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silviculture

Efficacy and Associated Factors of Even- and Uneven-Aged Management to Promote Oak Regeneration in the Missouri Ozarks

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Oak regeneration problems have been noted in the Missouri Ozarks and elsewhere in the eastern United States. Alteration of disturbance regimes, competition from nonoak species, and high overstory stocking are believed to be major barriers that impede oak regeneration. We studied regeneration in upland oak forests that were harvested by both even-aged (clearcutting) and uneven-aged (single-tree selection and group selection) regeneration methods, focusing on differences in oak regeneration among stands that received alternative harvest treatments. Ten years after treatments, the density of oak regeneration generally increased with increased removal of overstory trees, but only the clearcutting treatment resulted in a statistically significant increase in the density of oak seedlings and saplings over that in the no harvest treatment (the control). There were no differences among treatments in the relative proportions of oak seedlings and saplings as a whole or by size classes among the treatments. Successful oak regeneration after removal of overstory trees highly depends on the number and size of advance oak reproduction and is closely related to site conditions such as aspect and bedrock geology. Both site factors and advance oak reproduction must be considered when a regeneration method to promote oak is chosen. Compared with the uneven-aged methods (single-tree selection and group selection), clearcutting favored the red oak species over the white oak species.

Keywords: oak regeneration, advance reproduction, timber harvesting, Missouri Ozarks, Missouri Ozarks Forest Ecosystem Project (MOFEP)

Oaks (*Quercus* spp.) have been a dominant genus in eastern deciduous forests for thousands of years (Lorimer 1993, Spetich 2004). However, many oak stands harvested in the past several decades are now dominated to various degrees by other deciduous species (Loftis 1990a). A suite of biotic and abiotic factors (e.g., acorns, seedbed condition, vegetative competition, animal browsing, light availability, temperature, moisture, nutrients, fire, ice damage, and wind disturbance) contribute to the process of oak regeneration and recruitment (Barnes et al. 1980, Fei and Steiner 2008). Like other disturbance-dependent species, disturbance (e.g., logging, fire, or windthrow) is integral to regenerating oaks and sustaining oak-dominated forests (Johnson 2004). It has been hypothesized that widespread fire suppression and lack of disturbance that regulates understory light and competition are major causes of oak regeneration failures (Hicks 1998).

Oak species are less shade tolerant than many of their competitors (Dey 2002), so sufficient light is important for oaks to compete effectively with other hardwoods and to eventually recruit into the forest overstory (Lorimer 1993, Jensen and Kabrick 2007, Johnson et al. 2009). Light intensity near the floor of undisturbed or lightly disturbed hardwood stands is usually equal to or lower than the compensation point for oaks: the light intensity at which the amount of carbon gained from photosynthesis equals the amount lost from respiration (Barnes et al. 1980, Hodges and Gardiner 1993). Under a dense canopy, initial survival and growth of oak seedlings primarily depend on cotyledon reserves. Once the reserves

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; millimeters (mm): 1 mm = 0.039 in.; hectares (ha): 1 ha = 2.47 ac.

are depleted, adequate photosynthesis is necessary for survival. In low light beneath a mature forest overstory, the inability to sustain a positive carbon balance is a primary reason for the lack of oak advanced regeneration (Lorimer 1993). Under heavily shaded growing conditions (<5% full sunlight), oak seedlings have only one flush of shoot growth (Lockhart et al. 2003). Therefore, reducing overstory and/or midstory density is commonly recommended to promote oak regeneration by increasing light in the understory (Loftis 1990b, Johnson 1993, Larsen et al. 1997).

The amount of light reaching the forest floor after overstory removal is related to the size of canopy openings, the vertical structure and layers of vegetation canopy, and the aspect, slope, and physiographic position of the site. Even-aged regeneration methods such as clearcutting produce relatively large openings that allow the maximum amount of light to reach the forest floor (e.g., minimum diameter of canopy opening at least twice the height of surrounding trees). Even-aged forest regeneration via clearcutting and shelterwood methods has been recommended to regenerate oaks on xeric and xero-mesic sites in the Central Hardwood region (Roach and Gingrich 1968, Sander 1977, Johnson 1993, Johnson et al. 2009). Uneven-aged regeneration methods (single-tree selection and group selection) are potentially applicable to regenerate oaks on xeric sites by regulating light intensity and understory on sites where moisture stress favors oaks over most nonoak competitors (Johnson et al. 2009). Typically, the available light in the understory is <5% of full sunlight in productive hydric and mesophytic forests, where single-tree selection does little in the way of increasing light levels (Gardiner and Yeiser 2006, Parker and Dey 2008, Lhotka and Loewenstein 2009). In contrast, available light may approach 20% in mature xeric forests before harvesting (Blizzard et al. 2013), and selection management may be able to sustain stocking of the more shade-tolerant oak species (Loewenstein et al. 2000, Loewenstein 2005, Johnson et al. 2009).

Clearcutting or large aggregated overstory removals that create canopy openings increase the amount of light reaching the forest floor, which generally increases oak regeneration and growth, but at the same time may promote the regeneration of competing species (Beck and Hooper 1986, Loftis 1990a, 1990b, Schuler and Miller 1995, Parker and Dey 2008). The open forest canopy in clearcuts may also favor some invasive species (e.g., *Rosa multiflora* Thunb) that regenerate vigorously when mineral soil is exposed or favor growth of other shade-intolerant, fast-growing species such as yellow poplar (*Liriodendron tulipifera* L.) (Beck and Hooper 1986, Abrams and Nowacki 1992, Jenkins and Parker 1998, Groninger and Long 2008). Single-tree and group selection create smaller canopy gaps and may favor shade-tolerant species such as red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and American beech (*Fagus grandifolia* Ehrh.) (Johnson et al. 2009).

After overstory removal, oaks reestablish on the site from three sources: regeneration from seed, previously established seedlings and saplings in the understory, and stump sprouts. The effectiveness of forest overstory removal in promoting oak regeneration depends on numerous other factors including site condition, number, size, and spatial arrangement of oak advance reproduction and nonoak competitors, and species composition of the parent stand. Johnson et al. (2009) used the term "intrinsic accumulator" to describe those sites that naturally accumulate oak advance reproduction on certain physiographic positions and under certain moisture and disturbance regimes. To quantify the capacity of oak species to occupy and dominate growing space at a specified time after a stand regeneration harvest, Sander et al. (1984) proposed the concept of oak regeneration potential, which can be computed before harvest for a given stand from an inventory of the number and size of oak seedlings, saplings, and overstory trees. Appropriate regeneration methods are selected based on the estimate of a stand's oak regeneration potential (e.g., adequate, marginal, or poor), the suite of competing species, the degree of herbivory, and site conditions.

On mesic sites with low to moderate oak reproduction potential, for instance, the shelterwood method may be preferred over clearcutting to increase light intensity at the forest floor and promote growth of oak advance reproduction while still suppressing growth of nonoak competitors (Loftis 1990a, 1990b, Brose et al. 2008, Parker and Dey 2008).

Considering the enormous value of oak forests, improving oak regeneration success is exigent to researchers and forest managers. In 1989, the Missouri Department of Conservation (MDC) launched a long-term, landscape-scale experiment (Missouri Ozarks Forest Ecosystem Project [MOFEP]) to compare three alternative silvicultural systems on oak-dominated forests and the response of key ecosystem variables. The three treatments are even-aged management with clearcutting, uneven-aged management (UAM) with single-tree and group selection, and no harvest, which also serves as an experimental control (Brookshire and Shifley 1997, Brookshire and Dey 2000, Shifley and Kabrick 2002). Because regeneration is fundamental to the sustainability of a species (Dey 2014), the primary objective of this article was to use the MOFEP data to examine the effects of the alternative treatments on changes in the composition and size structure of oak seedlings, oak saplings, and competing tree species through one treatment cycle from 1990 to 2006. Given greater variation in site conditions and stand characteristics, specifically, we examined temporal changes in populations of oak and nonoak (all species combined) seedlings and saplings in different size classes by prescribed treatments to identify stand and site factors associated with significant differences in the regeneration response of oaks. These results can guide forest managers who wish to design harvest treatments that can retain or restore oaks in regenerated stands in the Missouri Ozarks.

Methods

Study Area

The MOFEP experiment includes nine sites ranging in size from 309 to 508 ha, located in Carter, Reynolds, and Shannon Counties in the southeast Missouri Ozarks (Figure 1). Before harvesting, trees in the study area were largely free from manipulation for at least the previous 40 years (<5% of area disturbed). The study area is mostly within the Current River Oak Forest Breaks and the Current River Oak-Pine Woodland Hills landtype associations of the Ozark Highlands (Kabrick et al. 2000). Mean annual precipitation in the study area is 1,140 mm, with most of the precipitation occurring as rainfall in the spring and fall. Mean annual temperature is 13° C. Mean daily temperature ranges from −0.5° C in January to 24.8° C in August. The elevation ranges from 171 to 360 m with slopes from 0 to 60%. The dominant soil parent materials include hillslope sediments, loess, and residuum (Meinert et al. 1997, Kabrick et al. 2000).

Wildland fire has been pervasive on the landscape surrounding the MOFEP sites with variable frequencies ranging from 2 to 40 years before the 1950s (Guyette et al. 2002). The increase in European population (1821–1940) was accompanied by periods of intensive logging for timber, open range grazing for livestock, frequent

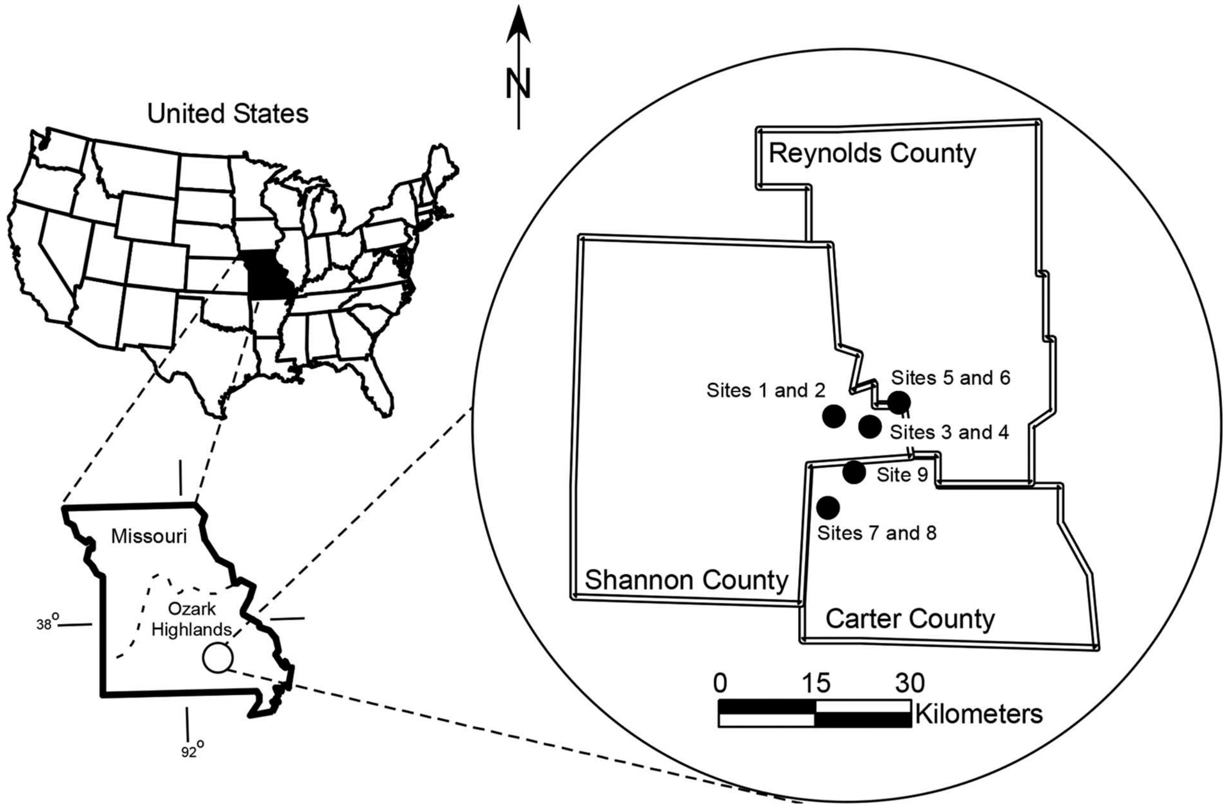

Figure 1. Location of nine MOFEP experimental sites (no harvest, sites 1, 6, and 8; uneven-aged management, sites 2, 4, and 7; and even-aged management, sites 3, 5, and 9).

woods burning, and forest clearing for agriculture. Marginal agricultural lands were abandoned to revert back to forest, and the 1950s began a period of widespread fire suppression that continues today. The former open oak woodlands and abandoned farms were gradually replaced by the currently dominant dense oak-hickory forests (Hanberry et al. 2014). Most forests have reached 70+ years of age with high stocking levels due to the lack of active natural and human disturbances (e.g., timber harvesting, fire) in the study area during at least the past 40 years (Shifley and Brookshire 2000).

Study Design and Timber Harvest Treatments

The nine MOFEP sites (administrative compartments) are grouped geographically into three replicated blocks. Each block contains one even-aged, one uneven-aged, and one no harvest treatment site (Brookshire and Shifley 1997) (Figure 1). Ecological landforms and forest species composition were used to divide each site into approximately 70 forest stands (management units) that were typically 2–10 ha in size. As described below, harvest treatments were applied to entire stands, but only a portion of the stands on a site were treated in any given harvest cycle. This approximates long-term, compartment-scale, sustained-yield management.

Each stand had at least one permanent monitoring plot, and depending on the treatment applied to the stand, each plot could be classified as receiving one of the following treatments during the 1996 harvest cycle: clearcut, group selection harvest, single-tree selection harvest, or no harvest. The first-entry harvests were initiated in May–November of 1996 after preharvest inventories were performed in 1990 and 1995. On the even-aged management sites, 129 ha in the compartments were clearcut (11%). On the uneven-aged management sites, 860 ha (57%) were treated with single-tree and group selection (Kabrick et al. 2000).

Based on the preharvest inventory, oaks accounted for >70% of total basal area in the overstory but <20% of all trees in the understory across all sites to be treated (Table 1). On these study sites, white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Münchh.), and post oak (*Quercus stellata* Wangenh.) were the four dominant species accounting for 71% of the stand basal area (Kabrick et al. 2004). Additional details of the study design are described by Brookshire and Shifley (1997), Shifley and Brookshire (2000), and Jensen and Kabrick (2007).

Even-aged management was implemented according to MDC Forest Land Management Guidelines established in 1986 and followed recommendations by Roach and Gingrich (1968). Stands selected for harvest typically had mature or over-mature trees, poles, or small sawtimber that would support a commercial timber harvest without reducing residual growing stocking below the B-level (Gingrich 1967). Rotation lengths for each site are 80–100 years. This results in a regulated harvest of 10–12% of the managed area per entry on a 10-year reentry schedule. The principal means of stand regeneration was use of clearcutting with a few residual overstory trees (e.g., den trees or snags) per acre retained for the benefit of wildlife. Ten percent of each treated site was left as "old-growth" and excluded from harvest in perpetuity. For the remainder of the even-aged management area, the MDC Forest Land Management Guidelines are intended to create an age-class distribution across administrative compartments (i.e., sites) comprising 10% seedlings, 20% small trees (6–14 cm dbh), 30% poles (14–29 cm dbh), and 40% sawtimber (>29 cm dbh) (Brookshire and Shifley 1997).

Table 1. Mean basal area and trees/ha of major oak species of MOFEP plots by treatment before timber harvesting (1995).

	All oaks	White oak	Black oak	Scarlet oak	Post oak	Other oaks	Nonoak
Trees/ha in the understory (for trees >1 m tall, but dbh <11.4 cm)							
No harvest	1,621 (13)	878 (7)	311 (3)	215 (2)	136 (1)	81 (1)	10,559 (87)
Single-tree selection	1,606 (13)	975 (8)	235 (2)	169 (1)	135 (1)	92 (1)	10,336 (87)
Group selection	1,810 (19)	1,110 (12)	259 (3)	218 (2)	182 (2)	41 (<1)	7,583 (81)
Clearcut	1,503 (12)	829 (7)	421 (3)	198 (2)	36 (<1)	19 (<1)	11,079 (88)
BA (m^2/ha) and trees/ha in the overstory (for trees >11.4 cm)							
No harvest	14.9 (77)	3.8 (20)	5.0 (26)	4.3 (22)	1.3 (7)	0.5 (3)	4.4 (23)
	2,670 (70)	962 (25)	685 (18)	670 (18)	245 (7)	108 (3)	1,120 (30)
Single-tree selection	15.4 (76)	3.8 (19)	5.5 (28)	4.8 (24)	1.1 (6)	0.2 (1)	4.7 (24)
	2,834 (70)	1,038 (26)	789 (20)	754 (19)	201 (5)	52 (1)	1,194 (30)
Group selection	16.2 (78)	3.0 (14)	6.1 (29)	6.0 (29)	1.0 (5)	0.1 (<1)	4.6 (22)
	2,841 (71)	833 (21)	919 (23)	906 (23)	170 (4)	13 (<1)	1,144 (29)
Clearcut	15.1 (78)	4.4 (23)	5.2 (26)	4.1 (21)	1.5 (8)	0.1 (1)	4.3 (22)
	2,423 (71)	957 (28)	669 (20)	571 (17)	214 (6)	12 (<1)	1,002 (29)

Numbers in parentheses represent the species proportion as a percentage (rounded to integers).

Uneven-aged management also followed the MDC Forest Land Management Guidelines and was based on the prescriptions of Law and Lorimer (1989). Ten percent of each site was initially reserved as old-growth and the remaining 90% was treated with uneven-aged management. For single-tree and group selection harvests, the cutting cycle of 10 years coincided with harvesting in the even-aged management units. Group selection harvests created openings with diameters that were one to two times the height of the surrounding overstory trees, depending on slope and aspect (21 m in diameter on south-facing slopes, 32 m in diameter on level areas, and 43 m in diameter on north-facing slopes). Single-tree selection was applied between group openings to improve timber quality and to promote regeneration and overstory recruitment through harvest regulation of the tree size distribution (Smith 1986). Management objectives for each stand were established based on targets set for largest diameter tree, residual basal area, and *q* value (e.g., see Johnson et al. 2009). The target residual basal area was chosen for the stand to be equivalent to B-level stocking. The target largest diameter tree varied from 46 to 66 cm dbh on low-quality and high-quality sites, respectively. The *q* value ranged from 1.3 to 1.7.

The no-harvest management sites were untreated. As for all sites, wildfire was suppressed, but otherwise natural disturbances occurred as on other surrounding forestlands.

Data

Since the initial inventory in 1990, woody vegetation has been remeasured every 3–5 years (1995, 1998, 2002, and 2006) across the nine study sites. A total of 648 (including 45 intermediate thinning plots not included in this study) permanent, circular inventory plots (0.2 ha each) were established for sampling vegetation on the nine MOFEP sites with 70–76 plots per site (Shifley and Brookshire 2000). Larger woody vegetation ≥11.4 cm (4.5 in.) dbh was measured on the main 0.2-ha plot. Smaller woody vegetation (3.8 cm ≤ dbh < 11.4 cm) (1.5–4.5 in.) was measured on four 0.02-ha subplots located within the 0.2-ha main plot. Woody vegetation <3.8 cm dbh but at least 1 m tall was measured on a 0.004-ha subplot nested within each 0.02-ha subplot.

To capture the dynamics of oak seedlings and saplings under various treatments, small woody vegetation or regeneration (trees <11.4 cm dbh) for four major oak species and collectively for nonoak species was regrouped into three size classes: size class 1 (height >1 m, dbh <1.3 cm), size class 2 (1.3 cm ≤ dbh < 3.8 cm), and size class 3 (3.8 cm ≤ dbh < 11.4 cm). Total stem density and the relative proportion of oaks and nonoak species were measured and calculated for each of the 603 plots in 1995 (preharvest), and in 1998, 2002, and 2006 (postharvest). The posttreatment inventory data indicated that <3% of reproduction was developed from stump sprouts, so stump sprouts after treatments were combined with other sources (seeds and previously established seedling and sapling reproduction) of regeneration. Overstory trees (≥11.4 cm dbh) were measured each year on each plot, recording species, dbh, crown class (dominant, codominant, intermediate, and suppressed), and status (live, dead, blown-down, den tree, and cut). In addition, canopy closure (0–100%) before and after treatments in each 0.2-ha (0.5 acre) study plot was measured using a canopy tube of 50 cm (20 in.) in diameter placed at 1.52 m (5 ft) high off the ground in 16 points nested in four 0.02-ha (0.05 acre) subplots in the growing seasons of 1994, 1995, 1997, 2001, and 2006. Canopy closure data will be analyzed as a surrogate to the changes in light condition between treatments.

For data analysis and modeling, we calculated both reproduction density and proportion for all oak species combined and by size class (dependent variables) and a number of contributing factors (independent variables) based on field measurement data. The proportion of oak reproduction was calculated as the overall percentage of oak reproduction among all understory reproduction including both oak and nonoak species, whereas the proportion of oak reproduction by size class was calculated as the percentage of oak reproduction among all understory reproduction of the same size class. The contributing factors measured or derived for each plot included overstory density (trees/ha) and basal area (m^2/ha) of all trees and oak trees before harvest (1995), total and oak tree densities and basal areas removed in 1996, advance oak reproduction density as a whole and by size classes (1, 2, and 3) before harvest, and site slope, slope position, aspect, geo-landform and ecological land type.

Data Analysis

Multivariate analysis of variance (MANOVA) was used to compare the differences in densities and proportions of oak seedlings and saplings as a whole and by size class in 1995 (before the 1996 harvest), 1998, 2002, and 2006 among the silvicultural treatments. In addition, analysis of covariance (ANCOVA) was used to compare the oak reproduction density and proportion difference in 2006, the most recent inventory year with data available for analysis, by using the corresponding oak reproduction densities and proportions from 1995 (preharvest) as the covariate. For data analyzed as proportions, the arc sine square root transformation was applied before statistical tests. The statistical significance for all tests was evaluated at the 95% confidence level.

Classification and regression tree analysis (CART) was applied to the 2006 oak reproduction observations to investigate the influence of spatial heterogeneity (e.g., among geo-landforms and bedrock) of the experimental units (MOFEP sites), differences in stand and site conditions (e.g., slope, aspect, stem density, and species composition) of plots treated within and among treatments, and stochastic events such as wind disturbances after timber harvest. CART is a nonparametric statistical technique useful for analyzing large data sets under heterogeneous experimental conditions to explore a variety of scientific questions on classification, prediction, and association (Breiman et al. 1984, Fan et al. 2006). It recursively partitions a heterogeneous population into subsets of relatively homogeneous data populations. The target population in CART is represented by the root node in the regression tree diagram, and a set of more homogeneous subpopulations obtained during the recursive partition process are illustrated by internal and terminal nodes, respectively. Classification or regression is evaluated based on the relatively homogeneous terminal nodes. Patterns in the data are thus explicitly and intuitively exhibited by diagrams of the hierarchical classification or regression.

To construct the regression tree model analyzing overall density and proportion of oak reproduction in 2006 (10 years after harvesting), the predictor variables included the following: (1) harvest treatment (no harvest, single-tree selection, group selection, or clearcut); (2) the stem density (trees/ha) and basal area (m^2/ha) of oaks, nonoaks, and all trees mechanically removed in 1996 or blown down by natural disturbances (e.g., wind) from 1995 to 2006; (3) overstory stem density (trees/ha) and basal area (m^2/ha) of oaks, nonoaks, and all trees and the proportion of oaks and nonoaks that were alive in 1995 (pretreatment); (4) stem density (trees/ha) and the proportion of oak and nonoak advance reproduction by size class in 1995; and (5) site conditions including slope, slope position, aspect, geolandform, depth to bedrock, and ecological land type of each plot. In this study, 603 MOFEP plots were used to construct the best regression tree model to predict oak reproduction density and proportion based on the complexity parameter (Breiman et al. 1984). Considering the relatively small sample size (number of plots) of a split resulting from a CART analysis (particularly for terminal nodes), the Random Forest (an ensemble model) was run with the same data used to construct the best single regression tree model to evaluate the importance of variables based on the mean squared error and to compare the coincidence/consistency between the ensemble model and the single regression tree model. The R statistical package *stats* was used for MANOVA and ANCOVA analyses, and *rpart* and *RandomForest* were used for regression tree and random forest analyses, respectively (Therneau and Atkinson 1997, Crawley 2007).

Results

Before harvesting (1995), the mean density of oak advance reproduction (trees ≥1 m tall and <11.4 cm dbh) in the understory predominantly consisted of white oak, black oak, scarlet oak, and post oak and ranged from 1,503 to 1,810 trees/ha in the stands designated to be treated. Collectively, oaks accounted for about 12–19% of advance reproduction for all tree species in the understory. Nonoak species, mainly including red maple, hickories (*Carya* spp.), flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum*[Nutt.] Nees), winged elm (*Ulmus alata* Michx.), and black gum (*Nyssa sylvatica* Marsh.) consisted of >80% of the understory reproduction with mean densities varying from 7,583 to 11,079 trees/ha (Table 1). In 1998, 2 years after harvesting, there were slight decreases in the density of both oak and nonoak reproduction due largely to harvest damage to advance reproduction on all treated stands, particularly the clearcut stands. By 2002, 6 years after treatment, the density of reproduction (all species) had increased with a trend (from high to low): clearcut > group opening > single-tree selection. An increase in reproduction density continued through 2006 (10 years after treatment) for the single-tree and group selection treatments, but a decrease occurred within the clearcut treatment, even though the trend/rank in reproduction density among the three treatments by 2006 remained the same as that observed in 2002. Compared with that for the treated stands, the density of reproduction in the no harvest stands (the control) changed little for oak and nonoak species during the same time period (Figure 2A).

Ten years after treatment (2006), oak reproduction had increased over pretreatment levels in all treated stands with mean densities of 9,857, 3,909, and 1,982 trees/ha, respectively, for the clearcut, group, and single-tree selection treatments. Oak reproduction density had decreased slightly in the no harvest stands and averaged 1,192 trees/ha by 2006 (Figure 2B). Both MANOVA and ANCOVA tests indicated that the increase in oak reproduction density in the clearcut stands was significantly greater than that in the no harvest stands. However, there were no statistically significant differences among all other pairwise treatment comparisons (e.g., clearcut versus group selection, clearcut versus single-tree selection, group selection versus single-tree selection, group selection versus no harvest, or single-tree selection versus no harvest) because of the great within-treatment variation in reproduction density.

From 1995 to 2006, the density of oak reproduction by size class varied differently among the treated stands. An increase was observed in all three reproduction size classes in the clearcut stands, whereas the increase occurred only within size classes 1 and 2 in the group openings and within size class 1 where single-tree selection harvesting occurred (Figure 2B). The proportion of oak reproduction as a whole and within the two smallest size classes (1 and 2) remained relatively stable, fluctuating between 8 and 14% for all treatments. However, the proportion of the largest oak reproduction had continually decreased in the no harvest, single-tree selection, and group selection stands compared with the generally increasing trend in the clearcut stands (Figure 2C). The proportion of oak reproduction as a whole and by size class did not differ statistically among all treatments.

The Random Forest model (including 500 individual regression trees) for posttreatment oak reproduction density showed that all covariates explained 64.3% of mean squared residuals, among which the three most important (in terms of mean decrease in squared residuals) independent predictor variables were oak advance reproduction density before treatment (22.8%), overstory oak basal area removed (16.0%), and site aspect (7.4%). The best regression tree model (i.e., a model that was statistically pruned based on the complexity measure) revealed the pattern of posttreatment oak reproduction density by these three variables (Figure 3A). Given similar amounts of overstory oak removal (e.g., ≥15 m^2/ha), the density of oak reproduction reached up to 13,000 trees/ha on southern and western aspects (azimuth 103–359°, node VIII), which was two to three times greater than that on the northeastern aspects (azimuth

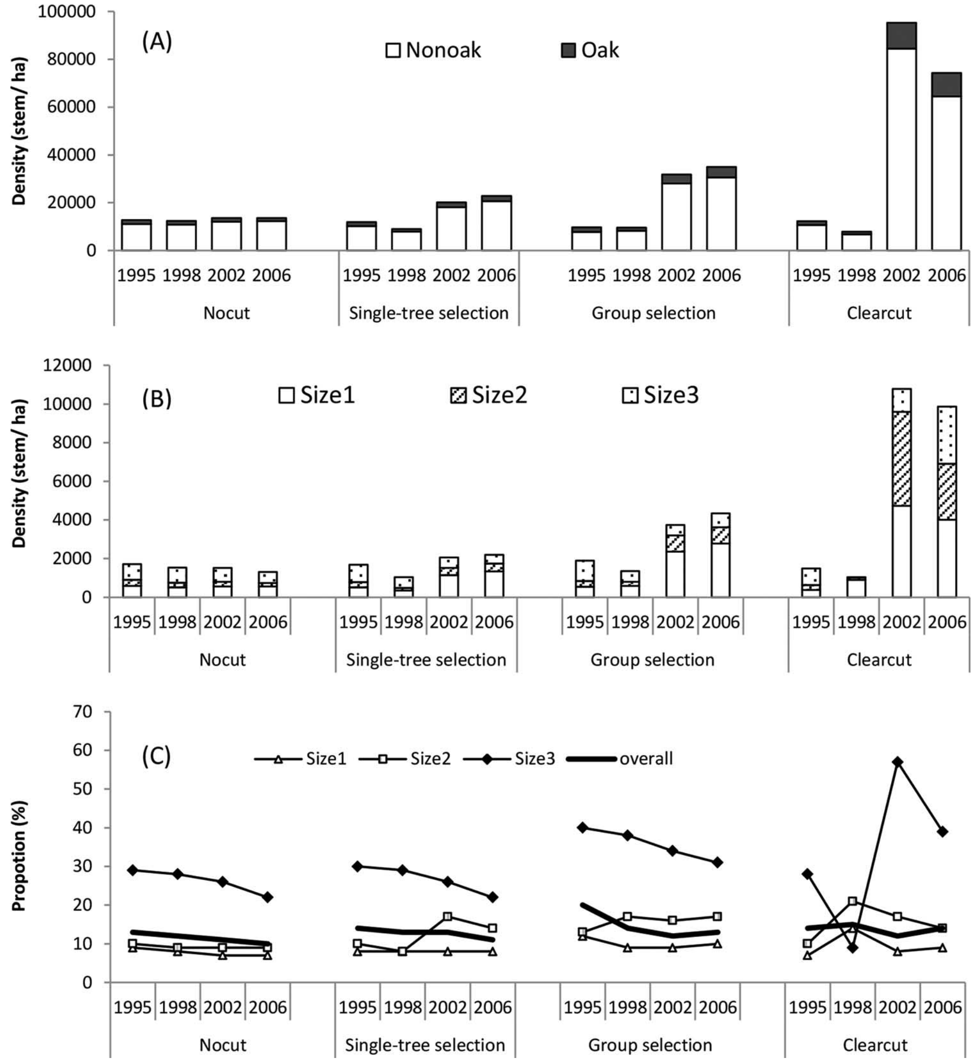

Figure 2. Change in the density of all oak reproduction combined (A) and by size class (B), and proportion of all oak combined and by size class (C) after the harvesting treatments. The harvest took place in 1996; therefore, 1995 shows preharvest conditions and 1998, 2002, and 2006 are postharvest inventories. Size 1: height > 1 m but dbh <1.3 cm; size 2: 1.3 cm ≤ dbh < 3.8 cm; size 3: 3.8 cm ≤ dbh < 11.4 cm.

0–103°, node VII). In the stands where oak basal area removal ranged from 9.5 to 15 m^2/ha and where oak advance reproduction was >1,075 trees/ha before harvesting (node VI), the density of oak reproduction averaged 6,236 trees/ha, more than double that for stands with similar levels of overstory removal but where the pretreatment density of oak advance reproduction was <1,075 trees/ha (node V). Stands with overstory oak basal area of <9.6 m^2/ha removed were predominantly the no harvest stands (nodes I, III, and IV) and the uneven-aged treatments (node II) (Tables 2 and 3). Four major oak species (white oak, black oak, scarlet oak, and post oak) comprised >70% of total stand basal area (Table 1). The differential responses of these four oak species to timber harvesting were captured in the terminal nodes II, V, VI, VII, and VIII of the CART model (Figure 3A), which were predominantly composed of treated sites (Table 2). White oak reproduction maintained its dominant position among the four major oaks (Figure 3B).

The Random Forest model for the posttreatment proportion of oak reproduction showed that all covariates explained 62.1% of mean squared residuals. The three most important (in terms of mean decrease in squared residuals) independent predictor variables were oak advance reproduction density before treatment (61.9%), bedrock (12.6%), and overstory basal area removed (11.4%). Figure 4 is the best single regression tree model, which showed that the proportion of oak reproduction 10 years after treatment was primarily associated with the first two factors: the density of oak advance reproduction before treatment and the type of bedrock. Where the initial density of oak advance reproduction was <1,075 trees/ha (terminal node I), oak reproduction accounted for only 5% of all understory reproduction after 10 years; the proportion doubled to 13% in stands where initial oak advance reproduction density ranged from 1,075 to 2,175 trees/ha (terminal node II). Where oak advance reproduction density was initially ≥2,175 trees/ha, the proportion of oak reproduction increased to 23% (terminal node III) over 10 years in stands located on the Eminence, Gasconade, or Precambrian bedrock formations and to 36% (terminal node IV) in stands on the Roubidoux formation.

Discussion

The disjunction in the size distribution for oaks in the overstory and understory (Table 1) is evidence of a potential problem in

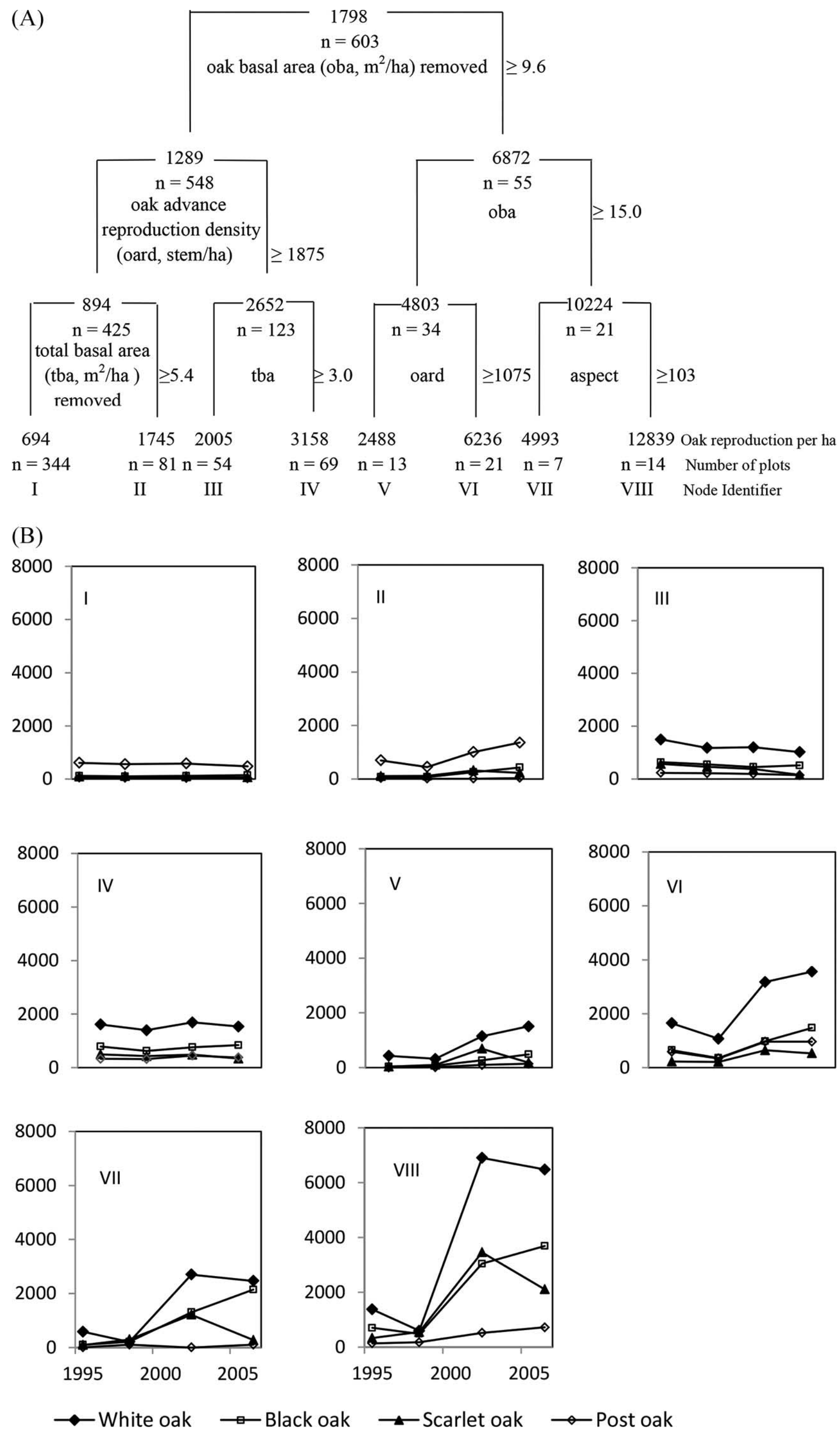

Figure 3. Regression tree model showing change in average oak reproduction density (stems/ha) 10 years after overstory treatments by significant factors (A) and distribution of seedlings and saplings of white oak, black oak, scarlet oak, and post oak within the identified terminal nodes in the regression tree model (B). In total, 603 treated and untreated MOFEP study plots were included to generate the best-sized regression tree model. The average oak reproduction density, number of MOFEP plots, and splitting variable are shown at each node. Terminal nodes I–VIII from left to right are labeled using Roman letters. Note that post oak never does very well where there is competition on average and better sites. It is more shade intolerant than many other oak species. White oak is the most shade tolerant of the oak species in this study, one reason they are most abundant regardless of overstory treatment.

sustaining oaks in future forests and is symptomatic of forests where oaks are being successionally replaced by shade-tolerant species (Lorimer 1984, Abrams 1992, Nowacki and Abrams 2008, Johnson et al. 2009). This is a relatively recent phenomenon that is attributed to changes in historical disturbance regimes, once largely characterized by anthropogenic fire (Guyette et al. 2002), but now driven by settlement and land-use changes that followed European colonization (Lorimer 1984, Crow 1988, Williams 1989, Abrams 1992, Dey 2002). The historic disturbance regime was thought to reduce stand density, create canopy openings to allow for the establishment and recruitment of oaks into the overstory, and reduce the number of aforementioned nonoak competitors (Johnson et al. 2009).

Table 2. Distribution of MOFEP plots by treatment within the terminal nodes of regression trees (Figure 3A).

Terminal node	Oak reproduction density (SE)	No. (%) of plots in regression tree model				
		Total	No harvest	Clearcut	Single-tree selection	Group selection
I	694 (32)	344	323 (94)	0 (0)	18 (5)	3 (1)
II	1,745 (337)	81	22 (27)	0 (0)	40 (49)	19 (24)
III	2,005 (146)	54	51 (94)	0 (0)	3 (6)	0 (0)
IV	3,158 (186)	69	58 (84)	0 (0)	8 (12)	3 (4)
V	2,488 (747)	13	1 (8)	4 (31)	4 (31)	4 (31)
VI	6,236 (442)	21	2 (10)	2 (10)	8 (38)	9 (42)
VII	4,993 (986)	7	0 (0)	4 (57)	0 (0)	3 (43)
VIII	1,2839 (1,382)	14	0 (0)	11 (79)	0 (0)	3 (21)
Total		603	457 (72)	21 (3)	81 (13)	44 (7)

Table 3. Distribution of MOFEP plots by treatment within the terminal nodes of regression trees (Figure 4).

Terminal node	Proportion (%) of oak reproduction (SE)	No. (%) of plots in regression tree model				
		Total	No harvest	Clearcut	Single-tree selection	Group selection
I	5 (<1)	265	200 (75)	8 (3)	39 (15)	18 (7)
II	13 (<1)	195	147 (75)	9 (5)	25 (13)	14 (7)
III	23 (1)	82	59 (72)	4 (5)	11 (13)	8 (10)
IV	36 (2)	61	51 (84)	0 (0)	6 (10)	4 (6)
Total		603	457 (76)	21 (4)	81 (13)	44 (7)

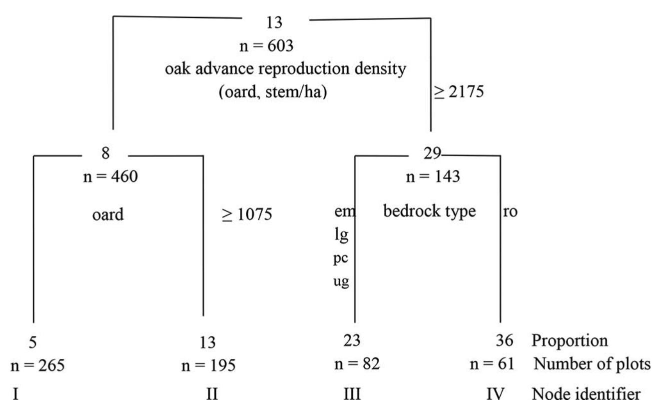

Figure 4. Regression tree model showing change in average proportions (%) of oak reproduction 10 years after overstory treatments by significant factors. In total, 603 treated and untreated MOFEP study plots were included to generate the best-sized regression tree model. The average proportion of oak reproduction, number of MOFEP plots, and splitting variable are shown at each node. OARD, oak advance reproduction density (stems/ha) before overstory treatments in 1996; bedrock types: em, Eminence; 1g, Gasconade; pc, Precambrian; ro, Roubidoux. Terminal nodes I–IV 4 from left to right are labeled using Roman letters.

Hanberry et al. (2014) have reported that historic (pre-1850) tree density was lower, and trees were larger in diameter than those in modern conditions based on the analysis of General Land Office Survey data and Forest Inventory and Analysis data. Therefore, reducing overstory density through harvesting as well as controlling competing vegetation has been recommended to regenerate oaks (Loftis 1990b, Johnson 1993).

In the Ozark Highlands, even-aged management (using clearcutting as the primary regeneration method) has generally proven to be effective as indicated by the significant posttreatment increase in oak reproduction in this study (Figure 2) and others (e.g., Johnson et al. 2009). Ten years after treatments, as many as 81% (17 of 21) of the stands treated with clearcutting had oak reproduction that was either close to or exceeded 5,000 trees/ha (nodes VI, VII, and VIII in Figure 3A). Within the same reproduction levels (e.g., nodes VI, VII, and VIII), however, the proportion of stands treated by the group selection and single-tree selection methods was merely 34% (15 of 44 stands) and 10% (8 of 81 stands), respectively (Table 2). Thus, uneven-aged methods should be applied judiciously for regenerating oaks in the Ozarks. Studies conducted elsewhere in the Ozarks have shown that a prerequisite for uneven-aged management to successfully regenerate oaks is to maintain a relatively large population of oak advance reproduction beneath a relatively low density (<15 m^2/ha in basal area or below B-level stocking) residual overstory (Gingrich 1967, Larsen et al. 1999, Loewenstein 2005). Sustaining oak forests using uneven-aged systems will be more successful on xeric (upper south- and west-facing slopes or ridges) to dry-mesic (upper north- and east-facing slopes) sites. This underscores the importance of light as one of the most significant limiting factors in oak regeneration in the Ozark forests. A closer examination of the demographic (or size structure) change in oak reproduction among the regeneration treatments from no harvest and single-tree selection to clearcutting (that represent gradients in overstory removal or increasing light availability) further reflects the pivotal role of light in oak seedling growth and recruitment.

The no harvest stands showed a decreasing trend in both densities and proportions of oak reproduction within three size classes (size 1: height > 1 m, dbh < 1.3 cm; size 2: 1.3 cm ≤ dbh < 3.8 cm; and size 3: 3.8 cm ≤ dbh < 11.4 cm) (Figure 2B and C). This finding indicated that high stand stocking and lack of periodic management disturbances, resulting in lower available light, had greatly limited the survival and growth of oak seedlings. In 2006, oak reproduction for the no harvest stands averaged 1,192 trees/ha and accounted for 10% of the total understory reproduction. The concave distribution (3:1:3) of oak reproduction by size class suggests that light and competition from nonoak species greatly limited the growth and recruitment of small-sized seedlings (Figure 2B). Although the canopy disturbances created by single-tree and group selection treatments increased oak reproduction densities in size class 1 in an increasing order relative to the no harvest treatment, oak reproduction densities in size classes 2 and 3 only increased slowly and resulted in a highly skewed negative exponential (reverse-J) distribution of oaks by size class (size 1 ≫ size 2 ≥ size 3 with much lower densities of oak reproduction in sizes 2 and 3 relative to size 1). As indicated by canopy closure data, light remains a limiting factor, particularly to the recruitment of oaks from size class 1 into successively larger classes (Figure 2B). Mean canopy closure in 1995 (1 year before the treatment) ranged from 82.4 to 86.2%, and 1 year after the treatments (in 1997), the single-tree selection, group opening, and clearcut treatments greatly reduced mean canopy closure to 59.7, 43.5, and 3.5%, respectively. However, mean canopy closure quickly increased to 69.8, 62.4, and 53.2% in 2001 and was restored to the pretreatment level (82.5, 84.1, and 80.9%) in 2006. This suggests that the improvement in light conditions due to treatments lasts no longer than 10 years. Larsen et al. (1997) has shown that the probability of large oak advance reproduction being present decreases significantly as overstory density increases, and they suggested keeping density at <15 m^2/ha to promote development of large oak seedlings. MOFEP overstory density in single-tree selection stands was near or exceeded this limiting threshold. By 2006, only the clearcut stands maintained a pattern that is typical of a population of trees that is increasing in diameter: size 1 > size 2 > size 3 with a negative exponential distribution of low or moderate skewedness. This fact suggests that large populations of oak reproduction are unlikely to occur unless overstory density, along with midstory and understory density, is greatly reduced through harvesting or other disturbances.

Overstory removal increased both oak and nonoak competitor reproduction densities, but had little effect on their overall proportions. However, further analysis of the proportions of oaks and of their competitors by size class suggested that competition from nonoak species differed by size class and treatment (Figure 2C). In contrast to the clearcut stands, oak reproduction had more competition from nonoak species in all other treatments. This was indicated by the relatively low abundance of large oak reproduction (i.e., oaks in size class 3) in the no harvest stands and in stands treated with uneven-aged methods. When oak seedlings are released by overstory removal, their shoot growth will be slow if they do not have a large root system or if competition from other species overwhelms them (Sander 1972, Hodges and Gardiner 1993). Even though the single-tree and group selection methods applied in this study allowed oak advance reproduction to grow, the light conditions created by these treatments favored regeneration growth of oak competitors, particularly species such as red maple, hickories, and black gum that are more shade tolerant than are oaks. In clearcuts, where light availability was greater, oaks maintained a greater ability to compete for growing space and occupied a greater proportion of the reproduction cohort.

The CART model (Figure 3A) showed that the response of oak regeneration to overstory removal varied with the density of oak advance reproduction and site factors (e.g., aspect). Not only are oaks less shade-tolerant than many of their major competitors, but they also grow at rates slower than or equal to those of their competitors, particularly species such as sassafras, red maple, black cherry (*Prunus serotina* Ehrh.), and ash (*Fraxinus*) on mesic (floodplain and bottomland with gentle slopes) sites in the Ozarks (Shifley and Smith 1982, Crow 1988). Oaks have a conservative growth strategy in which young seedlings invest photosynthates preferentially to root development, producing a high root/shoot ratio and supply of carbohydrates to support rapid shoot growth after a regeneration event (Johnson et al. 2009). Such a survival and growth strategy gives oaks a competitive advantage on dry-mesic or xeric sites where moisture may be limited or in environments characterized by frequent moderate to severe disturbances that cause topkill in trees (Dickson 1991). Therefore, oak reproduction is most often successful when fully released from the overstory on poorer-quality, xeric sites (south- or southwest-facing slopes represented by node VIII in Figure 3A), where adequate natural populations of larger oak advance reproduction are most likely to exist under the canopy of the parent stand; sites that Johnson et al. (2009) called "intrinsic accumulators of oaks" (e.g., node VI in Figure 3A) (Sander 1977). Development of larger oak advance reproduction that has high regeneration potential on more mesic and productive sites often requires silvicultural intervention to "xerify" the sites by reducing stand density and exposing the understory by midstory removal (e.g., application of herbicides or prescribed fire), thereby reversing the process of mesophication (Nowacki and Abrams 2008).

Unlike posttreatment oak reproduction density, the proportion of oak reproduction after timber harvesting was predominately related to the site/stand conditions before treatment (the abundance of oak advance reproduction before harvesting) and to site conditions (e.g., bedrock type) (Figure 4), regardless of the harvesting methods or intensity (Table 3). Stands having abundant oak advance reproduction, particularly when located on sites underlain by the Roubidoux bedrock formation, had a greater proportion of oaks 10 years after harvesting. Four classes of oak reproduction success in term of proportions of oak reproduction were identified based on bedrock formation and advance oak reproduction density: (I) low: advance oak reproduction $<$1,075 stems/ha; (II) moderate-low: advance oak reproduction between 1,075 and 1,875 stems/ha; (III) moderate-high: bedrock formations other than Roubidoux and advance oak reproduction ≥2,175 stems/ha; and (IV) high: Roubidoux formation and advance oak reproduction ≥2,175 stems/ha. A cross-analysis of posttreatment oak reproduction densities (terminal nodes I–VIII in Figure 3A) and proportions (terminal nodes I–IV in Figure 4) by treatment indicated that 80% (8 of 10) stands with the Roubidoux bedrock formation, advance oak reproduction ≥2,175 stems/ha (in the high oak reproduction success class), and treatment by the uneven-aged method had achieved the desired levels (terminal nodes VI, VII, and VIII in Figure 3A) of posttreatment oak regeneration. The soils that are derived from the Roubidoux formation have a coarse fragment concentration comprising gravel- and cobble-size chert and quartzose that occupies 20–30% of the soil's volume (Kabrick et al. 2011). Because these coarse fragments do not store water or release nutrients when they weather, soils formed in parent materials derived from the Roubidoux formation have a low water-holding capacity and have a low nutrient supply (Kabrick et al. 2004, 2008, 2011), and it appears that the occurrence of this formation is a proxy for dry and nutrient-deficient site conditions. These soil conditions limit the abundance of nonoak competitors in the stand, which in turn allows oaks to remain relatively abundant when released by harvesting. Abrams and Sands (2010) also observed that bedrock lithology was an important determinant of oak advance reproduction density at the Mohonk Preserve in eastern New York.

The success rates, measured by the proportion of stands in terminal nodes VI, VII, and VIII in Figure 3A, of the uneven-aged method were only 37% (7 out of 19 stands), 15% (6 of 39 stands), and 0% (0 of 57 stands) for stands in the moderate-high class, the moderate-low class, and the low class, respectively. Comparatively, the success rates of the even-aged method (e.g., clearcut) were much greater, reaching 100% (4 of 4), 100% (9 of 9), and 50% (4 of 8), respectively. In this study, there were no stands treated by clearcut in the high success class, and in this case the success rate could not be estimated (Tables 2 and 3). As a result, these four oak reproduction success (proportion) classes coupled with the eight oak reproduction density classes (Figure 3A) can guide management decisions on the selection of regeneration methods on a specific site/stand. For instance, the uneven-aged regeneration method is limited to stands with the Roubidoux bedrock formation and initial advance oak reproduction density ≥2,175 stems/ha to achieve high posttreatment oak reproduction density. On the low reproduction success sites/stands (oak advance reproduction density <2,175 stems/ha or on sites with bedrock formations other than the Roubidoux), active control of the nonoak competitors will be necessary to promote oak regeneration. On mesic sites where competitors are more abundant, prescribed fires, herbicides, or mechanical methods after timber harvesting to control oak competitors have proven to be necessary to enhance oak survival and growth (Schlesinger et al. 1993, Weigel and Johnson 2000, Spetich et al. 2002, Brose et al. 2008). A broader range of site/stand conditions, however, will be suitable for the even-aged (e.g., clearcut) method (Tables 2 and 3) (Hodges and Gardiner 1993).

Among the four major oak species, white oak reproduction maintained its dominant position after the treatments (Figure 3B), largely because of its greater shade tolerance compared with that of the other associated oak species (Johnson et al. 2009). Black oak displayed a slight trend in increasing density with increasing harvest removal. In contrast, scarlet oak, the most shade intolerant and fastest growing species of upland oaks in our study area, showed a rapid increase in reproduction density during the first 6 years after clearcut harvesting. This was followed by an abrupt decrease by the 10th year after harvest. This pattern of increasing reproduction density followed by a reduction 10 years after harvesting was also observed for white oaks in clearcuts (Figure 3B). The reduction in both scarlet oak and white oak reproduction density was due to the combination of mortality and to recruitment (ingrowth) of the largest oaks into the overstory size class (≥11.4 cm) as observed in the field. Post oak is shade intolerant and slow growing, which explains its insignificant presence and response in this study.

By 2006, the mean ratios of reproduction density between the red oak group (black oak + scarlet oak) and the white oak group (white oak + post oak) were 0.47, 0.40, 0.44, 0.94, and 0.89 for plots within terminals II, V, VI, VII, and VIII, respectively, suggesting that removal of more overstory trees (e.g., clearcut) tended to favor the red oak group species, whereas partial cutting (uneven-aged methods) favored the white oak group species (Groninger and Long 2008, Kabrick et al. 2008). Kabrick et al. (2008) indicated that the regeneration of the red oak group species was also related to ecological land type. They observed that the red oak group species were most abundant after harvesting on the drier ecological land types but that there was no relationship between oak abundance and ecological land type for the white oak group species, which was similar to our results. Others have documented the comparatively rapid growth rate of many of the red oak group species compared to the white oak group species, particularly on drier sites (Campbell 1965, McGee 1981, Hicks 1998).

Conclusions

Compared with the preharvest condition, a decrease in oak seedlings and saplings was observed 2 years after timber harvesting for all of the treatments, mostly due to slashing damage, particularly in group openings and clearcuts. However, an increase in oak reproduction density was observed 6 years after all harvest treatments, which was sustained for up to 10 years after harvest treatments, except for the clearcut treatment. Clearcutting was the only method that significantly increased total oak reproduction (seedling/sapling) density (>10,000 stems/ha) and resulted in reproduction growth into successively larger size classes. This is probably adequate to provide a significant oak component in future stands. The observed decrease in oak reproduction density from year 6 to 10 for the clearcut treatment was primarily due to the stem mortality (i.e., as regenerated stands entered into the stem exclusion stage of development) as well as to the ingrowth of larger reproduction out of reproduction size class 3 and into the overstory size class.

Oak regeneration increased significantly with increasing intensity of overstory oak removal, increasing initial density of advance oak reproduction, and southerly and westerly aspects. The rates of recruitment and development (growth) of oak seedlings under the single-tree selection and group selection methods generally are lower than for clearcutting, although on certain sites (e.g., with higher initial density of oak advance oak reproduction on south-facing slopes), group selection harvests have the potential to regenerate oaks. No treatments changed the relative proportion of oak seedlings and saplings in the understory, suggesting that the nonoak competitors remained as prevalent as before the treatments, and control of competitors after treatments will be crucial to the success of oak seedlings and saplings in future stands. Control of competitors can result from natural events such as periodic droughts or wildfires or through other silvicultural methods.

The proportion of advance oak reproduction and bedrock category can be used to predict the oak regeneration potential of a stand. Based on the four identified oak regeneration potential classes, resource managers and foresters can estimate the proportion of future oak regeneration. Our study indicated that the sites with initial advance oak reproduction density of >2,175 stems/ha and on the Roubidoux bedrock formation have the highest regeneration potential. To regenerate oaks (primarily white oak), uneven-aged silviculture (i.e., group selection method) is applicable on sites with high oak regeneration potential, but even-aged methods showed greater success on sites of low oak regeneration potential. MOFEP used a more classic approach to the single-tree selection method that limited oak reproduction development and recruitment into the overstory and caused species shifts to the more shade-tolerant white oak. Adoption of an approach to the uneven-aged method similar to that of Loewenstein (2005) may permit increased recruitment of red oak species by maintaining a lower density (B-level) overstory with periodic (e.g., every 30 years) reductions to lower stocking to permit recruitment.

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