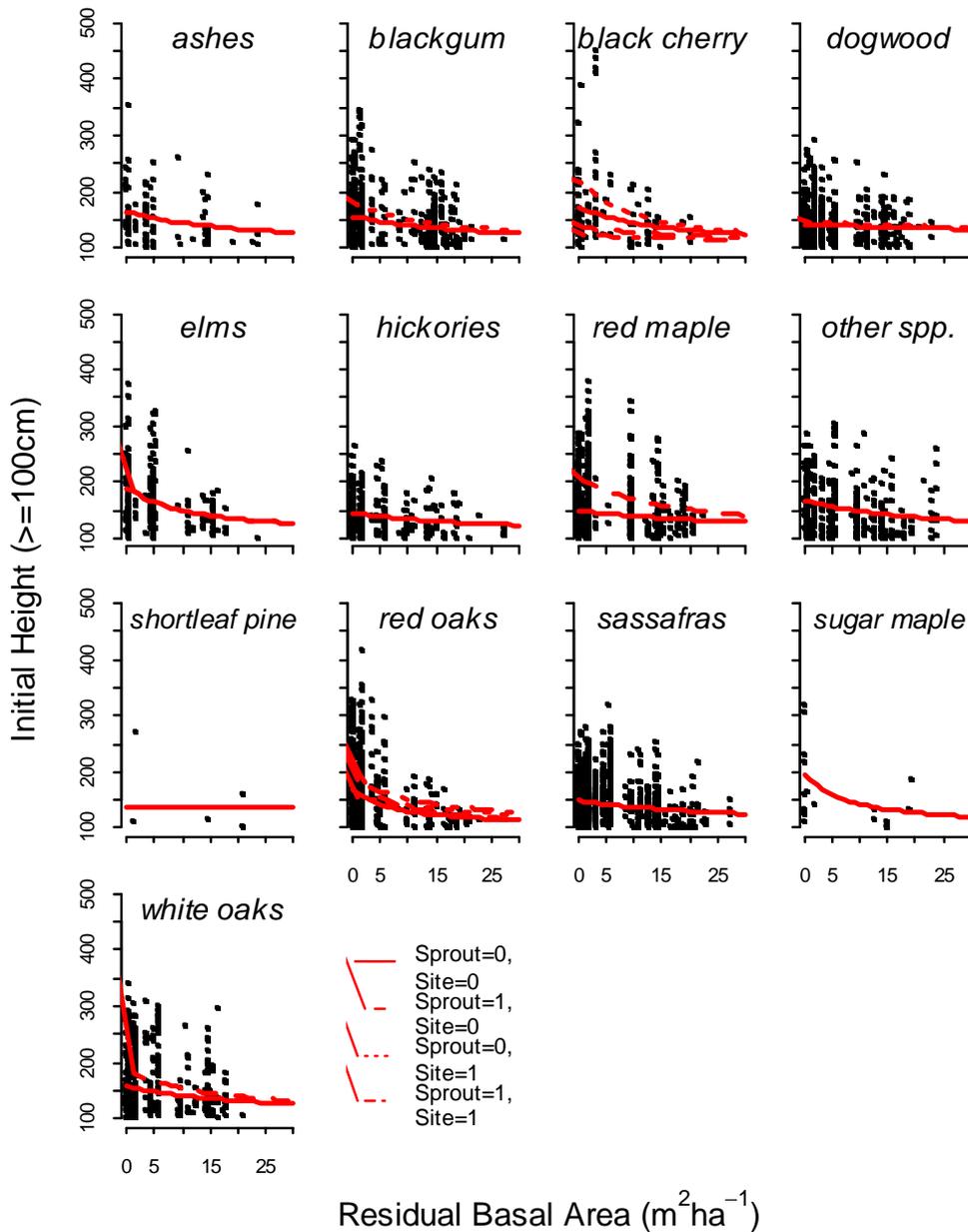
Acer negundo L.
Amelanchier arborea Michx.
Asimina triloba (L.) Dunal
Carpinus caroliniana Walt.
Celtis spp.
Cercis canadensis L.
Corylus americana Marshall
Crataegus spp.
Diospyros virginiana L.
Elaeagnus umbellata Thunb.
Gleditsia triacanthos L.
Gymnocladus dioica (L.) K. Koch.
Juglans nigra L.
Juniperus virginiana L.
Lindera benzoin L.
Morus spp.
Ostrya virginiana Mill.
Platanus occidentalis L.
Prunus americana Marshall
Rhamnus caroliniana Walt.
Rhus spp.
Robinia pseudoacacia L.
Sideroxylon lanuginose Michx.
Vaccinium spp.
Viburnum spp.
Unknown



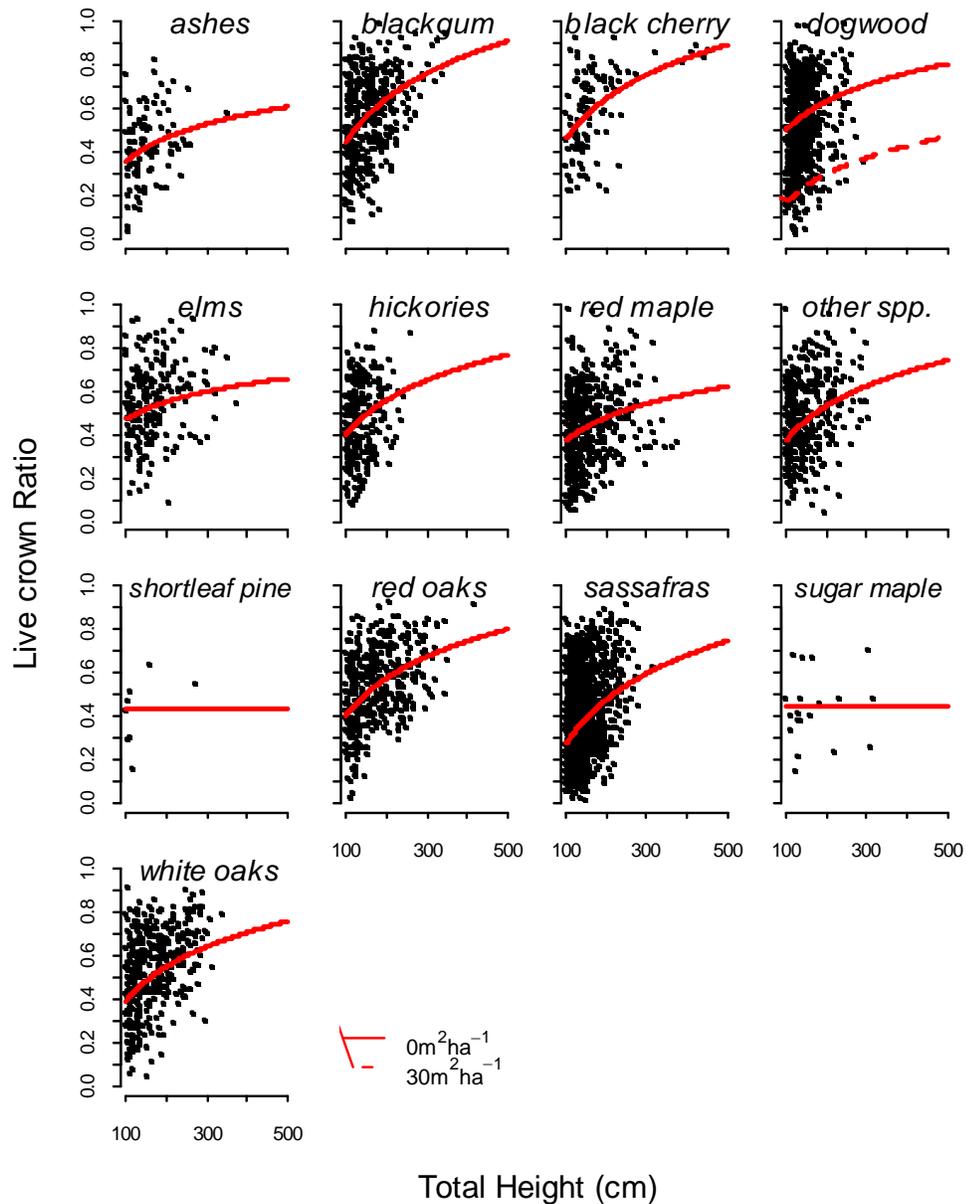
Appendix 2.2. Scattergraph of mean reproduction establishment in the Missouri Ozarks as a function of residual overstory density, presence of advance reproduction, and presence of a residual seed source. Curves are drawn using the establishment models and parameters from Table 2.9 multiplied by 250 to obtain stems·ha⁻¹. Solid line depicts establishment without advance reproduction ($X_2 = 0$) and without a residual seed source ($X_3 = 0$). Coarse broken line depicts establishment with advance reproduction ($X_2 = 1$) but without a residual seed source ($X_3 = 0$). Fine broken line depicts establishment without advance reproduction ($X_2 = 0$) but with a residual seed source ($X_3 = 1$). Variable broken line depicts establishment with advance reproduction ($X_2 = 1$) and with a residual seed source ($X_3 = 0$).



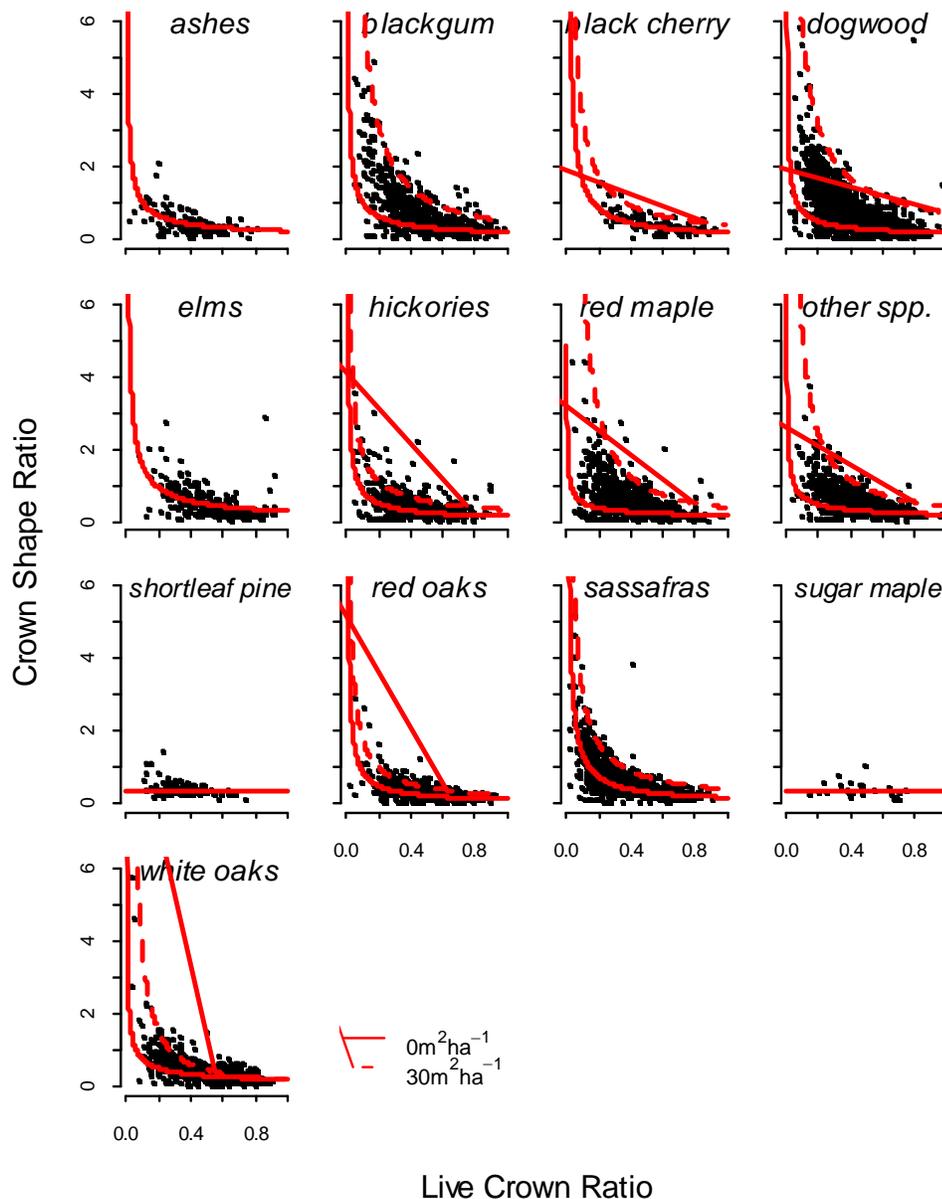
Appendix 2.3. Scattergraph of probability of initial height $\geq 100\text{cm}$ for new reproduction (non-sprout origin) as a function of residual overstory density and site class in the Missouri Ozarks for reproduction. Curves are drawn using the probabilistic models and parameters from Table 2.10. Curves on the left column depict probabilities for initial height $\geq 100\text{cm}$ on exposed backslopes ($X_2 = 0$) or grand mean if site was not included in “best” models; whereas, curves on the right column depict probabilities for initial height $\geq 100\text{cm}$ on protected backslopes ($X_2 = 1$). All sprout-origin stems in the dataset were $\geq 100\text{cm}$ at year 3.



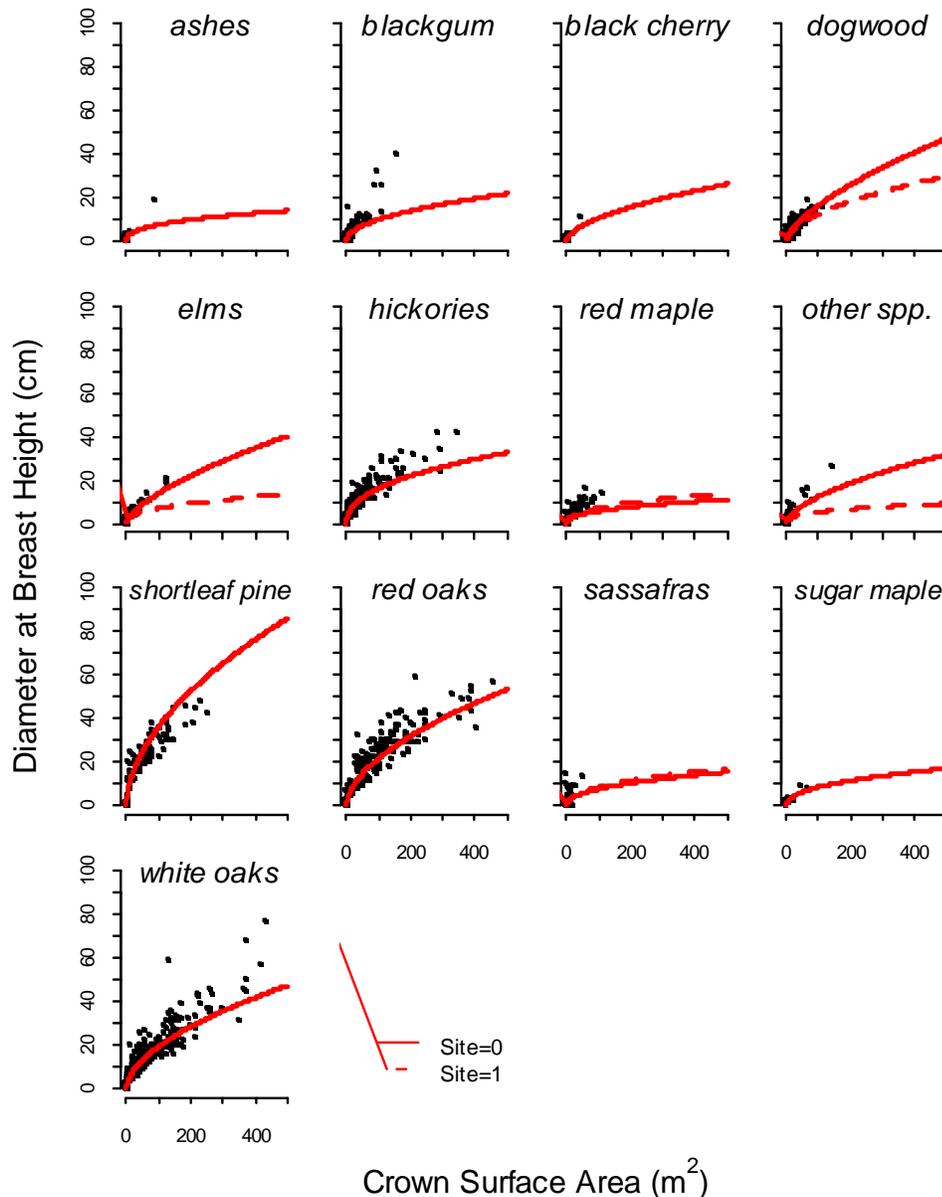
Appendix 2.4. Scattergraph of mean initial height for new reproduction (height $\geq 100\text{cm}$) as a function of residual overstory density, stem origin, and site class in the Missouri Ozarks. Curves are drawn using the initial height models and parameters from Table 2.11. Because those models were fit with 100cm subtracted from the initial height, 100cm was added to the estimates here. Solid line depicts mean initial height for non-sprout origin stems ($X_2 = 0$) on exposed backslopes ($X_3 = 0$). Coarse broken line depicts mean initial height for sprout origin stems ($X_2 = 1$) on exposed backslopes ($X_3 = 0$). Fine broken line depicts mean initial height for non-sprout origin stems ($X_2 = 0$) on protected backslopes ($X_3 = 1$). Variable broken line depicts mean initial height for sprout origin stems ($X_2 = 1$) on protected backslopes ($X_3 = 0$).



Appendix 2.5. Scattergraph of mean initial live crown ratio for new stems (height ≥ 100 cm) as a function of total height and residual overstory density in the Missouri Ozarks. Curves are drawn using the initial live crown ratio models and parameters from Table 2.12. There are two curves for dogwood, one depicting live crown ratio for low residual overstory density ($X_2 = 0\text{m}^2\text{ha}^{-1}$, solid line) and one depicting live crown ratio for high residual overstory density ($X_2 = 30\text{m}^2\text{ha}^{-1}$, broken line). Residual overstory density was only included as a continuous variable in the “best” model for dogwood.



Appendix 2.6. Mean crown shape ratio (crown radius/crown length) for trees of all sizes (height $\geq 100\text{cm}$) as a function of live crown ratio and residual overstory density in the Missouri Ozarks. Curves are drawn using the crown shape ratio models and parameters from Table 2.13. All species groups except shortleaf pine and sugar maple included live crown ratio (X_1) as a covariate. Only shortleaf pine, sugar maple, ashes, and elms did not include residual overstory density (X_2) as a covariate. Solid lines depict crown shape ratio for low residual overstory density ($X_2 = 0\text{m}^2\text{ha}^{-1}$) or grand mean if residual overstory density was not included in the “best” model, broken lines depict crown shape ratio for high residual overstory density ($X_2 = 30\text{m}^2\text{ha}^{-1}$). Residual overstory density was included as a continuous covariate.



Appendix. 2.7. Scattergraph of diameter at breast height for trees of all sizes (height ≥ 137.5 cm) as a function of crown surface area and site class in the Missouri Ozarks. Curves are drawn using the models and parameters from Table 2.14. All species groups included crown surface area (X_1) as a covariate. Crown surface area was calculated as the lateral surface area of a paraboloid with radius and length equal to crown radius and crown length respectively. Only dogwood, elms, red maple, other species, and sassafras included site class (X_2) as a covariate. Solid lines depict diameter at breast height for exposed backslopes ($X_2 = 0$) or combined if site was not included in the “best” model, broken lines depict diameter at breast height for protected backslopes ($X_2 = 1$).

Chapter 3:

The Impact of Overstory Density on Sapling Height Growth in the Missouri Ozarks – Implications for Interspecific Differentiation during Canopy Recruitment

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C. Dey

Abstract

Successful canopy recruitment is one of the most important components of sustainable forestry practices. For many desirable species in oak-dominated forests, insufficient sapling growth is a common limitation to successful recruitment. The objectives of this study were to 1) examine the impact of overstory density on sapling growth in the Missouri Ozarks, 2) investigate the potential for overstory retention to promote compositional shifts via interspecific differences in sapling height growth, and 3) compare the use of mean and near maximum growth rates to quantify the impact of overstory density on sapling growth and height differentiation among species. We found that periodic annual height increment of saplings decreased with increasing overstory density for all species groups in this study (red oaks, white oaks, hickories, sassafras, blackgum, dogwood, red maple, ashes, and elms). There was evidence of interspecific differentiation in growth rates during the sapling stage and the observed differences were more pronounced at low overstory densities. Increasing overstory densities reduced or eliminated the differences in growth among species. Although red oaks displayed the greatest maximum growth rates of all species under low overstory densities ($< 5\text{m}^2\text{ha}^{-1}$), the growth advantage of red oaks was reduced with increasing overstory density. This may provide opportunities to shift species composition toward white oaks using partial harvesting regimes in the Missouri Ozarks. However, white oaks had little to no advantage in height growth over many competing species when overstory density exceeded about $10\text{m}^2\text{ha}^{-1}$. This implies that the probability of recruitment

under overstory densities greater than about $10\text{m}^2\text{ha}^{-1}$ is likely to decline for all oaks in the Missouri Ozarks. We found that using the 90th quantile of height growth rates to evaluate the impact of overstory density on sapling growth had two potential advantages over using the mean growth rate: 1) better models of the limiting effects of overstory density on sapling height growth, 2) focused on the growth rates of stems that were most likely to recruit into the canopy.

Keywords: silviculture, regeneration, recruitment, differentiation, quantile

Introduction

Regeneration and canopy recruitment are two vital ecosystem processes necessary for sustainable forestry (Dey 2014). Unfortunately, difficulties and failures to regenerate economically or ecologically important species are common in many forest ecosystems. Although these regeneration failures can result from inadequacies in seed production or poor seedling establishment, insufficient sapling recruitment into the canopy is also a major cause (Clark *et al.* 1999, Coates 2002, Peet and Christensen 1987).

Saplings compete with the overstory for space and resources both above and below ground (Horn 1985). The density, structure, and composition of the overstory has an influence on the quantity and quality of light reaching the forest floor (Canham *et al.* 1994, Larsen and Kershaw 1996), and the availability of water and nutrients (Coomes and Grubb 2000). Resource availability, in turn, affects the abundance, survival, and growth of saplings (*e.g.*, Kneeshaw *et al.* 2006, Kobe *et al.* 1995, Pacala *et al.* 1994). Consequently, the density of the regeneration layer is often reduced as resource competition intensifies among saplings, but the cohort may be eliminated altogether depending on the magnitude of release provided by canopy disturbance (Oliver and Larson 1996).

Successful canopy recruitment is largely disturbance-driven, and there have been several efforts to organize disturbance response patterns into a framework that offers insight into the suitability of a species to certain environmental conditions (*e.g.*, MacArthur and Wilson 1967, Noble and Slatyer 1980, Grime

2006). Yet, despite numerous investigations into the impacts of resource limitation on canopy recruitment, consensus is lacking on the relative importance of the underlying physiological mechanisms involved (Coomes and Grubb 2000, Valladares and Niinemets 2008). Stem analyses suggest that successful recruits typically do not experience suppression during their ascent into the canopy (Landis and Peart 2005). Faster-growing saplings generally have lower risk of mortality (Kobe *et al.* 1995) and are more likely to capture available growing space (Loftis 1990a, Dey *et al.* 1996). Individuals that successfully differentiate from their peers in stature often benefit from the advantages of asymmetric competition (Schwinning and Weiner 1998, Weiner 1990).

However, rate of growth, *per se*, may not be an entirely sufficient predictor of successful recruitment unless it provides a lasting advantage in relative stature among co-occurring species with differences in life histories (Clatterbuck and Hodges 1988). Moreover, growth is only beneficial to the extent that resource availability and/or efficiency exceed respiration costs (Givnish 1988, Messier *et al.* 1999). Tradeoffs between rapid growth with abundant resources and survival with scarce resources for many species suggest that efficiency and persistence should be favored as delays in recruitment extend exposure to suppression (Tilman 1982, Walters and Reich 2000). Thus, shade intolerant species are likely to exhibit growth reduction, carbon imbalance, frequent dieback, and increased mortality when recruitment is delayed due to insufficient release (Kobe *et al.* 1995, Poorter *et al.* 2005).

Increasingly, regeneration methods that leave a partial overstory are being favored throughout the United States. Concurrently, there has been increasing concern that widespread recruitment problems are leading to compositional shifts and reductions in oak importance across much of the eastern United States (e.g., Fei and Steiner 2007, Nowacki and Abrams 2008, Oliver *et al.* 2005). Because oak species (*Quercus* spp.) have historically been an important, and often dominant, component of these forests, this concern has prompted extensive research into the regeneration niche of many oak species (Johnson *et al.* 2009).

At one time, clearcutting followed by intermediate thinnings was advocated as the optimal method for maintaining oak-dominated forests in the Central Hardwood Forest Region (Roach and Gingrich 1968). However, clearcutting has led to oak recruitment failures on highly productive sites where intense and sustained competition from shade-intolerant species excludes oak saplings (Beck and Hooper 1986). Consequently, variations of shelterwood methods were developed to increase the relative performance of oak saplings by reducing the abundance and/or growth of competitors (e.g., Loftis 1990b, Brose *et al.* 1999). However, partial harvesting of oak dominated forests has allowed the proliferation of shade-tolerant species in some cases (e.g., Schuler 2004). This suggests that successful oak recruitment is a complex process that is dependent, in part, on stand structure and composition in addition to local site conditions.

Tree recruitment dynamics in the Missouri Ozarks may be rather unique compared with much of the eastern United States. The soils, climate, and flora throughout much of the Missouri Ozarks favor an oak-hickory (*Carya* spp.) forest

type by limiting the composition, stature, and/or longevity of potential competitors (Johnson *et al.* 2009). There are few long-lived, shade-intolerant species, and most shade-tolerant species are not capable of persisting through stand development to ascend into the canopy of mature forests (Dey *et al.* 1996). This phenomenon is believed to be due, in part, to relatively xeric conditions that provide opportunities for oaks to persist where less drought tolerant species cannot (Larsen and Johnson 1998). Consequently, several silvicultural systems may be appropriate to sustain oak-hickory forests in the Missouri Ozarks, including single-tree selection (Loewenstein *et al.* 2000). However, partial harvesting likely delays recruitment and may promote a successional shift from mixed oaks to predominantly white oaks in the Missouri Ozarks (Kabrick *et al.* 2008b).

To date, results from longitudinal studies suggest that the effects of varying levels of residual overstory density on recruitment dynamics in oak-dominated forests are not yet fully understood (Kabrick *et al.* 2008b, Atwood *et al.* 2011, Schweitzer and Dey 2011). Moreover, there is some uncertainty regarding how the effects of overstory density on recruitment should be quantified (Oliver *et al.* 2005). Overstory density is highly influential on sapling populations, but growth can be constrained by several limiting factors (Canham *et al.* 1996, Niinemets and Valladares 2006). Because of this complexity, when growth is plotted as a function of a single limiting factor, the resulting graph is often a scatter of points with increasing or decreasing variance (heteroscedasticity) with a conspicuous upper boundary (Cade *et al.* 1999, Kaiser *et al.* 1994). Although the means of

such distributions are informative, an alternative is to use the maxima which may provide a more ecologically meaningful description of the effect of a single limiting factor in the presence of many (Cade *et al.* 1999). In addition, individuals that are most likely to be lasting participants in the recruitment process often exhibit above average growth (Landis and Peart 2005, Oliver *et al.* 2005). This provides opportunities for differentiation in stature, domination of neighbors, and continued ascent towards the canopy (Oliver and Larson 1996, Schwinning and Weiner 1998, Weiner 1990). Thus, the maxima of growth-resource relationships are likely to better represent the growth displayed by successful canopy recruits.

Applying knowledge of physiological and ecological principles to simultaneously meet regeneration and multiple-use objectives is a hallmark of scientific forest management, but changes in community composition, structure, and function should be intentional and well-reasoned. The ability to quantify and understand the competitive dynamics that result in successful recruitment and dominance of desired species is essential to prevent unintended shifts in forest composition and ecosystem function. Therefore, the objectives of this study are to: 1) examine the effect of overstory density on sapling growth in the Missouri Ozarks, 2) investigate the potential for overstory retention to promote shifts in composition via interspecific differences in sapling height growth, and 3) compare the use of mean and near maximum growth rates to quantify the impact of overstory density on sapling growth and height differentiation among species..

Methods

The data used in this study were collected from the Missouri Ozark Forest Ecosystem Project (MOFEP), which encompasses more than 3700 hectares within the Current River watershed in Carter, Reynolds, and Shannon Counties of southeastern Missouri. The study region is an unglaciated, deeply dissected plateau primarily comprising Ordovician and Cambrian dolomites and sandstones (Kabrick *et al.* 2000). Average annual precipitation is 115 cm and average annual temperature is 13.5° C (Kabrick *et al.* 2008b). Slope aspect and slope position are important characteristics used for site classification in the region (Nigh *et al.* 2000). The sites used in this study were on exposed (aspect: 136 - 315°) and protected (aspect: 316 - 136°) backslopes with an average site index (*Quercus velutina* Lam., base age 50) of 21.0 ± 1.3m and 22.0 ± 1.1m, respectively (McQuilkin 1974). Overstory species composition on both site classes are heavily dominated (>70% basal area) by oak species (primarily *Q. velutina*, *Q. alba* L., *Q. coccinea* Münchh., *Q. stellata* Wangenh.) and compositional differences between the two site classes are subtle (Kabrick *et al.* 2004). Protected backslopes usually have a slightly higher *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* Mill. are more common on exposed backslopes (Kabrick *et al.* 2004). Shifley and Brookshire (2000) provide a detailed documentation of the abundance and diversity of species found on MOFEP.

MOFEP is a long-term, landscape-scale experiment initiated in 1989 by the Missouri Department of Conservation (MDC) to evaluate the effects of forest management on ecosystem composition, structure, and function within the

Missouri Ozark Highlands (Brookshire and Shifley 1997). The forest management systems under evaluation at MOFEP include even-aged, uneven-aged, and no-harvest management. The even-aged treatments included clearcutting with reserves ($\sim 5\text{m}^2\text{ha}^{-1}$) for stands to be regenerated and intermediate thinning elsewhere, as prescribed by Roach and Gingrich (1968). In the clearcut stands, all live trees $> 3\text{m}$ in total height or $> 4\text{cm}$ dbh were felled, with the exception of trees left as reserves (Missouri Department of Conservation 1986). The uneven-aged regime consisted of single-tree selection on a 15-year harvest cycle with group-openings that ranged from one to two tree heights (0.03-0.15ha) interspersed throughout and summed to 5% of the harvested land area, as prescribed by Law and Lorimer (1989). Areas designated for a no-harvest management regime were maintained as experimental controls. In 1996, stands were harvested and followed MDC Forest Land Management Guidelines (1986). For additional information on MOFEP, including study rationale, experimental design, site conditions, inventory methods, and early findings, see Brookshire and Shifley (1997), Shifley and Brookshire (2000), and Shifley and Kabrick (2002).

Woody overstory vegetation on MOFEP was sampled via 648 circular 0.2-ha permanent plots that were randomly located throughout the study area with the constraint that each stand must have at least one plot located therein. On these 0.2-ha plots, the dbh and species of trees $\geq 11\text{cm}$ dbh were recorded. The dbh and species of woody understory vegetation 4 - 11cm dbh was sampled on four 0.02-ha subplots nested within each 0.2-ha plot. A stratified random sample of

eighty-eight 0.02-ha understory subplots (17 that were clearcut, 23 that were thinned, 16 harvested with single-tree selection, 8 in group-openings, 24 in stands that were not harvested), equally allocated to exposed and protected backslopes, received measurements additional to those described above. Due to the random determination of plot locations, the proportion of a subplot occupied by a group opening or single-tree gap varied. On the eighty-eight subplots, the species, dbh (1.37m), and total height were recorded for all stems ≥ 1 m in 1999 (3 yrs post-treatment) and again in 2004 (8 yrs post-treatment). Other variables, including the apparent origin of stems (seed or sprout) were recorded, but these largely categorical data were not included in the analyses that follow.

Given the number of species included in this dataset, some species were grouped for analyses at the genera or sub-genera level. All species, genera, or sub-genera that had ≥ 100 trees in the dataset were included in our analyses. The nine species groups used in this study were: 1) red oaks (*Q. rubra* L., *Q. velutina*, *Q. coccinea*, *Q. marilandica* Münchh.), 2) white oaks (*Q. alba*, *Q. stellata*, *Q. muehlenbergii* Engelm.), 3) hickories (*Carya tomentosa* Sarg., *C. glabra* Mill., *C. ovata* (Mill.) K. Koch., *C. texana* Buckley, *C. cordiformis* (Wangenh.) K. Koch.), 4) sassafras (*Sassafras albidum* J. Presl.), 5) blackgum (*Nyssa sylvatica* Marsh.), 6) dogwood (*Cornus florida* L.), 7) red maple (*Acer rubrum* L.), 8) ashes (*Fraxinus americana* L., *F. pennsylvanica* Marsh.), and 9) elms (*Ulmus alata* Michx., *U. rubra* Muhl., *U. americana* L.). Within the red oaks group, *Q. velutina* (75% TPHa) and *Q. coccinea* (23%) were the most common species. *Q. alba* (86%) and *Q. stellata* (12%) were the most common species in

the white oaks group. *C. texana* (45%), *C. tomentosa* (34%), and *C. glabra* (20%) were the major components of the hickories group. *F. americana* (94%) was the most common species in the ashes group and *U. alata* (58%) and *U. rubra* (34%) were the most common elms.

The response variable analyzed in this study was periodic annual height increment (PAI_{HT}) of saplings (trees > 1m tall, \leq 5cm dbh). PAI_{HT} was calculated as the mean annual height increment between the 1999 and 2004 measurements. Only stems that were alive at both measurement intervals and had a $PAI_{HT} \geq 0$ were included in our analyses. The random location of the study plots and variability in post-treatment overstory densities offered a gradient to estimate the effects of overstory density on sapling PAI_{HT} (Table 3.1, Fig. 3.1). PAI_{HT} was calculated from the trees within the 0.02-ha understory subplots, whereas, overstory density (basal area per hectare of stems \geq 11.5cm dbh) was calculated from the 0.2-ha overstory plot that each understory subplot was nested within. Although overstory basal area is an imperfect descriptor of stand density, it is widely used in silvicultural prescriptions because it is simple to measure. Overstory basal area is strongly correlated with canopy openness in the Missouri Ozarks (Blizzard *et al.* 2013), and has proven a useful indicator of the competitive pressure exerted by overstory trees in other locales (Biging and Dobbertin 1995, Lorimer 1983).

Plots of PAI_{HT} vs overstory basal area suggested that there was an exponential decline in growth with increasing overstory basal area (Fig. 3.1). Eight variants of a negative exponential function were used as candidate models to describe

this relationship (Table 3.2). Model I was a basic negative exponential model with only an intercept (a) and decay parameter (b) used to estimate the reduction in sapling growth (PAI_{HT}) as a function of increasing overstory basal area (x_1). It was expected that site differences between exposed and protected backslopes would impact sapling growth, thus models II, III, and IV incorporated site effects in different ways. Model II posits that differences in site have the greatest influence on sapling growth in the absence of overstory competition and includes a parameter (s_2) and indicator variable (x_2) for site class (0 for exposed backslopes, 1 for protected backslopes) with the intercept parameter of the basic model. Model III posits that differences in site have the greatest influence on the rate that sapling growth declines with increasing overstory competition and includes a parameter (s_3) and indicator variable (x_2) for site class with the decay parameter of the basic model. Model IV posits that differences in site influence growth through both the mechanisms described in model II and III and therefore includes site parameters and indicator variables with both the intercept and decay parameters of the basic model.

There was evidence of a nonlinear relationship between initial sapling height and PAI_{HT} in this dataset. Although there is clear biological precedent for such relationships (Weiner and Thomas 2001), differences in sapling establishment dates between clearcut subplots and partial or no-harvest subplots also likely contributed to perceived “size” effects on PAI_{HT} . At the beginning of the study period, the maximum initial height of saplings in the clearcut subplots, which were three years post-harvest at the start of the study period, was about 4.5m.

Saplings in the partial- and no-harvest subplots may have established several years earlier than the study period and therefore had a broader range of initial heights. Models of periodic growth (absolute or relative) that do not appropriately account for initial size may be subject to bias (MacFarlane and Kobe 2006). Thus, the effect of initial height was parameterized by including an initial height covariate (x_3) and exponent (θ) parameter (Pacala *et al.* 1994, MacFarlane and Kobe 2006) to all models described above, resulting in models i, ii, iii, and iv listed in Table 3.2.

Parameter estimates for mean PAI_{HT} were obtained via the generalized nonlinear least squares function (GNLS) within the NLME package (Pinheiro *et al.* 2011) in R version 2.13.0 (R Development Core Team 2011). Generalized nonlinear least squares extend nonlinear regression by allowing for correlated errors and/or non-constant variance (Pinheiro and Bates 2000). In this dataset, variance was clearly non-constant and was modeled as a power function of the conditional mean. The data were structured as repeated measurements (trees) in space (subplot), making it likely that trees on the same subplot had correlated errors. Thus, a compound symmetric covariance structure was incorporated to account for within-subplot error correlation.

Nonlinear quantile regression (Koenker 2005) was used to model the near-maxima of the growth-resource distributions in this study (Cade and Noon 2003). Quantile regression allows estimation of conditional quantiles (e.g., 25th, 50th, 75th, etc.) instead of the conditional mean of a response variable as a function of covariates (Koenker 2005). The maximum quantile that can be estimated

precisely varies with sample size and data distribution; thus, estimates of the absolute maxima (e.g., 99th quantile) may not be reliable without very large samples due to potential for bias from measurement error and other sources (Cade *et al.* 1999). To avoid limitations due to sample size, the 90th quantile was chosen to represent the near-maxima (PAI_{HT-Q90}). Parameter estimates for the quantile regression analyses were obtained via the nonlinear quantile regression function (NLRQ) within the QUANTREG package (Koenker 2012) in R version 2.13.0 (R Development Core Team 2011).

The candidate models were compared using Akaike's Information Criterion (AICc) corrected for small sample sizes (Burnham and Anderson 1998). For a species group, the model with the lowest AICc value was selected as the "best" model among those considered (Burnham and Anderson 1998). Goodness of fit for the best models was calculated using the square of Pearson's correlation coefficient (r^2) of predicted values against observed values. Paired bootstrapping (2000 iterations, percentile method) was used to construct pointwise 95% confidence bands (Harrell 2001) for the best models of both mean and near-max PAI_{HT} . These confidence bands were used for visual statistical inference among groups. Non-overlapping confidence bands indicate statistical differences among groups at a significance level ≤ 0.05 (*i.e.*, $\alpha \leq 0.05$), although statistical differences may also exist where confidence bands overlap slightly.

Results

The best models (according to lowest AICc) explained between 28 and 55 percent of the variation in mean PAI_{HT} (r^2 , Table 3.3). Initial sapling height was a significant predictor of mean PAI_{HT} for all species groups. There was considerable uncertainty in parameter estimates for some species, particularly the parameters associated with site productivity. The best models of mean PAI_{HT} for all species groups included one or more parameter(s) to account for differences between exposed and protected backslopes. Sassafras, blackgum, red maple, and elms were best represented by model iv, which included a site modifier for both the intercept and decay parameters. Red oaks, white oaks, hickories, and dogwood were best represented by model ii, which included a site modifier for only the intercept parameter. Ashes were best represented by model iii which included a site modifier to the decay parameter only.

The parameter estimate for initial sapling height (θ) varied among species (Table 3.3). For all species θ was positive but < 1 which indicated that larger stems had an advantage over smaller stems (Fig. 3.2), but the magnitude per unit size diminished with increasing size (MacFarlane and Kobe 2006). The growth advantage exhibited by larger saplings was greatest at low overstory densities and diminished considerably with increasing overstory density (Fig. 3.2).

Periodic annual height increment of saplings decreased within increasing overstory density for all species groups (Fig. 3.3). As overstory density increased, decreases in mean PAI_{HT} were similar among most species except sassafras and red maple on exposed backslopes, which declined less in growth rate than the other species. Few changes in rank occurred amongst species as

mean PAI_{HT} converged with increasing overstory density. The range of separation in mean PAI_{HT} among all species groups was about $50\text{cm}\cdot\text{yr}^{-1}$ with no residual overstory and was reduced to about $25\text{cm}\cdot\text{yr}^{-1}$ at the highest densities in this study ($30\text{m}^2\text{ha}^{-1}$). There was evidence of differentiation among species groups in mean PAI_{HT} at the lowest levels of overstory density and on exposed backslopes, particularly for those that occupy different strata in mature forests in the Missouri Ozarks. Oaks exhibited an advantage over many species at low overstory densities but the difference decreased with increasing overstory density.

In general, mean PAI_{HT} was somewhat greater on protected than exposed backslopes for most species groups (Fig. 3.3). However, the increases in mean PAI_{HT} related to slope aspect were only statistically significant for sassafras (s_1 Table 3.3). Red maple and elms exhibited considerable, but nominal increases in mean PAI_{HT} at low overstory densities as site quality increased. In contrast, blackgum and dogwood were much less competitive on protected backslopes, particularly at low overstory densities. According to the site parameter estimates, mean PAI_{HT} for blackgum and dogwood was lower (nominally for blackgum) on protected than exposed backslopes, but the rank changes across site classes was driven more by greater mean PAI_{HT} for sassafras, red maple, elm than lower mean PAI_{HT} for blackgum and dogwood (s_1 , Table 3.3). Ashes and blackgum exhibited nominally lower reductions in mean PAI_{HT} as overstory density increased on protected backslopes than on exposed backslopes (s_2 , Table 3.3). Hickories exhibited modest, but nominal increases in mean PAI_{HT} at low

overstory densities on protected backslopes. Both red oaks and white oaks exhibited only slight nominal increases in mean PAI_{HT} at low overstory densities on protected backslopes.

The best models of near maximal growth using PAI_{HT-Q90} were more parsimonious than the models of mean PAI_{HT} (Table 3.4). Except for sassafras, the best model of PAI_{HT-Q90} was model I, which included only the intercept and scale parameters. The best model for sassafras (Model II) included a site modifier for the intercept. The interval estimates for the decay parameter (b , Table 3.4) largely overlapped across species groups and provided little evidence of species segregating into distinct tolerance classes related to growth decline at the sapling stage. PAI_{HT-Q90} of most species was reduced by half ($\ln(2) \cdot b$) between $10m^2ha^{-1}$ and $15m^2ha^{-1}$. Sassafras exhibited the greatest tolerance in growth to overstory density, reducing in growth by half at about $28m^2ha^{-1}$.

Quantile regression analyses of PAI_{HT-Q90} provided evidence of greater interspecific differentiation in sapling growth than was suggested by mean PAI_{HT} . Among species groups in this study, PAI_{HT-Q90} suggested a four- tiered growth hierarchy at low overstory densities. Red oaks were the fastest-growing species and exhibited significantly greater growth than all other species in the absence of an overstory (Fig. 3.4). The difference in PAI_{HT-Q90} between red oaks and the second tier, which included white oaks, hickories, red maple, and sassafras (protected aspects), was approximately $15cm \cdot yr^{-1}$. Red oaks were able to maintain a statistical advantage over the second tier only when overstory densities were $< \sim 5m^2ha^{-1}$. At low overstory densities, PAI_{HT-Q90} for red oaks was

approximately $40\text{cm}\cdot\text{yr}^{-1}$ greater than blackgum, ashes, elms, and sassafras (exposed aspects), which comprised the third tier of growth. Red oaks were statistically indistinguishable from the third tier once overstory density reached about $10\text{m}^2\text{ha}^{-1}$. The difference in $\text{PAI}_{\text{HT-Q90}}$ between red oak and dogwood (fourth tier) was greatest in the absence of an overstory ($\approx 50\text{cm}\cdot\text{yr}^{-1}$), but the difference decreased as overstory density increased and was only statistically significant below about $18\text{m}^2\text{ha}^{-1}$.

$\text{PAI}_{\text{HT-Q90}}$ for the second tier was significantly greater ($\approx 15\text{cm}\cdot\text{yr}^{-1}$) than the third tier without a residual overstory, but the two tiers were largely indistinguishable once overstory density exceeded about $5\text{m}^2\text{ha}^{-1}$. Dogwood had a $\text{PAI}_{\text{HT-Q90}}$ significantly lower than all other species when overstory density was less than about $5\text{m}^2\text{ha}^{-1}$. Beyond that threshold, dogwood and elms were statistically indistinguishable, and at overstory densities greater than about $20\text{m}^2\text{ha}^{-1}$ dogwood was only significantly different from sassafras, blackgum, and white oak.

Discussion

The influence of overstory density on recruitment is a critical component of community dynamics (Oliver and Larson 1996). We found that the method of statistical analysis was an important factor in quantifying and interpreting these dynamics. By placing greater emphasis on saplings with the best intraspecific growth rates, quantile regression analyses of $\text{PAI}_{\text{HT-Q90}}$ provided evidence of greater interspecific differentiation in sapling growth than was suggested by

mean PAI_{HT} . Moreover, AICc scores ranked the basic negative exponential models for PAI_{HT-Q90} better than the more complex models using quantile regression. In contrast, AICc scores ranked the more complex models better for the mean, supporting the notion that the maxima of growth-resource distributions provide more ecologically meaningful estimates of the effect of a single limiting factor in the presence of multiple limiting factors (Cade *et al.* 1999, Cade and Guo 2000). Growth differentiation is often difficult to quantify with traditional statistical procedures (*e.g.*, Oliver *et al.* 2005); our results support the use of quantile regression to quantify a more meaningful response by targeting the population of above-average performers that are most successful.

The species analyzed in this study span a range of reported shade tolerance (Baker 1949, Burns and Honkala 1990, Niinemets and Valladares 2006). The growth of all species declined as overstory density increased and the rate of decline differed among some species (parameter b , Table 3.4). Thus, there was some evidence of rank changes among species in the magnitude of growth along the gradient of overstory density analyzed in this study (Fig. 3.4). We found that overstory density affected the growth of sassafras the least. In fact, the overstory density at which growth was reduced by half for sassafras was almost double that of all other species (Table 3.4). Moreover, the magnitude of growth for sassafras became greater than most other species as overstory density increased, especially on protected backslopes (Fig. 3.4). Although sassafras is generally considered intolerant of shade, Bazzaz and others (1972) reported that sassafras was able to photosynthesize efficiently at low light intensities.

However, reliable recruitment of sassafras via small openings in the canopy of mature forests in the Missouri Ozarks has not been reported.

Interpreting the observed differences among species in the magnitude of growth, albeit statistically significant, as ecologically meaningful may be premature. We do not yet know if there are threshold rates of growth for a species to successfully recruit into the canopy or how such thresholds might vary with ontogeny or other factors such as site, overstory composition and structure, and disturbance regime (Poorter *et al.* 2005, Wright *et al.* 2000). Nonetheless, canopy recruitment is a process rather than an event; thus, the cumulative effects of even minor sustained advantages could prove influential.

Previous studies in the Missouri Ozarks have suggested that interspecific differences in reproduction abundance are related to site quality and residual overstory density (Green 2008, Kabrick *et al.* 2008b, Larsen *et al.* 1997). Our results showed that species also exhibited differentiated growth rates during the sapling stage and that differences were most pronounced at relatively low overstory densities ($< 10\text{m}^2\text{ha}^{-1}$). Residual overstory densities $> 5\text{m}^2\text{ha}^{-1}$ eliminated the growth advantage of red oaks over white oaks. In the Missouri Ozarks, susceptibility to episodic red oak decline events may be a catalyst for foresters to favor white oaks over red oaks (Shifley *et al.* 2006, Kabrick *et al.* 2008a). Our results suggest that there is potential for partial harvesting methods to reach such an objective. However, the growth advantage exhibited by white oaks over competing species also decreased with increasing overstory density. White oaks had little to no advantage in height growth over many competing

species when overstory density exceeded about $10 \text{ m}^2\text{ha}^{-1}$. Moreover, the sprouting probabilities and subsequent growth rates of oaks have also been reported to decrease with increasing overstory density (Dey *et al.* 2008, Atwood *et al.* 2009). This implies that the probability of recruitment under overstory densities greater than about $10 \text{ m}^2\text{ha}^{-1}$ is likely to decline for all oaks in the Missouri Ozarks, which is consistent with the residual overstory densities recommended to sustain oak recruitment by Larsen and others (1997, 1999). Oliver and others (2005) reported similar recruitment dynamics with increasing overstory density in bottomland forests of the southern United States, but the threshold densities recommended for oak recruitment were lower.

Many of the species analyzed in this study rarely (ashes, blackgum, elms, red maple, sassafras) or never (dogwood) attain overstory stature in mature forests of the Missouri Ozarks (Burns and Honkala 1990, Johnson *et al.* 2009).

However, these species groups are often among the most abundant members of the seedling and sapling layer during stand development (Dey 1991, Johnson *et al.* 2009, Schlesinger *et al.* 1993). Because of this, these common associates in oak-hickory forests play an influential, albeit temporally constrained, role in the canopy recruitment process by limiting spatial opportunities for recruitment and delaying or, perhaps, eliminating the release of neighboring oaks and hickories from the sapling strata by exhibiting increasingly comparable growth under increasing overstory density. The temporal importance of this limiting influence is likely more constrained in the Missouri Ozarks than in more mesic parts of the eastern United States where many of the competing species we analyzed and

several others have greater potential to reach the overstory and are a more lasting source of competition (Atwood *et al.* 2011, Loftis 1990b, Nowacki and Abrams 2008, Oliver *et al.* 2005, Schuler 2004). As increasing overstory density progressively reduces sapling abundance and differences in growth rates, repeated disturbance, stochasticity, and differentiation along other gradients may become more important determinants of recruitment success (Beckage and Clark 2003, Grubb 1977). In general, oaks and hickories are thought to predominately utilize persistence strategies for regeneration and recruitment and exhibit various degrees of tolerance to both drought and fire (Arthur *et al.* 2012, Brose *et al.* 2013, Burns and Honkala 1990). The ability to persist in temporarily unfavorable conditions via dieback, vegetative reproduction, and seedling storage increases longevity (Bond and Midgley 2003, Warner and Chesson 1985). It is likely that differential mortality plays an important role in recruitment dynamics (Coates 2002, Pacala *et al.* 1996, Wright *et al.* 1998). Given the relatively xeric conditions of the Missouri Ozarks, differences in mortality rates among species may provide additional opportunities for differentiation during the sapling stage, but this is an area in need of quantitative research.

Undoubtedly, factors in addition to overstory density affect sapling growth, as evidenced by the spread of response in Figure 3.1. One likely source of the variation in growth we observed was an inability of the overstory metric used in this study to capture the spatial heterogeneity of resource availability. Varying spatial arrangement while maintaining the same stand-level basal area can substantially alter competitive neighborhoods and influence regeneration and

other ecosystem processes (Boyden *et al.* 2012, Palik *et al.* 2003). The models of mean PAI_{HT} , suggest that another source of the observed variation in growth was site quality. Despite many non-significant site parameters (Table 3), models of mean PAI_{HT} that included site differences were ranked better by AICc for all species groups. It is possible that the non-significance of site parameters was due to inherent variation, model misspecification, and/or the coarse-scaled site delineation used in these analyses. Another possible explanation is the limited observation period of this study, although greenhouse studies have found site effects on tree seedling growth after a single growing season (Latham 1992).

The influence of site was greatest for the four species that were best described by model iv. We observed a relatively large increase in growth on protected backslopes compared to exposed backslopes for sassafras, red maple, and elms in this study. This is consistent with several other studies that reported increased importance of these species on more productive sites (*e.g.*, Kabrick 2008b, Schlesinger *et al.* 1993). However, the increase in mean PAI_{HT} from exposed to protected backslopes was accompanied by nominal increases in the rate that growth declined with increasing overstory density (s_2 , Table 3.3). This suggests that growth/tolerance tradeoffs may exist for these species (Kaelke *et al.* 2001, Niinemets and Valladares 2006, Walters and Reich 2000) but is inconclusive because overstory composition, structural arrangement, and other potentially confounding differences among plots were not accounted for.

Increases in mean PAI_{HT} from exposed to protected backslopes were expected and observed (sometimes nominally) for most species, but not all (s_1 , Table 3.3).

Blackgum showed evidence of reduced growth on better sites at low overstory densities, but a nominal reduction in the rate that growth declined with increasing overstory density. This is consistent with Abrams' (2007) suggestion that blackgum should be most successful in xeric upland forests. There, the disadvantages of relatively slow inherent growth rates may be somewhat mitigated by considerable stress tolerance and a reduction in the number and competitive capacity of associated species (Abrams 2007). Our results suggest that the species that were best described by model ii (oaks, hickories, and dogwood) were also influenced by differences in site class, but the relationship between site class and overstory density on mean PAI_{HT} was not as dynamic as the species described by model iv. Mean PAI_{HT} of oaks and hickories at low overstory densities was nominally greater on protected backslopes than exposed backslopes. However, we observed a significant reduction in mean PAI_{HT} on protected backslopes compared to exposed backslopes for dogwood. Given the reported shade tolerance and drought intolerance of this understory species (Horn 1985, McLemore 1990) this result was not expected.

It has long been known that a seedling bank of *large* advance reproduction is often vital to successful canopy recruitment of oaks due to the inherently slow growth of seedlings that lack well-developed root systems (Johnson *et al.* 2009). Due to frequent dieback and resprouting of upland oaks, root-collar diameter is a better predictor of root biomass than height (Knapp *et al.* 2006). Nonetheless, we found that initially taller oak saplings exhibited a growth advantage in mean PAI_{HT} over shorter ones (Fig. 3.2). The magnitude of the initial height effect on mean

PAI_{HT} was much more pronounced for red oaks ($\theta = 0.64$, Table 3.3) than white oaks ($\theta = 0.30$, Table 3.3) which is consistent with previous estimates of the relative impact of size on reproduction growth among oak species (Dey 1991). In fact, an initial height effect on mean PAI_{HT} was significant for all species in this study (θ , Table 3.3). However, the effect of size on competitive capacity under a dense overstory was limited due to intrinsically low growth for all saplings in that setting (Fig. 3.2).

Our results provide insight into how overstory density manipulation alters the composition and structure of the regeneration layer in Missouri Ozark forests. This information could be valuable to foresters considering regeneration techniques that utilize partial cutting and multiple entries. Although we have not yet established longitudinal growth thresholds for successful canopy recruitment across a range of overstory density, the models of mean PAI_{HT} presented herein should provide inference into the timing required to attain recommended size thresholds for advance reproduction prior to a planned harvest (*e.g.*, Brose *et al.* 2008, Sander *et al.* 1984). This potentially extends the application of existing regeneration simulators (*e.g.*, Dey *et al.* 1996) by providing insight into how preparatory partial harvesting might alter the structure of the regeneration layer prior to a clearcut harvest. Of course, this potential is constrained by the species and sizes reported in this study and the inherent assumptions of existing regeneration simulators.

Conclusion

Periodic annual height increment of saplings decreased within increasing overstory density for all species groups (Objective 1). Secondly, species differentiation in growth rates occurred during the sapling stage, but differences were most pronounced at lower overstory densities. We identified thresholds in overstory densities that are related to possible shifts in species composition on certain sites in the Missouri Ozarks (Objective 2). This information should be valuable to foresters and improve the likelihood of achieving regeneration objectives. Finally, we suggest that the near-maxima of growth resource distributions have two potential advantages over the mean: 1) better models of the limiting effects of overstory density on sapling height growth 2) focused on the growth rates of stems that were most likely to recruit into the canopy (Objective 3). Additional research into the role of recruitment fluctuation is certainly warranted. Longitudinal monitoring of individuals in addition to populations on established studies like MOFEP will be essential to better understand the biology and ecology of forest dynamics and provide science-based management guidelines.

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References

- Abrams, M.D. 2007. Tales from the blackgum, a consummate subordinate tree. *Bioscience* 57(4): 347-359.
- Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., Loftis, D.L. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. Forestry*.110: 257-266.
- Atwood, C.J., Fox, T.R., Loftis, D.L. 2009. Effects of alternative silviculture on stump sprouting in the southern Appalachians. *For. Ecol. Mgmt.* 257: 1305-1313.
- Atwood, C.J., Fox, T.R., Loftis, D.L. 2011. Effects of various silvicultural systems on regeneration in mixed hardwood stands of the Southern Appalachians. *J. Sust. For.* 30: 419-440.
- Baker, F.S. 1949. A revised tolerance table. *J. Forestry*. 47:179-181.
- Bazzaz, F.A., Paape, V., Boggess, W.R. 1972. Photosynthetic and respiratory rates of *Sassafras albidum*. *For. Sci.* 18:218-222.
- Beck, D.E., Hooper, R.M. 1986. Development of a Southern Appalachian hardwood stand after clearcutting. *South. J. Appl. For.* 10: 168-172.
- Beckage, B., Clark, J.S. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology*. 84(7): 1849-1861.
- Biging, G.S., Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41(2): 360-377.
- Blizzard, E.M., Kabrick, J.M., Dey, D.C., Larsen, D.R., Pallardy, S.G., Gwaze, D.P. 2013. Light, canopy closure, and overstory retention in upland Ozark forests. p.73-79 *in*: Guldin, J.M. (ed). 2013. Proceedings of the 15th biennial southern silvicultural research conference. USDA For. Serv. Gen. Tech. Rep. SRS-GTR-175.
- Bond, W.J., Midgley, J.J. 2003. The evolutionary ecology of sprouting in woody plants. *Int. J. Plant. Sci.* 164(3 Suppl.): S103-S114.
- Boyden, S., Montgomery, R., Reich, P.B., Palik, B. 2012. Seeing the forest for the heterogeneous trees: Stand-scale resource distributions emerge from tree-scale structure. *Ecol. Appl.* 22(5): 1578-1588.
- Brookshire, B.L., Shifley, S.R. (Eds.) 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium.: An experimental approach to landscape research. St. Louis, MO, June 3-5, 1997. USDA For. Serv. Gen. Tech. Rep. NC-193.

- Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59(3): 322-334.
- Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic Region. USDA For. Serv. Gen. Tech. Rep. NRS-33.
- Brose, P.H., Van Lear, D.H., Keyser, P.D. 1999. A shelterwood-burn technique for regenerating productive upland oak sites in the Piedmont region. *South. J. Appl. For.* 23: 158-163.
- Burns, R.M., Honkala, B.H. (eds.). 1990. *Silvics of North America, Volume 2, Hardwoods*. USDA For. Serv. Agriculture Handbook 654. Washington, D.C. 675p.
- Burnham, K.P., Anderson, D.R. 1998. *Model Selection and Inference. A Practical Information-Theoretic Approach*. Springer. 353p.
- Cade, B.S., Guo, Q. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos* 91: 245-254.
- Cade, B.S., Noon, B.R. 2003. A gentle introduction to quantile regression for ecologists. *Front. Ecol. Environ.* 1(8): 412-420.
- Cade, B.S., Terrell, J.W., Schroeder, R.L. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology*. 80(1): 311-323.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Can. J. For. Res.* 26: 2632-1530.
- Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24: 337-349.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P. 1999. Interpreting recruitment limitation in forests. *Am. J. Botany.* 86(1): 1-16.
- Clatterbuck, W.K., Hodges, J.D. 1988. Development of cherrybark oak and sweet gum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. *Can. J. For. Res.* 18(1): 12-18.
- Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *For. Ecol. Mgmt.* 155: 387-398.

- Coomes, D.A., Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Mon.* 70(2): 171-207.
- Dey, D.C. 1991. A comprehensive Ozark regenerator. Ph.D. Dissertation, University of Missouri, Columbia, Missouri. 283p.
- Dey, D.C. 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* *in press*.
- Dey, D.C., Jensen, R.G., Wallendorf, M.J. 2008. Single-tree harvesting reduces survival and growth of oak stump sprouts in the Missouri Ozark Highlands. P. 26-37 in Proc. 16th Central Hardwood Forest Conf. Jacobs, D.F., and C.H. Michler (eds.). USDA For. Serv. Gen. Tech. Rep. NRS-P-24.
- Dey, D.C., Johnson, P.S., Garrett, H.E. 1996. Modeling the regeneration of oak stands in the Missouri Ozark Highlands. *Can. J. For. Res.* 26(4): 573-583.
- Fei, S., Steiner, K.C. 2007. Evidence for increasing red maple abundance in the Eastern United States. *For. Sci.* 53(4): 473-477.
- Givnish, T.J. 1988. Adaption to sun and shade: a whole plant perspective. *Aust. J. Plant. Physiol.* 15: 63-92.
- Green, J.L. 2008. Overstory density and its effect on oak regeneration abundance and oak understory height growth in the Missouri Ozark Highlands. M.S. Thesis. University of Missouri. Columbia, Missouri. 87p.
- Grime, J.P. 2006. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons. 456p.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review.* 52: 107-145.
- Harrell, F.E. 2001. *Regression Modeling Strategies with Applications to Linear Models, Logistic Regression, and Survival Analysis*. Springer. 571p.
- Horn, J.C. 1985. Responses of understory tree seedlings to trenching. *Am. Midl. Nat.* 114(2): 252-258.
- Clabo, D.C. 2014. Shortleaf pine sprout production capability in response to disturbances. M.S. Thesis. University of Tennessee-Knoxville. http://trace.tennessee.edu/utk_gradthes/2800
- Johnson, P.S., Shifley, S.R., Rogers, R. 2009. *The Ecology and Silviculture of Oaks*. CABI. 600p.
- Kabrick, J.M., Dey, D.C., Jensen, R.G., Wallendorf, M. 2008a. The role of environmental factors in oak decline and mortality in the Ozark Highlands. *For. Ecol. Mgmt.* 255: 1409-1417.

- Kabrick, J.M., Meinert, D., Nigh, T., Gorlinsky, B.J. 2000. Physical environment of the Missouri Ozark forest ecosystem project sites. In Shifley, Stephen R.; Brookshire, Brian L. ed. Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station. 41-70.
- Kabrick, J.M., Shifley, S.R., Jensen, R.G., Larsen, D.R., Grabner, J.K. 2004. Oak forest composition, site quality, and dynamics in relation to site factors in the southeastern Missouri Ozarks. In Spetich, M.A. ed. 2004. Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Dept. of Agriculture, Forest Service, Southern Research Station. 94-101.
- Kabrick, J.M., Zenner, E.K., Dey, D.C., Gwaze, D., Jensen, R.G. 2008b. Using ecological land types to examine landscape-scale oak regeneration dynamics. *For. Ecol. Mgmt.* 255: 3051-3062.
- Kaelke, C.M., Kruger, E.L., Reich, P.B. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. *Can. J. For. Res.* 31: 1602-1616.
- Kaiser, M.S., Speckman, P.L., Jones, J.R. 1994. Statistical models for limiting nutrient relations in inland waters. *J. Am. Stat. Assoc.* 89: 410-423.
- Knapp, B.O., Wang, G.G., Van Lear, D.H., Walker, J.L. 2006. Predicting root biomass of burned and unburned white oak advance reproduction from diameter and height. *South. J. Appl. For.* 30(1): 40-45.
- Kneeshaw, D.D., Kobe, R.K., Coates, K.D., Messier, C. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *J. Ecology.* 94: 471-480.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5: 517-532.
- Koenker, R. 2005. *Quantile Regression*. Cambridge University Press. 368p.
- Koenker, R. 2012. Quantreg: Quantile Regression. R package version 4.91. <http://CRAN.R-project.org/package=quantreg>.
- Landis, R.M., Peart, D.R. 2005. Early performance predicts canopy attainment across life histories in subalpine forest trees. *Ecology* 86(1): 63-72.
- Larsen, D.R., Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Mgmt.* 106: 1-7.

- Larsen, D.R., Kershaw, J.A. 1996. Influence of canopy structure assumptions on predictions from Beer's law. A comparison of deterministic and stochastic simulations. *Agr. Forest Meteorol.* 81: 61-77.
- Larsen, D.R., Metzger, M.A., Johnson, P.S. 1997. Oak regeneration and overstory density in the Missouri Ozarks. *Can. J. For. Res.* 27(6): 869-875.
- Larsen, D.R., Loewenstein, E.F., Johnson, P.S. 1999. Sustaining recruitment of oak reproduction in uneven-aged stands in the Ozark Highlands. USDA For. Serv. Gen. Tech. Rep. NC-203.
- Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology.* 73: 2129-2144.
- Law, J.R., Lorimer, C.G. 1989. Managing uneven-aged stands. In: Clark, F.B., Hutchinson, J.G. (eds.). *Central Hardwood Note 6.08.* USDA For. Serv. North Central Forest Experiment Station. 6p.
- Loewenstein, E.F., Johnson, P.S., Garrett, H.E. 2000. Age and diameter structure of a managed uneven-aged oak forest. *Can. J. For. Res.* 30: 1060-1070.
- Loftis, D.L. 1990a. Predicting post-harvest performance of advance red oak reproduction in the Southern Appalachians. *For. Sci.* 36(4): 908-916.
- Loftis, D.L. 1990b. A shelterwood method for regenerating red oak in the Southern Appalachians. *For. Sci.* 36(4): 917-929.
- Lorimer, C.D. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Mgmt.* 6: 343-360.
- MacArthur, R.H., Wilson, E.O. 1967. *The Theory of Island Biogeography.* Princeton University Press. 203p.
- MacFarlane, D.W., Kobe, R.K. 2006. Selecting models for capturing tree-size effects on growth-resource relationships. *Can. J. For. Res.* 36: 1695-1704.
- McLemore, B.F. 1990. *Cornus florida* L. Flowering Dogwood. in Burns, R.M., Honkala, B.H. (eds.). 1990. *Silvics of North America, Volume 2, Hardwoods.* USDA For. Serv. Agriculture Handbook 654. Washington, D.C. 675p.
- McQuilkin, R.A. 1974. Site index prediction tables for black, scarlet, and white oaks in southeastern Missouri. USDA For. Serv. Res. Pap. NC-108.
- Messier, C., Doucet, R., Ruel, J., Claveau, Y., Kelly, C., Lecowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* 29: 812-823.

- Missouri Department of Conservation 1986. Forest Land Management Guidelines. Missouri Department of Conservation, Jefferson City, Missouri. 81p.
- Nigh, T., Buck, C., Grabner, J., Kabrick, J., Meinert, D. 2000. Ecological Classification System for the Current River Hills Subsection. Missouri Department of Conservation Publication. Jefferson City, MO. 84p.
- Niinemets, U., Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Mon.* 76(4): 521-547.
- Noble, I.R., Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Nowacki, G.J., Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the Eastern United States. *Bioscience*. 58(2): 123-138.
- Oliver, C.D., Burkhardt, E.C., Skojac, D.A. 2005. The increasing scarcity of red oaks in Mississippi River floodplain forests: Influence of the residual overstory. *For. Ecol. Mgmt.* 210: 393-414.
- Oliver, C.D., Larson, B.C. 1996. *Forest Stand Dynamics*. John Wiley & Sons. New York.
- Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24: 2172-2183.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E. 1996. Forest models defined by field measurement: II Estimation, error analysis, and dynamics. *Ecol. Monogr.* 66:1-43.
- Palik, B., Mitchell, R.J., Pecot, S., Battaglia, M., Pu, M., 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. *Ecol. App.* 13: 674-686.
- Peet, R.K., Christensen, N.L. 1987. Competition and tree death. *Bioscience* 37(8): 586-595.
- Pinheiro, J.C., Bates, D.M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag New York, Inc. 528p.
- Pinheiro, J.C., Bates, D.M., Debroy, S., Sarkar, D, R Development Core Team. 2011. NLME: Linear and Nonlinear Mixed Effects Models. R package version 3.1-100.

- Poorter, L., Bongers, F., Sterck, F.J., Woll, H. 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *J. Ecol.* 93: 256-267.
- R Development Core Team. 2011. R: A language environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <http://R-project.org/>.
- Roach, B.A., Gingrich, S.F. 1968. Even-aged silviculture for upland central hardwoods. USDA For. Serv. Agriculture Handbook 355.
- Sander, I.L., Johnson, P.S., Rogers, R. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. USDA For. Serv. Res. Pap. NC-251.
- Schlesinger, R.C., Sander, I.L., Davidson, K.R. 1993. Oak regeneration potential increased by shelterwood treatments. *North. J. Appl. For.* 10(4): 149-153.
- Schuler, T.M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Can. J. For. Res.* 34: 985-997.
- Schweitzer, C.J., Dey, D.C. 2011. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA. *For. Ecol. Mgmt.* 262: 1729-1741.
- Schwinning, S., Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447-455.
- Shifley, S.R., Brookshire, B.L. (Eds.) 2000. Missouri Ozark Forest Ecosystem Project: Site history, Soils, Landforms, Woody and Herbaceous Vegetation, Down Wood, and Inventory Methods for the Landscape Experiment. USDA For. Serv. Gen. Tech. Rep. NC-208.
- Shifley, S.R., Kabrick, J.M. (Eds.) 2002. Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium. St. Louis, MO, October 17-18, 2000. USDA For. Serv. Gen. Tech. Rep. NC-227.
- Shifley, S.R., Fan, Z., Kabrick, J.M., Jensen, R.G. 2006. Oak mortality risk factors and mortality estimation. *For. Ecol. Mgmt.* 229: 16-26.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press. 296p.
- Valladares, F., Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Ann. Rev. Ecol. Evol. Syst.* 39: 237-257.
- Walters, M.B., Reich, P.B. 2000. Trade-offs in low-light CO₂ exchange: a component of variation in shade tolerance among cold temperate tree seedlings. *Func. Ecol.* 14: 155-165.

- Warner, R.R., Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *Am. Nat.* 125(6): 769-787.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5:360-364.
- Weiner, J., Thomas, S.C. 2001. The nature of tree growth and the “age-related decline in forest productivity”. *Oikos*. 94: 374-376.
- Wright, E.F., Canham, C.D., Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Can. J. For. Res.* 30: 1571-1580.
- Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia, *Can. J. For. Res.* 28: 871-886.

Tables

Table 3.1. Mean initial conditions of the five year measurement period.

Management Regime	Harvest Type	n	Overstory Density (≥ 11.5 cm dbh)		Saplings (>1 m height, ≤ 5 cm dbh)	
			Trees per ha	Basal Area ($\text{m}^2 \cdot \text{ha}^{-1}$)	Trees per ha	Initial Height (m)
Even-aged	clearcut	17	36.8 (15.5)	2.2 (0.8)	10635.8 (676.6)	1.6 (0.1)
	thinned	23	324.1 (15.2)	14.0 (0.6)	2276.5 (234.1)	2.2 (0.3)
Uneven-aged	single-tree	16	299.8 (16.6)	15.0 (0.9)	2476.2 (331.5)	2.1 (0.2)
	group opening	8	233.4 (25.7)	12.1 (1.3)	2914.6 (329.4)	1.9 (0.2)
None	no-harvest	24	366.8 (18.7)	21.0 (0.7)	2511.2 (373.4)	2.6 (0.3)

The number of subplots in each harvest type is denoted by n. Sapling characteristics were calculated from eighty-eight subplots (0.02-ha). Overstory density characteristics were calculated from the overstory plots (0.2-ha) that each subplot was nested within. Values in parentheses are standard errors. Harvest treatments were implemented in 1996; the measurement period analyzed in this study began in 1999 and ended in 2004. The initial conditions described in this table are from the 1999 measurement.

Table 3.2. Candidate models for estimating PAI_{HT} of saplings as a function of residual overstory density and other covariates.

Model	df	Form
I	3	$PAI_{HT} = ae^{x_1/b}$
i	4	$PAI_{HT} = [ae^{x_1/b}]x_3^\theta$
II	4	$PAI_{HT} = (a + s_1x_2)e^{x_1/b}$
ii	5	$PAI_{HT} = [(a + s_1x_2)e^{x_1/b}]x_3^\theta$
III	4	$PAI_{HT} = ae^{x_1/(b+s_2x_2)}$
iii	5	$PAI_{HT} = [ae^{x_1/(b+s_2x_2)}]x_3^\theta$
IV	5	$PAI_{HT} = (a + s_1x_2)e^{x_1/(b+s_2x_2)}$
iv	6	$PAI_{HT} = [(a + s_1x_2)e^{x_1/(b+s_2x_2)}]x_3^\theta$

Where: x_1 = Overstory Basal Area ($m^2 ha^{-1}$); x_2 = Site Class (0 if exposed backslopes, 1 if protected backslopes); x_3 = Initial Sapling Height (m); a (intercept), b (decay), s_1 (site class modifier to intercept), s_2 (site class modifier to decay), and θ (initial sapling height modifier) are parameters estimated from the data. Parameter estimates for the mean were fit using generalized nonlinear least squares with the variance modeled as a power function of the conditional mean and a compound symmetric error correlation structure. These additional parameters are not included in the reported degrees of freedom. Parameter estimates for the near-maxima were fit using nonlinear quantile regression which does not account for variance heterogeneity or error correlation.

Table 3.3. Parameter estimates for best models of mean PAI_{HT} of saplings as a function of overstory density and other covariates.

Species	N/n	Model	<i>a</i>	<i>b</i>	<i>s</i> ₁	<i>s</i> ₂	θ	Power	Rho	RSE	<i>r</i> ²	Akaike Weights
Red Oaks	320/35	ii	0.443 (0.03)	-13.591 (1.70)	0.043 (0.03)	-	0.636 (0.08)	0.492	0.039	0.343	0.39	0.60
White Oaks	365/48	ii	0.547 (0.05)	-10.552 (1.12)	0.041 (0.05)	-	0.301 (0.07)	0.141	0.217	0.227	0.46	0.59
Hickories	343/61	ii	0.497 (0.08)	-12.198 (1.74)	0.096 (0.09)	-	0.169 (0.08)	0.612	0.514	0.459	0.48	0.33
Sassafras	968/58	iv	0.446 (0.06)	-21.762 (6.33)	0.176 (0.08)	6.922 (7.14)	0.109 (0.04)	0.032	0.608	0.199	0.26	0.57
Blackgum	455/62	iv	0.422 (0.05)	-12.612 (1.81)	-0.062 (0.06)	-6.964 (3.83)	0.392 (0.08)	0.369	0.213	0.274	0.42	0.93
Dogwood	455/81	ii	0.347 (0.03)	-12.418 (0.85)	-0.054 (0.02)	-	0.339 (0.06)	0.588	0.162	0.325	0.41	0.54
Red Maple	646/44	iv	0.289 (0.06)	-29.076 (13.15)	0.133 (0.07)	15.921 (13.24)	0.409 (0.06)	0.742	0.205	0.472	0.38	0.99
Ashes	122/20	iii	0.414 (0.05)	-13.493 (3.11)	-	-2.060 (4.43)	0.397 (0.13)	0.346	0.387	0.223	0.55	0.65
Elms	249/24	iv	0.351 (0.09)	-16.767 (6.61)	0.158 (0.12)	5.496 (7.25)	0.169 (0.08)	0.461	0.411	0.297	0.34	0.74

Where: N/n is the total number of trees in the understory subplots and total number of overstory plots in which a species was measured, respectively. Model lists the best model for a species according to AICc from the candidate models described in Table 2. *a* (intercept), *b* (decay), *s*₁ (site class modifier to intercept), *s*₂ (site class modifier to decay), and θ (initial sapling height modifier) are model parameters estimated from the data. Parameter estimates were fit using generalized nonlinear least squares with the variance modeled as a power function of the conditional mean (Power) and a compound symmetric error correlation structure at the overstory plot level (Rho). RSE is the residual standard error of the model. Goodness of fit was assessed using the square of Pearson's correlation coefficient (*r*²) of predicted values against observed values. The Akaike Weights indicate the proportional weight of evidence for the best model relative to the other candidate models in Table 3.2. Values in parentheses are standard errors. Bold text indicates parameters included in a model that were not statistically significant ($\alpha=0.05$).

Table 3.4. Parameter estimates for best models of PAI_{HT-Q90} of saplings.

Species	Model	<i>a</i>	<i>b</i>	<i>s</i> ₁	Akaike Weights
Red Oaks	I	1.066 (0.04)	-14.371 (2.02)	-	0.29
		[1.00 , 1.16]	[-18.13 , -11.29]		
White Oaks	I	0.907 (0.03)	-22.282 (2.82)	-	0.34
		[0.85 , 0.96]	[-27.67 , -16.75]		
Hickories	I	0.878 (0.03)	-15.315 (1.70)	-	0.41
		[0.84 , 0.91]	[-18.93 , -13.23]		
Sassafras	II	0.658 (0.01)	-40.927 (5.77)	0.271 (0.02)	0.38
		[0.63 , 0.69]	[-54.3 , -30.45]	[0.21 , 0.31]	
Blackgum	I	0.707 (0.02)	-26.117 (2.92)	-	0.36
		[0.68 , 0.74]	[-35.59 , -21.82]		
Dogwood	I	0.567 (0.01)	-18.488 (1.05)	-	0.39
		[0.54 , 0.58]	[-21.12 , -16.44]		
Red Maple	I	0.859 (0.02)	-18.195 (1.32)	-	0.31
		[0.82 , 0.89]	[-20.49 , -15.23]		
Ashes	I	0.646 (0.08)	-20.826 (6.01)	-	0.39
		[0.60 , 0.91]	[-39.53 , -13.08]		
Elms	I	0.657 (0.02)	-20.227 (3.91)	-	0.41
		[0.60 , 0.72]	[-28.34 , -14.85]		

Where: Model lists the best model for a species selected by AICc from the candidate models described in Table 3.2. *a* (intercept), *b* (decay), and *s*₁ (site class modifier to intercept) are model parameters estimated from the data. Parameter estimates were fit using nonlinear quantile regression of 0.9 conditional quantile of the response distribution. The Akaike Weights indicate the proportional weight of evidence for the best model relative to the other candidate models in Table 3.2. Values in parenthesis are standard error estimates from the nonlinear quantile regression. Values in brackets are bootstrapped confidence intervals for parameter estimates ($\alpha = 0.05$). All parameters were statistically significant.

Figures

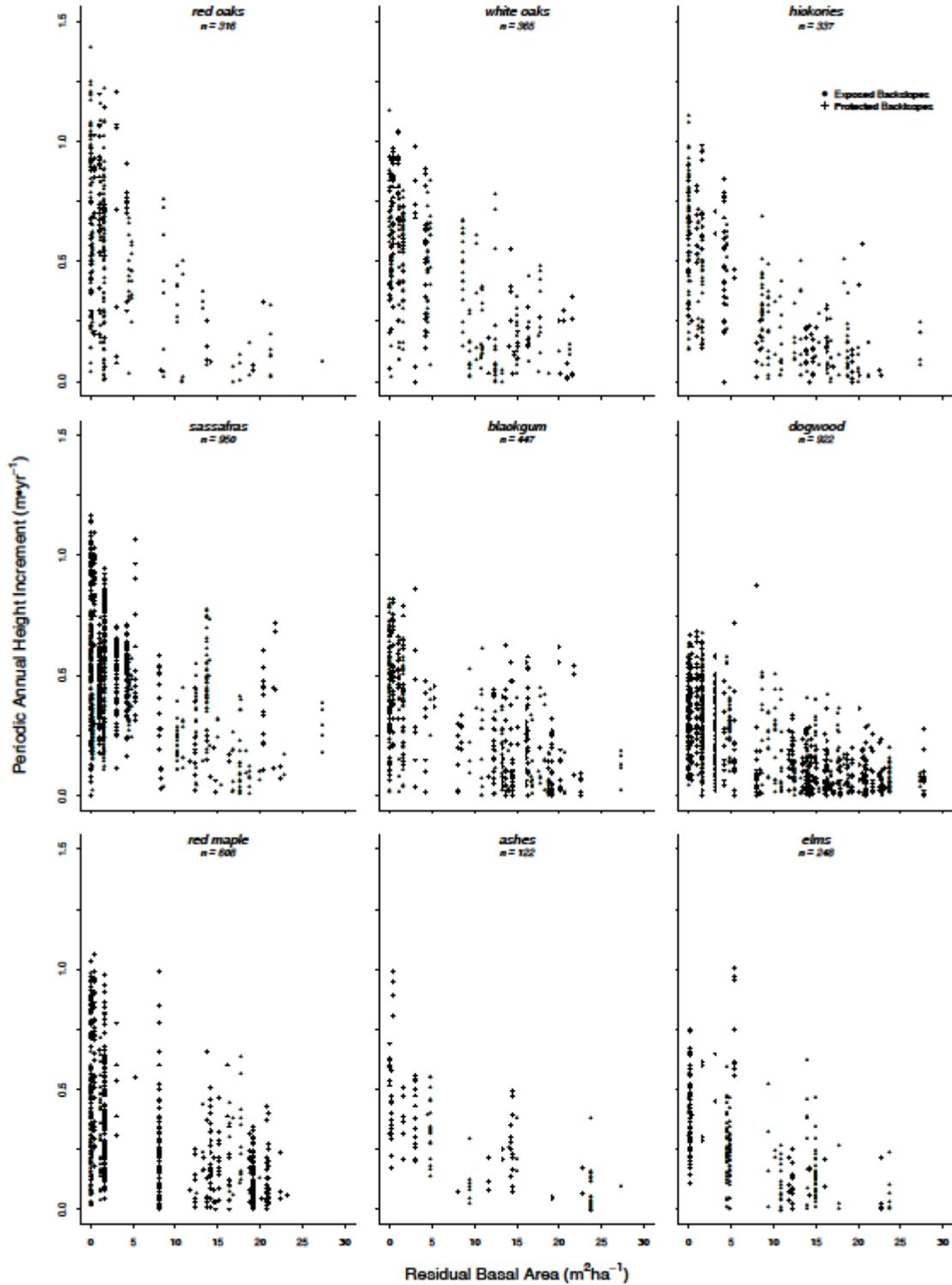


Figure 3.1. Periodic annual height increment of saplings along a gradient of overstory density.

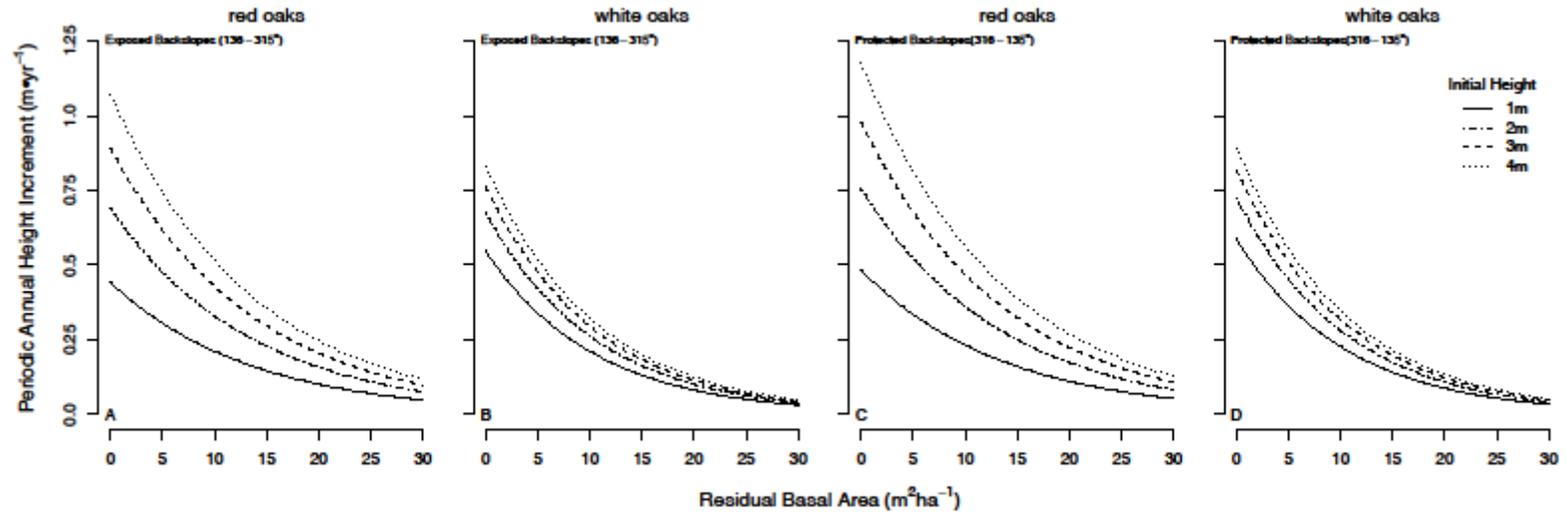


Figure 3.2. Impact of initial height on sapling mean periodic annual height increment for oaks along a gradient of overstory density.

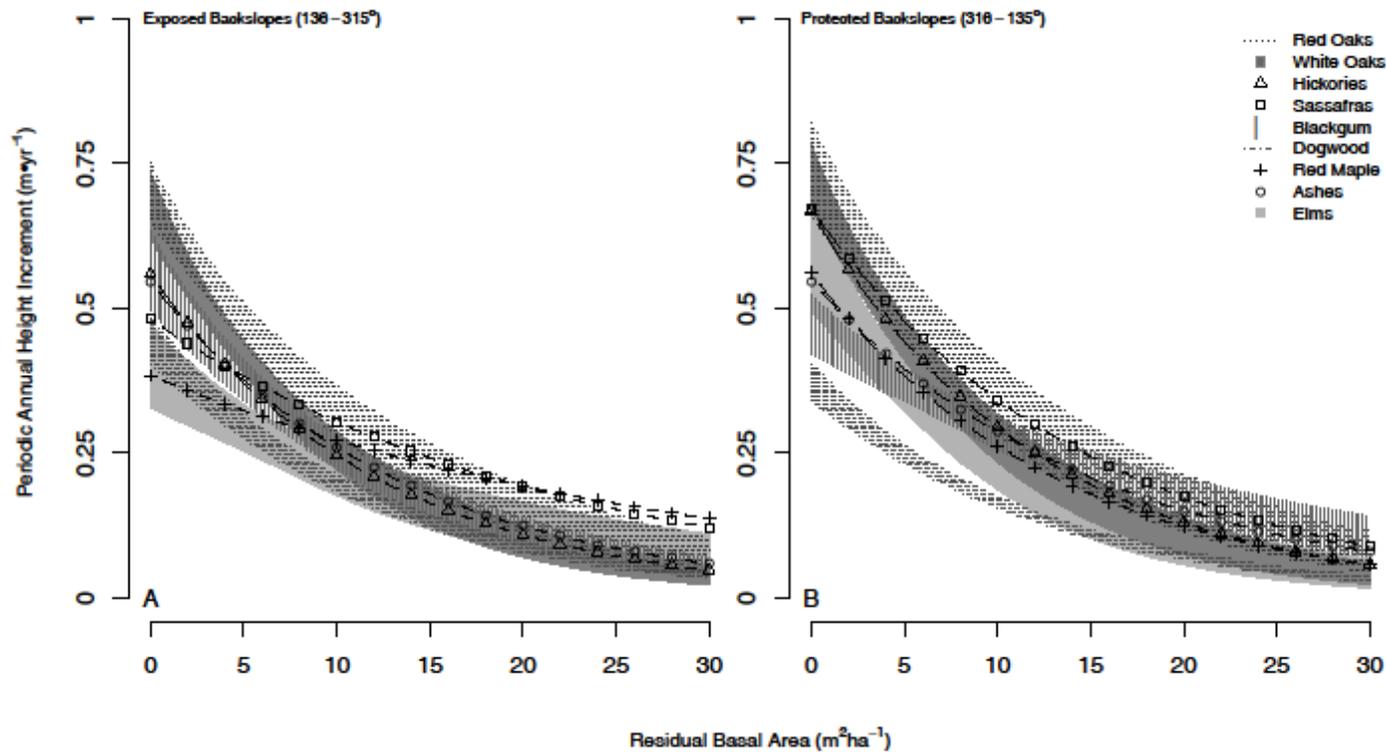


Figure 3.3. Mean regression curves and confidence bands for sapling periodic annual height increment along a gradient of overstory density. Figure adjusted to represent an initial sapling height of 2m, which was approximately average across the study. Regression curves are depicted for hickories, sassafras, red maple, and ashes. Confidence bands are depicted for red oaks, white oaks, blackgum, elms, and dogwood. Non-overlapping confidence bands indicate differences among groups at a significance level ≤ 0.05 . Statistically significant differences among groups may also exist in areas where their confidence bands slightly overlap.

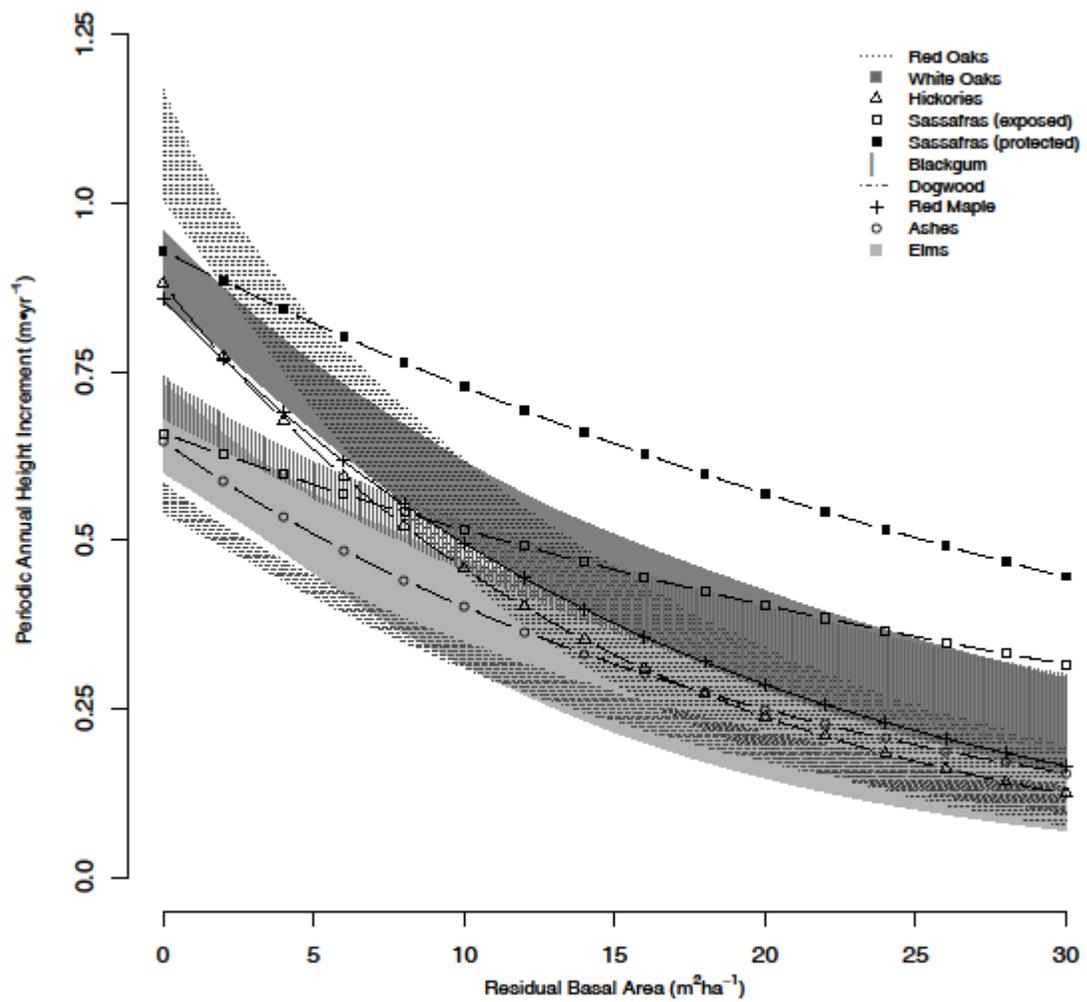


Figure 3.4. Quantile regression curves and confidence bands for the 90th quantile of sapling periodic annual height increment along a gradient of overstory density. Regression curves are depicted for hickories, sassafras, red maple, and ashes. Confidence bands are depicted for red oaks, white oaks, blackgum, elms, and dogwood. Non-overlapping confidence bands indicate differences among groups at a significance level ≤ 0.05 . Statistically significant differences among groups may also exist in areas where their confidence bands slightly overlap.

Chapter 4:

SAPLING HEIGHT INCREMENT AND DEVELOPMENTAL MILESTONES FOR
SUCCESFUL CANOPY RECRUITMENT IN THE MISSOURI OZARKS – AN
INITIAL EXAMINATION

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Abstract

Height development relationships have been successfully used to model growth and yield for a variety of species and regions. Unfortunately, there is little quantitative information to guide height development expectations during the regeneration period in naturally regenerated hardwood dominated forests of the eastern United States, particularly for those species with limited commercial value. A stem analysis study was initiated to examine height increment trends exhibited by juvenile trees during the first twenty years of stand development following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks. The objectives of the study were: 1) Quantify mean size related trends in height increment, 2) Develop a model to project size related trends in height increment, and 3) Quantify developmental milestones for recruitment into the upper canopy at the end of the regeneration period. Though highly variable, height increment of juvenile trees generally declined with increasing height during the first twenty years of stand development (Objective 1). There were some differences in the rate of decline, with *Sassafras albidum* and *Ulmus* spp. having the most rapid decline in height increment with increasing height of the species examined. There were differences in both mean height increment and mean height increment variability among trees that occupied different crown classes at the end of the regeneration period. Generally, as final crown class decreased from dominant to suppressed, both mean height increment and mean height increment variability declined. Although these differences were relatively minor initially, they were magnified as height increased. A model was developed that projects mean height increment as a function of height, species, stem origin, and

site class (Objective 2). This model provides a quantitative tool beyond site index extrapolation to fill a void of early height increment models. Developmental milestones for recruitment “success” were identified from the growth patterns exhibited by trees that occupied codominant and dominant crown classes at the end of the regeneration period (Objective 3). These milestones provide a tool to assess the height development of individual trees during the canopy recruitment process following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks.

Introduction

Foresters have long managed forests with the understanding that the ability of a species to flourish differed with the magnitude of disturbance (Büsgen and Münch 1929, Egler 1954, Puetmann *et al.* 2008). Consequently, the developmental patterns of mixed species stands can be complex, and it is common for the height profile of these stands to be dominated by a progression of species through time (Kelty *et al.* 1992, Oliver and Larson 1996). Species that exhibit rapid initial height growth tend to dominate young stands both in size and number immediately following major disturbance on many sites (Beck and Hooper 1986, Gould *et al.* 2005). However, species with rapid initial growth tend to be relatively intolerant to competition, short-statured, and short-lived and are eventually surpassed by relatively larger, longer-lived species with slower initial growth rates but greater tolerance of early competition (MacArthur and Wilson 1967, Noble and Slatyer 1980).

There is a considerable volume of observational and empirical evidence for interspecific differences in developmental patterns in a variety of mixed-species, single-cohort stands (*e.g.*, Doolittle 1958, Carmean 1979), particularly those with a *Quercus* component (*e.g.*, Clatterbuck and Hodges 1988, Oliver 1978, Johnson and Krinard 1988). These reports provide valuable information to foresters regarding the potential need of silvicultural intervention during canopy recruitment in even-aged stands (Brose *et al.* 2008, Ward 2009). Nevertheless, there has been less research focused on quantifying the developmental patterns of trees in young mixed species stands.

Height development is typically modeled as a function of age and site productivity. These relationships have been used to successfully model growth and yield for a variety of species and regions (Weiskittel *et al.* 2011, Burkhart and Tomé 2012, Pretzsch 2009). Unfortunately, height~age curves are seldom developed for species with limited commercial value though they may be important components of regenerating forests. When available for a species, height~age curves usually begin at age 10 to 20 years (*e.g.*, Carmean *et al.* 1989). Consequently, there is little quantitative information to guide expectations of height development for most or all of what is commonly considered the regeneration period (*sensu* Johnson *et al.* 2009) in naturally regenerated even-aged eastern forests. For example, modeling the height development of *Quercus rubra*, a species of great ecological and commercial value (*e.g.*, Loftis and McGee 1993), required extrapolation of height age curves below the age of twenty (Loftis 1990). Additionally, height~age curves are often produced from “site” or “top-height” trees (Helms 1998), which represent only the average growth of the “best” trees according to various selection criteria (Curtis 1964, Sharma *et al.* 2002, Garcia and Batho 2005). Therefore, far less is known about the growth of trees that become suppressed early in the development of a stand.

While quantitative height~age data would certainly be useful for modeling early stand development, it is not without limits. Often, the ages of individual stems are not known and stand age is substituted. Though stand and stem age data can be collected, it may have little correlation with biological age for species that regenerate via advance reproduction and/or vegetative reproduction. These

regeneration sources are common in eastern deciduous forest, particularly in the Missouri Ozarks (Johnson *et al.* 2009). It has been well documented that height growth and productivity in general, decreases with age (Ryan *et al.* 1997). However, there is growing evidence that the growth decline is better explained by biological limitations, particularly hydraulic conductivity, that result from increases in physical size, rather than age (Martínez-Vilalta 2007). This is a convenient relationship for modeling growth because of the aforementioned difficulty in obtaining appropriate age data.

Given the need to quantify height development trends of juvenile trees during early stand development, a study was initiated, in part, to examine the size related height increment patterns of developing trees via stem analysis. This initial examination of height development trends found in the stem analysis dataset had the following objectives:

- 1) Quantify mean size related trends in height increment exhibited by juvenile trees during the first twenty years of stand development in naturally regenerated mixed species even-aged stands.
- 2) Develop a model to project size related trends in height increment exhibited by juvenile trees during the first twenty years of stand development in naturally regenerated, mixed species, even-aged stands in the Missouri Ozarks.
- 3) Quantify developmental milestones of recruitment “success” from the growth patterns exhibited by juvenile trees that were ultimately in codominant and dominant crown classes following the first twenty years of

stand development in naturally regenerated, mixed species, even-aged stands in the Missouri Ozarks.

Methods

The data used in this project were collected from forest stands located in the Missouri Ozark counties of Carter, Reynolds, Ripley, Shannon, and Wayne. The study region is an unglaciated, deeply dissected plateau primarily comprising Ordovician and Cambrian dolomites and sandstones (Kabrick *et al.* 2000). Average annual precipitation is 115 cm and average annual temperature is 13.5° C (Kabrick *et al.* 2008). Slope aspect and slope position are important characteristics used for site classification in the region (Nigh *et al.* 2000). The sites used in this study were on exposed (aspect: 136 - 315°) and protected (aspect: 316 - 136°) backslopes with an average site index (*Quercus velutina* Lam., base age 50) of 21.0 ± 1.3m and 22.0 ± 1.1m, respectively (McQuilkin 1974). Overstory species composition on both site classes are typically dominated (>70% basal area) by oak species (primarily *Q. velutina*, *Q. alba* L., *Q. coccinea* Münchh., *Q. stellata* Wangenh.) and compositional differences between the two site classes are subtle (Kabrick *et al.* 2004). Protected backslopes usually have a slightly higher *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* Mill. are more common on exposed backslopes (Kabrick *et al.* 2004).

All stands were located on Missouri Conservation Areas under the management of the Missouri Department of Conservation. The stands sampled for this study were clearcut harvested with reserves ($\approx 5\text{m}^2\text{ha}^{-1}$) approximately twenty years prior to sampling. At the time of harvest, all live trees $> 3\text{m}$ in total height or $> 4\text{cm}$ dbh were felled, with the exception of trees left as reserves (Missouri Department of Conservation 1986). There was no evidence of stand-level disturbances since the time of harvest. According to harvest records, the stand ages (years since harvest) ranged from 18 to 28 years with a mean of 22 years. The purported age of each stand was confirmed by aging several obvious stump sprouts at ground level.

A total of twenty stands were sampled for this project from June to August, 2013. Ten stands were sampled on exposed backslopes and ten on protected backslopes. Within each stand, a single 0.05-ha circular search plot (12.6m radius) was established with a randomly determined center location. The following restrictions were placed on the location of plot centers: $\geq 32.72\text{m}$ from stand boundaries, $\geq 12.6\text{m}$ from obvious skid trail or landing area, $\geq 25.2\text{m}$ from any large trees that were obvious reserves from the previous rotation. In addition to the search plot, a 0.005-ha circular inventory plot (3.93m radius) was established at each plot center to record the species and diameter at breast height for all woody species.

On each search plot, the closest trees to the plot center that met the following criteria were identified as sample trees. The following species (or genera-based species groups) were targeted for sampling: ashes, blackgum, black cherry,

blackjack oak, black oak, dogwood, elms, hickories, northern red oak, shortleaf pine, post oak, red maple, southern red oak, sassafras, scarlet oak, sugar maple, white oaks. On each search plot, a sample from each species and across all crown classes (dominant, codominant, intermediate, suppressed) was obtained as available. A threshold height of 3m was required for a suppressed tree to be sampled. An additional sample was obtained from oak species in codominant or dominant crown classes on each plot, so that stems with different origins (obvious sprout vs not obvious sprout) were represented when possible. The sample sizes obtained for each species-crown class combination are provided in Table 4.1. Given a search plot size of 0.05ha (12.6m radius), any species/crown class combination not captured in the sample was an infrequent component of the sample stands.

Prior to felling by chainsaw, the distance and azimuth from plot center to each sample tree was recorded along with the diameter at breast height (1.375m), total height, and height to live crown base. Each sample tree was felled with a cut between ground level and 25cm above ground-level. Once the sample tree was felled, limbed and measured for felled length, a cross-section approximately 2cm thick was removed at ground level and every 25cm along the bole of the tree. An additional cross-section was cut at breast height (1.375m) for radial analyses. Each cross-section was labeled with an identifier and the sample height.

Samples were stored in paper bags and air dried under a covered, open-air facility up to a year prior to processing. Cross-sections were sanded using up to 600 grit sandpaper as needed, for ring identification. Each cross section was

aged at least twice along differing radii, and this was repeated by at least two technicians. Additional ages were taken until any disagreements were resolved. Optical microscopes with up to 3x magnification were used as necessary. The diffuse porous wood anatomy of blackgum and dogwood made aging difficult and has not yet been completed for all samples from these two species. Therefore, the analyses that follow do not include blackgum or dogwood.

When an age transition occurred between cross-sections, it was assumed that the completion of the preceding year's growth occurred at half the distance between the two cross-sections. For a 25cm distance between cross-sections, this provides yearly height with a precision of ± 12.5 cm assuming only one age transition occurred between cross-sections (Husch *et al.* 2003), which was almost always the case. Given this sampling intensity, more intricate methods of determining the height of hidden tips (*e.g.*, Cancino *et al.* 2013) were not used. Others have noted that the use of height-age data obtained via stem analysis could be problematic in regression analyses (Goelz and Burk 1996). However, the ± 12.5 cm precision allowed by the 25cm distance between cross sections in this study was comparable to published field estimates of standing tree heights (Larsen *et al.* 1987, Bragg *et al.* 2011). Furthermore, the ± 12.5 cm precision was much lower than the discrepancy between estimates of standing tree height and the measured length once felled for the sample trees in this study (mean: 58.7cm, sd: 116cm). Given this, it is assumed that the height-age data do not violate the assumptions of regression with any greater consequence than do the measurement errors associated with field estimates of standing tree heights.

Because the sampling began after the onset of growth in the Missouri Ozarks for 2013, the height-age data and ring width data for 2013 were not analyzed as growth for that year was not completed at the time of sampling.

It was hypothesized that annual increment rate was a function of species, height, stem origin, site class, stand age, and final crown class. Because final crown class cannot be known early in stand development, two model selection processes were completed. One model selection process included final crown class to derive a “best” model, and one did not include final crown class to produce a “projection” model for more general use. Candidate models were not developed from all possible combinations of the covariates and their interactions. Because height and species were the primary covariates of interest, they were included in all candidate models. Two-way interactions between height-species, height-stand age, height-stem origin, height-site class, and height-crown class were the only interactions considered.

All statistical analysis was completed in R statistical software version 3.0.3 (R Development Core Team 2014). The packages and functions used are mentioned in capital letters throughout the document. Because the data had a hierarchical grouping structure (cross-sections within trees within plots) mixed effects models were required (Pinheiro and Bates 2000, Zuur *et al.* 2009). The linear mixed effects model function (LME) within the NLME package (Pinheiro *et al.* 2013) was used for the mixed effects analyses. To accommodate this structure, random effects were included for each tree within plot and each plot. Possible serial autocorrelations for cross-sections within tree were assessed via

a continuous auto-regressive correlation structure (corCAR1) using cross-section height within tree as an ordering variable. The impact of including this correlation structure was evaluated during the model selection process. Heterogeneous errors were accounted for by modeling the variance as a power function of the mean (varPower). The impact of including separate parameter estimates of the variance power for different grouping variables (species, stem origin, crown class site class) was assessed during the model selection process.

Model selection for the mixed effects analyses was conducted using a combination of Akaike's Information Criterion (AICc) corrected for small sample sizes and likelihood ratio tests for nested models (Burnham and Anderson 1998, Pinheiro and Bates 2000, Zuur *et al.* 2009). Models fit via restricted maximum likelihood (REML) were used to determine the appropriateness of choices regarding random effects, correlation structures, and variance weights; whereas, selection of fixed effects were conducted using maximum likelihood (ML) fits (Pinheiro and Bates 2000, Zuur *et al.* 2009). To assess the contribution of fixed effects interactions of height with species, stand age, site class, and stem origin, each interaction was removed, in turn, from the full model, and compared via AICc. If an interaction was found to contribute little to model performance (difference < 2 units of AICc), then it was removed from the model and its respective main effect was assessed similarly. Finally, a model with all terms removed that were determined inconsequential in the previous steps was compared to the full model via AICc.

The reported parameter estimates were obtained via restricted maximum likelihood (REML) using effects coding (*i.e.*, sum,deviation) because there was no logical preference for a reference level among the categorical variables. Type 3 tests of fixed effects were obtained by effects coding using the CONTR.SUM function in the CAR package (Fox and Weisberg 2011) and the ANOVA.LME function in the NLME package (Pinheiro *et al.* 2011) with type = marginal.

Because of the grouping associated with the previously described data structure, a quantile estimation procedure that accommodated the random effects of plot and tree within plot was used. Quantile regression for clustered/panel data is an emerging area of statistical research (Koenker 2004, Geraci and Bottai 2014). There are currently two packages that exist to accommodate this application of quantile regression within R, the regression quantiles for panel data (RQPD) package (Koenker and Bache 2011) and the recently released linear quantile mixed model (LQMM) package (Geraci 2014, Geraci and Bottai 2014). The RQPD has limited availability, and convergence was difficult to achieve during preliminary analysis using the LQMM package. For this reason, quantile regression analyses were completed using the regression quantiles function (RQ) within the QUANTREG package (Koenker 2012) along with the b-splines function (BS) within the SPLINES package (R Development Core Team 2014). These functions were used to model the 10th percentile of height~age development trends of trees that were dominant and codominant at the end of the regeneration period. The default options for determining the number and placement of knots for the b-splines was utilized. Unfortunately, this analysis

cannot account for the possibility of correlated errors due to the grouped data structure.

Although linear regression was used for this analysis, the result is a nonparametric description of the conditional quantile of interest. This is desirable because parametric growth functions may impose assumptions and restrictions that are not generated by the underlying phenomenon of interest (Takezawa 2006). Nonparametric techniques such as functional data analysis, b-splines, and local linear regressions provide more flexibility in growth forms and analyses than parametric growth functions (Ramsay and Silverman 2002, Takezawa 2006). Nonetheless, these techniques are more often used for preliminary data analysis because they do not provide results that are easily reproducible or interpretable without training. Accordingly, pointwise reproductions of the lines produced by these analyses are provided as output along with the model results.

The minimum (or maximum) quantile that can be estimated precisely varies with sample size and data distribution; thus, estimates of the absolute minima (e.g., 1st percentile) may not be reliable without very large samples (Cade *et al.* 1999). To avoid limitations due to sample size, the 10th percentile was chosen to represent near-minima height~age development thresholds of trees. It was likely that some species that were relatively rare in the sample were too few in number to provide reliable quantile estimates. Thus, an arbitrary sample size of 5 trees was required for a species to be included in this analysis. By this criteria *Acer saccharum*, *Quercus falcata*, and *Ulmus* spp. were excluded from individual

species analyses. Two trees proved to be residuals from a previous rotation (heights > 8m at stand age 0) and they were excluded from analyses.

It was hypothesized that the near-minima height~age development thresholds may vary by site class. Therefore a separate regression was performed for each site class for those species with adequate representation (≥ 5 trees) in each site class.

Results

A model with random effects for tree and tree within plot was used given the data structure. AICc (REML) indicated that heterogeneous errors were best accounted for with variance modeled as a power function of the mean and separate power coefficients modeled for each final crown class. A model that incorporated a continuous autoregressive structure (CAR1) yielded a low estimate for correlation among consecutive cross sections within a tree (0.0677) and was not found to perform better per AICc (REML). Therefore the continuous autoregressive structure was not included in the “best” model. A model that included all covariates and their interaction with height except for a height·site class interaction was rated better per AICc (ML) than the full model (-855.3253 vs -844.9167). Models excluding other covariates, or their interactions, were found to be ranked worse than both the full model, and the model that only excluded the height·site class interaction per AICc (ML). Therefore, the model that excluded the height·site class interaction was chosen as the “best” model of

annual height increment. The parameter estimates for this “best” model are provided in Table 4.2.

Annual height increment was highly variable (Fig. 4.1). The residual standard deviation, or within group standard error, of the “best” model was 51.38cm (95% C.I. $\approx \pm 2.34$). The estimates for the random effects are presented in Table 4.3. The estimate of the random effect for plot was a standard deviation of 5.2cm (95% C.I. ≈ 3.56 -7.59cm), and tree within plot had a standard deviation of 6.37cm (95% C.I. ≈ 5.48 -7.39cm). The estimated parameters (δ) for the variance covariates, which were modeled as a power function ($\sigma^2 \cdot |v_{ij}|^{2\delta}$) of the fitted conditional mean (v_{ij}) for each final crown class tended to decline as crown class decreased from dominant to suppressed (Table 4.4). However, the estimates for intermediate and suppressed stems were similar and well within the 95% confidence regions of one another. Stems that were dominant at the time of sampling had a variance covariate power (δ) of 1.3451 (95% C.I. $\approx \pm 0.0912$), stems that were ultimately codominant had a variance covariate power (δ) of 1.2397 (95% C.I. $\approx \pm 0.0692$), intermediate trees had an estimated variance covariate power (δ) of 1.1281 (95% C.I. $\approx \pm 0.066$), and the variance covariate power (δ) for suppressed stems was 1.1453 (95% C.I. $\approx \pm 0.0662$).

For the sample trees in this study, average (unweighted) annual height increment was 71.8cm (95% C.I. $\approx \pm 4.07$ cm) (Table 4.2). Height was a statistically significant (p -value $<.0001$, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5). The effects coded parameters indicated that the main effect of height was to reduce annual height increment by

about 4cm (95% C.I. $\approx \pm 0.64$ cm) per meter increase in height (Table 4.2, Fig. 4.1). However, there were several significant interactions included in the “best” model that adjusted the rate at which height increment declined with increasing height (Tables 4.2,4.5).

Species was a statistically significant (p -value .0123, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5). There was a statistically significant (p -value $<.0001$, Type 3) interaction between height and species (Table 4.5). The interaction was significant individually only for *Pinus echinata* (p -value .0047), *Quercus coccinea* (p -value .0000), *Sassafras albidum* (p -value .0018), and *Ulmus* spp. (p -value .0020) (Table 4.2). The height-species interaction effect was negative for *Carya* spp., *Prunus serotina*, *Quercus alba*, *Quercus falcata*, *Sassafras albidum*, and *Ulmus* spp indicating that the rate of reduction in height increment with increasing height was greater than average; whereas, the rate of reduction was less than average for the remaining species. The decline in height increment with increasing height appeared most influential for *Sassafras albidum* and *Ulmus* spp. (Fig. 4.2). The effects coded parameters indicated that the main effect was lower than the unweighted grand mean for *Acer rubrum*, *Acer saccharum*, *Carya* spp., *Pinus echinata*, *Quercus alba*, *Quercus coccinea*, *Quercus marilandica*, and *Quercus stellata* but positive for all others. The species effects ranged from about -13cm to +21cm, but only *Acer rubrum* (p -value .0469), *Quercus stellata* (p -value .014), and *Ulmus* spp (p -value .0169) were statistically different ($\alpha=0.05$) from the unweighted grand mean.

Stem origin was a statistically significant (p -value <.0001, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5).

However, there was a statistically significant (p -value <.0001, Type 3) interaction between height and stem origin. Stems from obvious sprout origin exhibited a small reduction in annual height increment with increasing height ($-0.46\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.17\text{cm}\cdot\text{m}^{-1}$) (Fig. 4.3). The main effect for stems from obvious sprout origin was 4.71cm (95% C.I. $\approx \pm 1.56\text{cm}$) (Table 4.2).

Site class was a statistically significant (p -value .0045, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5).

Trees on protected backslopes had about a 4cm greater average increment (95% C.I. $\approx \pm 2.64\text{cm}$) than trees on exposed backslopes (Table 4.2). A

height-site class interaction was not included in the “best” model of size related annual height increment.

Stand age was a statistically significant (p -value <.0001, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5).

However, there was a statistically significant (p -value <.0001, Type 3) interaction between height and stand age (Table 4.5). The effect of the height-stand age interaction was negative (-0.11cm , 95% C.I. $\approx \pm 0.02\text{cm}$), implying that the effect of stand age on height increment was reduced by each unit increase in height.

The main effect of stand age was positive but small, indicating an average increase in height increment of 1.15cm (95% C.I. $\approx \pm 0.35\text{cm}$) with increasing stand age (Table 4.2).

Final crown class was a statistically significant (p -value $<.0001$, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.5). There was a statistically significant (p -value $<.0001$, Type 3) interaction between height and final crown class. The impact of the height-final crown class interaction was positive for trees that were ultimately dominant ($1.06\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.34\text{cm}$) and codominant ($0.82\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.25\text{cm}$) indicating that a growth advantage increased with increasing height (Fig. 4.4). The impact of the height-final crown class interaction was negative for trees that were ultimately intermediate ($0.41\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.31\text{cm}$) or suppressed ($1.46\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.39\text{cm}$) indicating that a growth disadvantage became more severe with increasing height. This implied that the effect of final crown class became more apparent with increasing height, and was strongest for trees that were ultimately dominant or suppressed trees. The height-final crown class interaction was statistically significant for all final crown classes. The main effect of final crown class was positive (9.79cm , 95% C.I. $\approx \pm 3.23\text{cm}$) to neutral (0.1cm , 95% C.I. $\approx \pm 2.18\text{cm}$) for trees that were ultimately dominant and codominant respectively (Table 4.2). The main effect of final crown class was negative for trees that were ultimately intermediate (-2.85cm , 95% C.I. $\approx \pm 2.5\text{cm}$) and suppressed (-7.05cm , 95% C.I. $\approx \pm 2.55\text{cm}$). The main effect was significantly different from the unweighted grand mean for trees that were ultimately dominant (p -value 0.0000), intermediate (p -value 0.0260), and suppressed (p -value 0.0000) (Table 4.2).

Because a model with final crown class may have restricted inference prior to the age at which final crown class was determined (stand ages 18-28 in this study), a model selection process was repeated without final crown class as a covariate. AICc (REML) indicated that heterogeneous errors were best accounted for with variance modeled as a power function of the mean and separate power coefficients modeled for each species. A model that incorporated a continuous autoregressive structure (CAR1) yielded a low estimate for correlation among consecutive cross sections within a tree (0.0687) and was not found to perform better per AICc (REML). Therefore the continuous autoregressive structure was not included in the “projection” model. A model that included all covariates and their interaction with height, except for stand age, was rated better per AICc (ML) than the full model (-454.1567 vs -386.3314). Another model that included all covariates and their interaction with height except for a height·site class interaction was rated better per AICc (ML) than the full model (-391.4509 vs -386.3314). Thus, an additional candidate model that included only height, species, stem origin, site class, height·species, height·stem origin was considered. This model was rated better per AICc (ML) than the full model (-457.5749 vs -386.3314) and the model that included all covariates except stand age (-457.5749 vs -454.1567). Models excluding other covariates, or their interactions, were found to be ranked worse than both the full model, and the model that excluded stand age and its interaction with height per AICc (ML). Therefore, the model that excluded stand age entirely and the height·site class interaction was chosen as the “projection” model of annual height increment rate

with unknown final crown classes. The parameter estimates for this “projection” model are provided in Table 4.6.

In terms of residual error, the “projection” model was only slightly worse than the “best” model. The residual standard deviation, or within group standard error, of the “projection” model was 51.45cm (95% C.I. \approx 49.11-53.89cm). However, there were differences in the variance components between the “best” and “projection” models. The estimates of the random effects for the “projection” model are presented in Table 4.7. The estimate of the random effect for plot was a standard deviation of 4.77cm (95% C.I. \approx 3.12-7.28cm) for the “projection” model which was slightly lower than the “best” model, but the tree within plot random effect for the “projection” model had a standard deviation of 10.13cm (95% C.I. \approx 9.24-11.12cm) which was considerably higher than the “best” model. The estimated parameters (δ) for the variance covariates, which were modeled as a power function ($\sigma^2 \cdot |v_{ij}|^{2\delta}$) of the fitted conditional mean (v_{ij}) for each species are provided in Table 4.8. Although the model with separate estimates for each species was ranked better per AICc, there was little difference in the estimates among species.

Per the “projection” model, average (unweighted) annual height increment was 75.7cm (95% C.I. \approx \pm 4.13cm) for the sample trees in this study (Table 4.6).

Height remained a statistically significant (p -value $<$.0001, Type 3) predictor of annual height increment (Table 4.9). The effects coded parameters indicated that the main effect of height was to reduce annual height increment by about 4cm (95% C.I. \approx \pm 0.36cm) per meter increase in height (Table 4.6). However,

there were significant interactions that adjusted the rate at which increment declined with increasing height (Tables, 4.6,4.9).

Species was a statistically significant (p -value .0004, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.9). There was also statistically significant (p -value <.0001, Type 3) interaction between height and species. The interaction was significant only for *Pinus echinata* (p -value .0047), *Quercus coccinea* (p -value .0000), *Sassafras albidum* (p -value .0018), and *Ulmus* spp. (p -value .0020). The height-species interaction effect was negative for *Acer rubrum*, *Carya* spp., *Quercus alba*, *Quercus falcata*, *Sassafras albidum*, and *Ulmus* spp indicating that the rate of reduction in height increment with increasing height was greater than average (Table 4.6); whereas, the rate of reduction was less than average for the remaining species. The species main effects ranged from about -16cm to +17cm, but only *Acer rubrum* (p -value .0134), *Carya* spp. (p -value .0215), and *Quercus stellata* (p -value .0002) were statistically different from the unweighted grand mean.

Stem origin was a statistically significant (p -value <.0001, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.9).

However, there was a statistically significant (p -value <.0001, Type 3) interaction between height and stem origin. Stems from obvious sprout origin exhibited a small reduction in annual height increment with increasing height ($-0.44\text{cm}\cdot\text{m}^{-1}$, 95% C.I. $\approx \pm 0.18\text{cm}\cdot\text{m}^{-1}$) (Table 4.6).The main effect advantage for stems from obvious sprout origin was 6.37cm (95% C.I. $\approx \pm 1.81\text{cm}$).

Site class was a statistically significant (p -value .0025, Type 3) predictor of annual height increment for the sample trees used in this study (Table 4.9). Trees on protected backslopes had about a 4cm advantage (95% C.I. $\approx \pm$ 2.59cm) over trees on exposed backslopes (Table 4.6). A height-site class interaction was not included in the “best” model of size related annual height increment.

The near-minima height~age development trends during the first twenty years of stand development in naturally regenerated, mixed species, even-aged stands in the Missouri Ozarks for trees that were ultimately in dominant and codominant crown classes is depicted for each species analyzed in Figure 4.5. The near-minima height of trees that were dominant and codominant at the time of sampling tended to increase in an approximately linear relationship with stand age for most species. The near minima for *Pinus echinata*, *Prunus serotina*, and *Sassafras albidum* tended to increase in a more sigmoidal pattern with increasing stand age. Point estimates of the lines produced by the non-parametric b-spline regression are provided in Table 4.10.

The impact of site class on the near minima appeared to be strongest for *Prunus serotina* throughout the first 20 years of development among those species with adequate representation on both classes (Fig. 4.5). As early as stand age 3 the near-minima height of *Prunus serotina* tended to be approximately 1-1.5m shorter on exposed backslopes compared to protected backslopes (Table 4.10). In addition to *Prunus serotina*, site class impacted the near-minima for *Carya* spp. and *Quercus alba*. The impact of site class on the near-minima for these

species increased with time, but was not immediately apparent. The divergence in near-minima height between site classes for *Carya* spp. was approximately 2m by age 20, but was ≤ 1 m through age 10. The difference in near-minima height among site classes was apparent much earlier for *Quercus alba* compared to *Carya* spp. The near-minima for *Quercus alba* on exposed backslopes was as much as approximately 1m shorter than on protected backslopes as early as stand age 6, but reached a peak difference similar to *Carya* spp. (≈ 2 m) by stand age 20. For other species with adequate representation on both site classes there was little difference in near-minima height~age trends between site classes during the first 20 years of stand development.

The near-minima for each species are plotted together for both site classes in Figure 4.6. There was little difference in the near-minima among most species through the first 20 years. However, there appeared to be an onset of increasing divergence among species beginning between ages 10-15 on exposed backslopes that was not evident on protected backslopes. Two notable exceptions to the general trends were *Pinus echinata* and *Prunus serotina* on exposed backslopes. The near-minima for these two species at a given age tended to be shorter than the other species on exposed backslopes until about age 10.

Discussion

Height development is typically modeled using variants of sigmoidal cumulative growth functions via nonlinear regression (Burkhardt and Tomé 2012, Weiskittel *et*

al. 2011). Increment curves derived from these sigmoidal cumulative growth functions indicate that annual increment is slow initially, reaches a peak, and declines thereafter. Assmann (1970) described these three phases as the juvenile phase, full vigor phase, and senescence phase respectively. This pattern of growth is well documented and several competing biological hypotheses have been posited to explain this phenomenon (Ryan *et al.* 1997). There is growing evidence that the decline in production is better explained by size-based relationships rather than age (Martínez-Vilalta 2007).

Preliminary analyses suggested that the classic sigmoidal pattern was not prevalent among the sample trees in this study (Fig. 4.7). Rather, most developmental trends appeared approximately linear, or asymptotically linear through much of the study period. This was likely due to a preponderance of advance reproduction regeneration and sprouting strategies for many species in the Missouri Ozarks (Johnson *et al.* 2009). These regeneration sources may be able to avoid or shorten the juvenile phase of growth, perhaps through belowground carbohydrate storage (Kobe *et al.* 2010). In this case, growth patterns would peak initially followed by the more linear senescence phase of growth during early stand development as opposed to true seedlings that would peak and decline later. This is consistent with the more rapid decline in height increment with increasing size in this study for obvious sprout origin stems compared to non-sprouts (Fig. 4.3). However, it must be noted that the identification of stem origin in this study was only approximate.

Vickers and others (2014) found that during canopy recruitment, saplings (height $\leq 4\text{m}$) that were taller initially had a significant advantage in periodic annual height increment over those that were shorter. There are at least three (probably more) possible mechanisms to explain this observed advantage: 1) the disparity in initial heights reflected inherent genotypic or phenotypic differences such as root mass (Dey *et al.* 1996), 2) initially taller individuals had successfully differentiated in stature from their peers and benefited from the advantages of asymmetric competition (Schwinning and Weiner 1998, Weiner 1990), and 3) differences in potential increment due to different phases of development (*sensu* Assmann 1970), *i.e.*, smaller saplings had not yet reached the phase of peak growth whereas larger saplings had. The decline in growth rate with increasing size suggests that the advantages of initial size on periodic annual height increment observed by Vickers and others (2014) among saplings in the Missouri Ozarks were not likely attributable to the different developmental phases described by Assmann (1970). The differences in growth observed between trees that ultimately occupied different crown classes in this study (Fig. 4.4) suggest that the first two explanations are complimentary. There were inherent differences that caused the initial disparity in height which were then magnified as the trees continued to develop.

The height increment of many of the species in this study declined at similar rates (Fig. 4.2), there were some notable rank changes among species, particularly the rapid decline of *Ulmus* spp. and *Sassafras albidum*. While height increment was modeled as a linear function in this analysis, additional analyses

that allow for the possibility of nonlinear trends may better capture differences due to species and stem origin during the first 20 years of stand development and are warranted. There was greater evidence of a nonlinear growth pattern for some species, particularly *Pinus echinata* (Fig. 4.7). However, there was considerable variability in height increment within species, thus the identification of more appropriate model forms may be difficult. The great variation in height increment observed within individuals, as well as within and among species in this study is characteristic of early growth analyses (Burkhardt and Tomé 2012, Weiskittel *et al.* 2011) and often increases modeling difficulty. This variability in height increment is likely an important contributor to species coexistence (Hara 1993, Kohyama *et al.* 2005) and warrants additional analyses within the dataset used in this study.

Given the high within group variation in height increment, the residual variation of the “projection” model was only slightly worse than the “best” model (Table 4.3, Table 4.7). Though inter-annual height increment was highly variable the projection model can be used to provide an expectation of individual tree growth during early stand development following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks. This model provides a quantitative tool to fill a void of early height increment models beyond site index extrapolation. Moreover, the inclusion of trees from all crown classes provides a more thorough representation of early growth than site index curves based solely on the selection of successful trees. However, given that the data used in this study was

collected at the end of the regeneration period, only those trees that survived were included, creating a selection effect in the “projection” model as well.

Because the model is size-based rather than age, it can provide an approximation of growth trends relative to initial conditions in more complex structures when age is not known. Vickers and others (2014) developed a size-based model of the decline in height increment with increasing overstory density. A combination of the trends in these two models may provide much needed inference into the developmental trends of saplings during canopy recruitment under a variety of management objectives. Nonetheless, additional research into the role of overstory density on sapling development is warranted.

The dataset used in this study provided an opportunity to examine the developmental milestones required to attain an upper canopy position at the end of the regeneration period following clearcutting for several species in naturally regenerated, mixed species stands in the Missouri Ozarks. The trees that were used to develop these milestones were dominant and codominant at the time of sampling (18-28 years post-harvest). There was remarkably little difference in the developmental milestones among species examined in this study during the first 15-20 years of stand development (Fig. 4.6). While the sample was dominated by *Quercus*, typical of forests in the Missouri Ozarks, the pathway to recruitment success for the minor associates such as *Carya* spp., *Acer rubrum*, and *Sassafras albidum* were virtually indistinguishable from *Quercus*. This may be a reflection of the ubiquity of *Quercus* and its role as the successional climax species pressuring other species to grow at a similar rate to avoid competitive

exclusion. This suggests that the developmental milestones presented here may be reflective of a vertical threshold of resource (light) availability that is a result of cumulative leaf area and below which growth is limited (Ellsworth and Reich 1993, Lewis *et al.* 2000, Yoda 1974). The reduction in both the mean and variability of height increment with increasing height for trees in lower final crown classes (Fig. 4.4, Table 4.4) is consistent with this hypothesis. The more rapid decline in height increment of *Sassafras albidum* and *Ulmus* spp. (Fig. 4.2) suggests that such thresholds, if predominantly driven by the developmental trends of *Quercus* would become exceedingly difficult to attain as stands continue to develop. Despite the apparent greater growth tolerance to shade of *Sassafras albidum* as an understory sapling (Vickers *et al.* 2014), the rapid decline of height increment with increasing size suggests it is a progressively weaker competitor in developing clearcuts following crown closure.

This may not be representative of the trends in early stand development in other regions. Oliver (1978) and Hibbs (1983) described *Quercus rubra* initially lagging behind both *Acer rubrum* and *Betula lenta* before eventually surpassing them to become dominant in even-aged stands in New England. Clatterbuck and Hodges (1988) and Johnson and Krinard (1988) described *Quercus pagoda* initially lagging behind *Liquidambar styraciflua* before eventually becoming dominant in bottomland hardwood forests of Mississippi and Arkansas. Dey and others (2009) found that the probability of *Quercus rubra* seedlings becoming a dominant or codominant tree increased slightly through time following shelterwood removal in upland hardwood stands in Missouri and Arkansas but

decreased sharply in Indiana. Despite the rapid initial growth of *Liriodendron tulipifera*, Morrisey and others (2008) reported that periodic droughts provided opportunities for the initially slower growing *Quercus* saplings to persist and exhibit sufficient growth to capture growing space during stem exclusion following clearcutting in Indiana. Zenner and others (2012) found that eventual dominant *Quercus* in even-aged stands on contrasting sites in Pennsylvania tended to be shorter than their direct competitors initially, but not more than 1-2m. This strategy of delayed ascent into the upper canopy has been coined “latent dominance” (O’Hara 1986).

Among the species examined in this study, only *Pinus echinata* and *Prunus serotina* on exposed backslopes exhibited this behavior. The developmental milestones for *Pinus echinata* on exposed backslopes tended to be lower than other species initially but taller later. This indicates that *Pinus echinata* stems that occupied the upper canopy at the end of the regeneration period tended to be among the tallest in the upper canopy, but also suggests that the developmental milestones for *Pinus echinata* become exceedingly difficult to attain for intermediate trees as the regeneration period progresses. Conversely, the developmental milestones for *Carya* spp., *Quercus alba*, and *Quercus stellata* were the lowest on exposed backslopes after 15 years.

In contrast to many of the studies mentioned earlier, the developmental milestones presented here do not describe the average development of eventual dominants and codominants. They are an approximation of the minimum height-development trends exhibited by eventual dominant and codominant trees. Thus,

latent dominance and other relative changes in mean height that may occur among the tallest trees would not necessarily be reflected by the near-minima presented here. Moreover, because these milestones represent the approximate minima rather than the absolute minima, it would not be unprecedented, though unlikely, for a tree to develop into an eventual dominant or codominant tree without reaching these milestones earlier in development. Conversely, reaching these milestones at an early age does not guarantee that a tree will remain on track to become a dominant or codominant tree. Canopy recruitment in even-aged stands has been described as an exclusionary process (Oliver and Larson 1996). Ward and Stephens (1994) reported that mortality rates of saplings were higher for trees occupying lower crown classes following clearcutting in Connecticut. Moreover, the probability of an individual maintaining or increasing crown class through time was lower for trees occupying lower crown classes (Ward and Stephens 1994). Additional analyses to determine the probability of remaining above these milestones, once reached or attaining these milestones if they are not reached initially are warranted. While it is unlikely that the trees used to develop these milestones experienced suppression early in development, they may not necessarily have been among the tallest trees earlier in the development process (Dahms 1963, Raulier 2003). The considerable within species inter-annual variation in height increment exhibited (Fig. 4.1) suggest that rank changes within and between species during development are likely.

There are developmental differences between individual trees and stands. These differences are likely magnified in mixed species stands (Kelty *et al.* 1992).

Measures of success based on stand development patterns may differ from those based on tree developmental patterns. Both approaches have been used to assess recruitment in the eastern hardwood forest. For example, Spetich and others (2002) defined success as 80% of the mean height of dominant competitors at a given stand age. In contrast, Loftis (1990) used an extrapolation of a site index curve as a success criterion. Sander and others (1984) intuited that a height of 2.7m at age 5 was an appropriate success threshold to evaluate regeneration adequacy in the Missouri Ozarks. This height represented 80% of the height of dominant oak stump sprouts at this age. Gould and others (2006) asserted that this point estimate criterion was too restrictive and suggested that plot based success criteria were a better representation of success at age 20 than criteria derived from individual trees. However, plot/stand based metrics of dominant height tend to be *higher* at earlier ages than those based on individual tree growth (Burkart and Tomé 2012, Raulier 2003, Weiskittel *et al.* 2011). The developmental milestones presented in Figure 4.6 were derived from the longitudinal growth of individual trees that occupied the upper canopy at age 20 and are virtually indistinguishable at age 5 (Table 4.10) to the cross-sectional success threshold suggested by Sander and others (1984). The early stature of the trees that ultimately occupied the upper canopy in this study relative to their known neighbors on the sample plot has not yet been examined.

If methodological differences produce drastically different interpretations of success, the practical implications could be considerable and result in misallocation of silvicultural resources. Therefore, further consideration into the

most appropriate criteria for success is warranted. Ideally, criteria for success would provide longitudinal inference so that intermediate action may be taken if deemed appropriate. For example, Dey and others (2009) demonstrated how longitudinal variation in plot based success criteria impacted the probability that a given seedling would attain canopy dominance through time. The developmental milestones presented here could be used in conjunction with reference chart methodology (Chapter 5) to gain greater inference into the marginal probability for a given species to attain them and the likely composition above and below those thresholds. Additional work to combine the inference obtainable from the developmental milestones presented here and the reference chart methodology presented in Chapter 5 is warranted. Spatially explicit competition indices may offer additional insight into recruitment dynamics and probabilities for success (Oliver *et al.* 1989).

Conclusion

Though highly variable, height increment of juvenile trees generally declined with increasing height during the first twenty years of stand development following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks (Objective 1). There were some differences in the rate of decline, with *Sassafras albidum* and *Ulmus* spp. having the most rapid decline in height increment with increasing height of the species examined. Mean height increment and mean height increment variability was lower for trees occupying

lower crown classes. These differences were minor initially, but were magnified with increasing height. A model was developed to project size related height growth trends exhibited by juvenile trees during the first 20 years of stand development following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks (Objective 2). This model projects mean height increment as a function of height, species, stem origin, and site class. This model provides a quantitative tool beyond site index extrapolation to fill a void of early height increment models. Developmental milestones for recruitment “success” were identified from the growth patterns exhibited by juvenile trees that were ultimately in codominant and dominant crown classes following the first 20 years of stand development following clearcutting in naturally regenerated, mixed species stands in the Missouri Ozarks (Objective 3). These milestones provide a tool that foresters can use to assess the status of individual trees during the canopy recruitment process in even-aged stands. While it is not guaranteed that tree that attains these milestones early in development will remain on track to become a member of the upper canopy at the end of the regeneration period, there is little chance that a tree will attain that goal without reaching these milestones at some point during the development of the stand. Additional research into the factors that influence the probability of continued success for those stems that attain these milestones early in development is warranted.

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References

- Assmann, E. 1970. *The Principles of Forest Yield Study*. Pergamon Press. 506p.
- Beck, D. E. and Hooper, R.M. 1986. Development of a Southern Appalachian Hardwood Stand after Clearcutting. *South. J. Appl. For.* 10: 168-72.
- Bragg, D.C., Frelich, L.E., Leverett, R.T., Blozan, W., Luthringer, D.J. 2011. The sine method: an alternative height measurement technique. *USDA For. Serv. Res. Note. SRS-22*. 12p.
- Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic Region. *USDA For. Serv. Gen. Tech. Rep. NRS-33*.
- Burkhart, H.E., Tomé, M. 2012. *Modeling Forest Trees and Stands*. Springer. 457p.
- Burnham, K.P., Anderson, D.R. 1998. *Model Selection and Inference. A Practical Information-Theoretic Approach*. Springer. 353p.
- Büsgen, M., Münch, E. 1929. *The Structure and Life of Forest Trees*. Chapman & Hall.
- Cade, B.S., Terrell, J.W., Schroeder, R.L. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology*. 80(1): 311-323.
- Cancino, J., Acuña, E., Espinosa, M. 2013. Combining ring counting and ring width for estimating height in stem analysis. *For. Sci.* 59(6): 599-609.
- Carmean, W.H. 1979. Site index comparisons among northern hardwoods in northern Wisconsin and Upper Michigan. *USDA For. Serv. Res. Pap. NC-169*. 20p.
- Carmean, W.H., Hahn, J.T., Jacobs, R.D. 1989. Site index curves for forest tree species in the eastern United States. *USDA For. Serv. Gen. Tech. Rep. NC-128*. 153p.
- Clatterbuck, W.K., Hodges, J.D. 1988. Development of cherrybark oak and sweetgum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. *Can. J. For. Res.* 18(1): 12-18.
- Curtis, R.O. 1964. A stem analysis approach to site index curves. *For. Sci.* 10: 241-256.
- Dahms, W.G. 1963. Correctio for a possible bias in developing site index curves from sectioned tree data. *J. For.* 61: 25-27.

- Dey, D.C. 1991. A comprehensive Ozark regenerator. Ph.D. Dissertation, University of Missouri, Columbia, Missouri. 283p.
- Dey, D.C., Johnson, P.S., Garrett, H.E. 1996. Modeling the regeneration of oak stands in the Missouri Ozark Highlands. *Can. J. For. Res.* 26: 573-583.
- Dey, D.C., Spetich, M.A., Weigel, D.R., Johnson, P.S., Graney, D.L., Kabrick, J.M. 2009. A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. *New. For.* 37: 123-135.
- Doolittle, W.T. 1958. Site Index Comparisons for Several Forest Species in the Southern Appalachians. *Proceedings of the Soil Science Society of America* 22: 455-458.
- Ellsworth, D.S., Reich, P.B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia.* 96: 169-178.
- Fox, J., Weisberg, S. 2011. *An R Companion to Applied Regression. 2nd ed.* Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Garcia, O., Batho, A. 2005. Top height estimation in lodgepole pine sample plots. *West. J. Appl. For.* 20(1): 64-68.
- Geraci, M. 2014. Linear quantile mixed models: the lqmm package for Laplace quantile regression. *J. Stat. Soft.* 57(13): 1-29. <http://www.jstatsoft.org/v57/i13/>.
- Geraci, M., Bottai, M. 2014. Linear quantile mixed models. *Statistics and Computing.* 24(3): 461-479.
- Goelz, J.C.G., Burk, T.E. 1996. Measurement error causes bias in site index equations. *Can. J. For. Res.* 26(9): 1585-1593.
- Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2005. Developmental Pathways Following the Harvest of Oak-Dominated Stands. *For. Sci.* 51(1): 76-90.
- Gould, P.J., Steiner, K.C., McDill, M.E., Finley, J.C. 2006. Modeling seed-origin oak regeneration in the central Appalachians. *Can. J. For. Res.* 36: 833-844.
- Hara, T. 1993. Effects of variation in individual growth on plant species coexistence. *J. Veg. Sci.* 4: 409-416.
- Helms, J.A. 1998. *The Dictionary of Forestry.* Society of American Foresters. 210p.

- Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology*. 64(6): 1394-1401.
- Husch B., Beers, T.W., Kershaw, J.A. 2003. *Forest Mensuration*. 4th ed. John Wiley. 443p.
- Johnson, P.S., Shifley, S.R., Rogers, R. 2009. *The Ecology and Silviculture of Oaks*. CABI. 600p.
- Johnson, R.L., Krinard, R.M. 1988. Growth and development of two sweetgum-red oak stands from origin through 29 years. *South. J. Appl. For.* 12(2): 73-78.
- Kabrick, J.M., Meinert, D., Nigh, T., Gorlinsky, B.J. 2000. Physical environment of the Missouri Ozark forest ecosystem project sites. In Shifley, Stephen R.; Brookshire, Brian L. ed. *Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment*. Gen. Tech. Rep. NC-208. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station. 41-70.
- Kabrick, J.M., Shifley, S.R., Jensen, R.G., Larsen, D.R., Grabner, J.K. 2004. Oak forest composition, site quality, and dynamics in relation to site factors in the southeastern Missouri Ozarks. In Spetich, M.A. ed. 2004. *Upland oak ecology symposium: history, current conditions, and sustainability*. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Dept. of Agriculture, Forest Service, Southern Research Station. 94-101.
- Kabrick, J.M., Zenner, E.K., Dey, D.C., Gwaze, D., Jensen, R.G. 2008b. Using ecological land types to examine landscape-scale oak regeneration dynamics. *For. Ecol. Mgmt.* 255: 3051-3062.
- Kelty, M.J., Larson, B.C., Oliver, C.D. 1992. *The Ecology and Silviculture of Mixed-Species Forests; a Festschrift for David M. Smith*. Springer.
- Kobe, R.K., Iyer, M., Walters, M.B. 2010. Optimal partitioning theory revisited: nonstructural carbohydrates dominate root mass responses to nitrogen. *Ecology*. 91(1): 166-179.
- Koenker, R. 2004. Quantile regression for longitudinal data. *J. Multivariate Analysis*. 91(1): 74-89.
- Koenker, R. 2005. *Quantile Regression*. Cambridge University Press. 368p.
- Koenker, R. 2012. Quantreg: Quantile Regression. R package version 4.91. <http://CRAN.R-project.org/package=quantreg>.
- Kohyoma, T., Kubo, T., Macklin, E. 2005. Effect of temporal autocorrelation on apparent growth rate variation in forest tree census data and an alternative distribution function of tree growth rate. *Ecol. Res.* 20: 11-15.

- Larsen, D.R., Hann, D.W., Stearns-Smith, S.C. 1987. Accuracy and precision of the tangent method of measuring tree height. *West. J. Appl. For.* 2(1): 26-28.
- Lewis, J.D., McKane, R.B., Tingey, D.T., Beedlow, P.A. 2000. Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and western hemlock canopy. *Tree Phys.* 20: 447-456.
- Loftis, D., McGee, C.E. eds. 1993. Oak Regeneration: Serious Problems, Practical Recommendations. Symposium Proceedings; 1992 September 8-10; Knoxville, TN. USDA For. Serv. Gen. Tech. Rep. SE-84. Pgs. 146-155.
- Loftis, D.L. 1990. Predicting post-harvest performance of advance red oak reproduction in the Southern Appalachians. *For. Sci.* 36(4): 908-916.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton, N.J.
- Martínez-Vilalta, J., Vanderklein, D., Mencuccini, M. Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia.* 150(4): 529-544.
- Missouri Department of Conservation 1986. *Forest Land Management Guidelines*. Missouri Department of Conservation, Jefferson City, Missouri. 81p.
- Morrissey, R.C. Jacobs, D.F., Seifert, J.R., Fischer, B.C., Kershaw, J.A. 2008. Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage. *Can. J. For. Res.* 38: 1419-1430.
- Nigh, T., Buck, C., Grabner, J., Kabrick, J., Meinert, D. 2000. *Ecological Classification System for the Current River Hills Subsection*. Missouri Department of Conservation Publication. Jefferson City, MO. 84p.
- Noble, I.R., Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- O'Hara, K.L. 1986. Developmental patterns of residual oaks and yellow-poplar regeneration after release in upland hardwood stands. *South. J. Appl. For.* 10: 244-248.
- Oliver, C.D. 1978. The development of northern red oak in mixed stands in central New England. *School of Environ. Stud. Bull.* 91. Yale University, New Haven CT.
- Oliver, C.D. 1980. Even-aged development of mixed-species stands. *J. For.* 78(4): 201-203.

- Oliver, C.D., Clatterbuck, W.K., Burkhardt, E.C. 1989. Spacing and stratification patterns of cherrybark oak and American sycamore in mixed, even-aged stands in the southeastern United States. *For. Ecol. Mgmt.* 31: 67-79.
- Oliver, C.D., Larson, B.C. 1996. *Forest Stand Dynamics*. 2nd ed. John Wiley & Sons, Inc. New York. 520p.
- Pinheiro, J.C., Bates, D.M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag New York, Inc. 528p.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., R Development Core Team. 2013. nlme: Linear and nonlinear mixed effects models. R package version 3.1-113.
- Pretzsch, H. *Forest Dynamics, Growth and Yield*. Springer. 664p.
- Puettmann, K.J., Coates, K.D., Messier, C.C. 2008. *A critique of silviculture: managing for complexity*. Island Press. 206p.
- R Development Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ramsay, J.O., Silverman, B.W. 2002. *Applied Functional Data Analysis: Methods and Case Studies*. Springer. 191p.
- Raulier, F., Lambert, M.-C., Pothier, D., Ung, C.-H. 2003. Impact of dominant tree dynamics on site index curves. *For. Ecol. Mgmt.* 184: 65-78.
- Ryan, M.G., Binley, D., Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27: 213-262.
- Sander, I.L., Johnson, P.S., Rogers, R. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. USDA For. Serv. Res. Pap. NC-251. 19p.
- Schwinning, S., Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447-455.
- Sharma, M., Amateis, R.L., Burkhardt, H.E. 2002. Top height definition and its effect on site index determination in thinned and unthinned loblolly pine plantations. *For. Ecol. Mgmt.* 168: 163-175.
- Spetich, M.A., Dey, D.C., Johnson, P.S., Graney, D.L. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. *For. Sci.* 48(3): 504-517.
- Takezawa, K. 2006. *Introduction to Nonparametric Regression*. John Wiley & Sons, Inc.

- Vickers, L.A., Larsen, D.R., Knapp, B.O., Kabrick, J.M., Dey, D.C. 2014. The impact of overstory density on sapling height growth in the Missouri Ozarks – implications for interspecific differentiation during canopy recruitment. *Can. J. For. Res.* 44(11): 1320-1330.
- Ward, J.S., Stephens, G.R. 1994. Crown class transisiton rates of maturing northern red oak (*Quercus rubra* L.). *For. Sci.* 40(2): 221-237.
- Ward, J.S. 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. *Can. J. For. Res.* 39: 118-130.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5:360-364.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A. Jr., Vanclay, J.K. 2011. *Forest Growth and Yield Modeling*. Wiley-Blackwell. 415p.
- Yoda, K. 1974. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Jpn. J. Ecol.* 24: 247-254.
- Zuur, A. Ieno, E.N., Walker, N., Saveliev A.A., Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer. 574p.

Tables

Table 4.1. Sample sizes (trees) for stem analysis dataset collected from twenty naturally regenerated mixed species even-aged stands in the Missouri Ozarks. All stands were sampled 18-28 years following a clearcut with reserves ($\leq 5\text{m}^2\text{ha}^{-1}$) harvest. The twenty plots were distributed evenly among exposed and protected backslopes. The closest tree that exhibited each categorical combination below (species, crown class) within 12.6m of a randomly determined point within each stand was sampled. Apparent stem origin (obvious sprout vs not) was recorded for each tree. A sample tree was selected from both stem origin categories within the dominant or codominant crown classes whenever possible for oak species. Analyses of blackgum and dogwood are not presented due to continued sample processing.

Species	Dominant	Codominant	Intermediate	Suppressed	Total
<i>Exposed Backslopes , Protected Backslopes</i>					
<i>Acer rubrum</i>	0,2	0,8	3,7	3,7	6,24
<i>Acer saccharum</i>	0,1	0,1	0,0	0,0	0,2
<i>Carya</i> spp.	2,4	5,10	8,9	9,9	24,32
<i>Cornus florida</i>	0,0	0,0	1,0	8,8	9,8
<i>Nyssa sylvatica</i>	0,0	3,6	8,7	8,9	19,22
<i>Pinus echinata</i>	4,2	8,0	6,1	4,0	22,3
<i>Prunus serotina</i>	1,7	5,10	3,5	3,4	12,26
<i>Quercus alba</i>	7,8	15,17	10,10	10,10	42,45
<i>Quercus coccinea</i>	7,8	15,11	4,4	3,3	29,26
<i>Quercus falcata</i>	1,0	1,0	0,0	0,0	2,0
<i>Quercus marilandica</i>	0,0	0,0	1,0	1,0	2,0
<i>Quercus rubra</i>	0,3	0,2	0,0	0,0	0,5
<i>Quercus stellata</i>	1,0	12,0	7,2	7,2	27,4
<i>Quercus velutina</i>	4,6	19,8	7,3	8,4	38,21
<i>Sassafras albidum</i>	0,0	0,5	2,7	3,5	5,17
<i>Ulmus</i> spp.	0,1	0,1	0,1	0,1	0,4
Total	27,42	83,79	60,56	67,62	237,239

Table 4.2. Effects coded fixed effects parameter estimates for the “best” model. For convenience the effects of the omitted category from the original category were obtained from a second regression and are provided below.

Fixed effect	Estimate	Std. error	DF	t-value	p-value
Intercept (Unweighted Grand Mean)	0.718	0.0208	7578	34.5531	0.0000
Height	-0.0417	0.0033	7578	-12.7559	0.0000
Stand Age	0.0115	0.0018	7578	6.4086	0.0000
<i>Acer rubrum</i>	-0.0578	0.029	382	-1.9937	0.0469
<i>Acer saccharum</i>	-0.1142	0.0889	382	-1.2853	0.1995
<i>Carya</i> spp.	-0.0407	0.0237	382	-1.7166	0.0869
<i>Pinus echinata</i>	-0.0116	0.0299	382	-0.3881	0.6981
<i>Prunus serotina</i>	0.0157	0.0273	382	0.5757	0.5652
<i>Quercus alba</i>	-0.0146	0.0208	382	-0.70223	0.4830
<i>Quercus coccinea</i>	-0.0159	0.0237	382	-0.673	0.5014
<i>Quercus falcata</i>	0.1296	0.1069	382	1.2122	0.2262
<i>Quercus marilandica</i>	-0.0713	0.0784	382	-0.9093	0.3638
<i>Quercus rubra</i>	0.0064	0.0733	382	0.0869	0.9308
<i>Quercus stellata</i>	-0.0869	0.0269	382	-3.2256	0.014
<i>Quercus velutina</i>	0.0051	0.0229	382	0.2219	0.8245
<i>Sassafras albidum</i>	0.0457	0.0353	382	1.2935	0.1966
<i>Ulmus</i> spp.	0.2105	0.0878	382	2.3983	0.0169
Non-sprout Origin	-0.0471	0.0079	382	-5.9468	0.0000
Sprout Origin	0.0471	0.0079	382	5.9468	0.0000
Exposed Backslopes	-0.0407	0.0126	18	-3.2452	0.0045
Protected Backslopes	0.0407	0.0126	18	3.2452	0.0045
Dominant Crown Class	0.0979	0.0164	382	5.9614	0.0000
Codominant Crown Class	0.001	0.0111	382	0.0905	0.9279
Intermediate Crown Class	-0.0285	0.0127	382	-2.2345	0.0260
Suppressed Crown Class	-0.0705	0.013	382	-5.4305	0.0000
Height·Stand Age	-0.0011	0.0001	7578	-8.5786	0.0000
Height· <i>Acer rubrum</i>	0.0009	0.0033	7578	0.2614	0.7938
Height· <i>Acer saccharum</i>	0.0089	0.0086	7578	1.0384	0.2991
Height· <i>Carya</i> spp.	-0.0004	0.0028	7578	-0.1543	0.8773
Height· <i>Pinus echinata</i>	0.009	0.0032	7578	2.8258	0.0047
Height· <i>Prunus serotina</i>	-0.0015	0.003	7578	-0.491	0.6235
Height· <i>Quercus alba</i> .	-0.0001	0.0023	7578	-0.0255	0.9797
Height· <i>Quercus coccinea</i>	0.0104	0.0025	7578	4.235	0.0000
Height· <i>Quercus falcata</i>	-0.0065	0.0102	7578	-0.6379	0.5236
Height· <i>Quercus marilandica</i>	0.0125	0.0106	7578	1.185	0.2361
Height· <i>Quercus rubra</i>	0.0041	0.007	7578	0.5928	0.5533
Height· <i>Quercus stellata</i>	0.0028	0.0033	7578	0.8484	0.3963
Height· <i>Quercus velutina</i>	0.0042	0.0025	7578	1.7188	0.0857
Height· <i>Sassafras albidum</i>	-0.0139	0.0040	7578	-3.1295	0.0018
Height· <i>Ulmus</i> spp.	-0.0305	0.0099	7578	-3.0857	0.0020
Height·Non-sprout Origin	0.0046	0.0009	7578	5.2904	0.0000
Height·Sprout Origin	-0.0046	0.0009	7578	-5.2904	0.0000
Height·Dominant Crown Class	0.0106	0.0018	7578	6.008	0.0000
Height·Codominant Crown Class	0.0082	0.0013	7578	6.5305	0.0000
Height·Intermediate Crown Class	-0.0041	0.0016	7578	-2.6378	0.0084
Height·Suppressed Crown Class	-0.0146	0.002	7578	-7.4051	0.0000

Table 4.3. Random effects parameter predictions for the “best” model.

Random Effect	Standard Deviation	95% C.I.
Plot	0.052	0.03561229-0.0758
Tree within plot	0.0637	0.0548472-0.0739
Residual	0.5138	0.4914-0.5372

Table 4.4. Parameter estimates for power of variance covariate function for each final crown class in the “best” model. The power function is as follows $(\sigma^2 \cdot |v_{ij}|^{2\delta})$ where σ^2 is residual model variance and v_{ij} is the conditional mean produced by the regression parameters in Table 4.2.

Final Crown Class	Power (δ)	95% C.I.
Dominant	1.3451	1.2539-0.4363
Codominant	1.2397	1.1704-1.309
Intermediate	1.1281	1.062-1.1942
Suppressed	1.1453	1.0791-1.2115

Table 4.5. Type 3 tests of fixed effects for the “best” model.

Fixed Effect	numDF	denDF	F-value	p-value
Intercept	1	7578	1193.9197	<.0001
Height	1	7578	162.7143	<.0001
Species	13	382	2.1243	0.0123
Stem Origin	1	382	35.3648	<.0001
Site Class	1	18	10.5311	0.0045
Stand Age	1	7578	41.0708	<.0001
Crown Class	3	382	14.9363	<.0001
Height-Species	13	7578	4.1284	<.0001
Height-Stem Origin	1	7578	27.9886	<.0001
Height-Stand Age	1	7578	73.5927	<.0001
Height-Crown Class	3	7578	27.7243	<.0001

Table 4.6. Effects coded fixed effects parameter estimates for the “projection” model. For convenience the effects of the omitted category from the original category were obtained from a second regression and are provided below.

Fixed effect	Estimate	Std. error	DF	t-value	p-value
Intercept (Unweighted Grand Mean)	0.7569	0.0211	7583	35.9187	0.0000
Height	-0.0402	0.0018	7583	-22.1582	0.0000
<i>Acer rubrum</i>	-0.0848	0.0341	385	-2.4854	0.0134
<i>Acer saccharum</i>	-0.0687	0.1009	385	-0.6803	0.4967
<i>Carya</i> spp.	-0.0631	0.0273	385	-2.309	0.0215
<i>Pinus echinata</i>	0.0241	0.036	385	0.6709	0.5027
<i>Prunus serotina</i>	0.031	0.033	385	0.9404	0.3476
<i>Quercus alba</i>	-0.0224	0.0244	385	-0.9181	0.3591
<i>Quercus coccinea</i>	0.0246	0.0275	385	0.8950	0.3713
<i>Quercus falcata</i>	0.174	0.1268	385	1.3718	0.1709
<i>Quercus marilandica</i>	-0.1645	0.1022	385	-1.6087	0.1085
<i>Quercus rubra</i>	0.086	0.0763	385	1.1265	0.2606
<i>Quercus stellata</i>	-0.1166	0.0314	385	-3.7058	0.0002
<i>Quercus velutina</i>	0.0083	0.027	385	0.3089	0.7576
<i>Sassafras albidum</i>	0.0291	0.0394	385	0.7379	0.4610
<i>Ulmus</i> spp.	0.1428	0.0946	385	1.5088	0.1322
Non-sprout Origin	-0.0637	0.0092	385	-6.9129	0.0000
Sprout Origin	0.0637	0.0092	385	6.9129	0.0000
Exposed Backslopes	-0.0434	0.0123	18	-3.5154	0.0025
Protected Backslopes	0.0434	0.0123	18	3.5154	0.0025
Height- <i>Acer rubrum</i>	-0.0029	0.0036	7583	-0.7995	0.4241
Height- <i>Acer saccharum</i>	0.0109	0.0082	7583	1.3228	0.1860
Height- <i>Carya</i> spp.	-0.0019	0.003	7583	-0.6363	0.5246
Height- <i>Pinus echinata</i>	0.0073	0.0034	7583	2.156	0.0311
Height- <i>Prunus serotina</i>	0.0000	0.0034	7583	0.0092	0.9926
Height- <i>Quercus alba</i>	-0.0000	0.0024	7583	-0.0102	0.9918
Height- <i>Quercus coccinea</i>	0.0097	0.0026	7583	3.8586	0.0002
Height- <i>Quercus falcata</i>	-0.0037	0.0116	7583	-0.3227	0.7469
Height- <i>Quercus marilandica</i>	0.0099	0.0128	7583	0.7701	0.4413
Height- <i>Quercus rubra</i>	0.005	0.0063	7583	0.7877	0.4309
Height- <i>Quercus stellata</i>	0.0038	0.0034	7583	1.1224	0.2617
Height- <i>Quercus velutina</i>	0.0047	0.0027	7583	1.7774	0.0755
Height- <i>Sassafras albidum</i>	-0.0202	0.0044	7583	-4.6418	0.0000
Height- <i>Ulmus</i> spp.	-0.0226	0.0099	7583	-2.2719	0.0231
Height-Non-sprout Origin	0.0044	0.0009	7583	4.8261	0.0000
Height-Sprout Origin	-0.0044	0.0009	7583	-4.8261	0.0000

Table 4.7. Random effects parameter predictions for the “projection” model.

Random Effect	Standard Deviation	95% C.I.
Plot	0.0477	0.0312-0.0728
Tree within plot	0.1013	0.0924-0.1112
Residual	0.5145	0.4909-0.5392

Table 4.8. Parameter estimates for power of variance covariate function for each species in the “projection” model. The power function is as follows $(\sigma^2 \cdot |v_{ij}|^{2\delta})$ where σ^2 is residual model variance and v_{ij} is the conditional mean produced by the regression parameters in Table 4.6.

Species	Power (δ)	95% C.I.
<i>Acer rubrum</i>	1.1259	1.0271-1.2248
<i>Acer saccharum</i>	1.3887	1.1063-1.6711
<i>Carya</i> spp.	1.1804	1.099-1.2618
<i>Pinus echinata</i>	1.1884	1.0798-1.2972
<i>Prunus serotina</i>	1.0451	0.9408-1.1493
<i>Quercus alba</i>	1.1938	1.1213-1.2662
<i>Quercus coccinea</i>	1.2561	1.1605-1.3517
<i>Quercus falcata</i>	1.1871	0.834-1.5401
<i>Quercus marilandica</i>	0.9433	0.6883-1.1983
<i>Quercus rubra</i>	1.6522	1.359-1.9455
<i>Quercus stellata</i>	1.222	1.1353-1.3087
<i>Quercus velutina</i>	1.1802	1.0964-1.2641
<i>Sassafras albidum</i>	1.2633	1.1571-1.3694
<i>Ulmus</i> spp.	1.3948	1.0784-1.7111

Table 4.9. Type 3 tests of fixed effects for the “projection” model.

Fixed Effect	numDF	denDF	F-value	p-value
Intercept	1	7583	1290.1516	<.0001
Height	1	7583	490.9861	<.0001
Species	13	385	2.9489	0.0004
Stem Origin	1	385	47.7889	<.0001
Site Class	1	18	12.3584	0.0025
Height·Species	13	7583	4.6963	<.0001
Height·Stem Origin	1	7583	23.2910	<.0001

Table 4.10. Height developmental milestones of recruitment success. These point estimates were derived from nonparametric (b-spline) quantile regression of the near-minima (10th percentile) height at a given age for trees that were in dominant or codominant crown classes at the end of the regeneration period.

Species	Stand Age (yrs)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Total Height (m)																			
<i>Acer rubrum</i> (protected)	0	0.6	1.2	1.9	2.5	3.1	3.7	4.2	4.8	5.3	5.8	6.2	6.7	7.1	7.5	7.9	8.3	8.7	9	9.4
<i>Acer saccharum</i> (protected)	0.7	1.3	1.9	2.5	3	3.6	4.1	4.6	5	5.5	5.9	6.4	6.8	7.2	7.6	8	8.4	8.8	9.2	9.6
<i>Carya</i> spp. (exposed)	0	0.6	1.2	1.7	2.3	2.8	3.3	3.8	4.3	4.7	5.1	5.5	5.9	6.3	6.6	6.9	7.3	7.5	7.8	8.1
<i>Carya</i> spp. (protected)	0	0.7	1.3	2	2.6	3.2	3.8	4.4	5	5.6	6.1	6.6	7.1	7.6	8	8.5	8.9	9.2	9.6	9.9
<i>Pinus echinata</i>	0	0.4	0.7	1.2	1.7	2.2	2.7	3.3	3.8	4.4	5.0	5.6	6.1	6.7	7.2	7.7	8.2	8.6	9	9.3
<i>Prunus serotina</i> (exposed)	0	0.2	0.6	1.1	1.5	2	2.6	3.2	3.7	4.3	4.9	5.5	6.1	6.6	7.2	7.6	8.1	8.4	8.7	9
<i>Prunus serotina</i> (protected)	0.2	0.9	1.5	2.1	2.8	3.4	4	4.7	5.3	5.9	6.5	7.1	7.6	8.1	8.6	9	9.4	9.7	10	10.2
<i>Quercus alba</i> (exposed)	0.4	0.8	1.2	1.6	2.1	2.5	3	3.5	3.9	4.4	4.9	5.3	5.8	6.2	6.6	7	7.4	7.7	8	8.3
<i>Quercus alba</i> (protected)	0.5	1.1	1.7	2.3	2.9	3.5	4.1	4.6	5.2	5.7	6.2	6.8	7.2	7.7	8.2	8.6	9	9.4	9.7	10
<i>Quercus coccinea</i> (exposed)	0.3	0.8	1.2	1.8	2.3	2.8	3.3	3.9	4.4	4.9	5.5	6	6.5	7	7.5	7.9	8.4	8.8	9.2	9.5
<i>Quercus coccinea</i> (protected)	0	0.6	1.3	1.9	2.5	3.1	3.7	4.3	4.8	5.4	5.9	6.5	7	7.5	8	8.5	8.9	9.4	9.8	10.2
<i>Quercus falcata</i> (exposed)	0	0.5	1	1.5	2.1	2.6	3.1	3.7	4.2	4.8	5.3	5.8	6.4	6.9	7.4	8	8.5	9	9.5	10
<i>Quercus rubra</i> (protected)	0.4	0.8	1.3	1.7	2.2	2.8	3.3	3.8	4.4	5	5.6	6.2	6.8	7.4	8	8.6	9.2	9.8	10.3	10.9
<i>Quercus stellata</i> (exposed)	0	0.5	1	1.5	2.1	2.6	3	3.5	4	4.5	4.9	5.3	5.8	6.2	6.5	6.9	7.3	7.6	7.9	8.2
<i>Quercus velutina</i> (exposed)	0.2	0.8	1.4	1.9	2.4	3	3.5	4	4.5	5	5.5	5.9	6.4	6.8	7.2	7.5	7.9	8.2	8.5	8.8
<i>Quercus velutina</i> (protected)	0.5	1	1.6	2.1	2.7	3.2	3.8	4.3	4.8	5.3	5.8	6.3	6.8	7.3	7.7	8.2	8.6	9	9.3	9.7
<i>Sassafras albidum</i> (protected)	0	0.5	1	1.6	2.2	2.9	3.5	4.1	4.8	5.4	6	6.5	7	7.4	7.8	8.2	8.4	8.5	8.6	-
<i>Ulmus</i> spp. (protected)	0	0.8	2	3	3.9	4.6	5.3	5.8	6.2	6.7	7	7.3	7.7	8	8.4	8.8	9.2	9.8	10.4	-

Figures

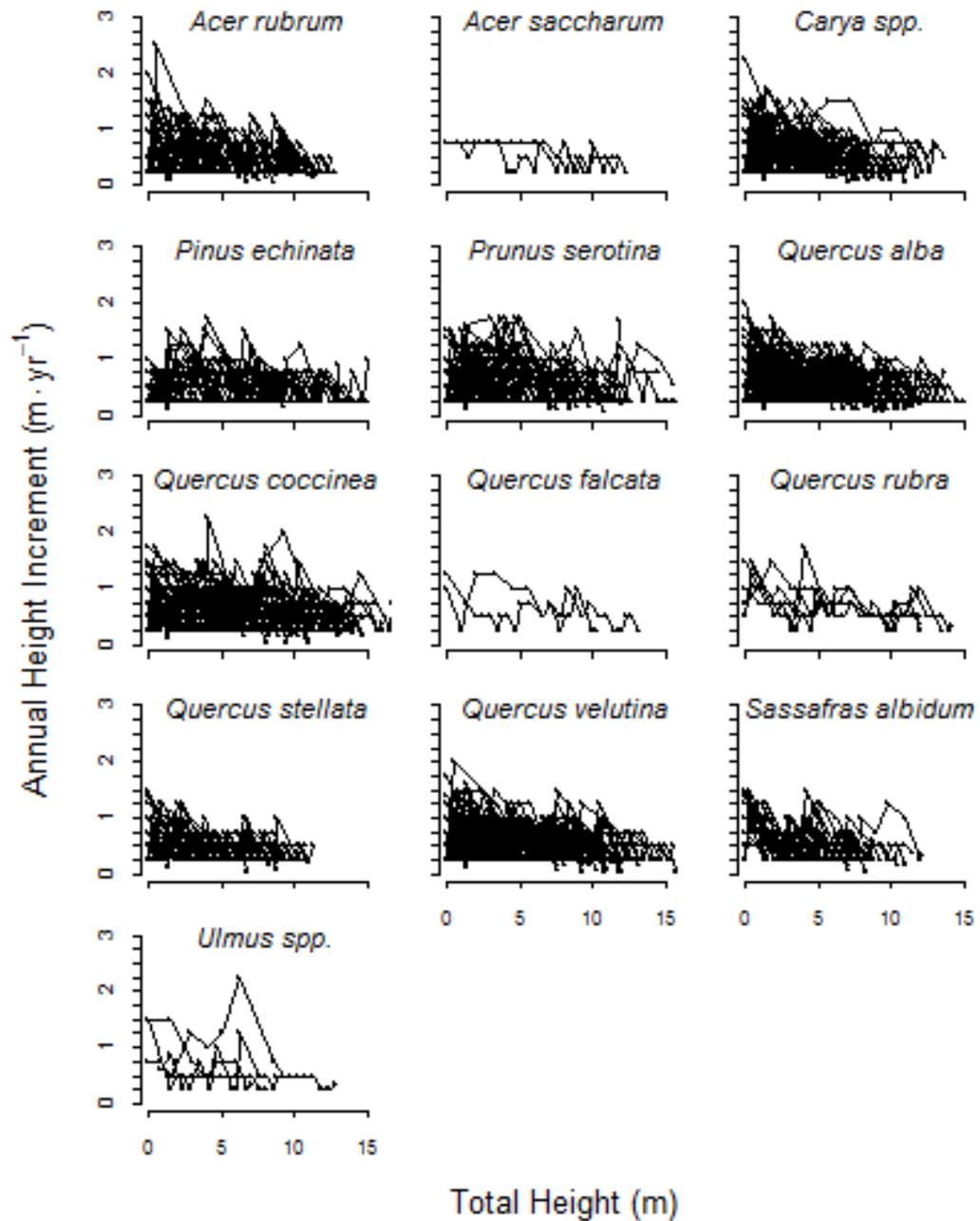


Figure 4.1. Height increment as a function of height for juvenile trees in naturally regenerated mixed species even-aged stands (18-28 yrs post-harvest) in the Missouri Ozarks.

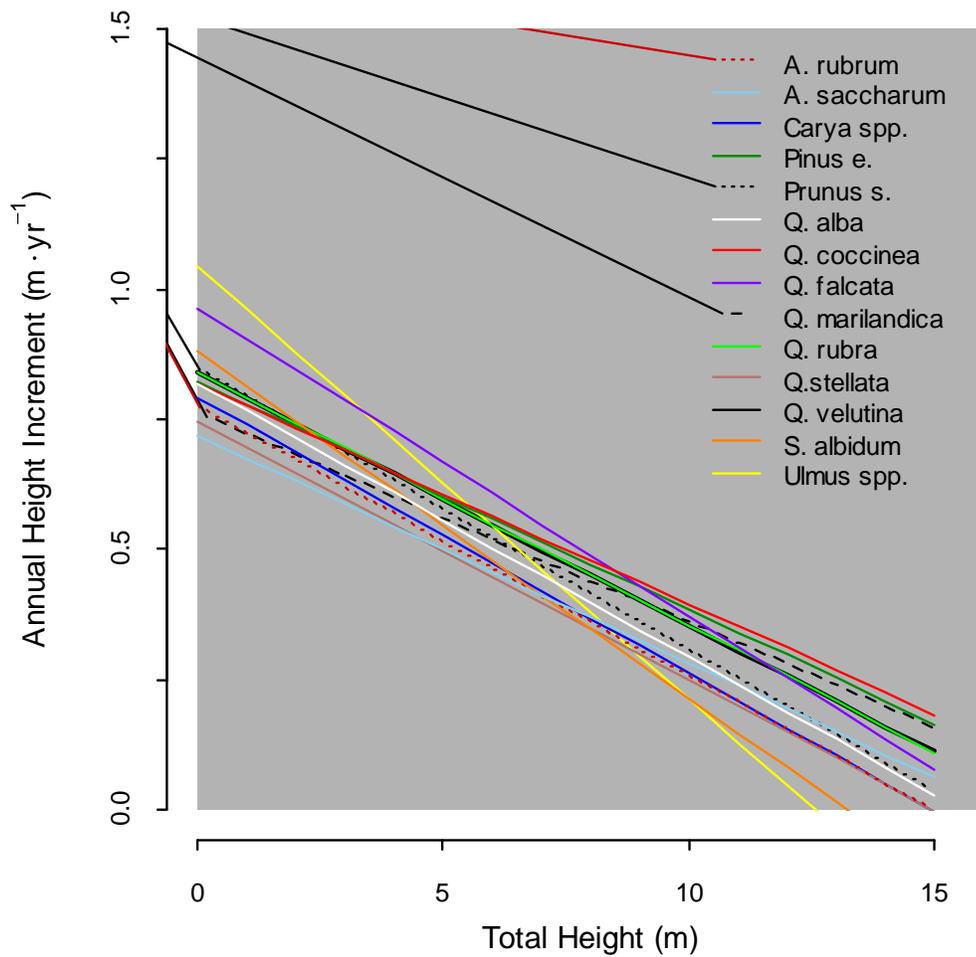


Figure 4.2. Impact of species on height increment trends from the “best” model as a function of height for juvenile trees in naturally regenerated mixed species even-aged stands (18-28 yrs post-harvest) in the Missouri Ozarks. Lines were drawn using the intercept, species, and stand age (held constant at 10) effects coded parameters from Table 4.2 along with their interaction with height and the main effect of height.

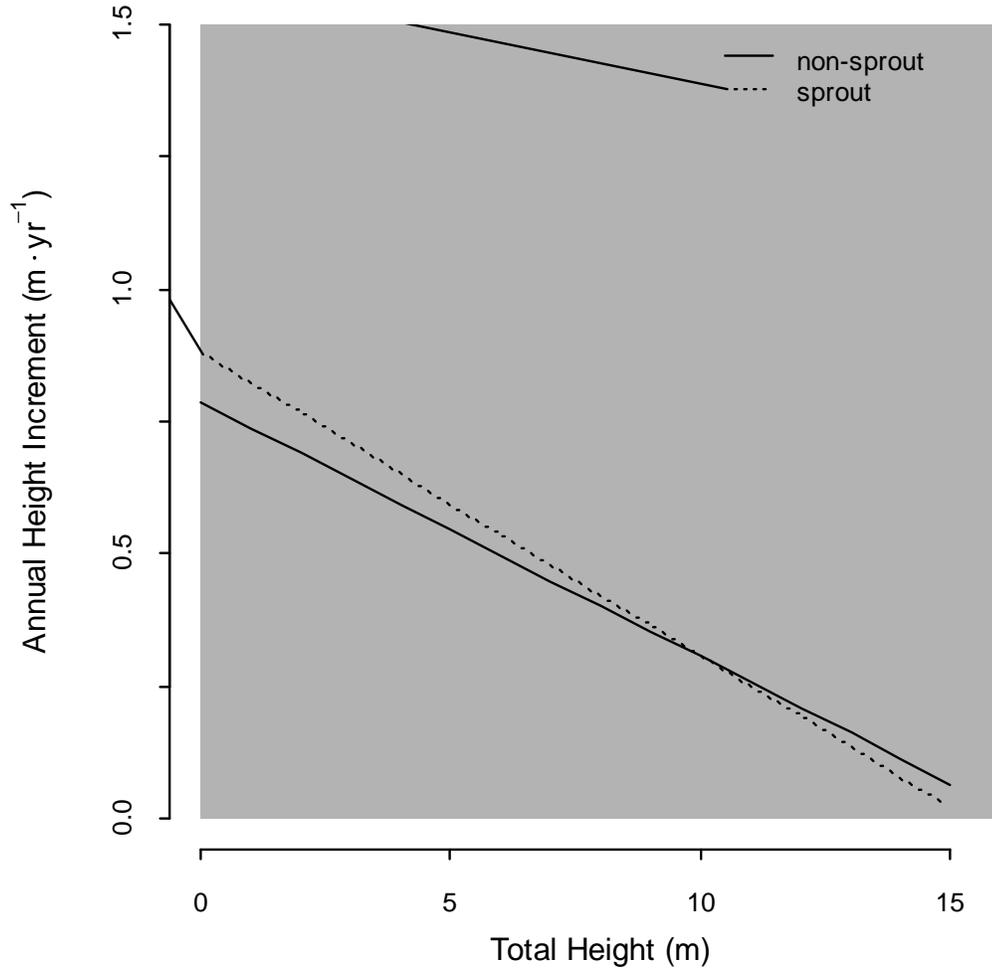


Figure 4.3. Impact of stem origin on height increment trends from the “best” model as a function of height for juvenile trees in naturally regenerated mixed species even-aged stands (18-28 yrs post-harvest) in the Missouri Ozarks. Lines were drawn using the intercept, stem origin, and stand age (held constant at 10) effects coded parameters from Table 4.2 along with their interaction with height and the main effect of height.

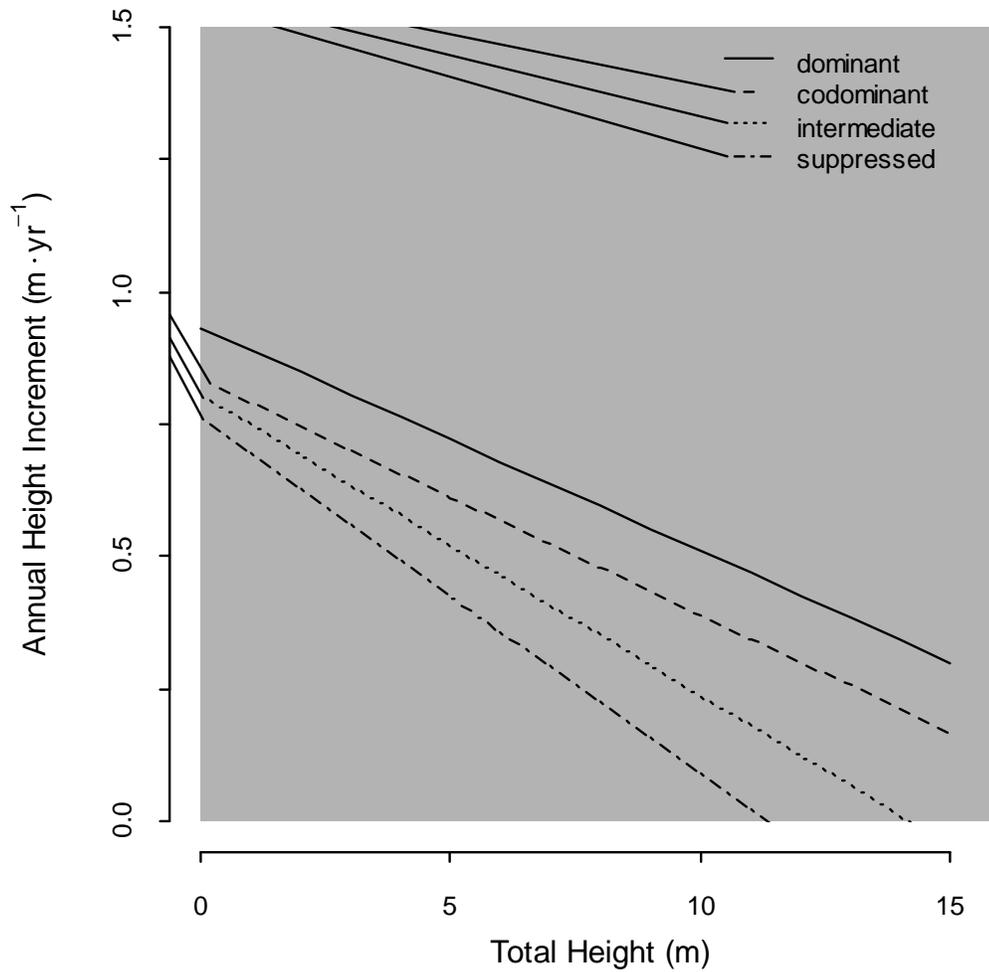


Figure 4.4. Impact of final crown class on height increment trends from the “best” model as a function of height for juvenile trees in naturally regenerated mixed species even-aged stands (18-28 yrs post-harvest) in the Missouri Ozarks. Lines were drawn using the intercept, crown class, and stand age (held constant at 10) effects coded parameters from Table 4.2 along with their interaction with height and the main effect of height.

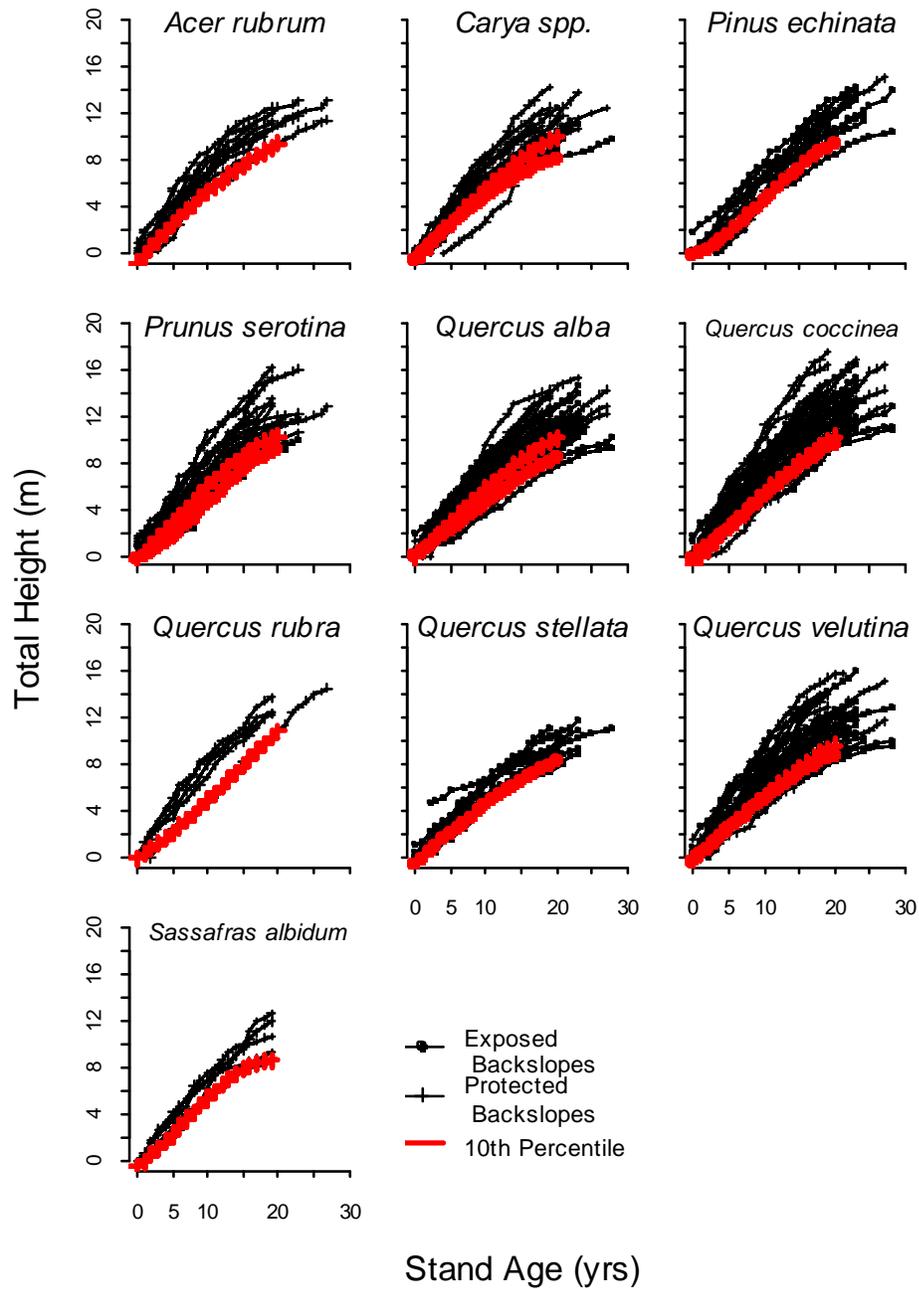


Figure 4.5. Height developmental milestones of recruitment success. These point estimates were derived from nonparametric (b-spline) quantile regression of the near-minima (10th percentile) height at a given age for trees that were in dominant or codominant crown classes at the end of the regeneration period.

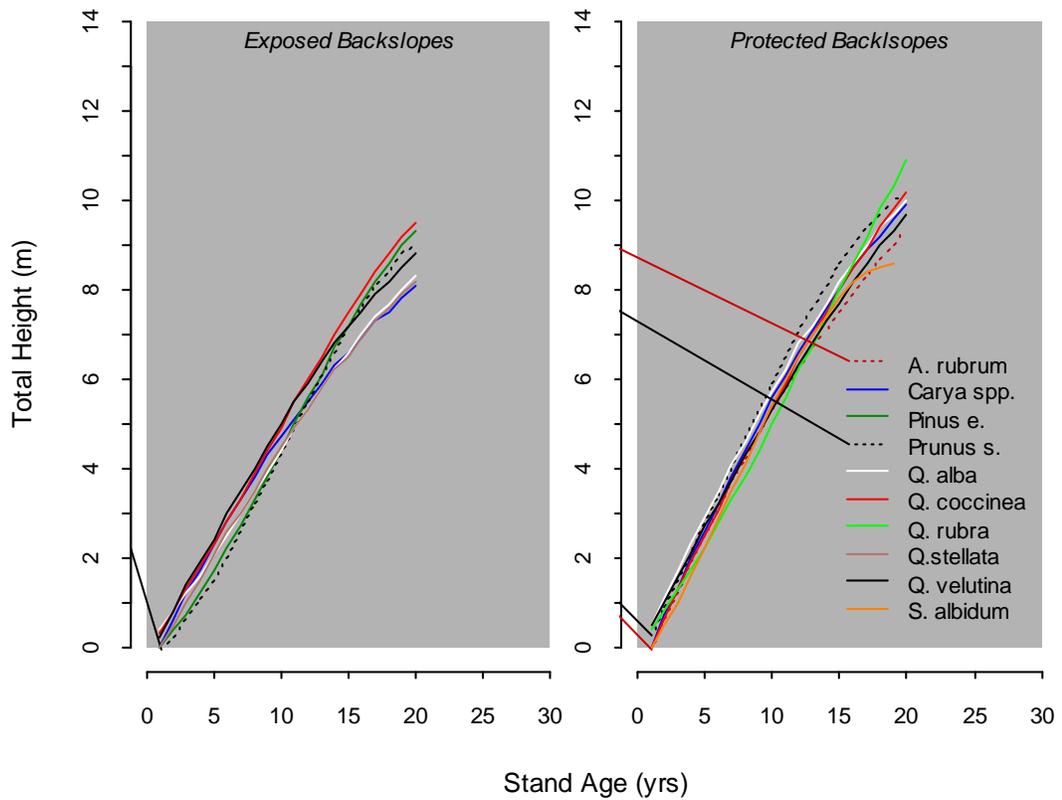


Figure 4.6. Differences in height developmental milestones of recruitment success among species. These point estimates were derived from nonparametric (b-spline) quantile regression of the near-minima (10th percentile) height at a given age for trees that were in dominant or codominant crown classes at the end of the regeneration period.

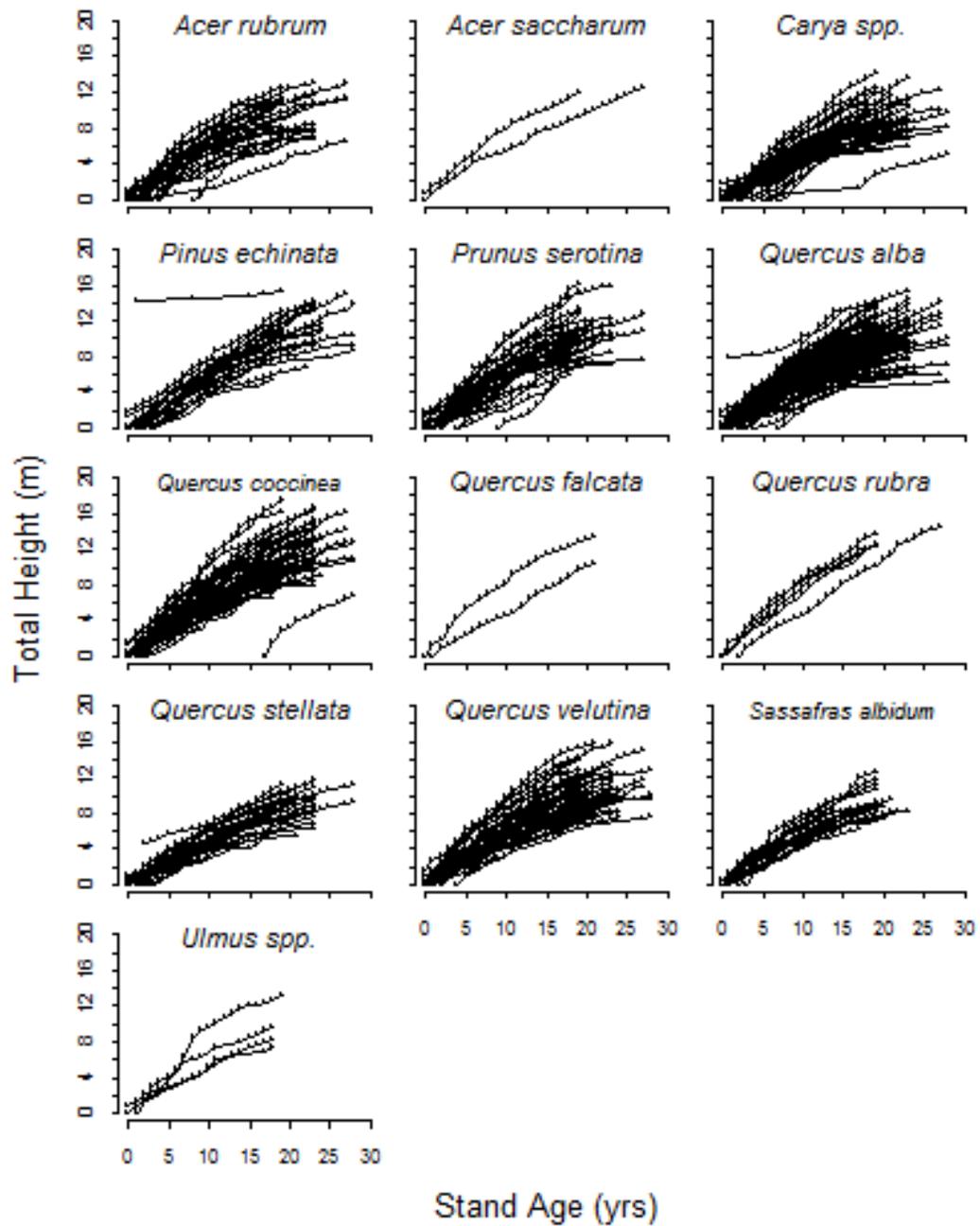


Figure 4.7. Height development as a function of age for juvenile trees in naturally regenerated mixed species even-aged stands (18-28 yrs post-harvest) in the Missouri Ozarks.

Chapter 5:

REFERENCE CHARTS – A QUANTITATIVE METHODOLOGY FOR
ASSESSING TREE PERFORMANCE

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C. Dey

Abstract

Reference charts have long been used in the medical field for quantitative clinical assessment of juvenile development by displaying distribution quantiles for selected anthropometric indicators (e.g., height) plotted against age for a specified peer population (e.g., girls 0-36 months in the United States). We propose that both the science and practice of forestry could benefit from the potential increase in quantitative descriptions and analyses offered by similar references for various tree measures. One area of study in particular that may benefit is stand dynamics. Because reference charts provide a flexible framework to quantitatively assess the performance of trees, it may be possible to achieve greater insight into the complex development patterns of trees than that provided by traditional categorical classifications (e.g., crown classes) at young ages. We have begun exploring this possibility by constructing height-age reference charts for several tree species in young, mixed stands and two site types within the Missouri Ozarks. The objectives of this manuscript are to describe the development of these tree-based reference charts and to demonstrate the potential utility of this methodology for quantitatively assessing the height development of young trees. We use the early height development of white oak (*Quercus alba* L.) throughout this manuscript as an illustrative example of the application of this method. Other potential applications for regeneration modeling, exploring early stand dynamics, and improving pre-commercial silvicultural prescriptions are also discussed.

Introduction

By what standard should a tree be judged? This question, perhaps unknowingly, is posed almost daily by practicing foresters. Unfortunately, there are few cases in which clearly defined, quantitative references have been established to assess and compare trees and stands. Yet, the utility of those few references that have been established is immense. For example, foresters use site index as a standard, quantitative reference for site productivity. Site index can be compared across stands because it is a reference that is widely used (Carmean 1975, Skovsgaard and Vanclay 2008). Other examples of quantitative references established by foresters include metrics for assessing density (*e.g.*, Reineke 1933, Gingrich 1967, Ducey and Knapp 2010), and those diagnosing nutrient deficiencies (*e.g.*, Vose and Allen 1988, Albaugh *et al.* 1998, Fox *et al.* 2007). Despite the demonstrated utility of these predominantly stand-level references, there is a general lack of quantitative references designed for assessing attributes such as the diameter or height of an individual tree. Though silviculture is generally prescribed at the stand level, foresters are often faced with decisions regarding the fate of individual trees during application. Therefore, a lack of quantitative references for attributes of individual trees may promote unnecessary error in silvicultural application and confounds efforts to understand the biology and ecology of forest development.

The early stand dynamics that follow a regeneration event is an area of study that could greatly benefit from the development of quantitative references for attributes that influence growth and survival. Regeneration is critical for

sustainable forest management, and concern over the efficacy of regeneration efforts is prevalent across many forest types and settings (Barrett 1995, Stanturf *et al.* 2001, Dey 2014). Qualitative or categorical metrics such as crown classes have proven useful for evaluating tree performance, particularly after intertree competition has increased vertical stratification in the stem exclusion stage of stand development (Ward and Stephens 1993, 1994, 1996). However, subjectivity and other constraints can complicate their application (Meadows *et al.* 2001) and traditional crown classes are not strictly applicable prior to canopy closure due to their reliance on relative canopy position and light availability as defining characteristics (Helms 1998). Consequently, regeneration evaluations that rely on crown classes as a benchmark of success usually are not applied until late in the post-harvest regeneration period. In turn, many regeneration projection systems endeavor to estimate post-harvest characteristics late in the regeneration period (*e.g.*, Dey 1991, Steiner *et al.* 2008, Vickers *et al.* 2011). Although treatments to ameliorate projected regeneration inadequacies late in the regeneration period are available (Brose *et al.* 2008, Steiner *et al.* 2008), opportunities to impose dramatic change diminish with stand age (Zenner *et al.* 2012, Ward 2013). It may be possible to improve the efficacy of such post-harvest interventions by providing more quantitative descriptions of those attributes that impact tree performance along with better estimates of windows of opportunity to impact the performance of desirable individuals (as discussed by: Heitzman and Nyland 1991, Miller 2000, Ward 2009).

The height of a tree and the relative height of neighbors influence growth and survival in developing stands (Assmann 1970, Oliver and Larson 1996, Weiner 1990). Single-cohort stands often contain mixtures of species that differ in growth rates, longevity, and other life-history traits. Empirical evidence of interspecific differences in development patterns has been reported in a variety of mixed-species, single-cohort stands (e.g., Doolittle 1958, Carmean 1979), particularly those with oak (*Quercus*) as a component (e.g., Clatterbuck and Hodges 1988, Oliver 1978, Oliver and Larson 1996). It is, therefore, common for the height profile of these stands to be dominated by a progression of species through time (Kelty *et al.* 1992, Oliver and Larson 1996). This implies that in young, mixed-species stands, an individual's current social position (height rank) among its neighbors is not necessarily an accurate representation of its performance or potential due to variance in development patterns. While discrepancies between current conditions and future potential are expected in most forecasting scenarios, that an individual's current social position may not be an accurate representation of its current performance is counterintuitive. This highlights what can be a strength and weakness of crown class evaluations and other localized estimates of relative stature: an individual's performance is necessarily defined by its current neighbors.

To clarify, consider the height development patterns of three species in a single-cohort stand from Figure 5.1.1. In this conceptual example, *Species C* exhibits inherently slow initial growth compared to the other two species but has the potential to eventually become the tallest of the three. An early crown class

evaluation (time 1, Fig. 5.1.1) may find that the greatest crown class attained by *Species C* is intermediate (Fig. 5.1.2). In contrast, a later crown class evaluation (time 2, Fig. 5.1.1), may find *Species C* capable of occupying all crown classes, including dominant (Fig. 5.1.3). In this conceptual example, an intermediate tree could be a superior specimen of a temporally inferior species (Fig. 5.1.2), or an inferior specimen of a temporally superior species (Fig. 5.1.3) depending on the timing of crown class evaluations and the differences in development patterns among the neighboring species. In other words, the relative stature of a tree in a young, mixed-species stand is a function of intraspecific, interspecific, and temporal variation in height development. Evaluations that do not explicitly consider each of these factors could be misleading.

The aforementioned inadequacies of using point estimates of relative stature as longitudinal indicators of regeneration success in mixed-species stands are subtle, but warrant a reexamination of potential frameworks or improvements available for assessing the early performance of individual trees. While there have been numerous quantitative studies of growth and mortality rates (*e.g.*, Pacala *et al.* 1994, Kobe and Coates 1997, Vickers *et al.* 2014), and several metrics designed to define competitive pressure (*e.g.*, Bella 1971, Lorimer 1983, Canham *et al.* 2004), there has seemingly been little effort to establish quantitative references for assessing an individual's development of an attribute of interest. Toward such improvements, we suggest that reference chart methodologies could be useful tools to quantitatively assess various attributes that may be of interest or importance.

Reference chart methodologies have long been used in the medical field for quantitative clinical assessment of human juvenile development (Quetelet 1871, Ulijaszek *et al.* 1998). These charts typically include selected quantiles of a reference distribution plotted against age for an attribute of interest (*e.g.*, height-age). Reference charts allow physicians to quantitatively compare the stature of an individual child at a given age to the distribution of statures attained by several other children with similar demographics at the same age. This assessment provides the physician valuable information to help determine if medical treatment for irregular development is warranted (Ulijaszek *et al.* 1998).

We have developed similar height-age reference charts for a limited number of sites, species, and scenarios and propose that they could be useful tools to quantitatively assess trees. These charts provide an explicit description of the intraspecific and interspecific variation in height development as well as the temporal dynamics of both. Moreover, these references can be applied to trees that are too young to be adequately evaluated by traditional crown classes.

Accordingly, our objectives are to: 1) describe the development of reference charts for forestry applications, and 2) demonstrate the potential utility of reference chart methodology for assessing the height development of young trees using data from the Missouri Ozarks as an example. We discuss how reference charts may extend the inference window of stand reconstruction techniques (*i.e.*, stem analysis) and have potential utility for applications in modeling regeneration and early stand dynamics, as well as refining pre-commercial silvicultural prescriptions. We note that though reference charts can

be developed for virtually any quantitative variable of interest, we focus solely on the assessment of height development in young trees for our analyses. The influence of height on tree performance during the early stages of stand development is well documented, but we recognize that it is not the only influential attribute. Though beyond the scope of this initial investigation into the utility of reference chart methodology for forestry applications, continued research into other attributes that influence early tree performance is warranted.

Methods

Data from two long-term studies were combined to establish reference data for height-age development in the southeast Missouri Ozarks. One study was administered by the USDA Forest Service (OH-466) and the other by the Missouri Department of Conservation (MOFEP). Both studies monitored stand development following clearcutting or clearcutting with reserves ($\leq 5 \text{ m}^2 \cdot \text{ha}^{-1}$ residual basal area). Retaining $< 5 \text{ m}^2 \cdot \text{ha}^{-1}$ of residual basal area has limited impact on the height growth of saplings in the study region (Vickers *et al.* 2014); therefore, we considered that postharvest growing conditions were comparable across the two studies.

The Ozark Highlands of southeast Missouri are unglaciated, deeply dissected plateaus primarily composed of Ordovician and Cambrian dolomites and sandstones (Kabrick *et al.* 2000). Average annual precipitation is 115cm and average annual temperature is 13.5° C (Kabrick *et al.* 2008). Slope-aspect and slope position are important delineating characteristics used for ecological classification in the region (Nigh *et al.* 2000). For this reason, the sample plots

used in this study were categorized as either exposed (aspect: 136 - 315°) or protected (aspect: 316 - 135°) backslopes. Average site index (*Quercus velutina* Lam., McQuilkin 1974) is approximately 21.0m (\pm 1.3m) on exposed backslopes and 22.0m (\pm 1.1m) on protected backslopes in this region.

The two studies followed different measurement protocols throughout the first twenty years post-harvest, which was the target period of our analyses. On the study OH-466, the height of woody stems was measured at 2, 5, and 10 years post-harvest. On the MOFEP study, the height of only the woody stems \geq 1m was measured 3 and 8 years post-harvest, but the height of all woody stems, including any $<$ 1 m tall, were measured 16 years post-harvest. Thus, we combined the height measurements from years 2, 5, and 10 from OH-466 with the year 16 measurements from MOFEP to provide 4 non-truncated measurements of height-age for all woody stems. All stems with a diameter at breast height (dbh) $>$ 6.3cm at year 2 from OH-466 or year 3 from MOFEP were considered residual saplings from the previous rotation and were not included in our analyses.

The objective of our statistical analyses was to estimate the longitudinal height-age quantiles of various reference populations (described later) derived from the dataset. The quantiles (quartiles, percentiles, etc.) of distribution define the probability that a random observation will fall below their corresponding value (*i.e.*, 99% of all observations will be below the value of the 99th quantile, and the probability that any new observation will exceed the 99th quantile is 1%). The most common techniques to estimate longitudinal quantiles for reference chart

construction in the medical literature are the LMS method (Cole and Green 1992) and quantile regression (Koenker 2005, Wei *et al.* 2006). Parametric quantile estimation was possible with our dataset, but the number of available parameters would be limited with only four measurements. Thus, the selection of growth functions flexible enough to apply across the entire height distribution with minimal parameters was not straightforward. Moreover, parametric growth functions may impose assumptions and restrictions that are not generated by the underlying phenomenon of interest (Takezawa 2006). Nonparametric techniques such as functional data analysis, b-splines, and local linear regressions provide more flexibility in growth forms and analyses than parametric growth functions (Ramsay and Silverman 2002, Takezawa 2006, Wei *et al.* 2006), but they do not provide results that are easily reproducible or interpretable for non-statisticians. Therefore, we simply estimated various height quantiles for each measurement using the *Type 8* algorithm (per Hyndman and Fan 1996) within the *quant* function of R version 2.13.0 (R Core Team 2011) and used linear interpolation to estimate values between the measurements (Fig. 2).

We used bootstrap procedures to investigate the impact of sample size on our quantile estimates. Because both inter- and intraspecific height variance increased with stand age and was greatest on protected backslopes, age 16 data from protected backslopes was used to provide conservative guidance for sample size requirements. The bootstrap procedure consisted of sampling with replacement for 10,000 iterations over a range of sample sizes from 100 to 1664 (sample size of original data) in increments of 100 stems. For each sample, the median and 95th quantile of the height distribution was estimated and subtracted

from the value reported from the original dataset (9.6, Table 5.1). Using this procedure, we were able to construct confidence intervals ($\alpha = 0.05$) of the impact of sample size on potential error in quantile estimation using the percentile method (Harrell 2001).

Logically identified and defined reference populations, or peer groups, are critical to the utility of reference charts. Just as gender is an important consideration in the assessment of human development, there are important considerations to promote logical assessments of a tree's development in an attribute of interest. Because species and site are two of the most important determinants of tree height at a given stand age, we developed a suite of reference charts that explicitly account for these two factors at differing scales. The peer groups we identified can be delineated into two categories: site-specific (exposed or protected backslopes) or species-specific. The site-specific peer groups used measurements for all woody stems on a particular site type as a reference distribution for tree height following a clearcut harvest. The primary application of these charts will be to assess the height development of an individual tree relative to the mainstream trends of stand development on a specified site type. In contrast, the species-specific peer groups used height-age measurements only for a specified species-group within mixed-species stands on a specified site type following a clearcut harvest. The primary application of these reference charts will be to assess the height development of an individual tree relative to the mainstream development trends for a particular species within mixed-species stands on a particular site type.

For the species-specific peer groups, six species groups were established at the genera or sub-genera level and included: 1) red oaks (*Q. rubra* L., *Q. velutina* Lam., *Q. coccinea* Münchh., *Q. marilandica* Münchh.), 2) white oaks (*Q. alba* L., *Q. stellata* Wangerh., *Q. muehlenbergii* Engelm.), 3) hickories (*Carya tomentosa* Sarg., *C. glabra* Mill., *C. ovata* (Mill.) K. Koch., *C. texana* Buckley, *C. cordiformis* (Wangerh.) K. Koch.), 4) sassafras (*Sassafras albidum* J. Presl.), 5) blackgum (*Nyssa sylvatica* Marsh.), and 6) dogwood (*Cornus florida* L.). A seventh group (other species) was comprised of species that were not included in previous groups but had insufficient representation to stand alone, including: *Acer* spp., *Amelanchier arborea* F. Michx., *Carpinus caroliniana* Walter, *Celtis* spp., *Cercis canadensis* L., *Corylus americana* Marshall, *Crataegus* spp., *Diospyros virginiana* L., *Fraxinus* spp., *Gymnocladus dioicus* (L.) K. Koch., *Juglans nigra* L., *Juniperus virginiana* L., *Morus* spp., *Pinus echinata* Mill., *Platanus occidentalis* L., *Prunus* spp., *Rhamnus caroliniana* Walter, *Rhus* spp., *Sideroxylon lanuginosum* Michx., *Ulmus* spp., and *Viburnum* spp.

Because these reference charts were constructed using data from trees that were likely deficient in one, or, perhaps, multiple resources (nutrients, water availability, etc.), the reported maxima do not necessarily reflect the physiological maxima for these species. It is also possible that our use of broad site type delineations masks some variation in height development that might be explained by higher resolution site delineation.

Results and Discussion

Error in quantile estimation was incrementally reduced as sample size increased (Fig. 5.3). For the median, the confidence band ($\alpha=0.05$) around the magnitude of error ranged from slightly over $\pm 0.5m$ (-0.7, 0.6) with a sample size of 100 to $\pm 0.2m$ with a sample size of 1664. As expected, the magnitude of error for the 95th quantile was greater than that found for the median. For the 95th quantile, the confidence band around the magnitude of error ranged from about $\pm 1.5m$ (-1.3, 1.5) with a sample size of 100 to a minimum of about $\pm 0.5m$ (-0.3, 0.5) with a sample size of 1664. Figure 5.3 suggests that sample sizes as low as 200 – 400 provided 95th quantile estimates with potential error $\leq 1.0m$ and that the incremental decrease in error with increasing sample size was minimal beyond about 400. To approach an error of $\pm 0.5m$ for the 95th quantile, 700-800 measurements were needed. While these results are informative, they should only be viewed as “ballpark” benchmarks of the sample sizes needed to adequately estimate the quantiles of a height-age distribution. Sample requirements will likely vary by age and species and perhaps regionally. Similar analyses should be conducted prior to data collection for reference chart construction for different purposes. Furthermore, the analyses above provide sample size inference only for point estimates of quantiles. Koenker (2005) describes the assumptions and asymptotic theory for quantile regression and discusses robustness to sample size.

The reference charts created for each of the peer groups we identified are shown in Figures 5.4, 5.5, and 5.6. These reference charts include only the 25th, 50th,

75th, 90th, and 99th quantiles for aesthetic considerations; however, estimates of the 5th, 10th, 20th, 25th, 30th, 40th, 50th, 60th, 70th, 75th, 80th, 90th, 95th, and 99th height-age quantiles are provided in Tables 5.1-5.3. Some users may prefer to employ various smoothing techniques to produce custom reference charts from Tables 5.1-5.3, but none were employed for the figures in this manuscript.

Because our reference charts were constructed with data from open populations rather than a finite number of individuals, changes in the reference population (*e.g.*, mortality, late germinants) can cause changes in the distribution of heights. Thus, sharp increases in the slope of quantile lines (*e.g.*, Fig. 5.6, sassafras ages 10-16) could be the result of the entire population exhibiting a “growth spurt,” an exclusion process that has a greater impact on the poorer performing trees, and/or extensive mortality. Conversely, sharp decreases in the slope of quantile lines (*e.g.*, Fig. 5.5, white oaks ages 10-16) could be the result of an exclusion process that has a greater impact on the better performing trees, extensive new germinants, and/or extensive mortality. In addition, stochastic disturbances and data deficiencies such as insufficient sample size or inherent differences in the combined datasets used to construct the reference charts could also contribute to seemingly erratic behavior in the quantiles of height distributions.

It has been recognized that the height distribution for a cohort of forest grown trees is often not symmetrical through time (Assmann 1970). The site-specific reference charts (Fig. 5.4) showed evidence of polymorphism across quantiles for both site types, particularly as stand age increased. The slope of all quantile lines tended to be positive through stand age 10 on both protected and exposed

backslopes. This indicates that the entire distribution of trees within the two site-specific peer groups increased in height during this period. However, after age 10 there was evidence of divergences within the height distributions. Some reference lines did not increase and others increased at varying rates. The timing of these divergences provides evidence that the onset of height development limitation occurs between age 10 and 16 in these forests. Similar estimates for the onset of development limitation and the beginning of height stratification in mixed oak forests have been documented elsewhere (Zenner *et al.* 2012). Though many reference lines were quite similar on both site types, by age 16 noticeable expression of within-site differences in developmental dynamics appeared to be underway. The slope of the reference lines was positive only for quantiles ≥ 75 on exposed backslopes after age 10, whereas on protected backslopes the slope was positive for quantiles ≥ 50 . This indicates that height development of trees is more limited on exposed backslopes than protected backslopes after age 10. Beyond those respective thresholds, the slope of the reference lines increased with increasing quantile.

The species-specific reference charts (Figs. 5.5 and 5.6) show considerable overlap in the height distributions of many species groups, particularly through age 5. However, both intergroup and intragroup differences in height development trends became more pronounced with stand age. The amount of intragroup variation in height was substantial for some species groups. For example, red oaks on both exposed (Fig. 5.5, Table 5.2) and protected backslopes (Fig. 5.6, Table 5.3) exhibited a broad distribution of heights. Red

oaks had attained the tallest height (*i.e.*, 99th quantile) of all species by the age of 16 and were among the tallest across the ages represented in the data though the advantage was most pronounced on exposed backslopes. However, the 5th quantile heights for red oaks were comparable to all other species across the age range of the data on both site types (Table 5.2, Table 5.3). Thus, the height advantage exhibited by red oaks over other species groups was exhibited only by upper quantile red oaks *i.e.*, those in the tail of the height distribution, though the degree of overlap among height distributions varied with species pairing and age. At age 16, when intergroup variation was greatest, about 90% of all red oaks fell within the distribution of heights for white oaks, hickories, sassafras, and the other species group, and about 60% of red oaks were within the range of heights for blackgum and dogwood on exposed backslopes (Table 5.2). The results were similar on protected backslopes, where about 95% of red oaks fell within the distribution of heights for white oaks and hickories, about 80% were within the distributions of the sassafras and the other species group (Table 5.3). The discrepancy between red oaks and blackgum was less pronounced ($\approx 75\%$ of red oaks were within the blackgum range), whereas the discrepancy was more pronounced between red oaks and dogwood (only $\approx 50\%$ of red oaks were within the dogwood range).

In contrast to the broad variation within the height distribution of red oaks (as well as white oaks, hickories, and other species), the sassafras, blackgum, and dogwood species groups exhibited much lower intragroup variation in heights. These species are rarely (sassafras, blackgum) or never (dogwood) components

of the overstory canopy in mature forests of the Missouri Ozarks (Burns and Honkala 1990, Johnson *et al.* 2009), but as was suggested by Dey (1991) and our species-specific charts (Figs. 5.5 and 5.6) they can be a source of competition in young clearcuts. For example, dogwood is the shortest at maturity of all species groups in these analyses, but through age 10 its height distribution overlapped with at least 80% of the trees from all species groups on both site types with the exception of oaks on exposed backslopes.

A clear advantage of reference chart methodology is the explicit consideration of the distribution of heights (or other variable) rather than a focus on a single average or categorical values. In addition to providing a reference for mainstream trends and outlier detection, the focus on distributions provides opportunities for comprehensive interpretation of developmental dynamics from the reference charts themselves. However, perhaps the greatest value provided by established reference charts is the flexible framework of inference available to new data. When combined with a field measured height, the reference charts provide an assessment of an individual's stature in relation to the mainstream development trends for a given peer group, even at an early age. For example, the 5th year height (3m) of a tree on a protected backslope in a Missouri Ozarks clearcut is displayed on the corresponding site-specific reference chart in Figure 5.7.1. A height of 3 meters at age 5 on this site type corresponds to the 75th quantile on the site-specific reference chart. This implies that at the time of measurement, the example tree was taller than about 75% of all trees in this peer group (or shorter than about 25% of all trees) without measuring any additional trees.

Further, comparing the height of this example tree to individual species groups via the species-specific references (Table 3) indicates that about 20% of red oaks, 30% of white oaks, 20% of hickories, 25% of sassafras, 40% of blackgum or dogwood, and about 20% of trees in the other species group would be taller at age 5 in clearcuts on protected backslopes in the Missouri Ozarks. Thus, reference chart methodology yields a measurement for an attribute of interest (*i.e.*, height) and provides a quantitative assessment of the performance of an individual tree regarding that attribute relative to a user-specified peer group.

Reference charts also provide opportunities to assess the development *pattern* of a tree. For example, consider the height development of the tree in Figure 5.7.2 derived from stem-analysis. At the time of sampling, this white oak (*Q. alba*) had attained a codominant canopy position in a 19 year old mixed-species, single-cohort stand on a protected backslope in the Missouri Ozarks (Vickers *et al.* unpublished data). Oak codominance around age 20 has long been a benchmark for regeneration success following clearcut harvests in the Missouri Ozarks (*e.g.*, Sander *et al.* 1984). Although this tree was in a favorable canopy position at the time of sampling, the reference chart suggests that prior to age 7, the height development of this tree (50-75th quantile), though not poor, was unexceptional relative to the mainstream trends for the specified peer group. However, between ages 7 and 11 this tree attained a height in the upper quantiles where fewer than 10% of other trees in clearcuts on protected backslopes in the Missouri Ozarks could have been taller.

When the height development pattern of the example white oak is plotted against the species-specific reference charts for protected backslopes, the height development of this tree relative to other white oaks that have grown in similar conditions can be examined (Fig. 5.8). The interpretation of the height development of this white oak in the species-specific analysis is similar to that found by the site-specific analysis. While unimpressive prior to age 7, this tree reached the upper 10% of the height distribution for white oaks in mixed stands by age 8 and maintained at least that status thereafter (Fig. 5.8). In addition to conspecific analyses, species-specific reference charts can also be used to provide inference into when this tree would likely outpace competitors and how that timing might vary with the species of the competitor (Fig. 5.8). Figure 8 shows that the height development of the example white oak was unexceptional relative to all other species groups through about age 6, only attaining between the 25th and 75th quantiles across all species groups. This implies that the example white oak would have been shorter than a majority of competing stems from any species group, including the short-statured dogwood. However after age 8-10 through age 16, an extant neighbor of many species had at most a 1% chance of being taller than this tree. A nearby red oak would have had at most about a 15% chance of being taller, while neighboring white oaks or hickories had at most about a 5% chance.

Without reference charts, opportunities to assess and interpret the development pattern of the tree used in the previous examples would be diminished. This additional information provided by reference charts could extend the inference

obtained from stand reconstruction by offering a comparative reference for longitudinal data. A long recognized shortcoming of stand reconstruction techniques has been the inability to account for the influence of trees that did not survive to be sampled. Although reference charts cannot replace this information lost to “ecological censoring”, they can offer a generalization of conditions by substituting various peer groups for targeted comparisons as was done by plotting the height development pattern of a white oak against the species-specific charts for other species groups in the previous example.

Our reference charts, like many of the most widely used anthropometric reference charts (Kuczmarski *et al.* 2002, de Onis *et al.* 2007), were developed with multiple datasets pieced together and analyzed cross-sectionally. Thus, the longitudinal component of each dataset, *i.e.*, the identity of individual trees, was not directly modeled to account for the developmental intricacies of each individual. Ideally, higher resolution data with annual measurements and tagged individuals could be used to construct the reference charts, but the paucity of longitudinally robust height-age measurements in the Missouri Ozarks precluded that possibility. As a result, interpretation of longitudinal assessments must be done with caution. The quantile lines reflect the *height* distribution of a peer group at a given point in time, rather than the distribution of *growth*. This seemingly minor distinction in stature vs growth has profound inferential consequences and has resulted in two categories of reference charts within the medical literature: 1) unconditional (growth distance) charts which are used for the purposes of assessing stature or 2) conditional (growth velocity) charts which

are used for the purposes of predicting and assessing growth (Cole 1994, Wei *et al.* 2006). To strengthen this distinction, recall the height development pattern of the white oak used in the previous examples. When the development pattern of this tree was plotted against the white oak species-specific reference chart (Fig. 5.8), it appeared to exhibit exceptional growth between stand ages 7-11, resulting in a much higher quantile assessment thereafter. However, this interpretation may be misleading. It cannot be determined from our unconditional (growth distance) charts if the growth displayed between ages 7-11 is atypical of what might be expected from other white oaks with a similar stature at the start of their 7th growing season. Therefore, as it occurs in children, it should also be expected that an individual tree may cross several quantile lines during the development process (Cole 1994). Indeed, several studies have found that longitudinal rank changes in height among trees are ubiquitous over the course of stand development (Dahms 1963, Rennolls 1978, Sharma *et al.* 2002).

Regardless of the attribute of interest, an adequate description of an individual's development is essential to increasing our understanding of the ecological and physiological drivers of stand development patterns. As mentioned in the introduction, performance assessments in young stands are often done via crown classes with no actual measurement of tree height. This level of examination may be sufficient for some objectives; however, the application of categorical point estimates such as crown classes in this dynamic period may be too general to capture the nuanced ecology of early stand development. We suggest the premise of crown class evaluations, if not their traditional application, should

absolutely be maintained. Differences in stature among neighbors in developing stands can have great biological importance (Assmann 1970, Oliver and Larson 1996, Weiner 1990). This long held tenet continues to be supported by several recent production ecology studies across a variety of forest types that found the largest 20 percent of trees within a stand (per biomass) had advantages over subordinate trees in both resource acquisition and resource use efficiency (Binkley *et al.* 2010, 2013, Campoe *et al.* 2013a, 2013b).

Although the focus of our study was not to identify the individuals responsible for the greatest growth or efficiency, we suggest that the methodology described herein could assist with the identification and description of those trees, especially in mixed-species stands. We note that the quantile reported from the reference chart methodology differs conceptually from the neighborhood or stand-level quantiles mentioned above and others that have been utilized previously (*e.g.*, Stage 1973, Bohora and Cao 2014). This is due to differences in the peer groups that the respective evaluations are drawing inference from. Generally, the peer groups used by reference chart methods represent a broader population derived from many individuals that share some common characteristic across multiple stands. In contrast, neighborhood or stand-level peer groups draw inference from a more restricted population. Neighborhood or stand-level evaluations have no replication within a neighborhood or stand, thus, the generality of that information will be a function of inter-neighborhood or inter-stand variance. We have demonstrated that a field measured height paired with an established suite of reference charts provides opportunities for robust

inference; however, the utility of reference charts for predicting future performance is unproven as of yet. We do not imply that localized inference is invalid or subsidiary to the reference chart methodology. Combining reference chart quantiles with localized stature hierarchies may provide improved predictions of growth and mortality and we suggest that this is an area worth exploring. Accordingly, analyses of growth based on reference quantiles in mixed-species, single-cohort stands in the Missouri Ozarks are underway (Vickers *et al. unpublished data*). Given the interspecific differences in height development trends described by the species-specific reference charts (Figs. 5.5, 5.6), it is likely that success criteria for stature, growth, survival, or other indicators of success will vary temporally and by species.

Much of our discussion has focused on illustrating various applications of height-age reference charts. Our examples are not exhaustive of the potential for the reference charts we have constructed or those that may be developed later. For example, reference charts for assessing the development of an individual tree relative to a conspecific monoculture could provide useful inference on the relative strength of intraspecific and interspecific dynamics but we did not have relevant data to construct such references. Although the reference charts we have presented are age-dependent and best suited for assessments of single-cohort stands, it may be possible to evaluate the impact of various management practices and regeneration treatments on the development of saplings by using reference charts for clearcuts as a benchmark. However, assessment of

regeneration success in multi-cohort stands will probably require repeat measurements and conditional growth charts.

Conclusion

We have described the development of reference charts for forestry applications (Objective 1). We also demonstrated some of the strengths and weaknesses of reference chart methodology for forestry applications (Objective 2) and identified areas that could be improved through continued research. While it is unlikely that a perfect method exists for assessing an individual's development in an attribute of interest, adopting a standardized methodology could increase our understanding of the causes and consequences of variation in the development process. Moreover, the act of adopting a common methodology itself might serve as a catalyst for innovation and advances in our understanding of early stand dynamics, production ecology, and other areas of study. For example, the sometimes flawed or difficult assumptions required by existing metrics of site productivity and stand density have become well known since their adoption, but the numerous efforts to strengthen, expand, refine, or debunk those assumptions have greatly advanced our knowledge of the impacts of site productivity and stand density on the biology and ecology of tree growth (e.g., Ducey and Knapp 2010, Skovsgaard and Vanclay 2008, Woods and Coates 2013).

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References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S. 1998. Leaf-area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* 44: 317-328.
- Assmann, E. 1970. *The Principles of Forest Yield Study*. New York. Pergamon Press. 506p.
- Barrett, J.W. 1995. *Regional Silviculture of the United States, Third Edition*. Wiley. 656p.
- Bella, I.E. 1971. A new competition model for individual trees. *For. Sci.* 17: 364-372.
- Binkley, D., Campoe, O.C., Gspaltl, M., Forrester, D.I. 2013. Light absorption and use efficiency in forests: why patterns differ for trees and stands. *For. Ecol. Mgmt.* 288: 5-13.
- Binkley, D., Stape, J.L., Bauerle, W.L., Ryan, M.G. 2010. Explaining growth of individual trees: light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. *For. Ecol. Mgmt.* 259: 1704-1713.
- Bohara, S.B., Cao, Q.V. 2014. Prediction of tree diameter growth using quantile regression and mixed-effects models. *For. Ecol. Mgmt.* 319: 62-66.
- Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic Region. USDA For. Serv. Gen. Tech. Rep. NRS-33.
- Burns, R.M., Honkala, B.H. (eds.). 1990. *Silvics of North America, Volume 2, Hardwoods*. USDA For. Serv. Agriculture Handbook 654. Washington, D.C. 675p.
- Campoe, O.C., Stape, J.L., Albaugh, T.J., Allen, H.L., Fox, T.R., Rubilar, R., Binkley, D. 2013b. Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation. *For. Ecol. Mgmt.* 288: 43-48.
- Campoe, O.C., Stape, J.L., Nouvellon, Y., Laclau, J.-P., Bauerle, W., Binkley, D., le Maire, G. 2013a. Stem production, light absorption and light use efficiency between dominant and non-dominant trees of *Eucalyptus grandis* across a productivity gradient in Brazil. *For. Ecol. Mgmt.* 288: 14-20.
- Canham, C.D., LePage, P.T., Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* 34: 778-787.

- Carmean, W.H. 1975. Forest site quality evaluation in the United States. *Advances in Agronomy*. 27: 209-269.
- Carmean, W.H. 1979. Site index comparisons among northern hardwoods in northern Wisconsin and upper Michigan. USDA For. Serv. Res. Pap. NC-169.
- Clatterbuck, W.K., Hodges, J.D. 1988. Development of cherrybark oak and sweetgum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. *Can. J. For. Res.* 18(1): 12-18.
- Cole, T.J. 1994. Growth charts for both cross-sectional and longitudinal data. *Statistics in Medicine*. 13(23-24): 2477-2492.
- Cole, T.J., Green, P.J. 1992. Smoothing reference centile curves: the LMS method and penalized likelihood. *Statistics in Medicine*. 11: 1305-1319.
- Dahms, W.G. 1963. Correction for a possible bias in developing site index curves from sectioned tree data. *J. For.* 61: 25-27.
- de Onis, M., Onyango, A.W., Borghi, E., Siyam, A., Nishida, C., Siekmann, J. 2007. Development of a WHO growth reference for school-aged children and adolescents. *Bull. World Health Organization* 85(9): 660-667.
- Dey, D.C. 1991. A comprehensive Ozark regenerator. Ph.D. dissertation. University of Missouri. Columbia, MO.
- Doolittle, W.T. 1958. Site Index Comparisons for Several Forest Species in the Southern Appalachians. *Proceedings of the Soil Science Society of America* 22: 455-458.
- Ducey, M.J., Knapp, R.A. 2010. A stand density index for complex mixed species forests in the northeastern United States. *For. Ecol. Mgmt.* 260: 1613-1622.
- Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A. 2007. Tree nutrition and forest fertilization of pine plantations in the Southern United States. *South. J. Appl. For.* 31(1): 5-11.
- Harrell, F.E. 2001. *Regression Modeling Strategies with Applications to Linear Models, Logistic Regression, and Survival Analysis*. Springer. 571p.
- Heitzman, E., Nyland, R.D. 1991. Cleaning and early crop-tree release in northern hardwood stands: a review. *North. J. Appl. For.* 8(3): 111-115.
- Helms, J.A. (Ed.) 1998. *The Dictionary of Forestry*. The Society of American Foresters. Bethesda, MD. 210p.
- Hyndman, R.J., Fan, Y. 1996. Sample quantiles in statistical packages. *American Statistician*. 50: 361-365.

- Johnson, P.S., Shifley, S.R., Rogers, R. 2009. *The Ecology and Silviculture of Oaks*. CABI. 600p.
- Kelty, M.J., Larson, B.C., Oliver, C.D. 1992. *The Ecology of Mixed-Species Forests: A Festschrift for David M. Smith*. Springer. 291p.
- Kobe, R.K., Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. F. Res.* 27: 227-236.
- Koenker, R. 2005. *Quantile Regression*. Cambridge University Press. 349p.
- Kuczumski, R.J., Ogden, C.L., Guo, S.S., *et al.* 2002. 2000 CDC growth charts for the United States: methods and development. *National Center for Health Statistics. Vital Health Stat* 11(246).
- Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Mgmt.* 6: 343-360.
- Meadows, J.S., Burkhardt, E.C., Johnson, R.L., Hodges, J.D. 2001. A numerical rating system for crown classes of southern hardwoods. *South. J. Appl. For.* 25(4): 154-158.
- Miller, G.W. 2000. Effect of crown growing space on the development of young hardwood crop trees. *North. J. Appl. For.* 17: 25-35.
- Oliver, C.D. 1978. The development of northern red oak in mixed stands in central New England. *Yale Univ. School For. Environ. Stud. Bull.* 91.
- Oliver, C.D., Larson, B.C. 1996. *Forest Stand Dynamics*. 2nd ed. John Wiley & Sons, Inc. New York. 520p.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr., Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24: 2172-2183.
- Quetelet, A. 1871. *Anthropometrie*. Brussels. Muquardt.
- Ramsay, J.O., Silverman, B.W. 2002. *Applied Functional Data Analysis: Methods and Case Studies*. Springer. 191p.
- Rennolls, K. 1978. "Top Height"; its definition and estimation. *Commonw. For. Rev.* 57: 215-219.
- Sander, I.L., Johnson, P.S., Watt, R.F. 1976. A guide for evaluating the adequacy of oak advance reproduction. *USDA For. Serv. Gen. Tech. Rep.* NC-23.

- Sharma, M., Amateis, R.L., Burkhart, H.E. 2002. Top height definition and its effect on site index determination in thinned and unthinned loblolly pine plantations. *For. Ecol. Mgmt.* 168: 163-175.
- Skovsgaard, J.P., Vanclay, J.K. 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. *Forestry.* 81(1): 13-31.
- Stage, A.R. 1973. Prognosis model for stand development. Res. Pap. INT-137. United States Dept. Agriculture, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Stanturf, J.A., Schoenholtz, S.H., Schweitzer, C.J., Shepard, J.P. 2001. Achieving restoration success: myths in bottomland hardwood forests. *Restor. Ecol.* 9(2): 189-200.
- Steiner, K.C., Finley, J.C., Gould, P.J., Fei, S., McDill, M. 2008. Oak regeneration guidelines for the Central Appalachians. *North. J. Appl. For.* 25(1): 5-16.
- Takezawa, K. 2006. *Introduction to Nonparametric Regression*. John Wiley & Sons, Inc.
- Ulijaszek, S.J., Johnston, F.E., Preece, M.A. 1998. *The Cambridge Encyclopedia of Human Growth and Development*. Cambridge University Press. 509p.
- Vickers, L.A., Fox, T.R., Loftis, D.L., Boucugnani, D.A 2011. Predicting forest regeneration in the Central Appalachians using the REGEN expert system. *J. Sust. For.* 30(8): 790-822.
- Vickers, L.A., Larsen, D.R., Knapp, B.O., Kabrick, J.M., Dey, D.C. 2014. The impact of overstory density on sapling height growth in the Missouri Ozarks – implications for interspecific differentiation during canopy recruitment. *Can. J. For. Res.* 44(11): 1320-1330.
- Vose, J.M., Allen, H.L. 1988. Leaf area, stemwood growth, and nutrient relationships in loblolly pine. *For. Sci.* 34: 547-563.
- Ward, J.S. 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. *Can. J. For. Res.* 39: 118-130.
- Ward, J.S. 2013. Precommercial crop tree release increases upper canopy persistence and diameter growth of oak saplings. *North. J. Appl. For.* 30(4): 156-163.
- Ward, J.S., Stephens, G.R. 1993. Influence of crown class and shade tolerance on individual tree development during deciduous forest succession in Connecticut, USA. *For. Ecol. Mgmt.* 60: 207-236.
- Ward, J.S., Stephens, G.R. 1994. Crown class transition rates of maturing northern red oak (*Quercus rubra* L.). *For. Sci.* 40: 1-17.

- Ward, J.S., Stephens, G.R. 1996. Influence of crown class on survival and development of *Betula lenta* in Connecticut, U.S.A. *Can. J. For. Res.* 26: 277-288.
- Wei, Y., Pere, A., Koenker, R., Xuming, H. 2006. Quantile regression methods for reference growth charts. *Statistics in Medicine.* 25: 1369-1382.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5: 360-364.
- Woods, A., Coates, K. David. 2013. Are biotic disturbance agents challenging basic tenets of growth and yield and sustainable forest management? *Forestry.* 86: 543-554.
- Zenner, E.K., Heggenstaller, D.J., Brose, P.H., Peck, J., Steiner, K.C. 2012. Reconstructing the competitive dynamics of mixed-oak neighborhoods. *Can. J. For. Res.* 42: 1714-1723.

Tables

Table 5.1. Quantile estimates for the site-specific reference groups used in this study. Quantile estimates are rounded to the nearest decimeter.

Reference group	Age	n	Quantile													
			5	10	20	25	30	40	50	60	70	75	80	90	95	99
			<i>Total Height (m)</i>													
exposed backslopes	2	336	0.3	0.5	0.7	0.8	0.9	1.1	1.2	1.5	1.7	2.0	2.1	2.4	3.0	4.4
	5	324	0.6	0.9	1.4	1.6	1.7	2.0	2.3	2.7	3.0	3.1	3.3	4.1	4.6	5.6
	10	307	0.5	1.2	2.2	2.4	2.7	3.3	3.8	4.2	4.9	5.2	5.5	6.5	7.1	8.3
	16	1839	1.4	1.7	2.1	2.3	2.5	3.0	3.7	4.3	4.9	5.3	5.9	7.4	8.6	11.1

protected backslopes	2	767	0.3	0.4	0.6	0.7	0.8	1.0	1.2	1.4	1.6	1.7	1.9	2.4	3.0	4.8
	5	731	0.6	0.8	1.3	1.5	1.6	2.0	2.3	2.5	2.8	3.0	3.2	3.7	4.2	5.5
	10	687	0.8	1.3	2.2	2.6	2.8	3.4	3.8	4.2	4.8	5.1	5.3	6.0	6.6	8.2
	16	1664	1.3	1.6	2.1	2.4	2.7	3.2	3.8	4.6	5.5	6.1	6.7	8.2	9.6	11.8

Table 5.2. Quantile estimates for the site- and species-specific reference groups on exposed backslopes used in this study. Quantile estimates are rounded to the nearest decimeter.

Species Group	Age	n	Quantile													
			5	10	20	25	30	40	50	60	70	75	80	90	95	99
			<i>Total Height (m)</i>													
red oaks	2	79	0.2	0.3	0.4	0.4	0.6	0.8	1.0	1.2	1.7	2.0	2.0	2.4	3.3	4.5
	5	74	0.3	0.4	0.8	1.1	1.4	2.0	2.3	2.7	3.1	3.6	4.1	4.7	5.5	7.3
	10	73	0.3	0.5	1.8	2.2	2.8	3.4	4.1	4.9	5.7	6.1	6.8	7.7	8.3	9.2
	16	214	1.6	2.0	2.7	3.3	3.7	4.4	5.5	6.8	7.7	8.3	8.9	10.7	11.9	13.9
white oaks	2	79	0.4	0.6	0.9	1.0	1.1	1.3	1.4	1.6	1.7	1.9	2.0	2.3	2.9	4.5
	5	79	0.9	1.2	1.9	2.1	2.4	2.6	3.0	3.2	3.5	3.7	4.1	4.5	4.7	5.3
	10	78	1.2	2.1	3.5	3.8	4.1	4.5	5.2	5.5	6.0	6.3	6.5	6.9	7.3	7.5
	16	522	1.3	1.6	1.9	2.0	2.2	2.5	3.0	3.8	4.7	5.2	5.9	7.6	8.5	10.5
hickories	2	58	0.3	0.4	0.5	0.6	0.7	0.9	1.0	1.1	1.2	1.5	1.6	2.2	2.6	3.0
	5	57	0.6	0.7	1.2	1.3	1.6	1.8	1.9	2.3	2.5	2.6	2.7	3.1	3.4	3.5
	10	58	0.6	0.8	2.0	2.2	2.4	2.7	3.0	3.6	4.2	4.3	4.8	5.2	5.3	5.7
	16	205	1.4	1.7	2.1	2.4	2.6	3.1	3.9	4.7	5.5	6.0	6.3	7.6	8.5	10.0
sassafras	2	39	0.6	0.6	0.8	0.8	1.0	1.1	1.2	1.3	1.8	1.9	2.1	2.4	3.4	4.4
	5	35	0.9	1.2	1.4	1.5	1.6	1.9	2.2	2.4	2.8	2.9	3.1	3.5	4.3	4.9
	10	29	0.4	0.5	1.6	2.0	2.2	2.8	3.1	3.3	4.0	4.1	4.2	4.8	5.3	6.2
	16	136	2.5	3.4	3.8	4.1	4.3	4.8	5.1	5.3	5.9	6.2	6.4	7.0	7.3	9.6
blackgum	2	26	0.8	0.9	1.0	1.1	1.1	1.5	1.7	2.0	2.1	2.2	2.3	2.7	3.2	3.4
	5	26	1.1	1.4	1.7	1.8	1.9	2.0	2.3	2.5	3.0	3.1	3.2	3.5	3.7	4.1
	10	26	1.5	2.1	2.4	2.5	2.7	3.2	3.3	3.5	3.7	3.9	4.2	4.6	5.2	6.2
	16	115	1.5	1.8	2.3	2.5	2.7	3.2	3.5	4.1	4.6	4.7	5.0	5.7	6.2	6.7
dogwood	2	27	0.7	1.1	1.2	1.4	1.4	1.7	1.9	2.1	2.3	2.5	2.6	3.0	3.2	3.4
	5	26	0.6	0.9	1.1	1.4	1.6	1.9	2.2	2.3	2.5	2.7	3.0	3.3	3.4	3.4
	10	17	0.6	0.8	2.2	2.4	2.6	2.8	3.1	3.5	3.8	4.0	4.3	5.0	5.4	5.5
	16	214	1.4	1.8	2.1	2.2	2.4	2.8	3.2	3.7	4.0	4.1	4.3	4.9	5.2	6.6
other species	2	28	0.4	0.5	0.7	0.8	0.8	0.9	1.0	1.1	1.5	1.5	2.0	2.3	2.6	2.9
	5	27	0.7	0.9	1.3	1.4	1.5	1.7	2.0	2.2	2.8	2.9	2.9	3.8	4.4	5.1
	10	26	1.1	1.5	2.2	2.4	2.4	2.5	2.9	3.8	4.4	4.9	5.2	5.7	6.7	7.4
	16	432	1.3	1.6	2.0	2.2	2.4	2.8	3.4	3.9	4.3	4.6	4.9	6.2	7.6	9.5

Table 5.3. Quantile estimates for the site- and species-specific reference groups on protected backslopes used in this study. Quantile estimates are rounded to the nearest decimeter.

Species Group	Age	n	Quantile													
			5	10	20	25	30	40	50	60	70	75	80	90	95	99
			<i>Total Height (m)</i>													
red oaks	2	209	0.3	0.4	0.5	0.6	0.6	0.9	1.0	1.2	1.4	1.5	1.6	2.1	2.6	4.1
	5	200	0.5	0.7	1.2	1.4	1.5	1.8	2.1	2.4	2.7	2.9	2.9	3.4	4.0	5.2
	10	188	0.9	1.3	2.3	2.8	2.9	3.5	4.3	4.9	5.2	5.4	5.6	6.4	7.2	9.2
	16	106	1.6	2.0	2.7	3.4	4.0	6.1	6.8	7.8	8.8	9.6	10.3	11.0	12.7	14.1
white oaks	2	145	0.2	0.3	0.5	0.5	0.7	0.8	1.0	1.2	1.4	1.6	1.8	2.8	3.4	5.0
	5	142	0.5	0.6	1.1	1.3	1.6	2.0	2.3	2.7	3.0	3.2	3.4	3.9	4.4	5.2
	10	141	0.5	1.0	2.0	2.5	2.8	3.5	4.2	4.7	5.2	5.5	5.8	6.2	6.9	7.9
	16	204	1.1	1.3	1.6	1.7	1.9	2.2	3.2	4.3	6.4	7.6	8.3	9.9	10.8	13.0
hickories	2	149	0.3	0.4	0.5	0.6	0.7	0.9	1.0	1.2	1.4	1.6	1.7	2.3	3.6	5.3
	5	151	0.7	1.0	1.3	1.4	1.5	1.8	2.0	2.3	2.5	2.7	2.8	3.5	4.3	5.7
	10	148	1.2	1.6	2.3	2.6	2.8	3.3	3.8	4.1	4.3	4.7	4.8	5.5	5.9	6.8
	16	173	1.1	1.5	2.0	2.1	2.5	2.9	3.2	3.9	5.1	5.5	6.1	7.6	8.4	11.9
sassafras	2	77	0.4	0.6	0.9	1.0	1.1	1.2	1.4	1.5	1.6	1.7	1.9	2.3	2.9	4.5
	5	61	0.7	0.8	1.3	1.4	1.6	2.0	2.1	2.3	2.7	3.0	3.1	3.4	3.9	5.4
	10	47	0.3	0.6	0.8	1.1	1.5	2.2	3.0	3.5	4.1	4.3	4.4	4.8	5.5	6.2
	16	170	2.7	3.9	5.0	5.2	5.3	5.8	6.5	7.0	7.6	7.9	8.2	9.1	9.6	10.4
blackgum	2	60	0.5	0.6	1.0	1.1	1.4	1.5	1.6	1.8	2.1	2.2	2.3	2.6	4.0	5.2
	5	57	0.9	1.2	1.6	1.7	1.9	2.3	2.5	2.9	3.5	3.7	3.8	4.2	4.7	5.1
	10	51	0.6	1.3	2.1	2.6	2.8	3.1	3.9	4.5	5.4	5.5	6.0	6.3	6.5	6.6
	16	81	1.4	2.1	2.7	3.0	3.2	4.0	4.6	5.3	5.6	5.8	6.6	7.6	8.8	9.4
dogwood	2	62	0.8	1.1	1.2	1.3	1.3	1.5	1.7	1.9	2.1	2.3	2.3	2.7	3.1	3.7
	5	56	1.3	2.0	2.3	2.4	2.4	2.5	2.7	2.9	3.1	3.3	3.4	3.7	3.8	4.0
	10	53	2.1	2.4	3.2	3.4	3.5	3.8	3.9	4.0	4.1	4.3	4.8	5.0	5.2	6.2
	16	246	1.5	1.9	2.3	2.4	2.7	3.0	3.4	3.7	4.1	4.3	4.5	5.2	6.1	6.9
other species	2	65	0.4	0.5	0.7	0.8	0.9	1.0	1.2	1.4	1.6	1.7	1.9	2.6	2.8	6.0
	5	64	0.8	1.1	1.5	1.5	1.7	2.0	2.2	2.4	2.6	2.7	2.9	3.8	5.5	7.5
	10	59	1.0	1.4	1.9	2.3	2.6	2.8	3.2	3.7	4.1	4.2	4.4	5.6	7.4	8.5
	16	684	1.2	1.5	2.0	2.2	2.4	3.0	3.5	4.3	4.9	5.3	5.9	7.3	8.1	10.6

Figures

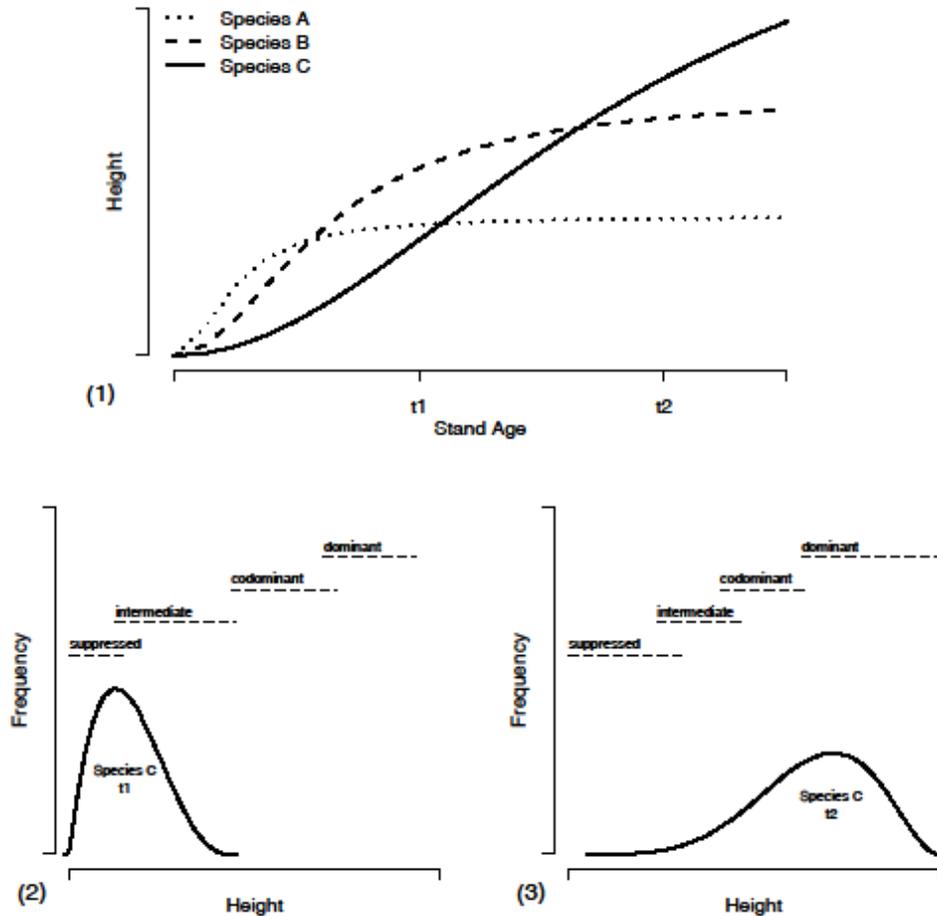


Figure 5.1. Conceptual example of the impact of intraspecific, interspecific, and temporal variation in height growth on relative stature. 5.1.1: Height-age curves for three co-occurring species. Note that although Species C exhibits the slowest initial growth, it has the potential to eventually be the tallest of the three species. A crown class evaluation for Species C at time 1 (5.1.2) finds that the greatest crown class attained by Species C is intermediate. In contrast, a crown class evaluation at time 2 (5.1.3) finds that Species C occupies all crown classes. This example shows that a point estimate of relative stature can be misleading by ignoring intraspecific, interspecific, and temporal variation in growth rates.

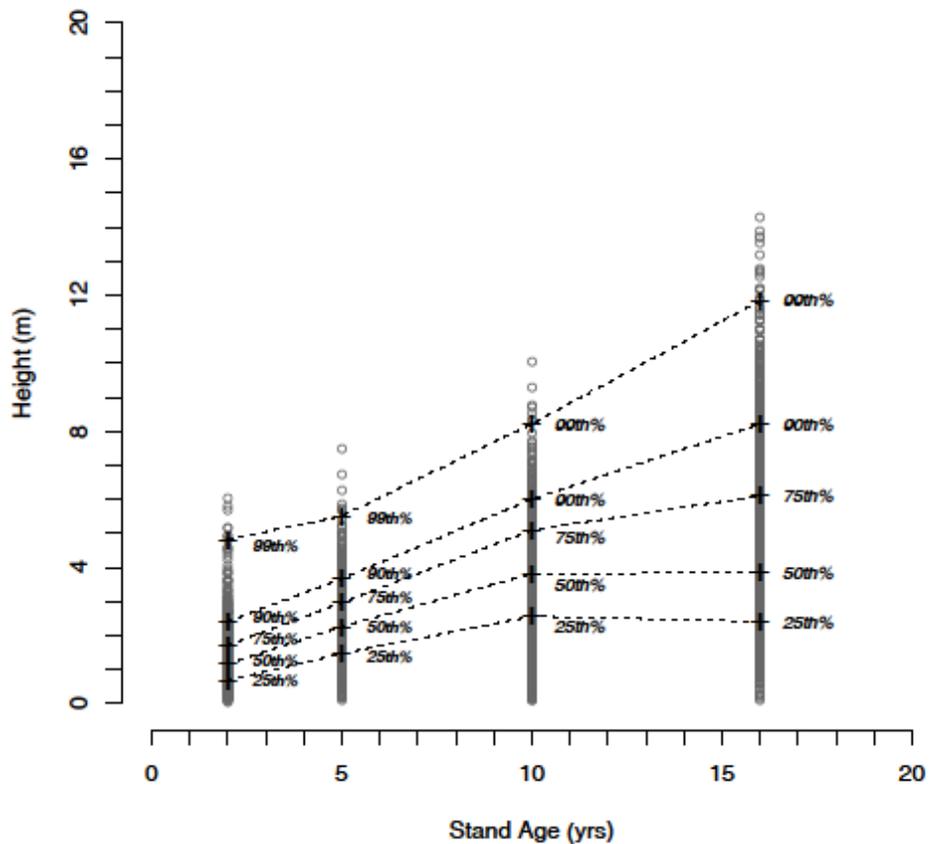


Figure 5.2. Quantile estimation and longitudinal interpolation of a height-age distribution. Reference charts were created by estimating the quantiles of a height distribution (open points) at each measurement interval (+ symbol) and using linear interpolation (broken lines) to estimate the quantiles between measurement intervals.

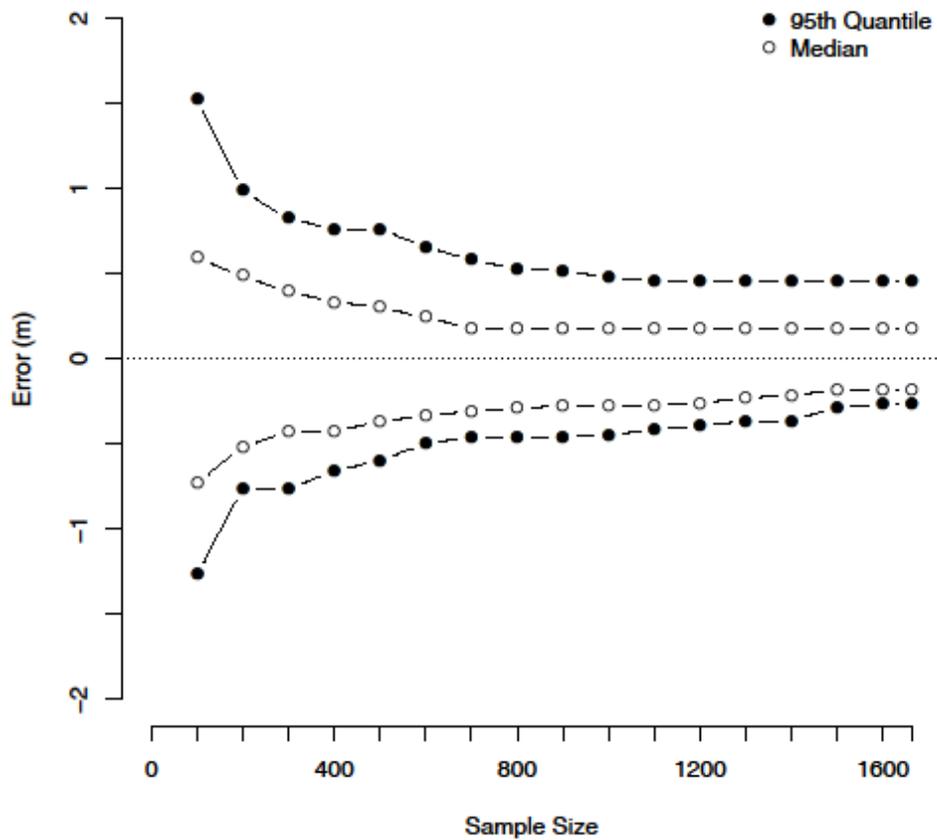


Figure 5.3. Impact of sample size on the magnitude of quantile estimation errors. Confidence bands ($\alpha=0.05$) for the magnitude of estimation error for the 95th quantile (filled points) and median (open points) on protected backslopes at stand age 16. Errors were calculated by sampling with replacement from the distribution of heights using sample sizes from 100 to 1664 (size of original data) and calculating the 95th quantile and median for the sample. These values were subtracted from the original estimates (Table 5.1) and the percentile method (10000 iterations) was used to construct confidence bands.

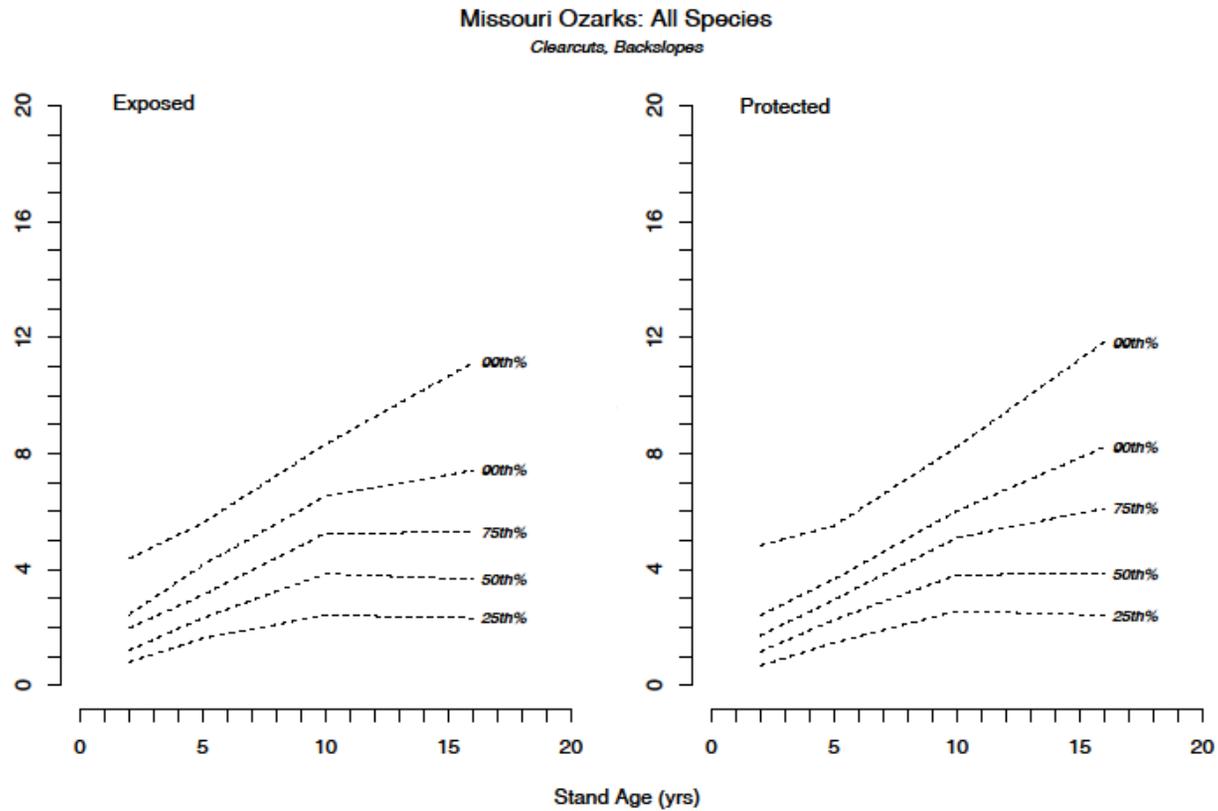


Figure 5.4. Site-specific height-age reference charts for mixed-species stands following a clearcut (residual basal area $\leq 5\text{m}^2\cdot\text{ha}^{-1}$) on exposed or protected backslopes in the Missouri Ozarks. Average site index (*Quercus velutina* Lam., base age 50) is approximately 21.0m ($\pm 1.3\text{m}$) on exposed backslopes (aspect: 136 - 315°) and approximately 22.0m ($\pm 1.1\text{m}$) on protected backslopes (aspect: 316 - 135°) in this region. Measurements for all woody species encountered (see text) are included.

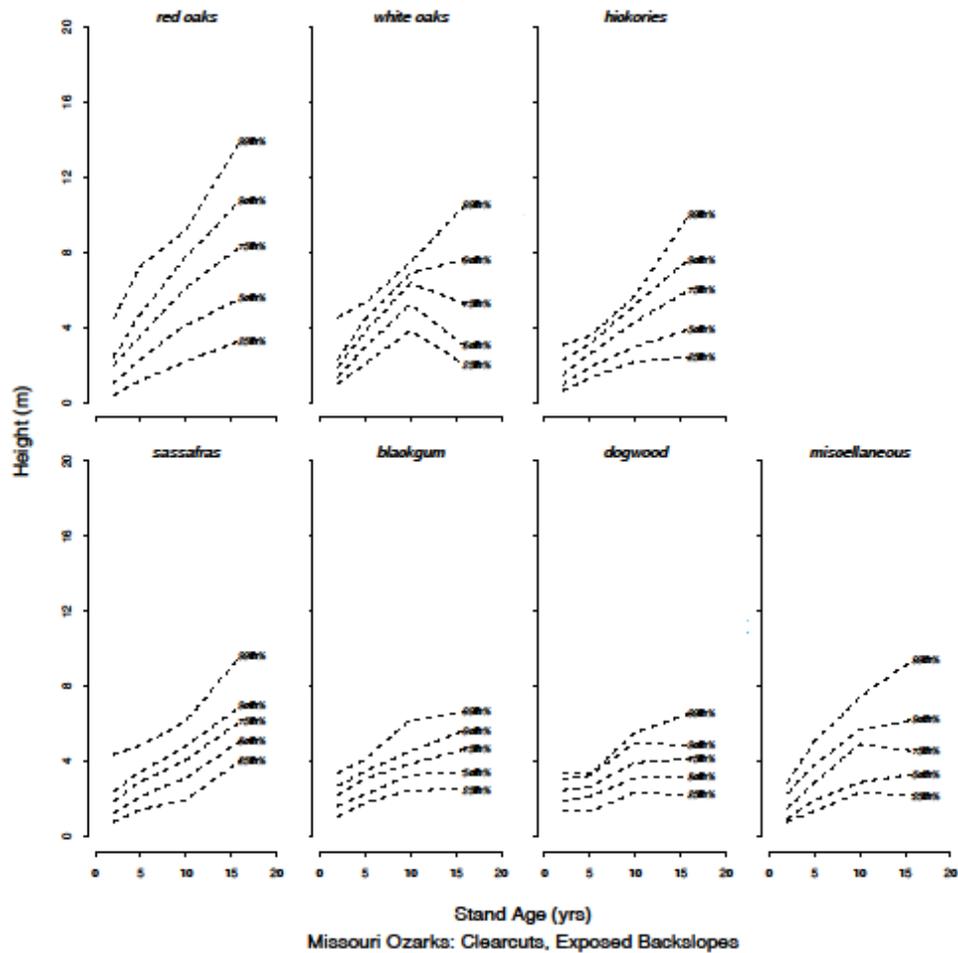


Figure 5.5. Species-specific height-age reference charts for mixed-species stands following a clearcut (residual basal area $\leq 5\text{m}^2 \cdot \text{ha}^{-1}$) on exposed backslopes in the Missouri Ozarks. Average site index (*Quercus velutina* Lam., base age 50) is approximately 21.0m ($\pm 1.3\text{m}$) on exposed backslopes (aspect: $136 - 315^\circ$) in this region. See text for species group definitions.

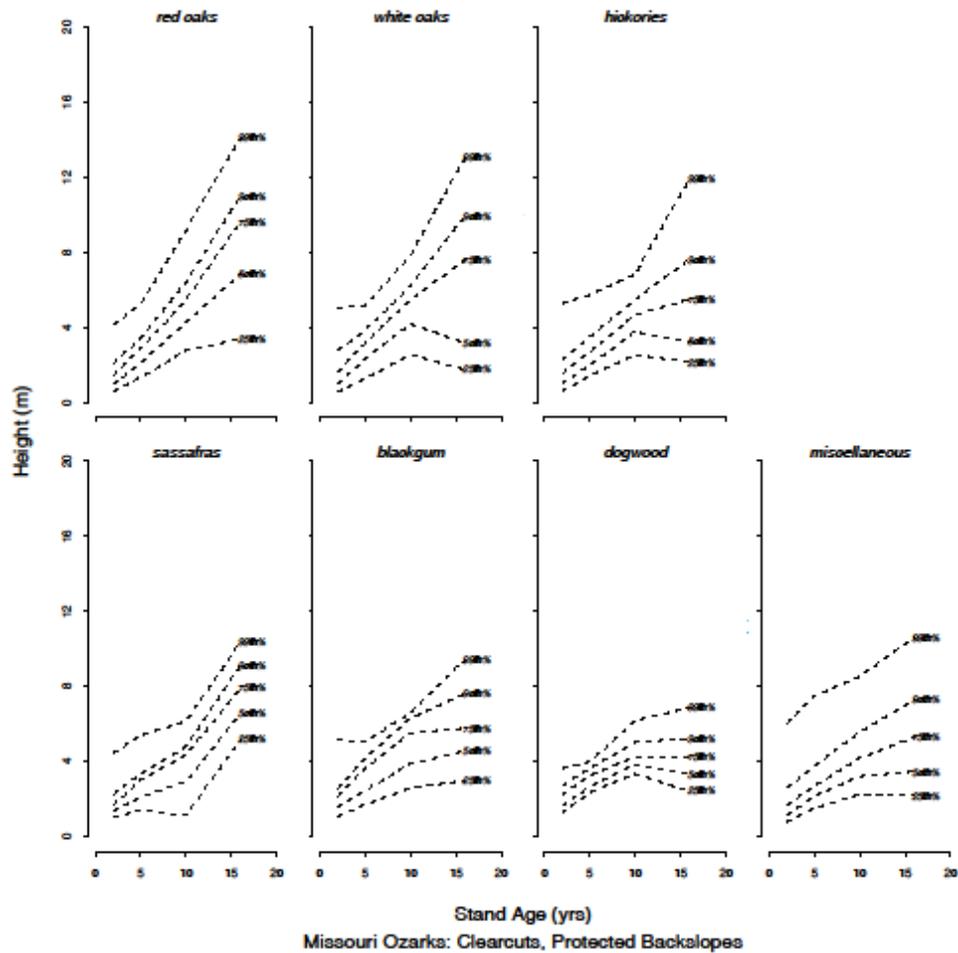


Figure 5.6. Species-specific height-age reference charts for mixed-species stands following a clearcut (residual basal area $\leq 5\text{m}^2 \cdot \text{ha}^{-1}$) on protected backlopes in the Missouri Ozarks. Average site index (*Quercus velutina* Lam., base age 50) on protected backlopes (aspect: $316 - 135^\circ$) is approximately 22.0m ($\pm 1.1\text{m}$) in this region. See text for species group definitions.

Missouri Ozarks: All Species
Clearcuts, Protected Backslopes

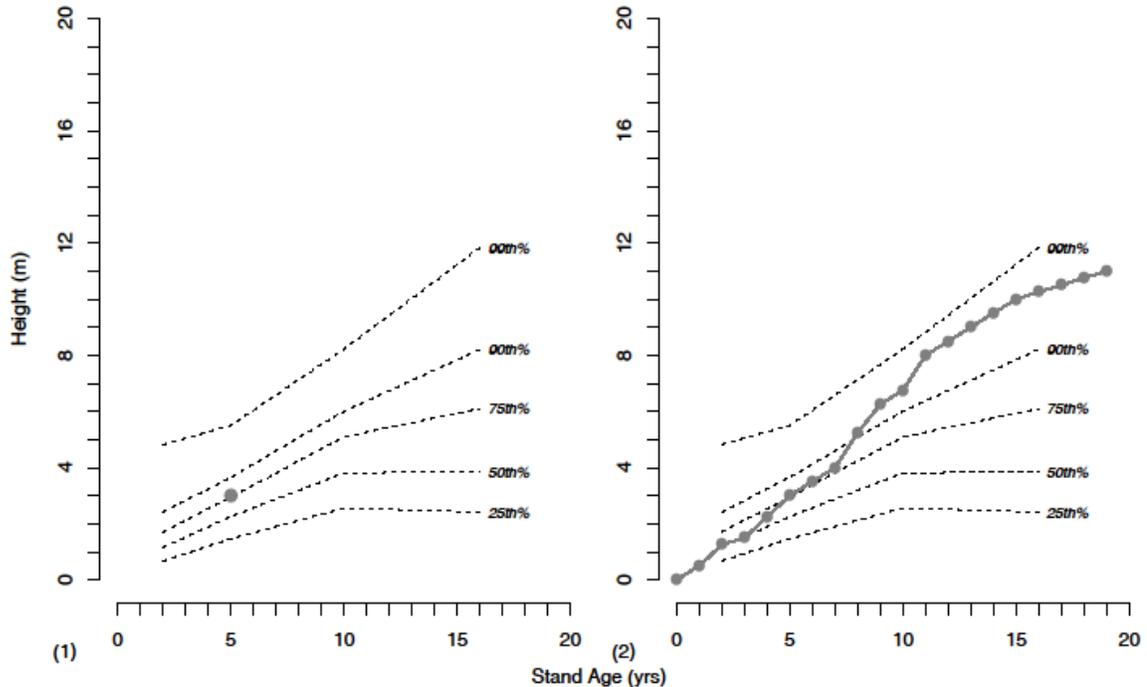


Figure 5.7. Application of site-specific reference charts for a one-time assessment (5.7.1) and a longitudinal assessment (5.7.2) of height. Reference charts can be used to evaluate the development of an individual relative to a specified peer group (protected backslopes here) using a single measurement (5.7.1). A height of 3 meters at age 5 on this site type corresponds to the 75th quantile. This implies that at the time of measurement, the example tree was taller than about 75% of all trees in this peer group (or shorter than about 25% of all trees) without measuring any additional trees. Reference charts also provide opportunities to assess the development pattern of a tree (5.7.2). The height development shown in 5.7.2 was obtained via stem analysis from a 19 year old white oak (*Quercus alba*) that, at the time of sampling, had attained a codominant canopy position in a mixed-species, single-cohort stand on a protected backslope in the Missouri Ozarks. Although this tree was in a favorable canopy position at the time of sampling, the reference chart suggests that prior to age 7, the height of this tree (50-75th quantile), though not poor, was unexceptional relative to the mainstream trends for the specified peer group. However, between ages 7 and 11 this tree attained a stature in the upper quantiles where fewer than 10% of other trees in clearcuts on protected backslopes in the Missouri Ozarks could have been taller.

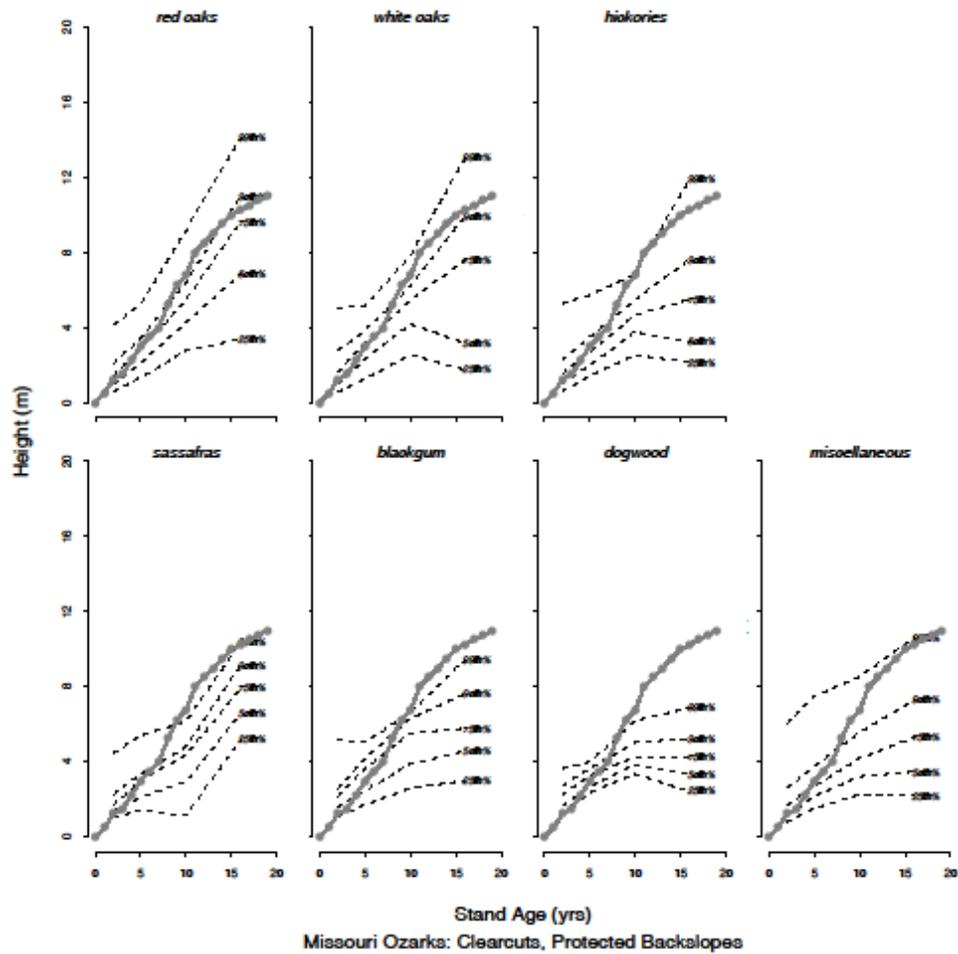


Figure 5.8. Application of species-specific reference charts for longitudinal assessment of height. The height development of the 19 year old codominant white oak (*Quercus alba*) from Figure 5.7.2 is plotted against the species-specific reference charts for all species groups on protected backslopes in the Missouri Ozarks. While unexceptional prior to age 7, this tree reached the upper 10% of the height distribution for white oaks by age 8 and maintained at least that status thereafter. In addition to conspecific analyses, species-specific reference charts can also be used to provide inference into when this tree would likely outpace competitors and how that timing might vary with the species of the competitor. Through about age 6 the height of this tree only attained between the 25th and 75th quantiles across all species groups. This implies that the example white oak would have been shorter than a majority of competing stems from any species group. However after age 8-10 through age 16, an extant neighbor of many species had, at most, a 1% chance of being taller than this tree. A nearby red oak would have had, at most, about a 15% chance of being taller. Neighboring white oaks or hickories had, at most, about a 5% chance.

Chapter 6: Conclusion

Regeneration is a dynamic process involving the establishment, growth, and mortality of individual trees and their neighbors. These three components are intimately connected and their interactions shape the composition and structure of the regenerating forest. The primary mechanism by which this process is initiated is overstory disturbance. Foresters have long understood that overstory manipulation offers a tool to influence regeneration dynamics due to interspecific differences in response to disturbance and resource limitation.

The preceding analyses focused exclusively on the establishment and growth components of regeneration. They indicate that as resource availability decreases in the understory due to increasing levels of overstory retention, interspecific differences in both sapling establishment and subsequent growth rates are muted. As residual overstory density exceeded about $15\text{m}^2\cdot\text{ha}^{-1}$ there was relatively little difference in sapling establishment and even less difference in growth among species.

The soils, climate, and flora throughout much of the Missouri Ozarks favor the *Quercus-Carya* forest type. Although *Quercus* establishment was not exceptionally high relative to other species at any level of residual overstory, there were growth advantages over the other species examined at low levels of overstory density. In this environment, relatively minor differences in initial growth rates were found to be magnified during the canopy recruitment process. However, interannual growth rates of individual trees were found to be highly variable. Moreover, intraspecific variation in height development was comparable to interspecific variation. This suggests that among neighboring individuals

longitudinal changes in dominance, both within and among species are to be expected.

The remarkable similarity in developmental milestones required for successful canopy recruitment in the absence of an overstory among species indicates that there are limits to the magnitude of height deficits that can be endured during the stem exclusion process. The deficit that can be endured likely decreases over the course of the stem exclusion process. Both mean height increment and variability thereof decreased with increasing height, and the rate of decline was greater for trees in lower canopy positions. Given the interannual variation in height increment, insurmountable deficits may be reached in a very short period of time. This suggests that while there are detectable advantages and disadvantages among species in both establishment and growth, stochasticity should be included alongside establishment, growth, and mortality as the fourth component of the regeneration process.

The stochastic models of establishment across a gradient of residual overstory density (Chapter 2) are consistent with the dynamic nature of the regeneration process. Linking establishment outcomes with models of annual height growth based on residual overstory density (Chapter 3) and size (Chapter 4) provides a powerful tool for both applied and empirical objectives. The combination of these models, while imperfect, should increase our ability to recreate the regeneration process, and as a result, our understanding of it. Areas in need of additional work have been suggested and use of the combined models as a simulation system

will undoubtedly highlight other weaknesses in the individual models and in our current ability to quantify the regeneration process.

The covariates chosen for the empirical models of reproduction establishment and the structure of the simulation module itself were strongly influenced by leading hypotheses and theories of tree and stand development. Therefore, the output should be sufficiently general to describe the establishment of a variety of species under a variety of scenarios. The output is provided as a treelist enumerated from inventoried and empirical parameters and individual tree attributes derived from allometrically derived relationships. This should foster compatibility with existing growth and yield models. Parameterization for the Missouri Ozarks was accomplished using a combination of existing data sources from tagged and untagged plots monitored before and after disturbance.

Parameterization of reproduction establishment could be accomplished in other settings by establishing tagged plots and tracking their development for a short period following planned disturbance. Simultaneous collection of a combination of stem analysis data and short term monitoring of additional tagged plots on stands/cohorts in different stages of development would likely expedite parameterization of growth and mortality functions.

Quantitative interpretation of the regeneration process is as important as simulation of it. Therefore, developmental milestones for recruitment “success” were identified from the growth patterns exhibited by juvenile trees that were ultimately in codominant and dominant crown classes following the first twenty

years of stand development in naturally regenerated, mixed species, even-aged stands in the Missouri Ozarks. These milestones provide a tool that foresters can use to assess the status of individual trees during the canopy recruitment process in even-aged stands. While it is not guaranteed that a tree that attains these milestones early in development will remain on track to become a member of the upper canopy at the end of the regeneration period, there is little chance that a tree will attain that goal without reaching these milestones at some point during the development of the stand. Reference chart methodology provides opportunities to increase the inference obtainable from regeneration and recruitment evaluations by providing interpretation of individual tree development in the context of a variety of peer groups.

Additional research into the role of recruitment dynamics is certainly warranted. In particular, greater insight into the developmental milestones of saplings that successfully attain upper canopy status in stands with complex size and age structures is needed. Likewise, additional study into the factors that influence the probability of continued success for those stems that attain these milestones early in development is warranted. Finally, variation in sapling mortality rates and those factors that influence it may be a strong source of differentiation during the canopy recruitment process, but one that remains largely unquantified in the Missouri Ozarks.

VITA

Lance Alan Vickers was born to Mark and Ginger Vickers of Hermitage, Arkansas in 1984. It was at Hermitage High School where two epochal events in his life occurred: 1) being introduced to Misty Temple, who would later become his wife, and 2) being introduced to the scientific study of forests, which would later become his career.

Lance attended the University of Arkansas at Monticello and earned the Bachelor of Science degree in Forestry with honors in 2006. Lance also worked as a Forestry Technician for Kingwood Forestry Services during that time. In 2007, Lance and Misty married and moved to Christiansburg, Virginia. Lance earned a Master of Science degree in Forestry from Virginia Tech under the supervision of Dr. Thomas R. Fox in 2009. Lance specialized in silviculture and regeneration of the Appalachian hardwood forests of Virginia and West Virginia. Afterwards, Lance worked as a Research Associate managing and analyzing several long-term silvicultural research studies of loblolly pine across the southeast United States for the Forest Productivity Cooperative.

Lance and Misty moved to Holts Summit, Missouri in 2011 and welcomed their first child, Scarlett. Their second daughter, Autumn, followed in 2014. Lance earned the doctor of philosophy in forestry degree from the University of Missouri in 2015 under the supervision of Dr. David R. Larsen. For his doctoral degree, Lance specialized in quantitative silviculture and focused on developing models and modeling strategies of the regeneration and early stand dynamics in Missouri Ozark forests. The Vickers' currently reside in Abilene, Texas. Lance continues

his efforts to improve scientific understanding of forest ecology and silvicultural manipulation through quantitative research into the factors and processes that influence early stand dynamics.