



Predicting the height growth of oak species (*Quercus*) reproduction over a 23-year period following clearcutting



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ARTICLE INFO

Article history:

Received 16 July 2015

Received in revised form 31 December 2015

Accepted 5 January 2016

Available online 18 January 2016

Keywords:

Competition

Long-term data

Stand development

Even-aged

Central hardwood region

ABSTRACT

We resampled plots from a repeated measures study implemented on the Hoosier National Forest (HNF) in southern Indiana in 1988 to investigate the influence of site and seedling physical attributes on height growth and establishment success of oak species (*Quercus* spp.) reproduction in stands regenerated by the clearcut method. Before harvest, an array of physical attributes were documented for individual stems of advance reproduction. Across all surveys, the same characteristics were remeasured in years 6, 12, and 23 for all reproduction types (advance reproduction, stump sprouts, and new seedlings). In order to characterize topo-edaphic conditions, soil samples were collected and analyzed in 2011, and slope aspect, slope percent, and slope position were measured in the field. Random Forest (RF) analysis was used to determine the best physical and environmental predictors of height growth for oak species and their competitors in developing stands. Overall, advance reproduction of oak species fared poorly following harvests. Sprout-origin oak stems proved stronger competitors in developing stands, although their abundance relative to competing species was quite low. Advance and sprout origin maple (*Acer* spp.) stems, along with new seedlings of black cherry (*Prunus serotina* Ehrh.) and yellow-poplar (*Liriodendron tulipifera* L.), quickly overtopped oak advance reproduction and established dominance in the developing canopy. The height of stems during prior sampling periods was the best overall predictor of stem height in subsequent sampling periods. Species was also an important predictor of stem height. Comparatively, environmental variables were poor predictors of height growth of individual stems throughout the study, although more mesic aspects, greater cation exchange capacity, and greater soil magnesium saturation were associated with greater height of non-sprout origin stems from species groups other than oak or hickory in year 6. Our results suggest that overstory removal has driven stand demographics towards species favored by infrequent large-scale disturbance events such as clearcutting. Without post-harvest treatments to control competitors, oak regeneration on more mesic sites is unlikely to recruit into developing stands.

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1. Introduction

During the late 20th century, silvicultural clearcutting was used extensively across the hardwood forests of the eastern United States (Roach and Gingrich, 1968; Sander and Clark, 1971; Smith, 1994; Walker, 1999). A major goal of this management technique was to regenerate new stands of shade-intolerant and mid-tolerant species, typically aspen (*Populus* spp.) and oak (*Quercus*

spp.) species, respectively. The open conditions created by clearcutting were thought to favor the establishment and persistence of oak reproduction over shade-tolerant competitors because oak reproduction rarely persists or grows successfully in the understory of mature hardwood forests due to shading from overstory and subcanopy cover (Dey, 2002). Furthermore, clearcutting was favored because it was considered economically advantageous due to high yields and ease of implementation (Clark and Watt, 1971; Sander and Clark, 1971).

Subsequent research has shown that the past widespread use of silvicultural clearcutting failed to perpetuate oak dominance,

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especially on productive sites (George and Fischer, 1991; Jenkins and Parker, 1998). This is cause for concern considering the economic and ecological importance of oak species within the Central Hardwood Region (CHR). For example, oak species comprise 28% of all growing stock in Indiana and are considered the most important timber species in the state (Bratkovich et al., 2007). In recent years, the desire to maintain oak ecosystems has intensified because oak is recognized as indispensable to addressing non-timber management objectives including maintaining understory plant diversity, sustaining wildlife populations, and providing habitat and food for neotropical migratory birds (Ellison et al., 2005; McShea et al., 2007; Groninger and Long, 2008).

Researchers have hypothesized that the success of oak species in post-harvest, even-aged stands largely depends on the abundance of advance reproduction that accumulates in the understory prior to harvest, as well as sprouts from stumps of harvested overstory trees (Sander and Graney, 1992; Dey, 2002; Weigel and Peng, 2002). The success of this advance reproduction may depend on the height and diameter of these stems prior to release (Belli et al., 1999), which has been related to the potential of the oak root systems to support vigorous growth after release and allow oak stems to successfully compete with early-seral species (Sander, 1971; Sander and Graney, 1992; Brose et al., 2012).

Research has also shown that upland oak species are better able to establish and persist on less productive sites because they are better adapted to more nutrient-poor or xeric site conditions than their primary competitors (Larsen and Johnson, 1998; Kabrick et al., 2008, 2014). Under such conditions, oak species are afforded a competitive advantage due to the rapid development of a large taproot, the ability to physiologically function under high water stress, flexibility in maintaining high root:shoot ratios through recurrent shoot dieback, and large genetic variability in drought tolerance within species (Abrams, 1990; Pallardy and Rhoads, 1993; Parker and Dey, 2008; Johnson et al., 2009). Therefore, site quality, in part, determines the abundance of advance oak reproduction that exists prior to harvest, with a greater abundance of oak species reproduction accumulating as site quality decreases (Kabrick et al., 2014).

To examine the competitive relationships between oak and other species, chronosequence studies have been widely used to represent different stages of post-harvest stand development (Hilt, 1985; Jenkins and Parker, 1998; Brashears et al., 2004; Morrissey et al., 2008, 2010). Generally, the substitution of space for time in chronosequence studies allows the generation of hypotheses related to long-term vegetation dynamics (Bakker et al., 1996), but actually testing these hypotheses depends upon long-term data (Pickett, 1989). In the case of oak species establishment, long-term data that tracks the fate of individual stems of advance reproduction and stump sprouts under a range of site conditions are critical to testing hypotheses related to the post-harvest establishment and survival of oak species under different site conditions. In controlled experiments, the physical attributes of individual stems have been shown to influence stem growth and survival under different light regimes (Dey and Parker, 1997). Understanding how growth varies through time in response to competition and environmental conditions provides valuable insight into the optimal timing of post-harvest treatments to release oak stems in developing stands. However, while studies have examined the effects of landtype on regeneration dynamics (Kabrick et al., 2008), and how physical characteristics of underplanted seedlings influence survival (Dey et al., 2009), we found no long-term studies that employed repeated measures to investigate the influence of both seedling attributes and the physical environment on height growth of multiple types of natural reproduction in post-harvest stands.

In 1988, a long-term, repeated measure study was implemented across six hardwood forest sites on the Hoosier National Forest (HNF) in southern Indiana to examine the competitive ability and development of individual stems of oak and competing species after clearcut harvesting. During a 23-year sampling period (1988–2011), morphological/physical attributes of advance reproduction were measured across six study sites. We also collected additional measurements of all stump sprouts and new seedlings, as well as a suite of physiographic and edaphic variables. Based upon these examinations, we address three primary questions and associated hypotheses in this study:

1. How well does advance reproduction of oak species compete against other species through time during early stages of stand development? We hypothesize that while advance reproduction of oak species will remain a component of developing stands, its relative density will decrease through time due to competition with other species.
2. How well do pre-harvest physical attributes of advance reproduction indicate the dominance of individual stems in post-harvest stands? We hypothesize that for any resample (years 6, 12, and 23), height and root collar diameter during the previous sample will be the strongest predictor of oak reproduction height regardless of origin type.
3. How well do site conditions predict the growth of advance reproduction in post-harvest stands? We hypothesize that while secondary to the physical characteristics of seedlings, environmental variables associated with low water and nutrient availability will be significant predictors of oak reproduction height during stand development. While poor site conditions reduce the growth of all tree species, including oaks, a greater reduction in the growth of mesophytic species results in reduced competition for oak species.

2. Methods

2.1. Study sites

Our six study sites were located within two adjoining natural regions in southern Indiana; the Highland Rim Natural Region and Shawnee Hills Natural Region (Homoya et al., 1985; Table 1). Both natural regions are unglaciated with terrain that varies from steep slopes and narrow ridges in the Highland Rim to broad ridgetops in the Shawnee Hills. Soils in both regions are acid silt loams derived from sandstone, siltstone, and loess. Uplands are dominated by oak species including chestnut oak (*Quercus prinus* L.) in the Highland Rim and black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), and scarlet oak (*Q. coccinea* Muenchh.) in the Shawnee Hills. Hickory species (*Carya*) are present as a secondary canopy component in association with oak species. Mesic ravines and slopes harbor species such as American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Q. rubra* L.), sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), and black walnut (*Juglans nigra* L.).

2.2. Plot establishment

In 1988, six mature oak-hickory stands ranging in size from 4.5 to 12.1 ha were harvested on the HNF (Table 1). All stands were clearcut for merchantable timber between the months of April and August. After removal of merchantable timber, all remaining trees ≥ 5.1 cm dbh (diameter at breast height) were cut and left on-site.; only trees < 5.1 cm remained standing on each site.

Prior to harvest, overstory stand data were collected from sixty-one 809 m² circular plots across the six stands. Between April 1 and June 22, 1988, six to 14 permanent overstory plots were

Table 1

Location and site descriptions of six study sites on the Hoosier National Forest in southern Indiana.

Site	Location lat/long (N/ W)	Size (ha)	# of plots	Topography ^a	Parent materials ^a	Soils ^a	Series	Soil classification	Basal area ^b (m ² ha ⁻¹)	Dominant overstory species ^c
1	38.9984153 –86.1810926	12.1	12	Dissected uplands with steep slopes	Siltstone, sandstone, shale	Acid silt loams	Brownstown-Channery silt loam and Gnowbone silt loam	Typic Dystrudepts and Typic Hapludults	27.3 ± 1.3	Chestnut oak, white oak, black oak
2	38.6208790 –86.8039782	7.6	10	Broad ridgetops and flats	Sandstone, loess	Acid silt loams	Wellston-Tipsaw- Adyeville complex	Ultic Hapludalfs	23.5 ± 2.3	Chestnut oak, white oak, black oak
3	38.6503353 –86.6736604	8.1	10	Broad ridgetops and flats	Sandstone, loess	Acid silt loams	Apalona-Zanesville silt loams	Oxyaquic Fragiudalfs	22.0 ± 0.9	Sugar maple, hickory spp., black oak, white oak
4	38.4774194 86.4103183	7.6	10	Rugged hills	Sandstone, limestone	Silt loams	Wellston-Adyeville-Ebal complex	Ultic Hapludalfs	15.7 ± 0.8	Hickory spp., white oak, black oak
5	38.4774194 –86.4103183	4.5	6	Rugged hills	Sandstone, limestone	Silt loams	Wellston-Adyeville-Ebal complex	Ultic Hapludalfs	16.0 ± 2.0	Yellow-poplar, maple spp., hickory spp., black oak
6	38.2292506 –86.5615854	9.3	7	Broad ridgetops and flats	Sandstone, loess	Acid silt loams	Wellston silt loam	Ultic Hapludalfs	22.7 ± 1.6	White oak, yellow- poplar, hickory spp.

^a From Homoya et al. (1985).^b Preharvest total across all species; mean ± 1 standard error.^c Dominant species, in order, based upon mean stand basal area (m² ha⁻¹) from Swaim (2013).

located and sampled in each stand (Table 2) using a stratified random design based upon topographic position. Plots were situated within each stand to encompass as many aspect-slope combinations as possible (Table 2) and were positioned a minimum of 12.2 m from the edge of the clearcut in order to avoid any edge effects from surrounding mature forest. During the summer of 2011, we resampled 55 of the original 61 plots. Two plots in Stand 1 were never harvested and therefore were not resampled in 2011. Four plots in Stand 6 could not be relocated.

Within each 809 m² overstory plot, three 16.2 m² circular subplots were established in 1988, prior to harvest, to assess reproduction. The 809 m² overstory plot was divided into thirds using a randomly chosen azimuth to locate the first dividing line. One hundred twenty degrees were added to this azimuth to locate the second line, and another 120 degrees added to locate the third line. Within each third, a permanent 16.2 m² circular plot was randomly located by adding a random number from between 1 and 120 to the azimuth of the dividing line. The 16.2 m² subplots were not allowed to overlap, therefore they were spaced at least 4.3 m

apart. Subplots were also spaced so they were at least 2.1 m from both the center and the outside edge of the main plot.

2.3. Plot sampling

All trees ≥4.1 cm dbh were measured by species in each 809 m² overstory plot during the 1988 and 2011 surveys. In 2011, we also collected replicate soil samples from each plot. A total of four samples per plot were collected from the top 10 cm of the A-horizon 10 m from plot center in each cardinal direction. In each plot, the samples were pooled for analysis. Additional site variables measured included aspect, percent slope, slope position, and site index of each plot (Table 3).

Within each 16.2 m² subplot during the 1988, 1994, 2000, and 2011 surveys, all reproduction was tallied by species into 0.3 m height classes with stems >2.4 m tallied into a single class. A representative sample of stems <3.8 cm dbh were selected for detailed measurements and mapped by azimuth and distance from the subplot center stake. Measurements taken prior to harvest in 1988 (year 0) on advance reproduction stems were form, ground diameter class, total height, dbh, and number of live stems (see Table 3 for detailed descriptions of measurements). The same individual advance reproduction stems were remeasured in 1994 (year 6), 2000 (year 12), and 2011 (year 23). New seedlings and post-harvest stump sprouts were mapped and measured beginning in year 6. Post-harvest measurements for all permanent stems included origin (advance reproduction vs. stump sprout vs. post-harvest seedling), form, total height, dbh, number of live stems, and crown class. When multiple stems were growing from a single root system, only the tallest stem was selected for measurements. Harvest induced damage to advance reproduction stems was documented and advance reproduction was reclassified into two origin classes: (1) undamaged during harvest or (2) damaged (cut or broken) and successfully respouted following harvest (see Table 3 for a full description of origins).

Table 2

Number sampled, aspect-slope position classes, and site index ranges of plots resampled in 2011 on the Hoosier National Forest.

Stand	No. plots sampled	Aspect-slope position of plots ^a	Site index range ^b
1	12	1 SL, 2 SM, 1 WM, 1 NM, 1 EL, 2 EM, 4 EU	41–80, chestnut oak
2	10	1 SM, 1 WL, 3 WM, 1 WU, 1 NM, 2 NU, 1 EM	49–68, chestnut oak
3	10	1 SU, 3 WL, 3 WM, 3 WU	45–70, black oak
4	10	2 SL, 3 SM, 2 SU, 1 WU, 1 NU, 1 EU	67–100, black oak
5	6	1 SL, 2 SM, 2 NL, 1 NM	97, black oak
6	7	2 NM, 1 NU, 3 EM, 1 EU	51–65, white oak

^a U = upper slope, M = mid slope, L = lower slope, N = north (315–45°), E = east (45–135°), S = south (135–225°), W = west (225–315°).^b Ranges are given for most common oak species in stand. Values represent mean SI for plots where species occurred. Stand 5 value based upon one black oak tree sampled.

2.4. Data preparation

Summary statistics calculated for each overstory plot included density (stems ha⁻¹) and basal area (m² ha⁻¹) by species. Soil

Table 3
Description of response and predictor variables used in RF analysis.

Variable code	Description	Median	Mean	Range
<i>Response variables</i>				
H23	Height of individual trees 23 years after clearcut harvests (m)	9.1	9.7	0.7–30.2
H12	Height of individual trees 12 years after clearcut harvests (m)	4.8	5.0	0.1–18.3
H6	Height of individual trees 6 years after clearcut harvests (m)	2.6 (all reproduction) 2.4 (advance reproduction only)	2.7 2.5	0.1–17.4 0.1–17.4
<i>Biological predictor variables</i>				
SP	Species class	WO = white oak group, RO = red oak group, HI = hickory group, RM = red maple, SM = sugar maple, YP = yellow-poplar, BC = black cherry, AB = American beech, OC = other commercial species, NC = non-commercial species		
H12	Height of individual trees 12 years after clearcut harvests (m)	4.8	5.0	0.1–18.3
H6	Height of individual trees 6 years after clearcut harvests (m)	2.6 (all reproduction) 2.4 (advance reproduction only)	2.7 2.5	0.1–17.4 0.1–17.4
H0	Height of advance reproduction prior to clearcut harvests; year 0 (m)	0.3	0.6	0.1–6.4
F12	Form class for individual trees 12 years after clearcut harvests	1 = true apical dominance, terminal had not died back, 2 = terminal had died back and a lateral branch had assumed dominance, 3 = no dominant leader, flat topped, bushy, or almost prostrate		
F6	Form class for individual trees 6 years after clearcut harvests	1 = true apical dominance, terminal had not died back, 2 = terminal had died back and a lateral branch had assumed dominance, 3 = no dominant leader, flat topped, bushy, or almost prostrate		
F0	Form class of individual trees prior to clearcut harvests; year 0	1 = true apical dominance, terminal had not died back, 2 = terminal had died back and a lateral branch had assumed dominance, 3 = no dominant leader, flat topped, bushy, or almost prostrate		
CC12	Crown canopy class 12 years after clearcut harvests	1 = suppressed or overtopped, 2 = intermediate, 3 = codominant, 4 = dominant		
CC6	Crown canopy class 6 years after clearcut harvests	1 = suppressed or overtopped, 2 = intermediate, 3 = codominant, 4 = dominant		
Or	Individual stem origin class	1 = advance reproduction, undamaged, 2 = advance reproduction, damaged during harvest and sprouted, 3 = stump sprout after harvest, 4 = new seedling established after harvest		
GD	Ground (root collar) diameter class for advance reproduction (cm)	1 = ≤0.64, 2 = 0.65–1.27, 3 = 1.28–1.91, 4 = 1.92–2.54, 5 = >2.54		
<i>Environmental predictor variables</i>				
Acode	Aspect class grouped by azimuth degrees	1 = 185–265°, 2 = 135–185° and 265–315°, 3 = 85–135° and 315–5°, 4 = 5–85°		
%C	Soil carbon (%)	2.99	3.06	2.01–6.41
%N	Soil nitrogen (%)	0.22	0.23	0.16–0.39
%Ca	Soil calcium cation saturation (%)	51.6	51.5	33.3–71.2
%Mg	Soil magnesium cation saturation (%)	14.8	15.2	6–25.2
%K	Soil potassium cation saturation (%)	3.6	3.7	2–7.1
%H	Soil hydrogen cation saturation (%)	28.5	29.6	14–47
ppmP	Soil phosphorus (ppm)	11	12	7–25
%OM	Soil organic matter (%)	4.6	4.8	3–8.5
pH	Soil pH	5.4	5.4	4.8–6.1
CEC	Soil cation exchange capacity (meq/100 g)	4.8	5	2.1–11.2
TSIPos	Slope position; 1 = plot located at base of slope, 100 = plot located at ridge summit (%)	62.5	64.2	1–100
%Slope	Slope (%)	20	19.8	2–44
SI	Site index class ^a	1 = poor (SI = 40–54), 2 = average (SI = 55–74), 3 = good (SI ≥ 75)		

^a Site index classes derived from Carmean, 1971; Carmean et al., 1989.

samples were analyzed for cation exchange capacity (meq/100 g), phosphorus content (ppm), potassium saturation (%), calcium saturation (%), magnesium saturation (%), hydrogen saturation (%), organic matter (%), and pH by A&L Analytical Laboratories in Memphis, Tennessee. Carbon (%) and nitrogen (%) were determined using an ECS 4010 CHNSO Analyzer (Costech Analytical Technologies, Inc., Valencia, CA) located in the Forest Ecology, Silviculture, and Soils Laboratory, Purdue University, West Lafayette, Indiana.

Aspect was transformed to a linear scale ranging from 0 to 2, with zero value at southwest [transformed aspect = cos(45-aspect) + 1; Beers et al., 1966]. Transformed aspects were then grouped into four classes ranging from most xeric (class 1) to most mesic (class3; Table 3). Slope position was assessed as a relative

proportion in relation to a ridge summit or drainage (e.g., ridge/summit = 100, mid slope = 50, drainage = 0). When possible, site index class (Carmean, 1971; Carmean et al., 1989) was determined in 1988 by measuring total heights and ages of between 2 and 6 dominant and/or codominant black oak trees within each 809 m² overstory plot. When there were too few or no black oaks on a plot, scarlet, white, or chestnut oak were substituted.

For ease of analysis, and to ensure sampling uniformity across stands, less common species were grouped with closely related species, or with species possessing similar silvical characteristics. For Random Forest analysis (described below), the white oak group (WO) included white oak, chestnut oak, chinkapin oak (*Q. muehlenbergii* Engelm.), and post oak (*Q. stellata* Wangenh.), although our

Table 4

Error statistics for RF runs with all response variables. Error for regressions is measured by percent variance explained and the mean of squared residuals (msr; Liaw and Wiener, 2002; Cutler et al., 2007). Response variables include individual stem heights in years 6 (H6), 12 (H12), and 23 (H23).

Response variable	Number of predictor variables	Number of RF trees	Number of variables per split	% Variance explained	msr
H6 (advance reproduction only)	18	5000	6	21.0	2.11
H6 (all reproduction)	16	5000	5	19.2	2.30
H12 (all reproduction)	19	5000	6	71.1	2.64
H23 (all reproduction)	22	5000	7	81.8	5.55

plots contained few individuals of these species other than white oak ($n = 2$ for post oak, $n = 2$ for chinkapin oak). The red oak group included northern red oak, black oak, and scarlet oak. Hickory species were not separated in previous sampling periods, but in 2011 the hickory group (HI) included shagbark [*C. ovata* (Mill.) K. Koch], pignut [*Carya glabra* (Mill.) Sweet], bitternut [*C. cordiformis* (Wan-genh.) K. Koch], and mockernut [*C. tomentosa* (Poir.) Nutt.] hickory. Red maple (RM; *A. rubrum* L.), sugar maple (SM), American beech, black cherry (*Prunus serotina* Ehrh.), and yellow-poplar (*Lirioden-dron tulipifera* L.) were used as individual species in RF analyses. All species with commercial value that are not mentioned above were placed into the commercial group (COM). The COM group included white ash, blackgum (*Nyssa sylvatica* Marshall), bigtooth aspen (*Populus tremuloides* Michx.), and elm (*Ulmus* spp.). Species of low commercial value were put into the non-commercial group (NC). Major species of the NC group included American hornbeam (*Carpinus caroliniana* Walter), eastern redbud (*Cercis canadensis* L.), flowering dogwood (*Cornus florida* L.), eastern hophornbeam [*Ostrya virginiana* (Mill.) K. Koch], and sassafras [*Sassafras albidum* (Nutt.) Nees].

2.5. Stand density analysis

We used Tukey HSD multiple comparison tests ($\alpha = 0.05$) to examine changes in the stem density of species groups through time at 6, 12 and 23 years following harvest. Stems were grouped into three height classes for analysis; <1.2 m, 1.2–2.4 m, and >2.4 m. For year 0, we included only advance reproduction (seedling and sprout origin), whereas for all other years we included only established individuals ≥ 0.3 m height. For this analysis, yellow-poplar and black cherry were combined with the COM group created for Random Forest analysis (“Other Commercial” in Table 5) and red maple, sugar maple and American beech were combined into a single group (“Maple and Beech” in Table 5).

2.6. Random Forest analysis

Because our dataset included a large number of categorical and continuous variables (Table 3), we used Random Forests (Breiman, 2001; Liaw and Wiener, 2002), an ensemble classifier that employs multiple decision trees. This nonparametric analysis technique requires few assumptions about data distributions and relationships between variables (Zhang and Singer, 2010). This and similar Monte Carlo randomization techniques have become popular in ecological studies because of their high classification accuracy, novel methods of determining variable importance, ability to model complex interactions between predictor variables, and flexibility to perform several types of statistical analysis, including regression (Cutler et al., 2007).

We used RF to model four response variables: (1) height of all individual reproduction types in year 6, (2) height of individual advance reproduction in year 6, (3) height of all individual reproduction in year 12, and (4) height of all individual reproduction in year 23 and (a detailed list of response and predictor variables

is provided in Table 3; a description of error statistics is provided in Table 4). We analyzed advance reproduction separately in year 6 because only advance reproduction would have a height prior to harvest (H0); therefore, origin could serve as a proxy for height in year 6. We also examined advance reproduction at year 6 separately to determine if any site variables were associated with regeneration in pre-harvest stands.

All data were analyzed using the R statistical computing program, version 2.15.0 (R Development Core Team, 2012); RF analyses were implemented using the packages *randomForest* (Liaw and Wiener, 2002) and *party* (Hothorn et al., 2006a, 2006b; Strobl et al., 2008, 2007).

3. Results

3.1. Stand density

Prior to harvest in 1988, densities of white and red oak group advance reproduction were lower than those of maple-beech, other commercial, and non-commercial species groups (Table 5). The density of hickory species was lowest overall (586 ± 126 stems ha^{-1}), while density of non-commercial species was the highest of any group (6332 ± 857 stems ha^{-1}). Most advance reproduction was small (<1.2 m tall), ranging from 75% (maple-beech) to 96% (red oak) of stems in a given species group (Table 5). In absolute terms, the maple-beech (607 stems ha^{-1}) and non-commercial groups (418 stems ha^{-1}) comprised most of the larger stems (>2.4 m), combining for roughly 84% of advance reproduction in that size class.

Six years after harvest the white oak, red oak, and hickory groups continued to occur in very low densities relative to the maple-beech, other-commercial, and non-commercial species groups. Maple-beech was the third most abundant group (1761 ± 317 stems ha^{-1}), behind other-commercial (3005 ± 475 stems ha^{-1}) and non-commercial (3825 ± 341 stems ha^{-1}) groups (Table 5). The non-commercial, other-commercial, and maple-beech groups continued to dominate the taller height classes (collectively 94% of stems 1.2–2.4 m tall and 96% of stems >2.4 m tall). The white oak was slightly more abundant than the red oak group in larger size classes in both absolute and relative terms, but both groups were still predominately in the shortest height class (<1.2 m; Table 5).

As stands entered stem exclusion and began to differentiate and self-thin, densities of all species declined in year 12 and again in year 23. The red oak, white oak, and hickory groups saw the least precipitous decline of all species (collectively-30% from year 6 to year 23), with a majority of remaining stems progressing into the largest size class (>2.4 m; Table 5). While non-commercial stems still dominated the stand in year 12 (2196 ± 341 stems ha^{-1} ; 36% of all stems), their density declined 60% by year 23, most notably in the largest size class (72% reduction; Table 5). By year 23, maple-beech and other commercial species comprised a majority of the stand (60%) and of the largest stems (65%; Table 5).

Table 5
Species composition and size distribution (mean \pm standard error; per ha) of study sites at harvest (0 years) and 6, 12 and 23 years following harvest. Year 0 includes only advance reproduction (seedlings and sprouts), whereas all other years include only established individuals 0.3 m or larger. Differences of total abundance within year were tested with Tukey HSD multiple comparison tests; letters denote differences with $p < 0.05$ among the species groups. Height classes are defined as S = <1.2 m, M = 1.2–2.4 m, and L = >2.4 m. Other commercial includes yellow-poplar, black cherry, and the COM group created for Random Forest analysis.

Year	Ht class	Species group						Total
		Red oak	White oak	Hickory	Maple-beech	Other commercial	Non-commercial	
0		1097 \pm 260 ^a	791 \pm 281 ^a	586 \pm 126 ^a	5660 \pm 1548 ^{bc}	2758 \pm 712 ^{ab}	6332 \pm 857 ^c	17,224 \pm 2657
	S	1058	688	549	4270	2613	5396	14,475
	M	17	19	21	782	77	519	1436
	L	29	84	16	607	68	418	1223
6		150 \pm 75 ^a	399 \pm 269 ^a	104 \pm 40 ^a	1761 \pm 317 ^b	3005 \pm 475 ^{bc}	3825 \pm 341 ^c	9244 \pm 603
	S	74	205	41	605	909	555	2390
	M	52	122	34	597	1204	1650	3660
	L	24	71	29	558	892	1619	3194
12		161 \pm 94 ^a	347 \pm 211 ^{ab}	89 \pm 62 ^a	1391 \pm 430 ^{bc}	1867 \pm 187 ^c	2196 \pm 380 ^c	6053 \pm 920
	S	25	114	27	84	134	60	445
	M	37	97	13	212	233	169	762
	L	98	136	50	1093	1500	1967	4846
23		155 \pm 38 ^a	212 \pm 81 ^{ab}	86 \pm 29 ^a	1109 \pm 236 ^c	919 \pm 131 ^c	869 \pm 269 ^{bc}	3353 \pm 414
	S	7	53	24	91	115	248	538
	M	0	0	16	95	15	73	199
	L	148	159	47	923	790	549	2616

3.2. RF models

Our RF analyses explained between 21% (advance reproduction, year 6) and 81% (all reproduction types, year 23; Table 4) of variance. The percent of variance explained increased with year since harvest (Table 4). Mean of squared residuals for all reproduction increased from 2.30 in year 6 to 5.55 in year 23.

3.2.1. Year 6 height of all reproduction

The most important predictors for height of all reproduction in year 6 were biological variables origin (Or; i.e., new seedlings, advance reproduction and stump sprouts) and species class (Fig. 1A and B). There was little difference in the importance of other predictor variables. The percent saturation of several ions (N, Mg, H, C) were the most important environmental predictors, but all were much less significant than origin and species class (Fig. 1A and B). In year 6, reproduction of oak, hickory, and American beech from stump sprouts ($n = 21$, Fig. 2A, Node 16) were taller when compared to that from advance reproduction of the same species class ($n = 277$, Node 17). The tallest groups in year 6 were stump sprouts of red maple and yellow-poplar ($n = 21$, Fig. 2A, Node 4). No new oak, hickory, or beech seedlings were documented in year 6. Mg saturation (%Mg) >13% and CEC >5.5 were associated with greater height of non-stump sprout reproduction (Fig. 2A, nodes 6 and 8).

3.2.2. Year 6 height of reproduction originating as advance reproduction

The most important predictors for the height of advance reproduction in post-harvest year 6 were the height of advance reproduction in year 0 (H0), i.e., before harvest, and species class (SP; Fig. 3A). These predictor variables were ≈ 3 times more important than the next greatest predictor in the model, ground diameter class (GD). There was little differentiation in importance of predictor variable other than height in year 0, species class, and ground diameter class. The most important environmental predictor variable was percent slope, followed by potassium cation saturation (%K) and aspect (Acode), although all environmental and edaphic variables displayed little importance relative to species class and height in year 0 (Fig. 3A). Stems of red oak species, white oak species, hickory species, red maple, and American beech that were ≤ 0.6 m height before harvest were associated with the

shortest overall heights in year 6 ($n = 117$, Fig. 3B, Node 7). The tallest reproduction in year six were stems that were >2.2 m height prior to harvest ($n = 57$, Fig. 3B, Node 13). The shortest black cherry and sugar maple advance reproduction in year 0 (≤ 0.6 m; $n = 24$, Fig. 3B, Node 4) were still taller by year 6 than even the tallest oak stems that originated as advance reproduction ($n = 57$, Fig. 3B, Node 9).

3.2.3. Year 12 height of all reproduction

Height in year 6 (H6) proved the strongest predictor for height of stems in year 12 (H12; Fig. 1C and D). Other important biological predictors included species class, crown class in year 6 (CC6), and origin. Environmental variables appeared to have little relationship to the height of stems in year 12 (Fig. 1C and D). Oak, hickory, black cherry, and yellow-poplar stems that were the tallest groups in year 6 remained in the tallest groups in year 12, although samples were smaller ($n = 27$, Fig. 2B, Nodes 17 and 18). Yellow-poplar from the second tallest height class in year 6 (≤ 4.7 m) appeared to be highly competitive in year 12 (node 11).

3.2.4. Year 23 height of all reproduction

Similar to year 12 models, only biological predictors proved significant when predicting the year 23 heights of all reproduction (Fig. 1E and F). Height in year 12 was the best overall predictor, followed by crown class year 12 (CC12), height in year 6, and species class. As in previous years, environmental variables were not strongly related to height in year 23 (Fig. 1E and F). The tallest individuals in year 23 were also the tallest individuals in year 12 (nodes 14 and 15; Fig. 2C).

4. Discussion

4.1. Advance reproduction

Due to the lack of large oak advance reproduction, clearcut stands in southern Indiana have shifted away from the oak-dominated forests that existed before harvest. In our study, most of the advance reproduction of oak species was <1.2 m tall prior to harvest (Table 5). This pool of small seedlings remained the shortest of all reproduction present in year 6. A small number of oak stems with heights >1.2 m did exist before clearcutting and

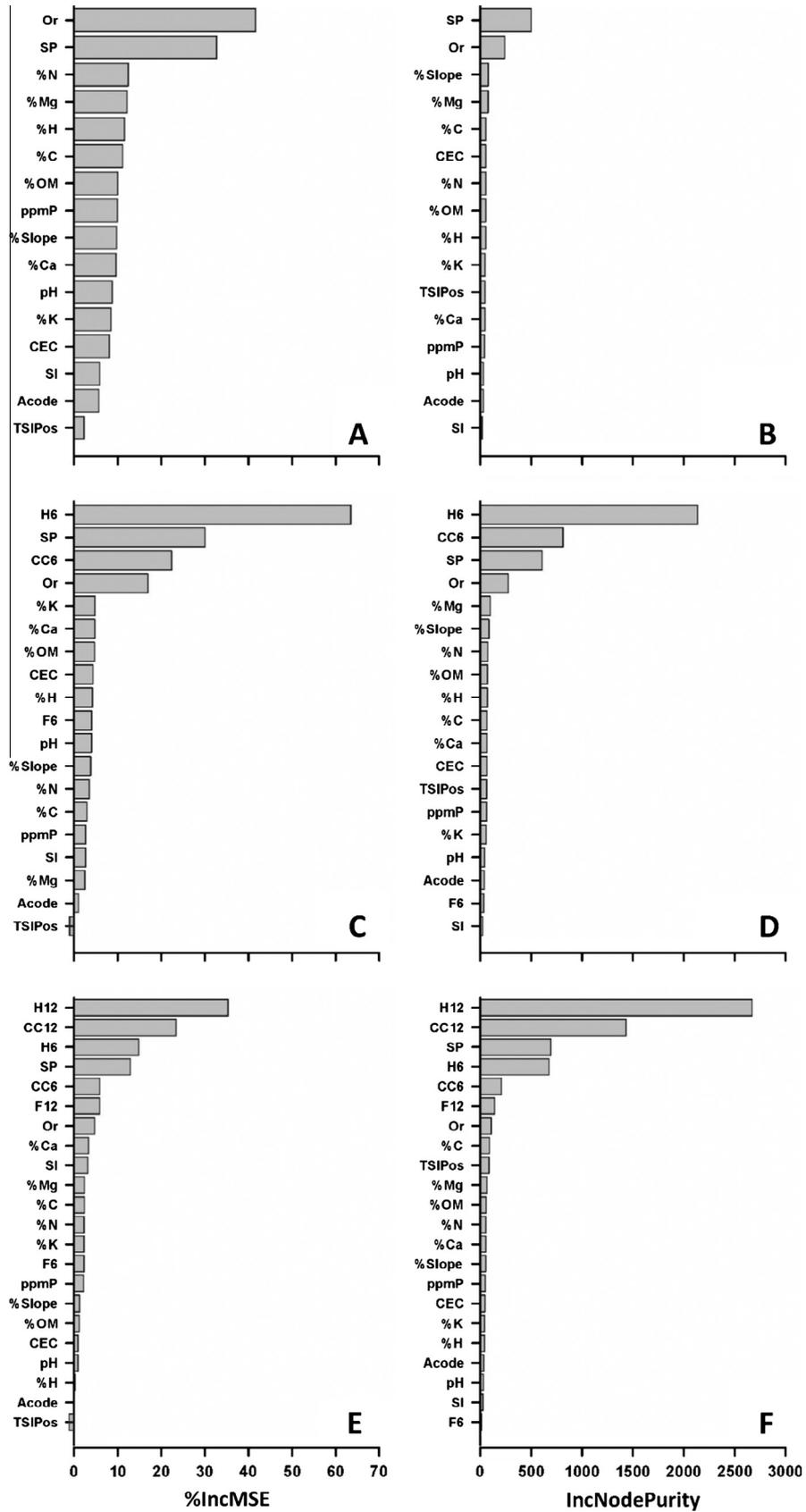


Fig. 1. Variable importance plots from RF model predicting heights of all reproduction types in year 6 (A and B), year 12 (C and D), and year 23 (E and F). %IncMSE = average increase in the mean square error when data for that variable are permuted while all others are left unchanged (Thompson and Spies, 2009). IncNodePurity = average increase in node purity from splitting on the variable; node purity is measured by residual sum of squares (Liaw and Wiener, 2002). The best predictors are those that produce the purest nodes. Predictor variables are described in Table 3.

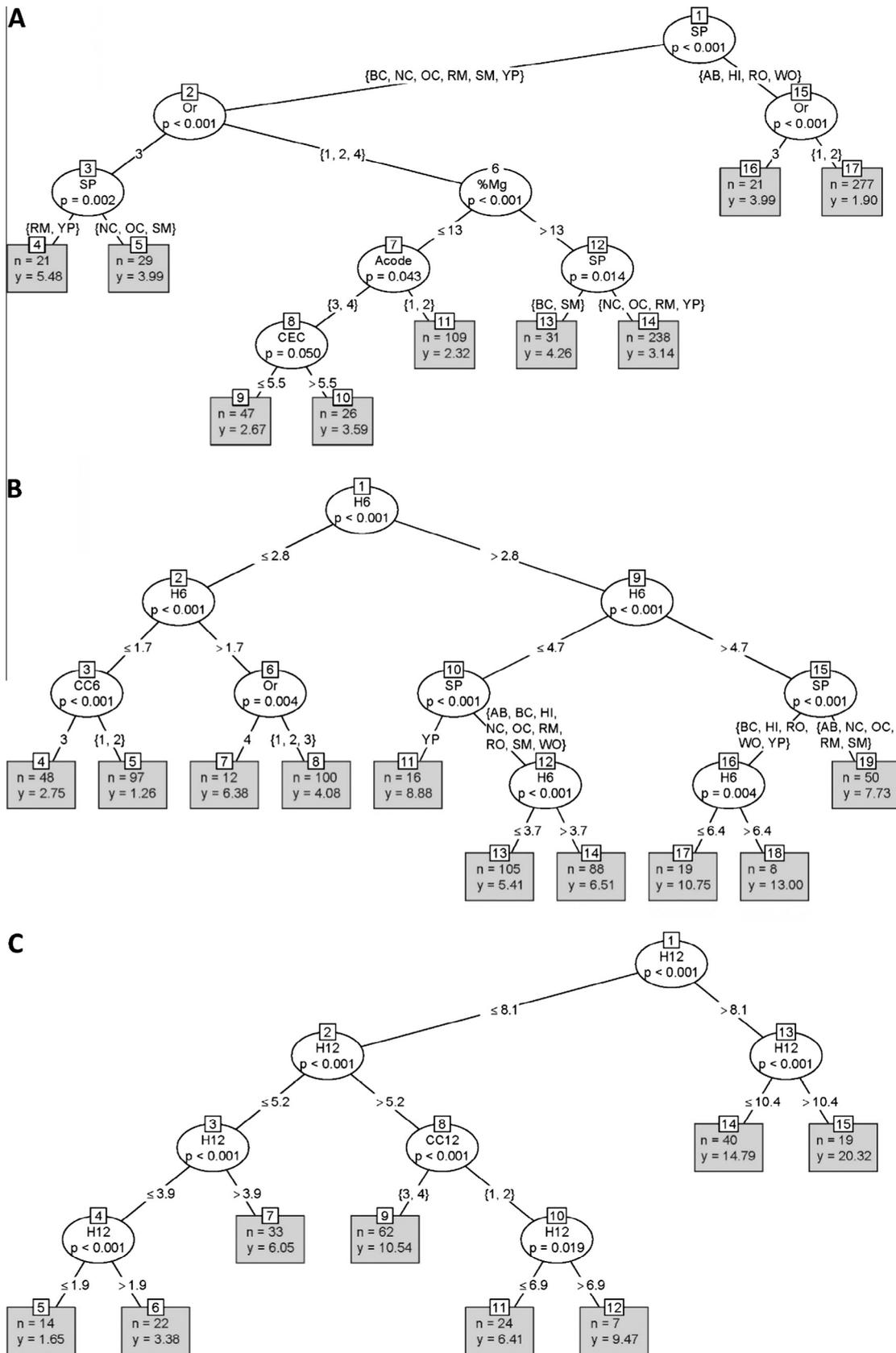


Fig. 2. Regression trees for individual tree height in year 6 (A), year 12 (B) and year 23 (C) using the five most important predictor variables as determined by random forests analysis. A Monte Carlo randomization test was used to assess p-values at each node; the length of individual lines represents strength of split. n = number of stems in category, y = mean height of category. Predictor variables are described in Table 3.

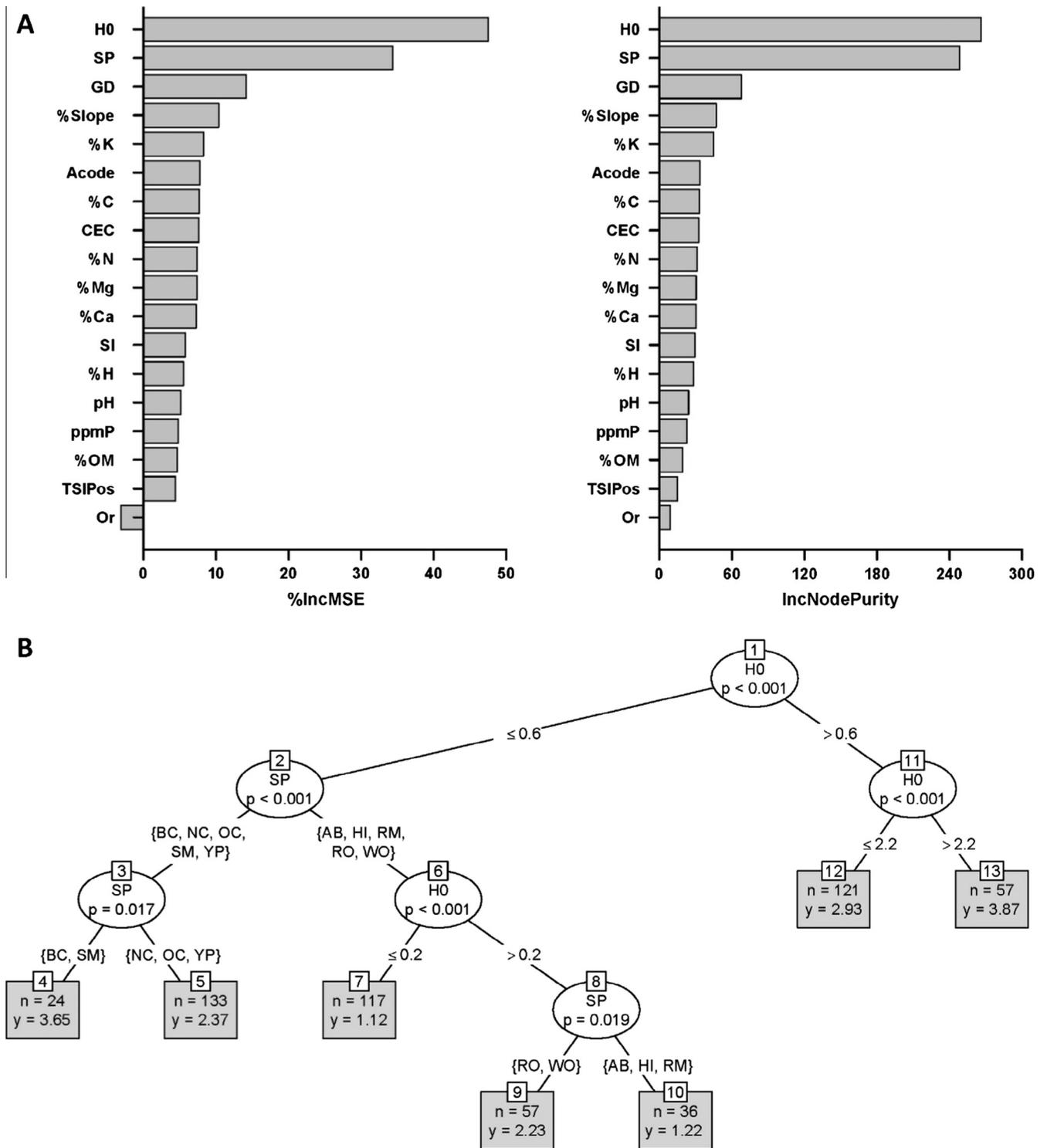


Fig. 3. (A) Variable importance plots from RF model predicting heights of advance reproduction in year 6. Predictor variables are described Table 3. %IncMSE = average increase in the mean square error when data for that variable are permuted while all others are left unchanged (Thompson and Spies, 2009). IncNodePurity = average increase in node purity from splitting on the variable; node purity is measured by residual sum of squares (Liaw and Wiener, 2002). The best predictors are those that produce the purest nodes. (B) Regression tree for individual advance reproduction height in year 6 using the five most important predictor variables as determined by random forests analysis. A Monte Carlo randomization test was used to assess *p*-values at each node; the length of individual lines represents strength of split. *n* = number of stems in category, *y* = mean height of category. Predictor variables are described in Table 3.

appeared to be competing for codominant positions in subsequent surveys. However, as we hypothesized, these larger stems were few in number compared to those of other species in the same canopy positions. Without surface fire or surrogate disturbances to limit competition and promote root and subsequent height

growth of oak seedlings, oak advance reproduction was unable to successfully compete against larger advance stems of competing species (Brose et al., 2001).

In partial support of our hypothesis, pre-harvest ground diameter class (GD) was the third most important predictor of advance

reproduction height in year 6 (Fig 3A), although its predictive value was much less than that of initial height and species. In planted red oak seedlings, Dey and Parker (1997) found that stem diameter near the root collar provided an integrated measure of seedling growth potential because of its strong relationship with both shoot and root characteristics associated with better field performance. In southeastern Ohio, Sander (1971) found that the most desirable ground diameter at time of clearcut harvest for oak advance reproduction was 1.3–2.5 cm; when damaged during harvest, sprouts from these larger stems averaged 1.4 m height by year 3 and successfully competed for codominant canopy positions. However, smaller damaged stems were unable to produce competitive sprouts in subsequent stands, likely due to their low biomass of roots prior to damage (Dey and Parker, 1997). In our study, 89% of the advance reproduction we tracked had root collar diameters less than 1.3 cm, below the minimum diameter recommended by Sander (1971). Whether advance reproduction was damaged or not during harvest had little to no importance in predicting height of stems 6 years later (Fig. 3A), suggesting that both damaged and undamaged stems lacked competitive ability in new stands.

The tallest stems of reproduction in year 6 were black cherry, sugar maple, red maple, and yellow-poplar (Fig. 2A). The relatively high number of maple advance reproduction in larger size classes before harvest allowed the genus to remain in dominant positions during subsequent stand development (Table 5). The shade-intolerance of black cherry and yellow-poplar seedlings suggests successful advance reproduction from those species germinated during the spring before harvest and benefitted from the light conditions created by complete overstory removal. Other studies across the region have also observed dominance of these species in post-harvest stands (Standiford and Fischer, 1980; Jenkins and Parker, 1998; Lhotka, 2013). For instance, in oak-hickory-dominated stands that were clearcut in southern Illinois during the 1980s, Groninger and Long (2008) found that maple, yellow-poplar, and black cherry were the most abundant species 15–26 years after harvest.

4.2. Other regeneration types

In year 6, the tallest stems from advance reproduction were black cherry, sugar maple, red maple, and yellow-poplar (Fig. 2A). Advance reproduction of red and white oak group species, along with hickory species and American beech, were found in the smallest height class in year 6. Some oak, hickory, and beech stump sprouts were competitive in year 6 (mean height = 4 m), but the sample was small (21 out of 799 total stems measured, Fig. 2A).

The low number of sprout origin oaks documented in the current study was likely due to the advanced age and large size of oaks within pre-harvest stands. The low disturbance intensities and long rotations that currently characterize management in southern Indiana may have profound effects on oak regeneration since vegetative reproduction in the form of stump sprouting in oaks declines as rootstocks continue to age and stems grow in size, thus becoming less likely to produce stump sprouts that are competitive (Groninger and Long, 2008; Johnson et al., 2009; Weigel and Peng, 2002; Weigel et al., 2011). No new oak seedlings were documented in 6 year old stands, likely due to the relatively poor seed dispersal within the genus and the lack of older, seed producing oaks left within harvest units.

The tallest stems of all reproduction in year 6 stands were from yellow-poplar and red maple stump sprouts. Repeated measure studies from the central and southern Appalachian Mountains have shown similar results; stems of black cherry, yellow-poplar, red maple and similar species originating from stump sprouts grow quickly (Keyser and Zarnoch, 2014) and remain dominant decades after harvest, outcompeting white, northern red, and chestnut oak

(Wendel, 1975; Beck and Hooper, 1986). While studies have shown that early seral species such as yellow-poplar and black cherry were common in pre-harvest overstories (Wendel, 1975; Beck and Hooper, 1986), the shade tolerance of red maple allowed it to establish in the pre-harvest subcanopy in densities much higher than those of other species, providing numerous sprout origin red maple stems in regenerating stands (Wendel, 1975; Gould et al., 2003).

As we hypothesized, by year 12 and 23 the heights of stems in the previous sampling periods were by far the strongest predictors of current height. Essentially, the height growth winners in year 23 were already among the tallest stems 6 years after harvest and remained in these positions through the end of the study. This result corroborates research demonstrating that intermediate and codominant oaks should be released with pre-commercial thinning 5–15 years post-harvest in order to recruit oak species into the overstory (Johnson et al., 2009; Ward, 2009). Because prior height and species were the strongest predictors of future height, site preparatory burns that limit competition and promote larger advance oak reproduction could offer an effective management strategy before overstory removal (Arthur et al., 1998). As observed with reproduction in year 6, basal diameter of advance reproduction in previous samples was a weak predictor of future height.

4.3. Environmental factors

Contrary to our hypothesis, site factors contributed little to the prediction of height growth in post-harvest stands relative to biological factors. However, in year 6 black cherry, sugar maple, and yellow-poplar displayed greater height on richer soils (high %Mg and CEC) located on north and east facing slopes (aspect code; Fig. 2A). Both advance and post-harvest seedlings of these species were able to establish codominant positions 6 years after harvest, unlike oak advance reproduction, which were largely relegated to intermediate canopy positions.

The rapid growth of black cherry, sugar maple, and yellow-poplar on productive sites suggests that they have some affinity for topographic and edaphic characteristics associated with more mesic conditions. Even though these species do establish on drier, more nutrient-limited sites (Hilt, 1985; Jenkins and Parker, 1998), the vigor of post-harvest stems decreased with decreasing site quality, likely limiting their competitive ability. Morrissey et al. (2008) showed that slightly older clearcut stands (cut before 1988) in our study region maintained higher densities of oak in post-harvest conditions. This was likely due to an exceptional drought that occurred from 1986 to 1988, which likely limited growth and caused mortality of seedlings from drought sensitive species such as yellow-poplar and black cherry (Morrissey et al., 2008). Seedling in this study developed in relatively drought-free conditions, therefore drought sensitive species remained highly competitive in young stands.

5. Conclusions

As observed in other forest systems (Bailey and Covington, 2002; Guyette et al., 2007), our study sites experienced historic harvesting and subsequent management practices that led to a simplified disturbance regime that drove composition and structure towards dense stands of shade-tolerant species. As observed in our study and many others (e.g., Beck and Hooper, 1986; George and Fischer, 1991; Jenkins and Parker, 1998; Groninger and Long, 2008), this shift in composition and structure has resulted in the oak recruitment failure that currently plagues much of the CHR. In our study, large oak reproduction was rare in pre-harvest stands, allowing more aggressive early seral species, such

as yellow-poplar, and large advance reproduction of shade-tolerant species, like sugar maple, to dominate new stands. Initial height was the best predictor of future height growth in all species, further highlighting the poor competitive status of small oak reproduction. Oak stump sprouts remained competitive in developing stands, but too few of these stems existed to successfully regenerate stands, likely due to the advanced age and wide dispersion of overstory stems in pre-harvest stands.

In our study, the physical environment, including slope position and aspect, were poor predictors of oak height growth in young, clearcut stands. The poor predictive power of site variables suggests that competition effects masked any direct site effects in this study. The productivity of southern Indiana forests, and lack of fire or surrogate disturbance to control mesophytic competition, has allowed developing stands to shift away from the oak-dominance that existed prior to harvest.

Because the tallest stems in 6-year-old stands were the tallest stems in years 12 and 23, stands should be cleaned as early as possible to release oak reproduction from competition. Alternatives to silvicultural clearcutting should also be considered, such as a two- or three-stage shelterwood combined with pre-harvest prescribed burns. These treatments would likely promote the large oak advance reproduction that is needed to successfully reproduce oak ecosystems in southern Indiana.

Acknowledgments

We thank Charlie Jackson, Lindsay Jenkins, Andy Meier, and Josh Shields for their assistance with fieldwork and analyses. We also thank the personnel of the Hoosier National Forest for their assistance and logistical support. Funding for this study was provided by the USDA Forest Service Northern Research Station and Hoosier National Forest under Joint Venture Agreement 11-JV-11242311-013.

References

- Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* 7, 227–238.
- Arthur, M.A., Paratley, R.D., Blankenship, B.A., 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *J. Torrey Bot. Soc.* 125, 225–236.
- Bailey, J.D., Covington, W.W., 2002. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. *For. Ecol. Manage.* 155, 71–278.
- Bakker, J.P., Olf, H.J., Willems, J.H., Zoebel, M., 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* 7, 147–156.
- Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. *South. J. Appl. For.* 10, 168–172.
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. *J. For.* 64, 691–692.
- 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 the Mississippi. *South. J. Appl. For.* 3, 133–138.
- Brashears, M.B., Fajvan, M.A., Schuler, T.M., 2004. An assessment of canopy stratification and tree species diversity following clearcutting in central Appalachian hardwoods. *For. Sci.* 50, 54–64.
- Bratkovich, S., Gallion, J., Leatherberry, E., Hoover, W., Reading, W., Durham, G., 2007. Forests of Indiana: Their Economic Importance. USDA Forest Service, Northeastern Area State and Private Forestry, NA-TP-02-04, 18p.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32.
- Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2012. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59, 322–334.
- Brose, P., Schuler, T., Van Lear, D., Berst, J., 2001. Bringing fire back: the changing fire regimes of the Appalachian mixed-oak forests. *J. For.* 99, 30–35.
- Carmean, W.H., 1971. Site Index Curves for Black, White, Scarlet, and Chestnut Oaks in the Central States. USDA Forest Service, North Central Experiment Station, St. Paul, MN, Research Paper NC-62.
- Carmean, W.H., Hahn, J.T., Jacobs, R.D., 1989. Site Index Curves for Forest Tree Species in the Eastern United States. USDA Forest Service General Technical Report NC-128.
- Clark, F.B., Watt, R.F., 1971. Silvicultural methods for regenerating oaks. In: White, D.E., Roach, B.A. (Eds.), *The Silviculture of Oaks and Associated Species*. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, Penn., pp. 37–43.
- Cutler, D.R., Edwards Jr., T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. *Ecology* 88, 2783–2792.
- Dey, D.C., 2002. The ecological basis for oak silviculture in eastern North America. In: McShea, W.J., Healy, W.M. (Eds.), *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press, Baltimore, pp. 60–79.
- Dey, D.C., Parker, W.C., 1997. Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. *New For.* 14, 145–156.
- Dey, D.C., Spetich, M.A., Wiegel, 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.
- Ellison, A.M., Banks, M.S., Clinton, B.D., Colburn, E.A., Elliot, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N. L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Houe, B.V., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- George, D.W., Fischer, B.C., 1991. The occurrence of oak reproduction after clearcut harvesting on the Hoosier National Forest. *North. J. Appl. For.* 8, 144–146.
- Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2003. Regenerating mixed-oak stands in Pennsylvania: a quarter century retrospective. In: Van Sambeek, J.W., Dawson, J.O., Ponder Jr. F., Loewenstein, E.F., Fralish, J.S. (Eds.), *Proc. of the 13th Central Hardwood Forest Conf. US For. Serv. Gen. Tech. Rep. NC-234*. pp. 254–258.
- Groninger, J.W., Long, M.A., 2008. Oak ecosystem management considerations for central hardwoods stands arising from silvicultural clearcutting. *North. J. Appl. For.* 25, 173–179.
- Guyette, R.P., Muzika, R., Voelker, S.L., 2007. The historical ecology of fire, climate, and the decline of shortleaf pine in the Missouri Ozarks. In: Kabrick, J.M., Dey, D. C., Gwaze, D. (Eds.), *Shortleaf pine restoration and ecology in the Ozarks: Proceedings of a symposium*. General Technical Report NRS-P-15. USDA Forest Service, Northern Research Station, Newton Square, PA, pp. 8–18.
- Hilt, D.E., 1985. Species composition of young central hardwood stands that developed after clearcutting. In: Dawson, J.O., Majerus, K.A. (Eds.), *Proceedings of the 5th Central Hardwood Forest Conference, 15–17 April 1985*, Champaign, Illinois. Department of Forestry, University of Illinois Urbana, Champaign, Ill., pp. 11–14.
- Homoya, M.A., Abrell, D.B., Aldrich, J.R., Post, T.W., 1985. The natural regions of Indiana. *Proc. Indiana Acad. Sci.* 94, 245–268.
- Hothorn, T., Bühlmann, P., Dudoit, S., Molinaro, A., Van Der Laan, M.J., 2006a. Survival ensembles. *Biostatistics* 7, 355–373.
- Hothorn, T., Hornik, K., Zeileis, A., 2006b. Unbiased recursive partitioning: a conditional inference framework. *J. Comput. Graph. Stat.* 15, 651–674.
- Jenkins, M.A., Parker, G.R., 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. *For. Ecol. Manage.* 109, 57–74.
- Johnson, P.S., Shifley, S.R., Rogers, R., 2009. *The Ecology and Silviculture of Oaks*. CABI Publishing, New York.
- 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. Manage.* 255, 3051–3062.
- 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, 1107–1117.
- 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. Manage.* 391, 29–35.
- Larsen, D.R., Johnson, P.S., 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manage.* 106, 1–7.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2, 18–22.
- Lhotka, J.M., 2013. Effect of gap size on mid-rotation stand structure and species composition in a naturally regenerated mixed broadleaf forest. *New For.* 44, 311–325.
- McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. *J. Wildlife Manage.* 71, 1717–1728.
- 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.
- Morrissey, R.C., Jacobs, D.F., Seifert, J.R., Kershaw, J.A., 2010. Overstory species composition of naturally regenerated clearcuts in an ecological classification framework. *Plant Ecol.* 208, 21–34.
- Pallardy, S.G., Rhoads, J.L., 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. *Can. J. For. Res.* 23, 1766–1774.
- Parker, W.C., Dey, D.C., 2008. Influence of overstory density on ecophysiology of red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) seedlings in central Ontario shelterwoods. *Tree Physiol.* 28, 797–804.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, pp. 110–135.
- R Development Core Team, 2012. *R: A Language and Environment for Statistical Computing*, Version 2.15.0. R Foundation for Statistical Computing, Vienna, Austria.

- Roach, B.A., Gingrich, S.F., 1968. Even-aged Silviculture for Upland Central Hardwoods. Forest Service, USDA Forest Service, Agricultural Handbook. 39 p.
- Sander, I.L., 1971. Height growth of new oak sprouts depends on size of advance reproduction. *J. For.* 69, 809–811.
- Sander, I.L., Clark, F.B., 1971. Reproduction of upland hardwood forests in the central states. In: Agriculture Handbook No. 405. U.S. Department of Agriculture, Forest Service.
- Sander, I.L., Graney, D.L., 1992. Regenerating Oaks in the Central States. In: Oak Regeneration: Serious Problems Practical Recommendations. USDA Forest Service GTR SE-84, pp. 174–183.
- Smith, D.W., 1994. The Southern Appalachian hardwood region. In: JBarrett, J.W. (Ed.), Regional silviculture of the United States, 3rd ed. Wiley, New York, pp. 173–225.
- Standiford, R.B., Fischer, B.C., 1980. Fifteen year results of three harvesting methods on composition and development of regeneration in southern Indiana upland hardwoods. In: Garrett, H.E., Cox, G.S. (Eds.), Proceedings of the 3rd Central Hardwood Forest Conference, 16–17 September 1980, Columbia, Missouri. University of Missouri Press, Columbia, Missouri, pp. 408–419.
- Strobl, C., Boulesteix, A.L., Kneib, T., Augustin, T., Zeileis, A., 2008. Conditional variable importance for random forests. *BMC Bioinformatics* 9, 307.
- Strobl, C., Boulesteix, A.L., Zeileis, A., Hothorn, T., 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinformatics* 8, 25.
- Swaim, J.T., 2013. Stand development and the competitive ability of oak (*Quercus* spp.) following silvicultural clearcutting on the Hoosier National Forest. M.S. Thesis. Purdue University, West Lafayette, IN, 106 p.
- Thompson, J.R., Spies, T.A., 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. *For. Ecol. Manage.* 258, 1684–1694.
- Walker, L.C., 1999. The North American Forests: Geography, Ecology, and Silviculture. CRC Press, New York, 398 p.
- 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.
- 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.
- Weigel, D.R., Dey, D.C., Peng, C.Y.J., 2011. Stump sprout dominance probabilities of five oak species in southern Indiana 20 years after clearcut harvesting. In: Proceedings of the 17th Central Hardwood Forest Conference GTR-NRS-P, p. 10.
- Wendel, G., 1975. Stump Sprout Growth and Quality of Several Appalachian Hardwood Species after Clearcutting. USDA Forest Service Research Paper, Northeastern Forest Experiment Station.
- Zhang, H., Singer, B.H., 2010. Recursive Partitioning and Applications, 2nd ed. Springer, New York, NY, 259 p.