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# Height development milestones for canopy recruitment after overstory removal in the Missouri Ozarks

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ABSTRACT

Tree height development has been studied extensively. Nonetheless, there is limited quantitative guidance for height expectations during the regeneration period, particularly for common species with low commercial value. Site index models, for example, often omit the initial 15–20 years of development. We examined height development of juvenile trees during the first twenty years after overstory removal in naturally regenerated, mixed stands in the Missouri Ozarks to identify milestones indicative of eventual recruitment into the upper canopy by the end of the regeneration period. Such milestones quantify minimum height requirements for recruitment success from trees that occupied codominant and dominant crown classes at the end of the regeneration period. Results show these milestones differed statistically by site class and those differences increased over time. Species-specific milestones were similar and while some statistical differences were observed, the practical, if not ecological, consequences of those differences appeared limited. The similarity in milestones among species suggests that there is a minimum height threshold for eventual canopy recruitment success after overstory removal in the Missouri Ozarks. This was validated using independent data from a nearby long-term study with tagged individuals. Less than 1% of trees that failed the milestones by year 3 met them after 16 years, and less than 1% of trees failing the milestones at year 8 met them by year 16. Thus, the presented milestones are a tool that can be used to assess individual tree height development during the recruitment process. A tree that attains these milestones early in development is not guaranteed to remain successful throughout the regeneration period, but success without first reaching these milestones is highly improbable.

## 1. Introduction

### 1.1. Early stages of post-disturbance stand development are complex, but critical

Early stand dynamics after overstory removal exert considerable influence on the future character of a stand. It is during this period in mixed species stands that the first opportunities to evaluate the culmination of regeneration efforts arise. It is also the last opportunity to use silvicultural practices to promote desirable species within the regenerating cohort (Ward, 2009). Within a few years of overstory removal, the new cohort usually begins to approach the limits of site occupancy and enters a period marked by increasing vertical stratification and competition-induced mortality (Oliver and Larson, 1996). During this period, it is critical for individual trees to maintain height development trajectories that avoid resource preemption by current and future neighbors (Weiner, 1990).

### 1.2. Techniques for evaluating recruitment success

The ability to evaluate and project the fate of individual trees, a necessary step in determining the need for silvicultural intervention, often involves a high degree of uncertainty (McGee and Bivens, 1984), particularly in mixed stands (Oliver and Larson, 1996). Several models and guidelines have been developed to aid evaluations of regeneration potential of a stand (e.g., Sander et al., 1984, Dey et al., 1996a). These tools typically have two major components: (1) a pre-harvest survey and (2) a post-harvest benchmark. The pre-harvest survey provides an estimate of the density and size tally of advance reproduction, a key determinant of post-harvest growth for species that rely on advance reproduction for success (Sander, 1971, 1972). The importance of advance reproduction to *Quercus* regeneration success has been demonstrated by several empirical studies (e.g., McQuilkin, 1975, Loftis, 1990, Dey et al., 1996b).

In contrast, the post-harvest benchmark is often based on (reasonable) assumptions that have received modest empirical examination. Research has shown that individuals in the upper canopy (i.e., the dominant or codominant crown classes) at the end of the regeneration period – around 20 years after complete overstory removal in many deciduous forests of the eastern United States (Johnson et al., 2009) - are likely to remain competitive in later stages (Ward and Stephens, 1994). On this premise, crown class or height-based analogues at various times after overstory removal are typically used as benchmarks for recruitment success. For example, Sander et al. (1976) used a

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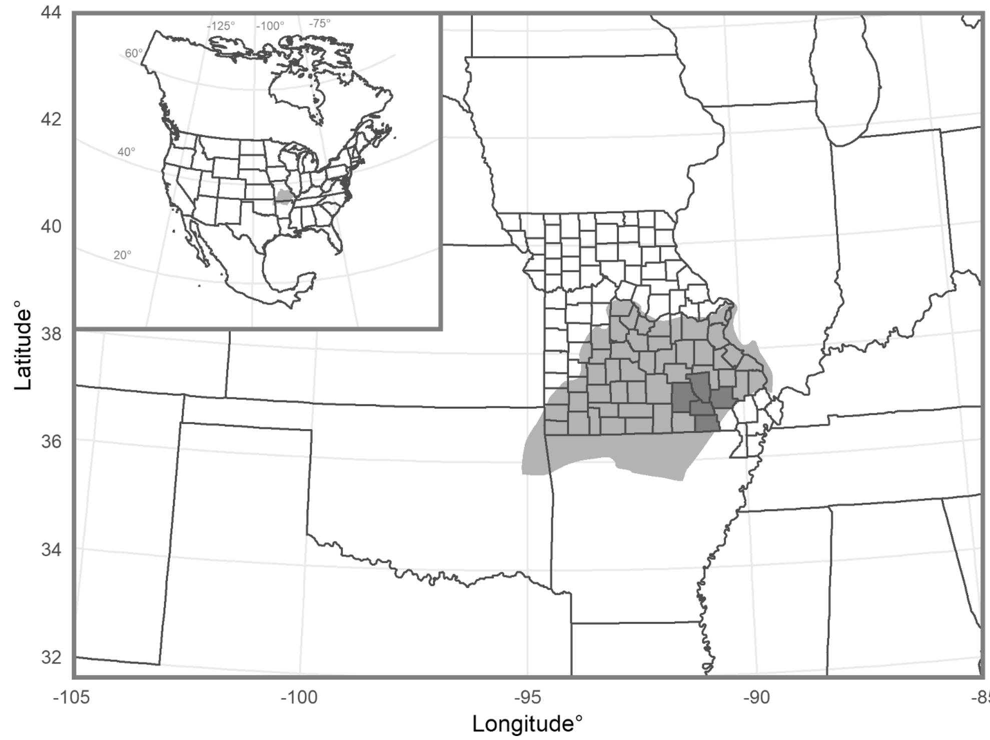


**Fig. 1.** The study included data from Carter, Reynolds, Ripley, Shannon, and Wayne counties (dark grey) of southeast Missouri within the Ozark Highlands Ecological Section (light grey).

benchmark of upper canopy attainment at age 12 after overstory removal in Illinois forests. Sander et al. (1984) used a relative height benchmark that corresponded to 80% of the height of dominant *Quercus* stump sprouts to denote *Quercus* sapling success five years after overstory removal in the Missouri Ozarks, reporting that nearly all stems that had attained this benchmark were in the upper canopy. Johnson and Rogers (1985) also used a relative height (80%) benchmark based on the expected height of *Q. rubra* sprouts 16 years after overstory removal in Wisconsin, reporting that trees that met the benchmark were generally in codominant or dominant crown positions. Loftis (1990) used a two-part benchmark that included specific height (≈ site index) and free to grow requirements 8 years after overstory removal. Spetich et al. (2002) used a benchmark of ≥ 80% of the mean height of competitors 8 years after shelterwood removal in the Boston Mountains of Arkansas. Steiner et al. (2008) used a third-decade crown class benchmark (dominant, codominant, or intermediate) for seed-origin *Quercus* (Gould et al., 2006) and an age 4 height benchmark (2 m) for sprout-origin *Quercus* (Gould et al., 2007). Brose et al. (in press) used a benchmark of upper canopy attainment at age 10. For these and similar tools, a fundamental assumption appears to be that approximating upper canopy status throughout the regeneration period is an appropriate benchmark of success.

### *1.3. The need for flexible, longitudinal evaluation methods*

Undoubtedly, one reason for the differing post-harvest benchmarks identified by researchers is related to constraints imposed by a limited number of available datasets and by the intricacies associated with them. Another reason is that understanding of the developmental patterns of individual trees that attain upper canopy status by the end of the regeneration period remains incomplete. Despite extensive research into height development, there is limited quantitative guidance for height expectations throughout the regeneration period in deciduous forests of the eastern United States. Dey et al. (2009) showed that for a given initial condition, the likelihood of upper canopy attainment varied considerably over time after shelterwood removal and was influenced by site productivity and suite of competitors. The authors highlighted the importance of a benchmark's timing, which may have as much influence on management implications as the specific requirements used.

Site index curves are commonly used to guide height development expectations. Representing both site- and species-specific longitudinal trends in average height development of eventual upper canopy trees, site index curves are seemingly well-suited to benchmark recruitment success through time in young stands. Unfortunately, applications in young stands are limited because they were developed to forecast tree height growth in the later stages of stand development. For example, among 129 site index curves compiled by Carmean et al. (1989), the average minimum applicable age was 15 years. Excluding conifers or plantations, the average minimum age was 18 years with only one-third of the curves applicable in stands < 20 years. Consequently, post-harvest benchmarks derived from site index curves must rely on extrapolation rather than an empirical basis (Loftis, 1990). Moreover, because site index represents the average height of the 'best' trees at a given time, it may be desirable to define some acceptable envelope around that average to avoid overly conservative benchmarks.

### *1.4. Objectives/research questions*

Further investigation into juvenile tree development after overstory removal is needed because of the variability in criteria previously used to assess recruitment success due to differences among ecoregions and species mixtures, and the limited quantitative data on early height development trends in many regions. To that end, this manuscript reports study results from a stem analysis project that examined early height development trends over 20 years after overstory removal in naturally regenerated, mixed stands in the Missouri Ozarks. Following the findings that upper canopy status at the end of the regeneration period is a critical measure of continued recruitment success (Ward and Stephens, 1994, Johnson et al., 2009), this study investigates the early growth patterns of trees that met this criteria. There were three objectives of this study. The first objective was to identify height development milestones indicative of successful upper canopy recruitment by the end of the regeneration period. Such milestones quantify minimum height requirements rather than an average, thereby simplifying interpretation and management applications. The second objective was to determine if the milestones varied among species and by site classes in the study region. The third objective was to examine the validity of the milestones using independent data from a nearby long-term study including individually tagged trees.

## 2. Material and methods

### 2.1. Study region

Data were collected from stands located in the Missouri Ozark counties of Carter, Reynolds, Ripley, Shannon, and Wayne (Fig. 1). The study region, within the Ozark Highlands Ecological Section (McNab et al., 2007), is an unglaciated, deeply dissected plateau primarily comprising Ordovician and Cambrian dolomites and sandstones (Kabrick et al., 2000). Average annual precipitation is 1150 mm 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 – 135°) backslopes with an average site index (*Q. velutina* [Lam.], base age 50) of 21.0 ± 1.3 m and 22.0 ± 1.1 m, respectively (McQuilkin, 1974). Mature 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 greater *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* (Mill.) are more common on exposed backslopes (Kabrick et al., 2004).

### 2.2. Data collection

All stands were located in Missouri Conservation Areas and managed by the Missouri Department of Conservation. The stands sampled for this study were harvested via clearcutting with reserves approximately twenty years prior to sampling. At the time of harvest, all live trees > 3 m in total height or > 4 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 19 to 29 years with a mean of 22 years. The purported age of each stand was confirmed by aging several stump sprouts at ground level.

Twenty stands were sampled in summer 2013. Ten stands were sampled on exposed backslopes and ten on protected backslopes. Within each stand, a single 0.05-ha circular search plot (12.6 m radius) was established around a randomly determined location. The following restrictions were placed on the location of plot centers: ≥32.72 m from stand boundaries, ≥12.6 m from obvious skid trail or landing area, ≥25.2 m from any large trees that were obvious reserves from the previous rotation.

The following species (or genera-based species groups) were targeted for sampling: *Acer* spp., *Carya* spp., *Fraxinus* spp., *Nyssa sylvatica* [Marshall], *Pinus echinata*, *Prunus serotina* [Ehr.], *Quercus* spp., *Sassafras albidum* [(Nutt.) Nees], and *Ulmus* spp. On each plot, the most central specimen from each species and across all crown classes (dominant, codominant, intermediate, suppressed) was sampled, as available, though suppressed trees were required to be ≥ 3 m tall for sampling. Codominant and dominant trees were the primary focus of this analysis and the sample sizes for each species are provided in Table 1.

Prior to felling by chainsaw, the distance and azimuth from plot center to each sample tree was recorded along with diameter at breast height (1.37 m), total height, and height to live crown base. Once the sample tree was felled, limbed and measured for felled length, a cross-section approximately 2 cm thick was removed at ground level and every 25 cm along the bole of the tree. An additional cross-section was taken at breast height.

**Table 1**
Final sample size for upper canopy stem analysis dataset collected from twenty naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks 19–29 years after harvest via clearcutting with reserves ($\leq 5\ m^2\ ha^{-1}$).

| Species | Codominant | Dominant | Total |
|---|---|---|---|
| | …# trees (exposed sites, protected sites)… | | |
| *Acer* spp. | 0,9 | 0,3 | 0,12 |
| *Carya* spp. | 5,10 | 2,4 | 7,14 |
| *Nyssa sylvatica* | 0,5 | 0,0 | 0,5 |
| *Pinus echinata* | 8,0 | 4,0 | 12,0 |
| *Prunus serotina* | 5,10 | 1,7 | 6,17 |
| *Quercus alba* | 15,16 | 7,8 | 22,24 |
| *Q. coccinea* | 14,11 | 8,8 | 22,19 |
| *Q. stellata* | 11,0 | 1,0 | 12,0 |
| *Q. velutina* + | 19,10 | 5,9 | 24,19 |
| *Sassafras albidum* | 0,5 | 0,0 | 0,5 |
| Total | 77,76 | 28,39 | 105,115 |

### 2.3. Data preparation

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 with up to 600-grit sandpaper as needed, for ring identification. Optical microscopes with up to 3× magnification were used as necessary to identify tree rings. Each cross section was aged at least twice along differing radii by two or more technicians until consensus was achieved. Because the sampling began before the 2013 growing season was completed, 2013 data were not further analyzed.

When an age transition occurred between cross sections within a given sample tree, it was assumed that the preceding year's growth ended at half the distance between the two cross-sections. For a 25 cm distance between cross-sections, this provided an estimate of annual height with a precision of ± 13 cm when only one age transition occurred between cross-sections (Husch et al., 2003), which was usually 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. Goelz and Burk (1996) noted that errors due to hidden tips in height-age data obtained via stem analysis could be problematic in some regression analyses. The ± 13 cm precision of the stem analysis data was comparable to published field estimates of standing tree heights (Larsen et al., 1987, Bragg et al., 2011) and much better than the average discrepancy between estimates of standing tree height and felled lengths for the sample trees in this study (62 cm, sd: 94 cm). Given this, it was assumed that any measurement errors in the stem analysis derived height-age data had no greater consequence than would measurement errors for field estimated standing tree heights.

### 2.4. Data analysis

All statistical analyses were completed in R statistical software version 3.4.4 (R Development Core Team, 2018).

#### 2.4.1. Identify height development milestones for upper canopy recruitment

Because the primary analytical objective was to estimate the minimum height at a given age for trees that successfully recruited into the upper canopy rather than an average height, quantile regression methods were preferred over ordinary least squares regression in this study. A quantile estimation procedure that accommodated the hierarchical grouping structure (cross-sections within trees within plots) of the data using random effects of plot and tree within plot was desired, but unavailable as this remains an emerging area of statistical research (Koenker, 2004, Geraci and Bottai, 2014). Quantile regression analyses for height-age were completed using the b-splines function (BS) from the SPLINES package (R Development Core Team, 2018) within the regression quantiles function (RQ) from the QUANTREG package (Koenker, 2017). The default options for determining the number and placement of knots for the b-splines were utilized. The result is a non-parametric description of the conditional quantile of interest. Non-parametric techniques minimize assumptions and restrictions not generated by the underlying phenomenon of interest and provide more flexibility in growth forms than parametric growth functions (Ramsay and Silverman, 2002, Takezawa, 2006), but they do not provide concise results for convenient reporting. Thus, tabular reports of the estimates produced by these analyses are provided. For convenience, simple linear regression was used to provide a linear approximation of the estimates provided in the tabular report.

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 such limitations, the 10th percentile was chosen for height development milestones, which represent the near-minima height-age development of trees that were dominant and codominant at the end of the regeneration period.

#### *2.4.2. Examine species and site differences in milestones*

It was expected that the height development milestones may vary by species and site class. Separate regressions were performed for each species-site class combination with a sample size ≥ 5 trees. Three species groups occurred exclusively on a single site class (*Acer* spp., *Sassafras albidum*, *Q. stellata*) while two other groups (*Pinus echinata*, *N. sylvatica*) occurred on both, but only in sufficient number for analyses on a single site class.

Differences in milestones among species and site classes could potentially vary with time, e.g., two species may be similar early but diverge over time. To evaluate if, and when statistical difference in estimates may occur, 95% confidence bands were constructed for each regression. Nonoverlapping confidence bands were used to visually indicate statistical differences among groups at a significance level of $\alpha \le 0.05$.

Given a search plot size of 0.05-ha (12.6 m radius), any species/crown class combination not captured in the sample was an infrequent component of the sample stands. Some relatively rare species in the sample were too few in number to provide reliable individual quantile estimates (*Acer saccharum* [Marshall], *Q. falcata* [Michx.], *Q. rubra*, *Ulmus* spp.). Thus, *A. saccharum* was combined with the more numerous *A. rubrum* [L.] (hereafter, *Acer* spp.). *Q. falcata* and *Q. rubra* were combined with *Q. velutina* (hereafter, *Q. velutina* + ). *Ulmus* spp. were excluded. Five trees proved to be large residuals from a previous rotation (heights ≥ 3 m at stand age 0) and excluded from analyses. One *Nyssa sylvatica* tree could not be analyzed and was excluded.

#### *2.4.3. Examine the validity of milestones for independent data*

An independent dataset from a nearby long-term study was used to evaluate the validity of the height development milestones. This independent dataset consisted of 7940 trees and was collected from 18 mixed stands within the Missouri Ozark counties of Carter, Reynolds, and Shannon, each with a single, randomly located 0.02-ha plot. The dataset included the following tree species: *Acer* spp., *Amelanchier arborea* [(Michx.) Fern.], *Carpinus caroliniana* [Walter], *Carya* spp., *Celtis* spp., *Cercis Canadensis* [L.], *Cornus florida* [L.], *Diospyros virginiana* [L.], *Fraxinus* spp, *Gleditsia triacanthos* [L.], *Juniperus virginiana* [L.], *Morus* spp., *Nyssa sylvatica*, *Ostrya virginana* [(Mill.) K. Koch.], *Pinus echinata*, *Platanus occidentalis* [L.], *Prunus serotina*, *Quercus* spp., *Rhamnus caroliniana* [(Walter) A. Gray], *Sassafras albidum*, and *Ulmus* spp. Similar to the stem analysis study, half of the plots were on exposed backslopes, the other on protected backslopes. These stands were also located on Missouri Conservation Areas and managed by the Missouri Department of Conservation. The stands were also harvested via clearcutting with reserves (leaving up to 5 $m^2\,ha^{-1}$, predominately *Pinus echinata*) and all stems > 3 m in total height or > 4 cm dbh were felled, with the exception of trees left as reserves (Missouri Department of Conservation, 1986). Harvesting for this study was conducted during the winter of 1995–1996. Three years after harvesting, all woody stems ≥ 1 m tall were tagged and measured. The trees were measured again at 8 years and at 16 years post-harvest. Stems > 1 m tall at year 8 were assumed present at year 3, but shorter than the 1-m threshold.

The estimated likelihood that a stem that initially lagged behind a milestone early in development but eventually ascended and met or exceeded them later in development was used to examine if the milestones identified were valid representations of minimum height requirements for recruitment success. In this analysis, if the proportion of trees that failed the milestones early (age 3 or 8) but attained them later (age 8 or 16) exceeded 10% it would suggest the milestones did not represent minimum height requirements for recruitment success. Tagged trees that died between measurement periods were categorized as failures for subsequent milestones.

The validation analysis was also conducted on a subset of the independent data restricted to those species with local life histories (stature, longevity) that readily permit upper canopy presence in mature Missouri Ozark forests (*Carya* spp., *Fraxinus* spp., *Pinus echinata*, *Platanus occidentalis*, *Quercus* spp.).

#### *2.4.4. Compare milestones to height development of lower canopy*

It became of interest to compare the milestones to the height development patterns of stems that were only able to reach the lower canopy at the end of the regeneration period (intermediate and suppressed crown classes). To do so, the average height development trajectory (across all species) for intermediate and suppressed crown classes on each site class was estimated. Those height-age analyses were completed using the b-splines function (BS) from the SPLINES package within the linear regression function (LM) from the STATS package (R Development Core Team, 2018). Again, default options for determining the number and placement of knots for the splines were utilized. This technique provided a nonparametric description of height development patterns over stand age similar to the quantile regression analyses; however, the result was an estimate of the average height at a given age rather than a specified height quantile as in the milestone analysis. For each regression, 95% confidence bands were constructed. The sample sizes for each site class-lower crown class combination by species are provided in Table 2.

**Table 2**
Final sample size for lower canopy stem analysis dataset collected from twenty naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks 19–29 years after harvest via clearcutting with reserves (≤5 $m^2ha^{-1}$).

| Species | Intermediate | Suppressed | Total |
|---|---|---|---|
| | *…# trees (exposed sites, protected sites)…* | | |
| *Acer* spp. | 3,7 | 3,7 | 6,14 |
| *Carya* spp. | 8,9 | 9,9 | 17,18 |
| *Nyssa sylvatica* | 8,7 | 8,9 | 16,16 |
| *Pinus echinata* | 6,1 | 4,0 | 10,1 |
| *Prunus serotina* | 3,5 | 3,4 | 6,9 |
| *Quercus alba* | 10,10 | 10,10 | 20,20 |
| *Q. coccinea* | 5,4 | 3,3 | 8,7 |
| *Q. stellata* | 7,2 | 7,2 | 14,4 |
| *Q. velutina+* | 7,3 | 8,4 | 15,7 |
| *Sassafras albidum* | 2,7 | 3,5 | 5,12 |
| Total | 59,55 | 58,53 | 117,108 |

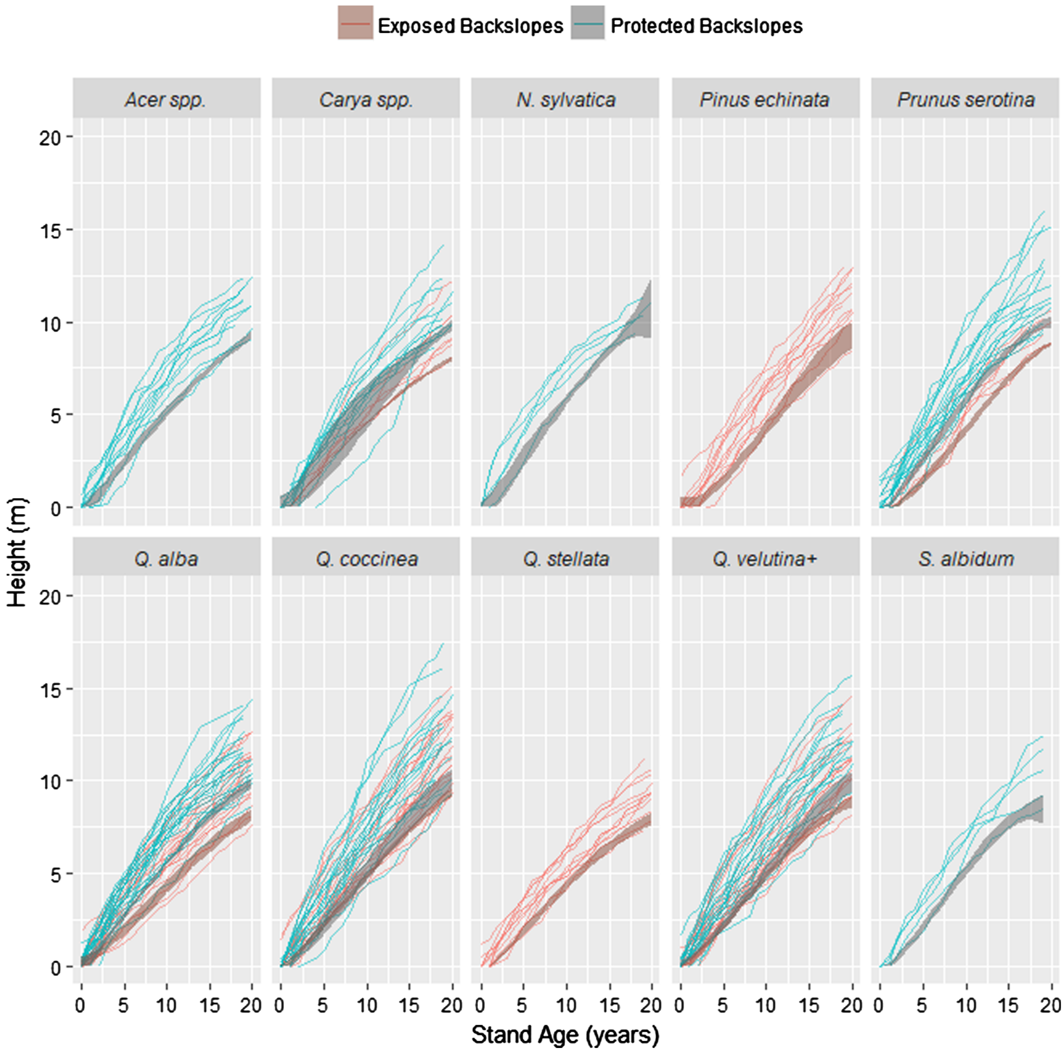


**Fig. 2.** Early height development of trees in codominant or dominant crown classes at the end of the regeneration period after overstory removal in naturally regenerated mixed stands in the Missouri Ozarks on two site classes. Lines depict individual tree development using stem analysis data. Ribbons depict 95% confidence bands for quantile regression estimates of near-minima (10th percentile) height at a given age.

## 3. Results

### *3.1. Identify height development milestones for upper canopy recruitment*

Within the naturally regenerated mixed stands of the Missouri Ozarks, codominant and dominant trees ranged in height from 7 to 17 m by the end of the regeneration period and averaged about 10 m on exposed backslopes and nearly 12 m on protected backslopes (Fig. 2). For most species, heights tended to increase approximately linearly across much of the range of stand ages, though there were exceptions. By age 10, *N. sylvatica* began exhibiting the concave curvature indicative of declining growth rates whereas *Pinus echinata*, *Prunus serotina*, and *S. albidum* tended more sigmoidal with increasing stand age. Confidence bands for the species-specific near-minima (10th percentile) estimates generally approximated the bottom of the height distribution on each site class except for rare cases where individual trees exhibited notably outlying growth patterns. *Carya* spp. on protected backslopes provides the most obvious example of an individual tree with an outlying growth pattern and difference between the near-minima and absolute minima.

### *3.2. Examine species and site differences in milestones*

There was clear statistical evidence (nonoverlapping confidence bands) of site differences in near-minima for most species that occurred on both site classes. Heights on exposed backslopes tended to be shorter than on protected backslopes (Fig. 2). Divergence in confidence bands between site classes increased with stand age. *Prunus serotina* exhibited the earliest site class differences with separation between confidence bands evident after the first growing season and reaching 1 m before age 10. For *Q. alba*, statistical differences between site class emerged after age 3 and separation between confidence bands exceeded 1 m by age 15. *Carya* spp. showed the greatest separation between confidence bands at the end of the regeneration period (> 1 m), but site class differences were not clear until early in the second decade of development. There was evidence of a difference between site classes for *Q. velutina* + by the end of the regeneration period, but the separation between confidence bands was slight. There was no evidence of site differences in near-minima for *Q. coccinea* as the confidence bands for the two site classes overlapped throughout the regeneration period.

There was remarkably little difference among species in the near-minima height trends on a given site class in this study (Fig. 3). Confidence bands for all species strongly overlapped for most of the regeneration period, providing limited evidence for statistical differences

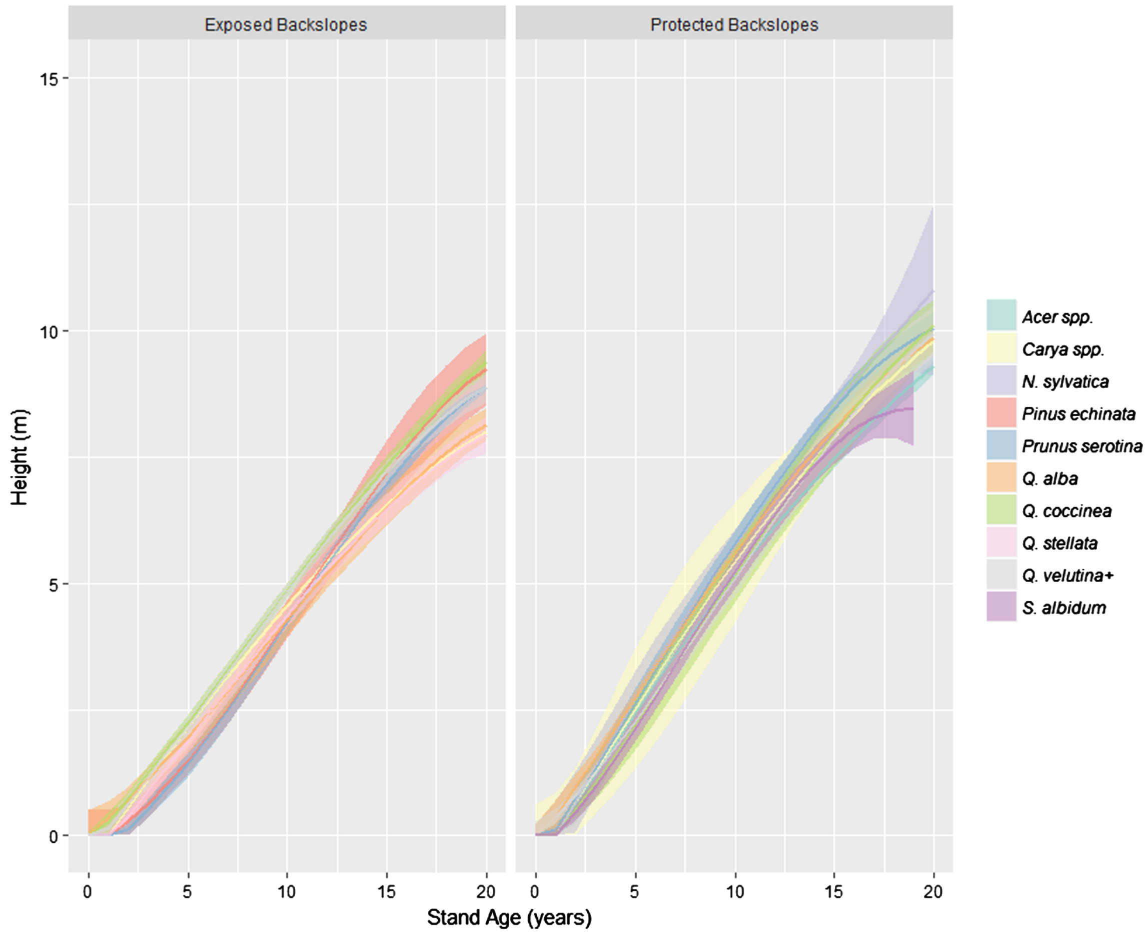


**Fig. 3.** Near-minima early height development of trees in codominant or dominant crown classes at the end of the regeneration period. Lines depict quantile regression estimates (10th percentile), ribbons depict 95% confidence bands.

between species. Some evidence for differences between species began emerging between ages 15–20 and those divergences were more prevalent on protected than exposed backslopes. The limited statistical evidence for species differences and the minor magnitude of separation where confidence bands did not overlap suggested that a more general site-specific model might efficiently describe the near-minima early height development trends of codominant and dominant trees.

A comparison of the site-specific model (all species on a given site class) to the species-specific models previously described generally supported adoption of the simpler site-specific model (Fig. 4). The species-specific confidence bands overlapped the site-specific point estimates across most ages for all species. In all nonoverlapping cases, the magnitude of separation between confidence bands was low, the largest being 37 cm for *Q. coccinea* on exposed backslopes at the end of regeneration period. This difference was less than the average discrepancy between estimates of standing tree height and felled lengths for the sample trees in this study (62 cm). Any divergences between species- and site-specific models generally increased over time, though not always. The most notable exceptions to this general trend were *Pinus echinata* and *Prunus serotina* on exposed backslopes where the degree of overlap was similar early and later in the regeneration period. The near-minima for these two species on exposed backslopes tended to be shorter than the site-specific model until about age 10, but was taller thereafter.

Because differences between the species- and site-specific models were few and minor, the more general site-specific estimates were identified as height development milestones for successful upper canopy recruitment by the end of the regeneration period. Nonparametric point estimates for these milestones are provided in Table 3 and linearly approximated ($R^2$: 0.99) by the equation $HT = -0.34 + 0.47 \times SA + 0.14 \times SC + 0.06 \times SA \times SC$, where: HT = milestone height (m), SA = stand age (yrs 1–20) and SC = site class (0 for exposed backslopes, 1 for protected backslopes.

### 3.3. Examine the validity of milestones for independent data

The application of the stem analysis derived height development milestones to independent data from a nearby long-term study with tagged individuals suggested that the milestones were indicative of minimum heights required for upper canopy attainment by the end of the regeneration period. Only 6% of trees from the independent study that failed the milestones at age 3 ascended to meet them at age 8 (Table 4) and 1% of trees that failed the milestones at age 3 ascended to meet them by age 16 (Table 5). Less than 1% of the trees that failed the milestones at age 8 ascended to meet them by age 16 (Table 6). The proportion of validation trees that met and maintained the milestones at all ages was low - only 10% of trees that met the milestones at age 3 met them again at age 16 (Table 5). A larger proportion of validation trees maintained the milestones from age 3–8 (44%, Table 4) than from age 8–16 (20%, Table 6).

The proportion of trees that failed the milestones at early ages but ascended to meet them later was also low for common overstory species in mature Missouri Ozark forests. Only 5% of trees in this subset of the validation data that failed the milestones at age 3 ascended to meet them at age 8 (Table 7). Only 1% of the subset trees that failed the milestones at age 3 ascended to meet them by age 16 (Table 8) and less than 1% that failed the milestones at age 8 met them by age 16 (Table 9). However, the proportion of trees in the mature overstory

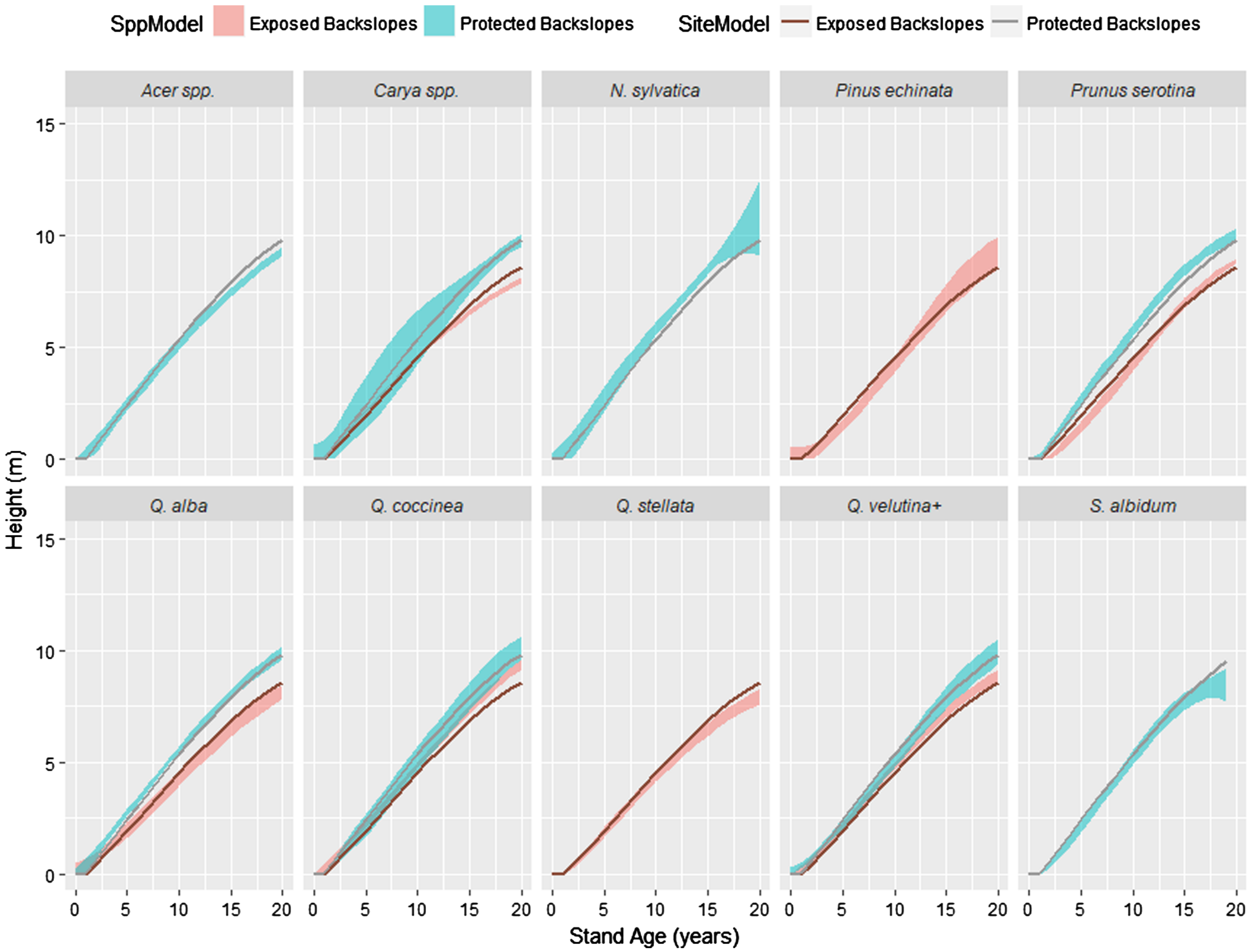


**Fig. 4.** Near-minima early height development by species and site class. Ribbons depict 95% confidence bands for quantile regression estimates (10th percentile) for species –specific models, lines depict quantile regression point estimates for models that are only site-specific (includes all species on a site class).

species subset that met and maintained the milestones at all ages was considerably higher than the full validation dataset – 27% of the subset trees that met the milestones at age 3 met them again at age 16 (Table 8). Similar to the full validation dataset, a larger proportion of the subset trees maintained the milestones from age 3–8 (59%, Table 7) than from age 8–16 (40%, Table 9).

### 3.4. Compare milestones to height development of lower canopy

The average height development patterns for trees that ultimately occupied intermediate or suppressed canopy positions tended to meet the milestones at young ages but fall increasingly short of those milestones over time (Fig. 5). The average height for ultimately suppressed trees began to fall short of the milestones by ages 6–7 on both site classes. By age 20, the average suppressed stem was approximately 2 m below the milestones. The average height for trees that were ultimately in an intermediate canopy position met the milestones for most of the regeneration period. The average intermediate stem fell below the milestones by age 16–17 on protected backslopes. The average height development pattern of intermediate stems was most similar to the milestones on exposed backslopes, only beginning to fall short by age 19.

**Table 3**

Height development milestones of recruitment success, trees that are shorter than the milestones at a given stand age are not likely to become canopy dominant or codominant trees by the end of the regeneration period. 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. A simple linear approximation ($R^2$: 0.99) can be obtained via $HT = -0.34 + 0.47 \times SA + 0.14 \times SC + 0.06 \times SA \times SC$, where: HT = milestone height (m), SA = stand age (yrs 1–20) and SC = site class (0 for exposed backslopes, 1 for protected backslopes.

| Site Class | Stand Age (years) | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| | Total Height (m) | | | | | | | | | | | | | | | | | | | |
| Exposed Backslopes | 0 | 0.5 | 0.9 | 1.4 | 1.9 | 2.5 | 3.0 | 3.5 | 4.0 | 4.5 | 5.0 | 5.5 | 6.0 | 6.4 | 6.9 | 7.3 | 7.7 | 8.0 | 8.3 | 8.6 |
| Protected Backslopes | 0 | 0.6 | 1.2 | 1.8 | 2.4 | 3.0 | 3.6 | 4.2 | 4.8 | 5.4 | 5.9 | 6.4 | 7.0 | 7.4 | 7.9 | 8.4 | 8.8 | 9.2 | 9.5 | 9.8 |

**Table 4**
Contingency table of height development milestone validation results from ages 3 to 8 after harvest via clearcutting with reserves (≤5 $m^2ha^{-1}$) using an independent dataset of 7940 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 3 | Age 8 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 4,347 (94%) | 300 (6%) | 4647 |
| ≥ Milestones | 1840 (56%) | 1453 (44%) | 3293 |
| Total | 6187 | 1753 | 7940 |

**Table 5**
Contingency table of height development milestone validation results from ages 3 to 16 after harvest via clearcutting with reserves (≤5 $m^2ha^{-1}$) using an independent dataset of 7,940 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 3 | Age 16 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 4619 (99%) | 28 (1%) | 4647 |
| ≥ Milestones | 2965 (90%) | 328 (10%) | 3293 |
| Total | 7584 | 356 | 7940 |

**Table 6**
Contingency table of height development milestone validation results from ages 8 to 16 after harvest via clearcutting with reserves (≤5 $m^2$ $ha^{-1}$) using an independent dataset of 7,940 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 8 | Age 16 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 6178 (99%) | 9 (< 1%) | 6187 |
| ≥ Milestones | 1406 (80%) | 347 (20%) | 1753 |
| Total | 7584 | 356 | 7940 |

**Table 7**
Contingency table of height development milestone validation results from ages 3 to 8 after harvest via clearcutting with reserves (≤5 $m^2$ $ha^{-1}$) using an independent dataset of 2,718 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Only species with local life histories (stature, longevity) enabling common upper canopy presence in mature Missouri Ozark forests (*Carya* spp., *Fraxinus* spp., *Pinus echinata*, *Platanus occidentalis*, *Quercus* spp.) are included. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 3 | Age 8 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 1701 (95%) | 94 (5%) | 1795 |
| ≥ Milestones | 377 (41%) | 546 (59%) | 923 |
| Total | 2078 | 640 | 2718 |

**Table 8**
Contingency table of height development milestone validation results from ages 3 to 16 after harvest via clearcutting with reserves (≤5 $m^2$ $ha^{-1}$) using an independent dataset of 2718 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Only species with local life histories (stature, longevity) enabling common upper canopy presence in mature Missouri Ozark forests *(Carya* spp., *Fraxinus* spp., *Pinus echinata*, *Platanus occidentalis*, *Quercus* spp.) are included. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 3 | Age 16 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 1779 (99%) | 16 (1%) | 1795 |
| ≥ Milestones | 678 (73%) | 245 (27%) | 923 |
| Total | 2457 | 261 | 2718 |

**Table 9**
Contingency table of height development milestone validation results from ages 8 to 16 after harvest via clearcutting with reserves (≤5 $m^2$ $ha^{-1}$) using an independent dataset of 2718 tagged trees from a nearby long-term study encompassing 18 naturally regenerated mixed stands on exposed or protected backslopes in the Missouri Ozarks. Only species with local life histories (stature, longevity) enabling common upper canopy presence in mature Missouri Ozark forests (*Carya* spp., *Fraxinus* spp., *Pinus echinata*, *Platanus occidentalis*, *Quercus* spp.) are included. Trees with heights < milestones for their respective site class at a given age failed the milestones, whereas those with heights ≥ milestones met them. Parenthetical values indicate row proportions.

| Age 8 | Age 16 | | Total |
|---|---|---|---|
| | < Milestones | ≥ Milestones | |
| < Milestones | 2073 (99%) | 5 (< 1%) | 2078 |
| ≥ Milestones | 384 (60%) | 256 (40%) | 640 |
| Total | 2457 | 261 | 2718 |

## 4. Discussion

### 4.1. Importance of identifying development milestones

This study quantified height development milestones from trees that successfully recruited into the upper canopy recruitment by the end of the regeneration period. Applying this information can increase the likelihood of desirable regeneration outcomes in two ways. First, the milestones can help researchers develop or improve pre-harvest evaluation models of regeneration potential by providing empirically derived benchmarks of post-harvest height requirements for plausible recruitment success. Second, because the milestones are longitudinal, they can assist post-harvest monitoring efforts identify when additional silvicultural efforts are needed to improve or maintain recruitment of desirables. These milestones can be applied in the field by comparing measured heights of subject trees to the corresponding milestone values for stands of the same age and site class. Trees that have fallen below the milestones have little precedent for successful upper canopy recruitment. Silvicultural investments on such trees could be less efficient than on trees still above the milestones, which may have a greater chance of continuing to meet future milestones following release treatments based on their greater precedent for success. The fate of borderline trees is an open question, with any chance of successful recruitment likely dictated by chance disturbances or silvicultural interventions that provide release from nearby competing stems.

In contrast to some techniques for evaluating canopy recruitment success, the milestones do not target the average height at a given age of eventual codominants and dominants. Instead, they approximate

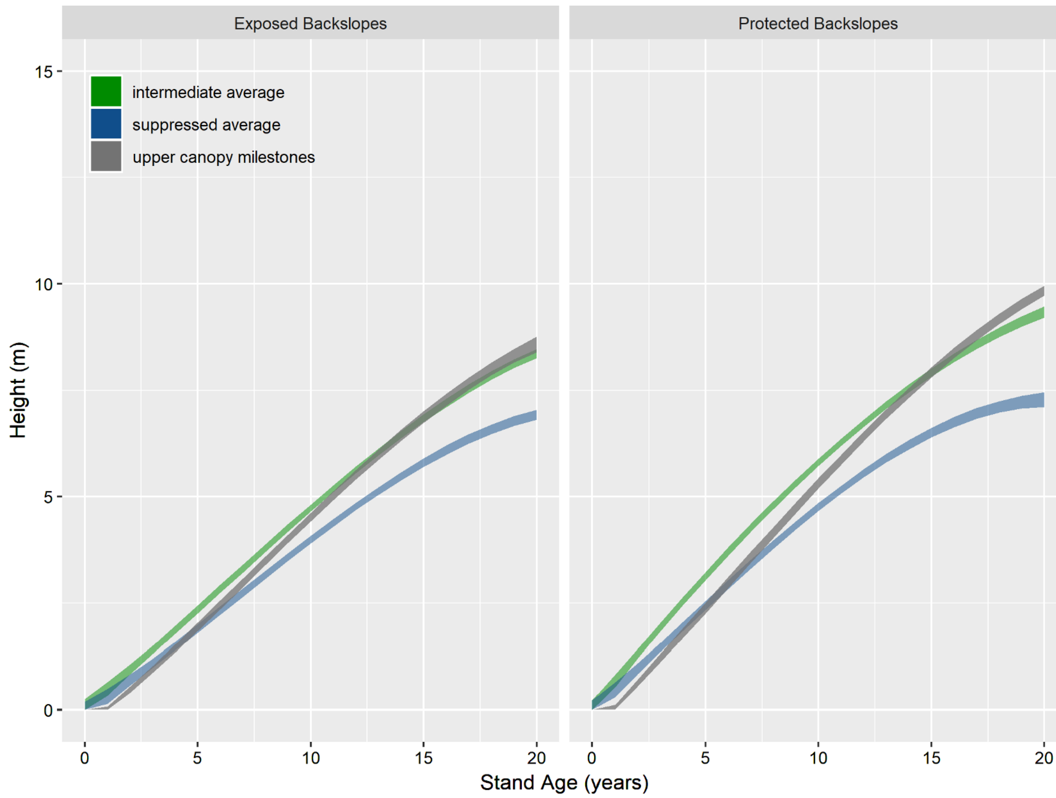


**Fig. 5.** Comparing upper canopy milestones (grey ribbons depict 95% confidence bands) to average height development for eventual intermediate and suppressed trees (green and blue ribbons depict 95% confidence bands) for two site classes in the Missouri Ozarks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

minimum height-age trends, providing a threshold value for binary assessments (i.e., success or failure). This threshold separates trees that are ‘on track’ for successful upper canopy recruitment from those that are clearly not. Thus, a key feature is an ability to distinguish trees that have precedent for success from those that do not. No more than 1% of validation trees deemed failures early became successful later. This indicates the milestones are an effective representation of longitudinal height development thresholds for eventual canopy recruitment. However, a consequence of this minimum threshold approach is that many trees deemed successful at an early age may ultimately succumb to competition, random events, and other factors over the course of stand development. Still, ‘on track’ trees are identified as the population likely to have the greatest management potential since there is greater precedent for their success. The larger this population, the more opportunities to exert meaningful influence on stand composition and growth through tending treatments.

### 4.2. Implications of species differences in milestones

The similarity in near-minima among species was somewhat unexpected, though Zenner et al. (2012) reported neighboring canopy dominants usually were within 1–2 m of total height during the regeneration period in Pennsylvania clearcuts. That the magnitude of differences in this study, when present, was lower than observed measurement errors for standing tree heights suggests that the practical, if not ecological, consequences of those differences are limited. The species included in this study are known to vary in shade tolerance, some widely (Burns and Honkala, 1990). A nearby study found significant differences in sapling height growth rates under varying levels of overstory density for many of the species in this study (Vickers et al., 2014). The milestones presented here may reflect a vertical threshold of resource (light) availability within the cumulative leaf area profile of a stand below which growth is limited by shading (Ellsworth and Reich, 1993, Lewis et al., 2000, Yoda, 1974). In this case, trees shorter than the milestones may experience intense side and low shade from neighboring stems (Oliver and Larson, 1996, *ch.*3). The similarity in near-minima among species may also be a temporary feature related to the point in stand development analyzed.

While *Quercus* dominated the sample, which is typical of forests in the Missouri Ozarks, the pathways to recruitment success for both major and minor associates were virtually indistinguishable from *Quercus*. This may be a reflection of *Quercus*’ (1) local ubiquity (Kabrick et al., 2004), (2) locally superior maximum growth rates (Vickers et al., 2014), and (3) local role as a successional climax (Gustafson et al., 2000) all pressuring other species to grow at a similar rate to avoid competitive exclusion in young stands. The milestones presented in this study may not be representative of early stand development trends in other regions. Oliver (1978) and Hibbs (1983) described *Q. rubra* initially lagging behind both *Acer rubrum* and *Betula lenta* [L.] before eventually surpassing them to become dominant in even-aged stands in New England. This strategy of delayed ascent into the upper canopy has been coined “latent dominance” (O’Hara, 1986) and some evidence of that dynamic has been reported for *Quercus* in studies from multiple locales (Clatterbuck and Hodges, 1988, Johnson and Krinard, 1988; Zenner et al., 2012; Steiner et al., 2018).

Latent dominance and other relative changes in mean or maximum height that may occur among dominant trees may not necessarily be reflected by the near-minima examined in this study. Among the species included, only *Pinus echinata* and *Prunus serotina* on exposed backslopes exhibited limited signs of this behavior and only for a limited period (< 10 years). The near-minima for *Pinus echinata* on exposed backslopes tended to be slightly lower than other species initially, but later, became slightly taller. Kabrick et al. (2015) reported that underplanted *Pinus echinata* in the Missouri Ozarks were shorter than competitors 5 years after planting due to a low first-year growth rate while maintaining a comparable growth rate after year 1.

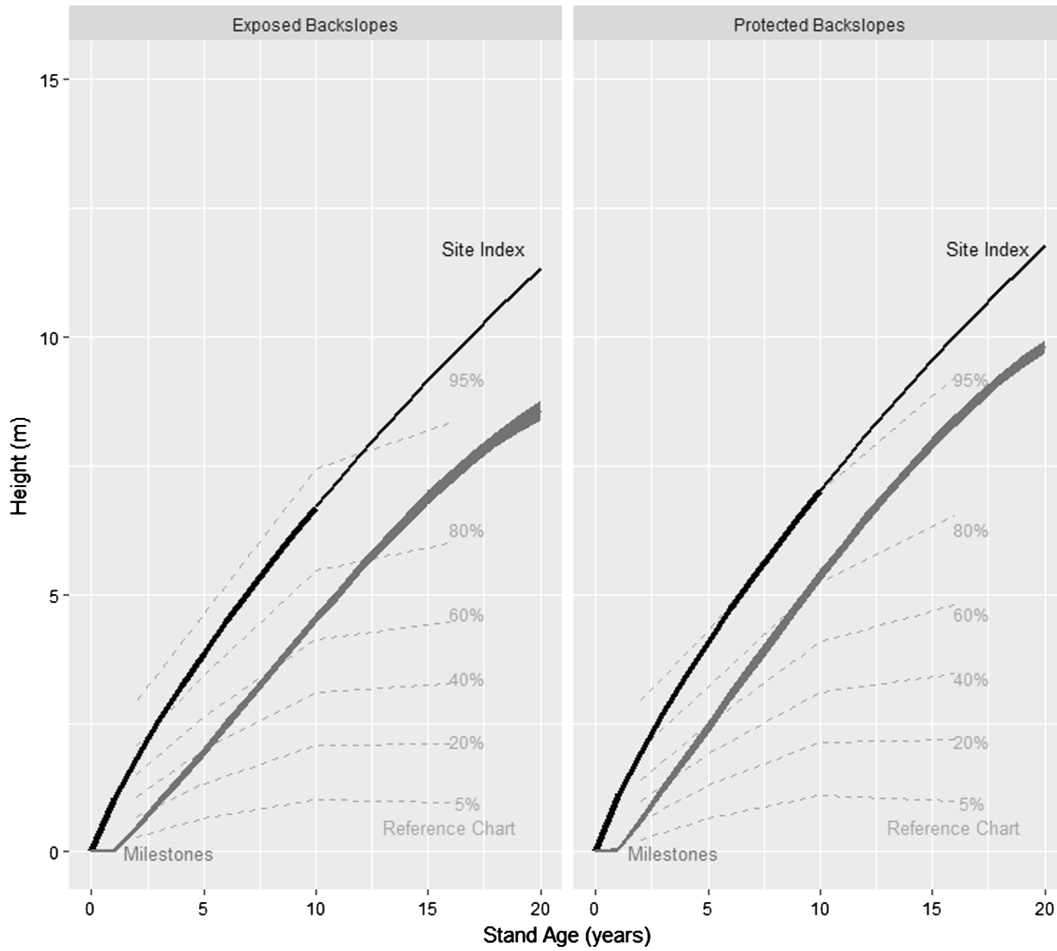


**Fig. 6.** Early height development milestones (grey ribbons depict 95% confidence bands) for eventual upper canopy attainment after overstory removal for two site classes in the Missouri Ozarks. Black lines depict average site index for the two site classes, thicker portions depict ages requiring extrapolation (< 10 years). Broken grey lines depict various distribution quantiles from site-class based height-age reference charts for all species in mixed stands on exposed or protected backslopes after harvest via clearcutting with reserves in the Missouri Ozarks (adapted from Vickers et al. 2017).

### 4.3. Implications of analytical techniques

There are developmental differences between individual trees and stands (Oliver and Larson, 1996). These differences are likely magnified in mixed stands (Kelty et al., 1992). Measures of success based on stand development patterns may differ from those based on tree development patterns. Both approaches have been used to assess recruitment in deciduous forests of the eastern United States. For example, Spetich et al. (2002) used a stand-based benchmark at a given stand age, i.e., 80% of the mean height of dominant competitors. Sander et al. (1984) used a tree-based benchmark at a given stand age, i.e., 80% of a dominant oak sprout height. The tree-based benchmark that Sander et al. (1984) seemingly intuited equates to a height of 2.7 m at age 5. Gould et al. (2006) postulated that this benchmark may be too restrictive. Several site index studies have shown that plot/stand based metrics of dominant height tend to be taller at earlier ages than those based on individual tree growth (Burkhart and Tomé, 2012, Raulier et al., 2003, Weiskittel et al., 2011). If methodological differences produce drastically different interpretations of success, the practical implications could be considerable and result in misallocation of silvicultural resources. The longitudinal milestones identified via stem analysis in this study (Table 3) generally align with the 2.7 m benchmark used by Sander et al. (1984) for age 5 point estimates. At age 5, the milestones are somewhat shorter (1.9–2.4 m), but by age 6 they are strikingly similar (2.5–3 m). Ideally, criteria for success would provide longitudinal inference so that silvicultural action may be taken when deemed appropriate. For example, Dey et al. (2009) demonstrated variation in the probability that a given seedling would attain canopy dominance over the course of early stand development, suggesting the efficacy of silviculture can vary with timing.

Loftis (1990) incorporated both stand and tree criteria into a two-part benchmark, i.e., free to grow and ≥ extrapolated site index, thus combining individual growth and environment to some degree. That approach is robust, as failure to recruit can be the result of either inferior subject growth or unfortunate location near fast-growing neighbors. As shown in Fig. 6, the milestones identified in this study are shorter than those provided by a local site index curve (McQuilkin, 1974 via Carmean et al., 1989). This was predictable as site index represents the average height of eventual upper canopy trees at a given time, whereas the milestones represent near-minima heights.

Due to inherent shortcomings with stem analysis data, the prior stature of the trees sampled in this study relative to their neighbors cannot be comprehensively examined. However, by using the milestones in conjunction with local reference charts for height development (Vickers et al., 2017), some inference into how the milestone heights compare with the probable height distributions for neighboring trees through time was attained. The reference chart lines in Fig. 6 depict height distribution quantiles at a given age for mixed stands (all species) on similar sites in the Missouri Ozarks. The reference charts show that benchmarks premised on relative height of competitors (e.g. 80%, Spetich et al., 2002), which is generally analogous to the corresponding 80% reference chart lines in Fig. 6, may be more stringent than the milestones when stand age is < 10–12 (depending on site class) but less stringent thereafter. When the same 80% reference chart line is compared to a site index based benchmark, it is increasingly less stringent through time, and considerably less so on protected backslopes compared to exposed. This suggests that relative height based evaluations aiming to identify trees likely to be part of the future dominant canopy may need to employ dynamic relative height values that vary based on age and site class. Further consideration into the most appropriate criteria for success is warranted.

### 4.4. Implications for stand development and management

Failing the milestones at an early age indicates that a tree is unlikely to attain the upper canopy by the end of the regeneration period. Canopy recruitment is often an exclusionary process and the probability of an individual maintaining or increasing crown class through time is lower for trees occupying lower crown classes (Ward and Stephens, 1994, Oliver and Larson, 1996). Note that reaching these milestones at an early age does not guarantee *continued* success recruiting into the upper canopy. The critical challenge for a given tree is to maintain sufficient height growth to remain above the milestones as the stand continues to develop. The validation results indicate 27% of trees from common overstory species were able to maintain the milestones from age 3 to 16.

The reference charts indicate that attaining the milestones is likely common early in the regeneration period but increasingly difficult as stands become older. The validation data showed a similar result with 59% of trees from common overstory species maintaining the milestones from ages 3–8, but only 40% able to maintain the milestones from ages 8–16. This was further evidenced by the failure of stems that ultimately occupied suppressed canopy positions to maintain heights above the milestones after about age 7, despite meeting them at young ages. The decreasing probability of maintaining the milestones in the latter half of the first decade following overstory removal likely follows the onset of canopy closure in the regenerating cohort, which has been reported at similar stand ages elsewhere (Zenner et al., 2012).

The higher milestones and earlier shortcoming of those milestones by ultimately intermediate and suppressed stems on protected backslopes suggests that vertical stratification and subsequent self-thinning occurs more rapidly on the higher quality site class, consistent with the commonly observed Sukachev effect reported by others (e.g., Leary, 1997). On exposed backslopes, a stem's categorization into an intermediate canopy position at the end of the regeneration period appeared to be as much a result of their immediate surroundings as their stature. Given that ultimately suppressed trees were closer to the milestones earlier it appears that the more closely a tree approximates the threshold, the less likely it would be to end up a canopy dominant. However, site index studies have reported that eventual upper canopy trees are not necessarily among the very tallest trees early in development process (Dahms, 1963, Raulier et al., 2003).

### 4.5. Future work

Additional research into the factors that influence the probability of continued success for those stems that attain these milestones early in development is warranted. Potential refinements could include exploring the efficacy of incorporating neighborhood characteristics for gaining additional insight into recruitment dynamics and probabilities for success. Logical extensions include identification of development milestones for additional regions, species, and silvicultural regimes.

## 5. Conclusions

Height development milestones for recruitment “success” were identified from the early growth patterns exhibited by trees ultimately in codominant and dominant crown classes 20 years after overstory removal in naturally regenerated, mixed stands in the Missouri Ozarks. These milestones may improve post-harvest evaluations of individual trees during the regeneration period. The remarkable similarity in 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. Independent data suggest the milestones effectively reflect heights required for upper canopy attainment by the end of the regeneration period. Successful canopy recruitment without first meeting the height milestones is highly unlikely.

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