Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 255 (2008) 3051–3062
Forest Ecology and Management
www.elsevier.com/locate/foreco

Using ecological land types to examine landscape-scale oak regeneration dynamics

John M. Kabrick [a,*], Eric K. Zenner [b], Daniel C. Dey [a], David Gwaze [c], Randy G. Jensen [d]

[a] USDA Forest Service Northern Research Station, 202 Natural Resources Building, Columbia, MO 65211, USA
[b] The Pennsylvania State University, School of Forest Resources, 305 Forest Resources Building, University Park, PA 16802, USA
[c] Missouri Department of Conservation, 1102 S. College Avenue, Columbia, MO 65201, USA
[d] Missouri Department of Conservation, RR 2 Box 198, Ellington, MO 63638, USA

Received 22 June 2007; received in revised form 13 September 2007; accepted 24 September 2007

Abstract

The long-standing interest in regenerating oaks stimulated the development of a number of research studies during the past several decades. Most studies have focused on addressing oak regeneration problems and many of these suggested that oak regeneration failures occur where site conditions favor the establishment and growth of competing species that capture the growing space following crown release. Because ecosystem classification regimes incorporate information about site conditions including many of the biophysical factors that largely govern site quality, some forest scientists have proposed that they be used for predicting oak regeneration dynamics. We used a large data set from a replicated landscape-scale experiment comprising nine, 400-ha forest management compartments to systematically examine oak regeneration dynamics following the application of a range of regeneration methods (clearcutting, group and single-tree selection) across differing ecological land types. We found that species of the red oak group appeared to be regenerating successfully only in stands harvested with clearcutting and that regeneration success was greatest in clearcut stands located on ecological land types of lower site quality where the density of competitors was relatively low. In contrast, species of the white oak group were regenerated with clearcutting and with the combination of group and single-tree selection but their regeneration response did not appear to be related to ecological land type. We conclude that an ecological classification framework is valuable for partitioning the landscape into finer-scale land units each having a similar propensity to (1) accumulate red oak reproduction in advance of harvesting and (2) respond to various regeneration methods each in a uniform manner. This framework was less important for examining species in the white oak group, which had similar regeneration dynamics across land types.

Keywords: Oak regeneration; Silviculture; Landscape-scales; Ecological land type; Ozark Highlands

1. Introduction

Interest in oak (*Quercus* L.) regeneration has prompted the implementation of a large number of research studies over the last several decades. These have served the dual purpose of examining the basic ecology of the oak regeneration process as well as the roles of management methods including harvesting practices, fire regimes, and other cultural practices for regenerating oaks (Johnson et al., 1989; Loftis, 1990; Schlesinger et al., 1993; Brose et al., 1999; Hutchinson et al., 2005). Several symposia and workshops have been held featuring oak regeneration as central themes (Loftis and McGee, 1992; Spetich, 2002; Weigel et al., 2004).

Furthermore, many studies have focused on the long-standing problems associated with regenerating oaks (Loftis and McGee, 1992). Throughout the natural range of oaks, regeneration failures generally occur where non-oaks in the reproduction cohort successfully out-compete oaks for growing space (Lorimer, 1993; Johnson et al., 2002). The reason oaks often fail to capture growing space is due to their growth habit where more photosynthate is initially allocated to root production than to shoot growth (Lorimer, 1993; Johnson et al., 2002). This physiological adaptation allows oaks to develop large root systems and consequently enables them to

* Corresponding author. Tel.: +1 573 875 5341x229; fax: +1 573 882 1977.
E-mail address: jkabrick@fs.fed.us (J.M. Kabrick).

0378-1127/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.09.068

persist on droughty sites and to resprout vigorously following fire, grazing, or other disturbances that kill or injure the shoot (Lorimer, 1993; Johnson et al., 2002). However, this same physiological adaptation also causes oaks to have a slow juvenile shoot growth rate, which is a disadvantage on high quality sites (*sensu* Helms, 1998) where fast-growing competitors can accumulate on the forest floor and/or rapidly capture growing space following crown release (Hodges and Gardiner, 1993).

Johnson et al. (2002) recognized the relationship between site quality and oak regeneration and developed terminology that describes an ecosystem's inherent ability to accumulate oak reproduction. They used the term *intrinsic accumulators* to refer to ecosystems having the natural tendency to accumulate oak reproduction over long periods and *recalcitrant accumulators* to refer to ecosystems where oak reproduction fails to naturally accumulate or persist in the understory. These terms are used to describe the tendency for oak reproduction to become established and remain in the understory of the parent oak stand in the absence of management interventions that favor the establishment of oaks relative to competing species, such as the application of prescribed fire or preparatory and establishment cuts used in the shelterwood method (Helms, 1998).

The natural tendency to accumulate oak reproduction is largely determined by climatic and site conditions, which in turn influence the overall density and composition of competitors. Ecosystems or sites that are intrinsic accumulators are generally dry to xeric and may have moderate to low productivity. These conditions support few understory competitors and sometimes lower overstory stocking allowing oak reproduction to accumulate even in the absence of moderate disturbances. Ecosystems or sites that are recalcitrant accumulators are generally mesic and productive and consequently have well-developed shade-tolerant competitors in the reproduction size class. This in turn prevents the accumulation of oak reproduction under closed canopies or produces fast-growing competitors which outgrow oak reproduction following major canopy disturbances that remove some or all of the overstory.

Although practicing foresters and forest scientists have long recognized the importance of site quality on forest growth and yield, the role of environmental factors on oak reproduction establishment and dynamics has not always been systematically investigated. For example, in North America, the severity of oak regeneration problems differs regionally and is more problematic in the Southern Appalachians than in the Ozark Highlands (Loftis, 1983; Johnson et al., 2002). Even within a region, successful regeneration of oaks is largely explained by the presence of oak advance reproduction, which are the seedlings, seedling sprouts, and small trees generally <4 cm DBH present in the stand prior to applying a regeneration method (Sander, 1972; Loftis, 1983; Beck and Hooper, 1986). The accumulation of oak advance reproduction is related to soil moisture availability (Larsen and Johnson, 1998) and other topographic factors affecting site quality (Carvell and Tryon, 1961; Sander et al., 1984; Loftis, 1990).

Ecological classification systems summarize information about the physical environment, plant community composition, and their interrelationships at multiple scales (Cleland et al., 1997). The most commonly used ecological classification framework used in the United States was developed by the USDA Forest Service (Keys et al., 1995; Cleland et al., 1997) and has been used to hierarchically organize, classify, and map land units from regional to site scales in an ecologically meaningful way based upon climate, geology, physiography, soils, and vegetation information (Table 1). This framework has been used to classify the United States to the ecological subsection level (Keys et al., 1995) and to classify many national and state forests as well as other public and private lands at finer scales (Hix, 1988; Van Kley, 1993; McNabb et al., 1999; Dolan and Parker, 2005).

Ecological classification systems are generally used for mapping land areas, identifying potential natural communities, and predicting the responses of forest ecosystems to natural and management-imposed disturbances (Dolan and Parker, 2005). Consequently, ecological classification is a useful management tool for both setting management objectives and implementing management regimes. However, because ecological classification systems incorporate information about the biophysical factors largely governing site quality, they likely provide a suitable framework for systematically examining oak regeneration dynamics from local scales (e.g., among stands within landscapes) to broad scales (e.g., among ecological sections and subsections). Larsen and Johnson (1998) suggested that ecological classification would be useful for silviculturists working in oak-dominated forests and woodlands by providing

Table 1
Ecological units used to classify forest ecosystems in the United States[a]

Scale	Ecological unit	Map scale (reference)	Differentiating criteria
Ecoregion	Domain, division, province	1:30 to 1:100 million (subcontinental)	Climate zones and climate patterns; geographical associations; vegetation types
Subregion	Section, subsection	1:125,000 to 1:1 million (multi-state)	Subregional climate patterns; broad geological patterns; vegetation types
Landscape	Land type association	1:100,000 (within-state)	Major landforms and general topography; soil associations; vegetation associations
Land unit	Ecological land type, ecological land type phase	1:24,000 (multiple to single stands)	Minor landforms and slope positions, slope-aspect, soil series, plant communities

[a] Adapted from Cleland et al. (1997) and Johnson et al. (2002).

a mechanism for identifying how different species of oaks respond to regeneration methods. However, the utility of the ecological classification framework for predicting oak regeneration dynamics has not been systematically evaluated.

The Missouri Ozark Forest Ecosystem Project (MOFEP) provided an opportunity to systematically examine the interaction between oak regeneration dynamics, ecological land types (ELTs), and regeneration methods at stand and landscape scales (i.e., 10–100 s of ha). MOFEP was initiated in 1989 by the Missouri Department of Conservation (MDC) to examine the cumulative effects of even-aged, uneven-aged, and no-harvest management systems on the sustainability of the flora and fauna of upland oak ecosystems. It is a fully replicated experiment designed to extend for a least one 100-year rotation from the first harvest entry in 1996. It was initiated largely because the impacts of forest management on songbirds and other non-commodity forest attributes such as diversity of native plant and animal species at large scales have been poorly understood in the Missouri Ozarks (Brookshire et al., 1997). At MOFEP, management systems are used in the same manner as operationally practiced by the Missouri Department of Conservation. Here, three management systems (e.g., even-aged, uneven-aged management, or no-harvest management) were each applied to three administrative compartments ranging in area from 300 to 500 ha. Within an administrative compartment, the same regeneration and tending treatments were applied to stands that differed in soils, plant communities, site quality, and consequently, ELTs.

Our main objective was to examine the interaction between each of three regeneration methods (clearcut, the combination of single-tree and group selection, single-tree selection) and ELT with respect to the regeneration of oaks. These regeneration methods provide a range of canopy cover from nearly open to nearly closed. At MOFEP they were implemented across a wide range of ELTs of differing site qualities. We hypothesized that oak regeneration dynamics resulting from a single regeneration method would differ by ELT within the same landscape. We proposed that the understanding of the stand-level interaction between regeneration method and ELT would further our understanding of oak regeneration dynamics at the landscape scale.

2. Methods

2.1. The MOFEP study sites

MOFEP consists of nine forest administrative compartments ranging in size from 314 to 516 ha, primarily within the Current River Oak Forest Breaks and the Current River Oak-Pine Woodland Hills landtype associations of the Ozark Highlands section (approximately 37°6′N, 91°7′W; Kabrick et al., 2000). In the study region, the mean annual precipitation is 115 cm and the annual temperature is 13.5 °C. During the growing season, the average daily minimum temperature is 13.8 °C and the average daily maximum is 28.7 °C. These compartments were initially selected because they contained mature, second-growth forests largely free of manipulation for >40 years, were the size of administrative compartments commonly used by the MDC for managing forests, and were in close proximity to each other. Prior to the study, compartments were subdivided into stands averaging 5 ha in size and having uniform, slope and slope-aspect and vegetation composition (Brookshire et al., 1997).

A detailed landscape-scale soil mapping and characterization project was conducted on MOFEP in 1994–1995 (Meinert et al., 1997; Kabrick et al., 2000), which included characterizing important physical and vegetation characteristics of each study compartment. These data were used in conjunction with other data collected elsewhere in the region to classify the sites at the ELT and phase levels (Nigh et al., 2000; Grabner, 2002). In this region, ELTs are defined by geologic formation, slope position and landform, slope aspect, soil depth to bedrock, and the presence of indicator plant species. To examine the interaction between regeneration method and ELT at the stand level, we selected the four most prominent but contrasting ELTs (ELTs 3, 4, 5, and 6) common to all nine MOFEP compartments (Table 2). Ecological land types 3 and 5 occur on south- and southwest-facing backslopes and ELTs 4 and 6 occur on

Table 2
Ecological land types (ELT) compared in this study

Ecological land type	Characteristics	Extent in study area (%)
3. Exposed Roubidoux/upper Gasconade backslopes	Slopes: >20%; aspect: 135–315°; soils: deep, gravelly or cobbly with low base saturation; overstory: *Quercus velutina* Lam., *Q. coccinea* Muenchh., *Q. alba* L., *Pinus echinata* Mill.; ground flora: *Vaccinium* spp., *Desmodium* spp.; *Q. velutina* Lam. Site $index_{50}$ = 20 m	21
4. Protected Roubidoux/upper Gasconade backslopes	Same as ELT 3 except aspect: 315–135°; overstory: *Q. velutina* Lam., *Q. coccinea* Muenchh., *Q. alba* L.; ground flora: *Vaccinium* spp., *Desmodium* spp., *Smilacena* spp.; *Q. velutina* Lam. Site $index_{50}$ = 22 m.	18
5. Exposed lower Gasconade/Eminence backslopes	Slopes: >20%; aspect: 135–315°; soils: deep, gravelly or cobbly becoming clayey with depth and having moderate base saturation; overstory: *Q. alba* L. *Q. velutina* Lam.; ground flora: *Vaccinium* spp., *Desmodium* spp.; *Q. velutina* Lam. Site $index_{50}$ = 21 m	10
6. Protected lower Gasconade/Eminence backslopes	Same as ELT 5 except aspect: 315–135°; soils: deep, gravelly or cobbly with moderate base saturation; overstory: *Q. alba* L. dominates; ground flora: *Cimicifuga* spp., *Desmodium* spp.; *Q. velutina* Lam. Site $index_{50}$ = 23 m	9

ELT names include slope aspect (for slopes >20%), bedrock formation, and slope position. Overstory or ground flora species are either dominant or diagnostic and are listed in order of importance. Detailed descriptions of the ELTs are provided by Nigh et al. (2000).

north- and northeast-facing slopes. Oaks presently are the dominant overstory species on all four ELTs with only minor compositional differences among them. These ELTs differ in water- and nutrient-supply capacities, site quality, and native vegetation. Together, these four ELTs occupy about 60% of the land area in the study sites.

2.2. MOFEP study design and harvest treatments

When MOFEP was initiated, groups of three compartments were allocated into statistical ''blocks'' by spatial proximity. Three compartments within each block were randomly assigned one of three treatments: (1) even-aged management with harvesting by clearcutting and intermediate thinning; (2) uneven-aged management with harvesting using single-tree selection and the combination of single-tree selection and group selection; and (3) no-harvest management. Sheriff and He (1997) provided a more detailed description of blocking and treatment allocation to compartments.

The even-aged management treatment uses clearcutting with reserves as the principal means of stand regeneration (Brookshire et al., 1997). With this method approximately 10% of the area in a forest compartment is initially designated as ''old growth'' and excluded from future harvesting. During each entry, about 10–15% of the remaining area in the compartment is clearcut (with reserves) in stands located within each even-aged compartment. Because reserve trees are retained, the stands are only nominally even-aged. However, only a small number of reserve trees are retained and they comprise oaks and other hardwoods are left to provide food and cover for wildlife or shortleaf pine to provide seed for natural regeneration and number fewer than 10–20 per ha and are generally >30 cm DBH. Thinnings (intermediate cuttings) are conducted periodically within stands to improve quality and increase growing space for residual trees. The thinning method used in Ozark forest stands varies with the overall quality of the standing timber. Most stands have a history of mismanagement before MDC ownership that has left poor-quality timber. Commonly a combination of free thinning and selection thinning (*sensu* Helms, 1998) is used to improve the stand. Rotation lengths for even-aged compartments are approximately 100 years with a 15-year entry. It is important to note that even though stands in compartments under even-aged management are nominally even-aged, at the compartment scale they are uneven-aged because only regenerating 10–15% of the compartment during each entry creates a mosaic of age and size classes over time.

Uneven-aged treatment follows the guidelines developed by Law and Lorimer (1989) and includes a combination of group selection and single-tree selection on a 15-year cutting cycle for timber harvest and forest regeneration. Just like with even-aged management, approximately 10% of the forest compartment is initially designated as ''old growth.'' The remaining area is grouped into stands of 8–32 ha. Within stands, group selection methods are used to create openings to regenerate shade-intolerant species. These group openings are approximately 1–2 tree heights in diameter, depending on aspect. At MOFEP, they are 21 m (0.03 ha) on south-facing slopes, 32 m (0.08 ha) on ridge tops, and 43 m (0.15 ha) on north-facing slopes. The total land area of openings is to sum to about 5% of the total harvested area. Elsewhere in the stand, single-tree selection is used with harvest objectives set by the desired residual basal area (B), the largest diameter to be left in the stand (D), and the change across consecutive diameter classes (q), sometimes referred to as the ''BDq'' method (Guldin and Baker, 1989). At MOFEP, the target residual basal area (B) is equivalent to B-level stocking (about 58%) with adjustments made for logging damage (Roach and Gingrich, 1968). The target largest diameter (D) is about 45 cm DBH in stands of low site quality to 65 cm DBH in stands of high site quality. The target q-value (q) averages 1.5 but can range from 1.3 to 1.7. For all harvesting, re-entries coincide with those of even-aged treatments. On uneven-aged sites, the B, D, and q were selected to create similar diameter distributions on a forest-wide basis as under even-aged management (see Brookshire et al., 1997).

The no-harvest management treatment, as the name implies, will not be harvested. Wildfires are suppressed and natural events such as tornadoes, fires, insect and disease outbreaks are treated the same as on any other forest land owned by the MDC, except that salvage harvests will not occur. At MOFEP, this treatment serves as an experimental ''control'' to compare with the two other management practices.

During the first harvest entry conducted between May 1996 and May 1997, 5600 m^3 of timber were harvested on the three even-aged sites (20 m^3 per harvested ha or 5 m^3 per site ha) and 8000 m^3 were harvested on the three uneven-aged sites (9 m^3 per harvested ha or 5 m^3 per site ha). On even-aged sites, 11% of the area was clearcut and 15% was thinned. On uneven-aged sites, 57% of the area was harvested with selection and group methods. Regardless of harvest method, black oak and scarlet oak in combination comprised 60% of the harvested basal area; white oak and post oak accounted for an additional 20–30%. On a percentage basis, harvested trees included more scarlet and black oak basal area and less white oak and shortleaf pine basal area than the sites had before harvest. In clearcut stands, harvesting removed about 93% of the basal area with the remaining 7% comprising the reserve trees. Canopy cover was 83–86% prior to harvesting and was reduced to 57% in single-tree selection stands, 40% in single-tree and group selection stands, and 3% in clearcut stands. Details can be found in Kabrick et al. (2002).

2.3. Woody vegetation sampling

Woody vegetation on MOFEP was initially sampled in 1991 and has been re-inventoried approximately every 3–4 years since. Woody vegetation was sampled during the dormant season in 648 permanent 0.2-ha plots distributed approximately equally among the nine MOFEP compartments. At least one plot was established in each stand on all compartments. Within permanent plots, live and dead trees $\geq$11 cm DBH were sampled in 0.2-ha circular plots; trees between 4 and 11 cm DBH were sampled in four 0.02-ha circular subplots; trees at least 1 m tall and less than 4 cm DBH were sampled in four, 0.004-acre circular subplots nested within the 0.02-ha subplots. Characteristics recorded for each tree included species, DBH (or height class for trees <1.37 m tall), status (e.g., live, dead, den, cut, blow-down), and crown class (e.g., dominant, codominant, intermediate, suppressed). Plot and subplot data were combined to obtain plot averages by DBH or size class and all values were converted to a per ha basis.

Pre-harvest inventories showed that oaks are the dominant trees on the MOFEP sites and four oak species, white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), and post oak (*Q. stellata* Wangenh.) comprise 71% of the basal area (Table 3). Other oaks found at MOFEP include chinkapin oak (*Q. muehlenbergii* Engelm.), blackjack oak (*Q. marilandica* Muench.), Shumard oak (*Q. shumardii* Buckl.), and northern red oak (*Q. rubra* L.), but in combination they comprise only 1% of the basal area. Shortleaf pine (*Pinus echinata* Mill.) (8%), pignut hickory [*Carya glabra* (Mill.) Sweet] (4%), black hickory (*C. texana* Buckl.) (4%), mockernut hickory (*C. tomentosa* Poir. Nutt.) (4%), flowering dogwood (*Cornus florida* L.) (3%), and blackgum (*Nyssa sylvatica* Marsh.) (2%) also are in the study area (Table 3).

Table 3
Trees and shrubs inventoried in the study area before harvesting

Scientific name	Common name	Basal area ($m^2\ ha^{-1}$)	Number per ha
Quercus velutina Lam.	Black oak	5.33	143
Quercus coccinea Muenchh.	Scarlet oak	4.67	121
Quercus alba L.	White oak	4.51	321
Pinus echinata Mill.	Shortleaf pine	1.84	52
Quercus stellata Wangenh.	Post oak	1.33	54
Carya glabra (Mill.) Sweet	Pignut hickory	0.87	121
Carya texana Buckl.	Black hickory	0.83	109
Carya tomentosa Poir. Nutt.	Mockernut hickory	0.78	138
Cornus florida L.	Flowering dogwood	0.74	862
Nyssa sylvatica Marsh.	Black gum	0.53	212
Quercus muehlenbergii Engelm.	Chinkapin oak	0.14	12
Quercus marilandica Muenchh.	Blackjack oak	0.11	7
Acer rubrum L.	Red maple	0.09	133
Sassafras albidum (Nutt.) Nees	Sassafras	0.09	257
Juglans nigra L.	Black walnut	0.07	2
Ulmus rubra Muhl.	Slippery elm	0.07	49
Ulmus alata Michx.	Winged elm	0.07	47
Fraxinus americana L.	White ash	0.05	44
Juniperus virginiana L.	Red cedar	0.02	7
Acer saccharum Marsh.	Sugar maple	0.02	7
Quercus shumardii Buckl.	Shumard oak	0.02	2
Quercus rubra L.	Northern red oak	0.02	<1
Carya cordiformis (Wangenh.) K. Koch	Bitternut hickory	0.02	2
Ulmus americana L.	American elm	0.02	10
Rhamnus caroliniana Walt.	Carolina buckthorn	0.02	89
Cercis canadensis L.	Redbud	0.02	40
Morus rubra L.	Red mulberry	<0.02	10
Diospyros virginiana L.	Persimmon	<0.02	15
Amelanchier arborea (Michx. f.) Fern.	Serviceberry	<0.02	17
Crataegus spp.	Hawthorn	<0.02	10
Prunus serotina Ehrh.	Black cherry	<0.02	12
Bumelia lanuginosa (Michx.) Pers.	Gum bumelia	<0.02	7
Carya ovata (Mill.) K. Koch	Shagbark hickory	<0.02	<1
Celtis occidentalis L.	Hackberry	<0.02	22
Viburnum rufidulum Raf.	Rusty black haw	<0.02	17
Fraxinus pennsylvanica Marsh.	Green ash	<0.02	5
Carpinus caroliniana Walt.	Hornbeam	<0.02	7
Gleditsia triacanthos L.	Honey locust	<0.02	<1
Prunus americana Ehrh.	Wild plum	<0.02	2
Ostrya virginiana (Mill.) K. Koch	Ironwood	<0.02	<1
Asimina triloba (L.) Dunal	Pawpaw	<0.02	20
Rhus copallina L.	Winged sumac	<0.02	2
Celtis laevigata Willd.	Sugarberry	<0.02	2
Celtis tenuifolia Nutt.	Dwarf hackberry	<0.02	5
Rhus glabra L.	Smooth sumac	<0.02	2
Elaeagnus umbellata Thunb.	Autumn olive	<0.02	<1
Robinia pseudoacacia L.	Black locust	<0.02	<1
Staphylea trifolia L.	Bladdernut	<0.02	<1

Includes all plants >1 m tall.

2.4. Data and analysis

To evaluate the effects of the regeneration methods, we compared the oak reproduction density prior to the first harvest entry to the post-harvest densities determined from three consecutive inventories completed in 1998, 2002, and 2006. We grouped the species into four groups: White oaks (Section Quercus), red oaks (Section Lobatae), competitors, and other species. The white oak group predominantly comprised white oak but also included some post oak and chinkapin oak. The red oak group predominantly comprised scarlet oak and black oak but also included northern red oak, Shumard oak, and blackjack oak. Red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.), and sassafras [*Sassafras albidum* (Nutt.) Nees] were grouped as ‘‘competitors’’ because the abundances of these species increased greatly following harvesting and they strongly competed for growing space for many years after crown closure. The group ‘‘other species’’ comprises the remaining tree species. These species do compete for growing space but are generally viewed as only a temporary problem for oak regeneration before crown closure (Johnson et al., 2002).

We conducted a randomized complete block analysis of split plots in space (e.g., ELTs within compartments) and time (e.g., repeated measures) as outlined by Steel et al. (1997) to examine the fixed effects of regeneration method, ELT, time since harvest, and all of the first-order interactions among these effects on the density of oaks in the large reproduction size class (trees at least 1 m tall and less than 4 cm DBH). To do this, we used PROC MIXED (SAS version 9.1, SAS Institute, Inc., Cary, NC, USA). Because of the MOFEP design, we were able to statistically examine four regeneration methods including (1) clearcutting; (2) single-tree selection; (3) the combination of single-tree selection and group selection when both were used in a single stand; and (4) no-harvest. Random effects in our analysis included block (i.e., the three MOFEP statistical blocks), block × treatment, block within treatment and ELT, block × year, and block × treatment × year. Our analysis included the stands within the four most common ELTs that were clearcut (14 stands) in the three even-aged compartments, harvested with single-tree selection (25 stands) or the combination of single-tree and group selection (43 stands) in the three uneven-aged compartments, and the unharvested stands within all nine compartments (222 stands). All estimates were averaged by block before analysis. We examined the effects of treatment, ELT, and time, but we were particularly interested in examining the differences among regeneration methods over time and by ELT over time. To do this, we examined treatment × time and treatment × time × ELT interactions. For significant interactions ($\alpha = 0.05$), differences between individual (least square) means were determined using Fisher’s least significant difference (LSD).

For clarity, we followed the conventions of Johnson et al. (2002) and used the term ‘‘regeneration’’ when discussing the process of regenerating a forest and the term ‘‘reproduction’’ when discussing the actual plants being regenerated. The term ‘‘advance reproduction’’ refers to the seedlings, seedling sprouts, and small trees (<4 cm DBH) that have accumulated prior to regeneration harvests. In this paper, large reproduction refers to the trees that are >1 m tall but <4 cm DBH.

3. Results

The pre-harvest density of oaks in the large advance reproduction size class ranged from 109 to 217 trees per ha

Table 4
Density of tree species >1 m tall and less than 4 cm DBH before harvesting

	White oaks[a] (trees per ha)	Red oaks[b] (trees per ha)	Competitors[c] (trees per ha)	Other species (trees per ha)
Block 1 (compartments 1, 2, 3)	130	90	223	1498
Block 2 (compartments 4, 5, 6)	108	110	245	1675
Block 3 (compartments 7, 8, 9)	250	184	116	1588
Overall	163	128	195	1587

Values are compartment-level estimates averaged by statistical block.
[a] Comprises primarily white oak and includes post oak and chinkapin oak.
[b] Comprises primarily scarlet oak and black oak and includes northern red oak, Shumard oak, and blackjack oak.
[c] Comprises blackgum, red maple, and sassafras.

Table 5
Density of tree species >1 m tall and less than 4 cm DBH by ecological landtype before harvesting

Ecological land type[a]	White oaks[b] (trees per ha)	Red oaks[c] (trees per ha)	Competitors[d] (trees per ha)	Other species (trees per ha)
ELT 3	186 a	231 a	147 a	1433 a
ELT 5	200 a	149 ab	102 a	1376 a
ELT 4	93 a	72 bc	187 a	1610 a
ELT 6	155 a	68 c	329 a	1803 a

Significant differences ($P > 0.05$) within species groups among ELTs are indicated by different letters. Ecological land types are arranged in increasing site quality from top to bottom.
[a] Descriptions of ELTs are included in Table 2.
[b] Comprises primarily white oak and includes post oak and chinkapin oak.
[c] Comprises primarily scarlet oak and black oak and includes northern red oak, Shumard oak, and blackjack oak.
[d] Comprises blackgum, red maple, and sassafras.

when averaged across compartments by statistical blocks without regard to ELT. In clearcut stands, oaks contributed approximately 7% of the all trees in the reproduction size class and white oak group species were slightly more abundant than species in the red oak group (Table 4). The principal competitors of oaks in the Ozark Highlands including red maple, blackgum, and sassafras contributed about 9% of the pre-harvest density. We found that the initial reproduction density of red oak group species decreased significantly ($P < 0.05$) as the site quality of the ELT increased (Table 5). The density of competitors and of other species showed similar trends although differences among ELTs were not statistically significant. The pre-harvest density of white oaks in the reproduction size class did not show consistent trends and appeared to be unrelated to ELT.

We found significant interactions between the regeneration method and time since harvest for both the white oak group ($P < 0.001$) and red oak group ($P < 0.001$). The reproduction density of oaks increased with increasing harvest intensity (Fig. 1a and b). For both the white oaks and red oaks, the reproduction density increased most rapidly in stands that were harvested by clearcutting. In clearcut stands, the oak reproduction density decreased by year 10 because of the combination of competition-induced mortality in the reproduction size class and recruitment of a large number of the oaks into a larger size class. When we examined oak densities in the larger size class (i.e., >4 cm DBH), we found little evidence of recruitment in stands harvested with the other methods.

White oaks responded differently than the red oaks to the other regeneration methods. For white oaks, the reproduction density in stands harvested with the combination of single-tree and group selection was significantly ($P < 0.05$) greater than in stands harvested with single-tree selection or in unharvested stands by the sixth year following harvesting (Fig. 1a). White oak reproduction was nominally but not significantly greater in stands harvested with single-tree selection compared to unharvested stands. For red oaks, the reproduction density in stands harvested with the combination of single-tree and group selection or with single-tree selection was not significantly different than in unharvested stands. Regardless of regeneration method, oaks remained only about 13–22% of the total stem

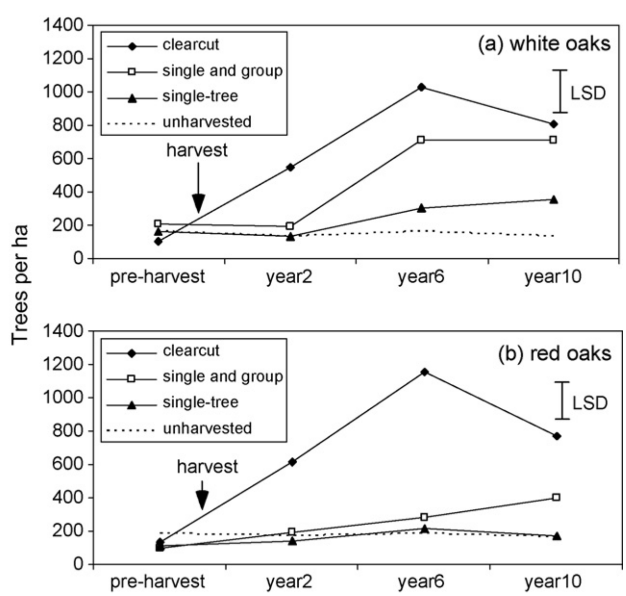

Fig. 1. Density of trees >1 m tall and <4 cm DBH for (a) the white oak group (white oak, post oak, and chinkapin oak) and (b) the red oak group (scarlet oak, black oak, northern red oak, Shumard oak, and blackjack oak) pre-harvest and for 10 years following harvests conducted in 1996. The vertical bar in each panel indicates the magnitude of the least significant difference (LSD, $\alpha = 0.05$).

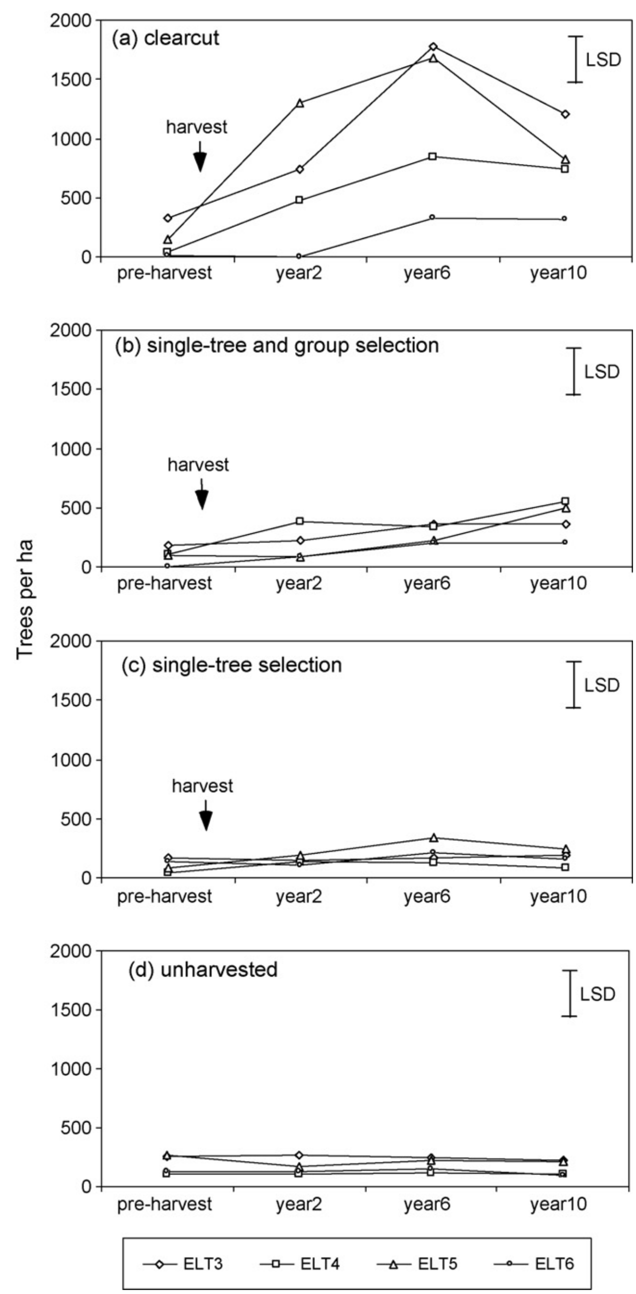

Fig. 2. Density of red oak group (scarlet oak, black oak, northern red oak, Shumard oak, and blackjack oak) trees >1 m tall and <4 cm DBH by ecological land type (ELT) pre-harvest and for 10 years after harvesting in 1996. Harvesting methods included (a) clearcuting; (b) the combination of single-tree and group selection; and (c) single-tree selection; compared to (d) unharvested stands. The ELTs are defined in Table 2. The vertical bar in each panel indicates the magnitude of the least significant difference (LSD, $\alpha = 0.05$).

Table 6
Proportion of tree species >1 m tall and less than 4 cm DBH by regeneration method 10 years following harvesting

	White oaks[a] (%)	Red oaks[b] (%)	Competitors[c] (%)	Other species (%)	All (trees per ha)
Clearcut	7	6	19	68	12587
Single-tree and group selection	14	8	13	65	5204
Single-tree selection	9	4	17	70	3899
Unharvested	6	7	26	61	2260

[a] Comprises primarily white oak and includes post oak and chinkapin oak.
[b] Comprises primarily scarlet oak and black oak and includes northern red oak, Shumard oak, and blackjack oak.
[c] Comprises blackgum, red maple, and sassafras.

density by year 10, about the same proportion as in unharvested stands (Table 6).

For the red oak reproduction density, we found a significant ($P < 0.001$) treatment × ELT × time interaction (Fig. 2). In clearcut stands, red oak reproduction density increased more rapidly and remained at higher levels throughout the 10-year-period following harvesting on the ELTs having lower site quality (ELTs 3 and 5) than on those having higher site quality (ELTs 4 and 6). In the clearcut stands, the density of the principal competitors (red maple, blackgum, and sassafras) also increased. However, unlike for the red oaks, the principal competitors increased the most in the ELTs having higher site quality (Fig. 3). For white oaks, there was no significant treatment by ELT by time interaction ($P = 0.13$). However, the white oak reproduction density in clearcut stands located on ELT 3 was nominally greater than on the other ELTs following harvesting (Fig. 4).

4. Discussion

4.1. Accumulation of advance reproduction

Much of the oak regeneration research has shown that the presence of large oak advance reproduction (i.e., seedlings, seedling sprouts, and small trees >1 m tall and <4 cm DBH) that have become established before harvesting, is critical for successful oak regeneration (Sander et al., 1984; Loftis, 1990; Johnson et al., 2002). This has led to the development of guidelines recommending threshold densities of advance

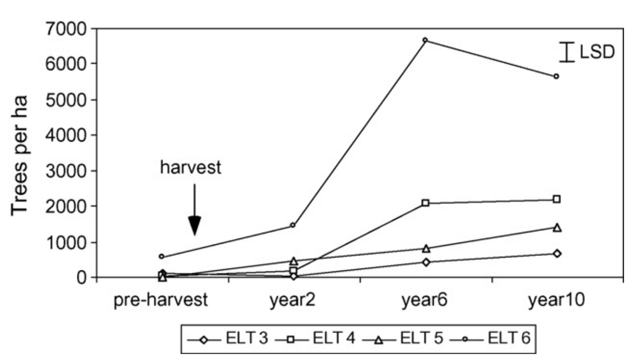

Fig. 3. Density of principal oak competitors (blackgum, red maple, and sassafras) >1 m tall and <4 cm DBH by ecological land type (ELT) pre-harvest and for 10 years after clearcutting in 1996. The ELTs are defined in Table 2. The vertical bar indicates the magnitude of the least significant difference (LSD, $\alpha = 0.05$).

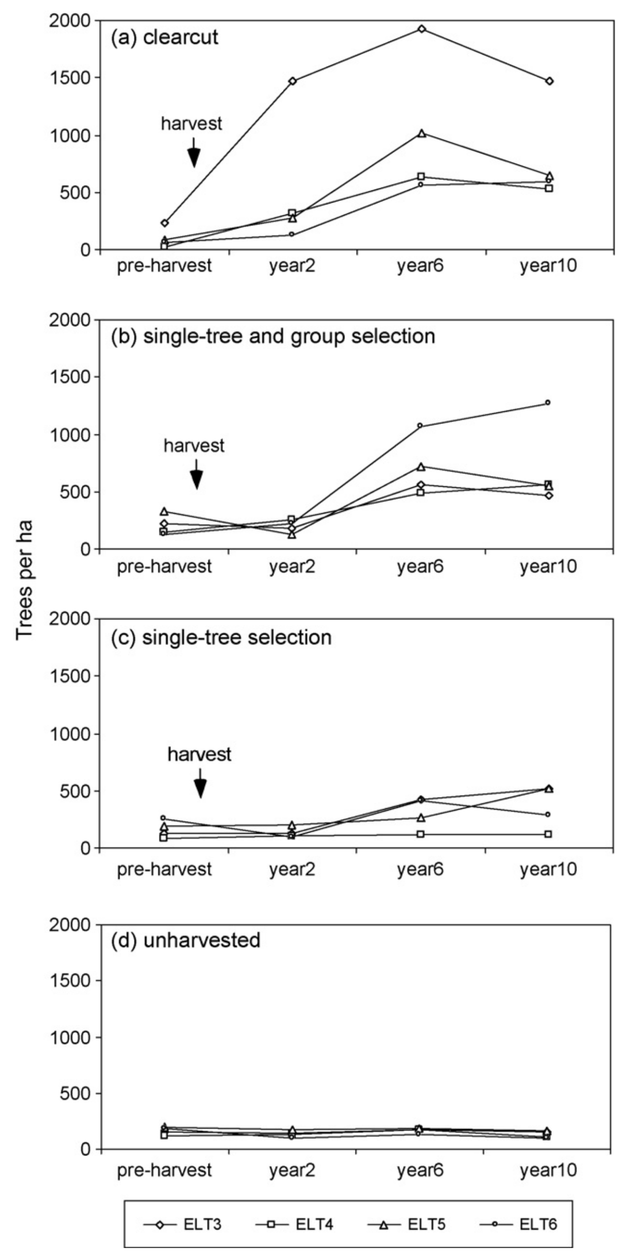

Fig. 4. Density of white oak group (white oak, post oak, and chinkapin oak) trees >1 m tall and 4 cm DBH by ecological land type (ELT) pre-harvest and for 10 years after harvesting in 1996. Harvesting methods included (a) clearcutting; (b) the combination of single-tree and group selection; and (c) single-tree selection; compared to (d) unharvested stands. The ELTs are defined in Table 2. There were no significant treatment × ELT × time interactions for the white oak group.

reproduction for the Ozark Highlands (Sander et al., 1984), the southern Appalachians (Loftis, 1983) and the Mississippi Alluvial Valley (Belli et al., 1999). The advance reproduction density on our study sites ranged from 109 to 217 trees per ha. This advance reproduction density is about a fifth of the number per ha recommended by Sander et al. (1984) prior to clearcutting in the Ozark Highlands. However, these values are similar to those reported elsewhere in the Central Hardwood Region (Hilt, 1985; Beck and Hooper, 1986). The low density of oak advance reproduction found in our study sites was somewhat surprising because the Ozark Highlands is considered to be an intrinsic accumulator of oaks. Here, the site conditions are generally much drier than in other ecoregions in eastern North America, generally limiting the number of other tree species competing for growing space on the forest floor. There also are relatively few mesphytic and shade-tolerant species such as ironwood (*Ostrya virginiana* L.), downy serviceberry (*Amelanchiar arborea* L.), or sugar maple (*Acer saccharum* L.) in the midstory of these forests shading the forest floor and preventing the accumulation of oak reproduction. However, Johnson et al. (2002) point out that oaks do not necessarily accumulate in large numbers on sites that are considered to be intrinsic accumulators. Rather, sites that are considered to be intrinsic accumulators are those where oak reproduction can persist in the understory for long periods of time and this cannot be determined from a single inventory.

The advance reproduction densities reported in Table 4 represent the average at a scale approaching that of a landscape (i.e., the 3800-ha area comprising the nine administrative compartments). However, the environmental conditions including slope gradient, slope aspect, soil properties, and consequently the site quality vary considerably across this landscape. When we partitioned the landscape into ELTs that account for combinations of these environmental and site variables we found that the density of the red oak advance reproduction varied significantly by ELT (Table 5). Red oak advance reproduction was significantly greater in the ELTs 3 and 5, which generally have a lower water- and nutrient-supply capacity compared to ELTs 4 and 6. We also found a concomitant but nominal inverse relationship between ELT and the density of principal competitors, suggesting that their increased density may have contributed to a large extent to the decreased density of red oak advance reproduction.

We found no relationship between the advance reproduction density of white oaks and ELT (Table 5). The principal species of this group was white oak (*Q. alba*), which is reportedly moderately shade tolerant and generally more shade tolerant than the species in our red oak group, and generally found under a wide range of site conditions (Burns and Honkala, 1990). We suspect that for these reasons the white oak advance reproduction did not differ appreciably among ELTs. Johnson (1992) showed that white oak reproduction accumulated to greater densities under higher overstory stocking levels than did black oak in xeric ecosystems of Michigan, demonstrating the relatively greater shade tolerance of white oak reproduction. We are not aware of studies showing differences in the accumulation of oaks by species group among undisturbed stands of differing site qualities.

Because the successful regeneration of oak stands requires the presence of large (>1 m tall) reproduction before harvesting (Sander et al., 1984; Dey et al., 1996; Johnson et al., 2002), some kind of management-imposed intervention targeting the advance reproduction cohort may be required on mesic sites to increase the density or proportion of oaks. Much has been written about using prescribed fire (Brose and Van Lear, 1998; Brose et al., 1999) for reducing the density of fire-sensitive competitors and increasing the advance reproduction density of oaks. However, the application of prescribed fires on mesic sites without reducing the overstory stocking and thereby increasing the amount of sunlight reaching the forest floor has been largely unsuccessful for increasing the density or the size of oak advance reproduction (see review by Brose et al., 2006). More promising results have been demonstrated where prescribed fires have been used in conjunction with harvesting, particularly when the fire-free period was at least 4 years and the stands were heavily cut as with shelterwoods and clearcuts (Brose et al., 2006). Others have demonstrated the utility of herbicides (Weigel and Johnson, 1998), and mechanical methods for controlling competitors (Johnson et al., 2002) to favor oaks in the reproduction cohort.

4.2. Response to harvesting

The two oak species groups responded slightly differently to harvesting and the differential response to harvesting by the two oak groups appeared to be strongly related to differences in the shade tolerances among the principal oak species in each group. The moderate shade tolerance of species in the white oak group allowed the large reproduction to increase in all regeneration treatments, although increases were modest in stands harvested with single-tree selection compared to those in stands harvested with the combination of single-tree and group selection or by clearcutting. Of the two principal red oak group species, scarlet oak is considered to be shade intolerant (Burns and Honkala, 1990) and black oak is considered to be moderately tolerant, but less so than white oak (Hardin et al., 2001). Accordingly, the red oak reproduction density increased more where harvesting created fairly large openings in the canopy (Fig. 1b). This suggests that the single-tree selection method or a combination of the single-tree and group selection as practiced in this study is causing a compositional shift from a mix of white oak and red oak group species to a composition predominately comprising the white oak group.

Although the clearcut stands had the greatest increases in the reproduction density of both white oak and red oak group species, clearcutting is not the only way to successfully regenerate red oak group species in the Ozark Highlands. Others have shown that oaks can be regenerated with other even-aged methods such as shelterwoods (Schlesinger et al., 1993) and with uneven-aged selection methods that reduced residual stocking to lower than B-level (Larsen et al., 1999). Our findings simply suggest that the red oak group species in our study site need considerably more light in order to recruit into the overstory than is afforded by the single-tree selection method or the combination of the single-tree and group selection methods as implemented in our study.

Even though clearcutting was the only regeneration method to significantly increase the reproduction density of the red oaks, the response differed by ELT (Fig. 2a). On ELTs 3 and 5, which had lower site qualities, clearcutting effectively increased the red oak reproduction rapidly to the point where recruitment into the larger size class began to occur after year 6. However, on ELT 6 where the site quality was greatest, clearcuts performed relatively poorly, largely because the relatively high density of competitors (Fig. 3) shaded the oak reproduction even in the absence of an overstory. This illustrates the increasing importance of the role that competitors in the reproduction layer play as site quality increases. Specifically, in oak stands having low site quality and few competitors, oak reproduction can be developed and recruited by reducing the overstory density. However, in oak stands having high site quality and more abundant competitors, simply reducing the overstory density may not allow red oak reproduction to develop or recruit. This increasing importance of competitors in the reproduction layer was also noted by Schlesinger et al. (1993) in the Ozark Highlands and Loftis (1990) in the southern Appalachians where the shelterwood method was used to regenerate oaks. These authors concluded that as site quality increased, additional methods to favor oaks and control competitors in the reproduction layer were needed. Some of the recommended methods included prescribed fire (Loftis, 1990), herbicides, and mechanical removal (Schlesinger et al., 1993). They also concluded that maintaining denser shelterwood overstories helped to control the competitors when used in conjunction with methods to favor oaks in the reproduction layer.

It may be too soon to know if there will be a red oak regeneration failure on ELT 6 in our study. Research in oaks stands in Ohio showed that the proportion of oaks commonly remains below 20% for more than the first 15 years following harvests, even on poor sites where oaks eventually become the dominant tree species (Hilt, 1985). In clearcut stands on ELT 6, undoubtedly some of the red oaks will eventually recruit into the overstory and there is evidence that some of the white oaks will as well (Fig. 4). Moreover, competing species such as blackgum, red maple, and sassafras will eventually succumb to drought and other mortality agents or will be overtopped by some of the oaks (Johnson et al., 2002). However, it appears that red oaks will not be as abundant in the future in stands on ELT 6 than on stands on ELTs of lower site quality. This also suggests that if maintaining high densities of red oaks is an objective for stands on ELT 6, then different management practices that not only decrease the overstory canopy cover but also decrease the density of competitors in the reproduction size class are required.

4.3. Landscape issues

Landscape-scale studies like MOFEP allow for the examination of the influence of environmental factors such as ELTs on the oak regeneration process across forested landscapes. However, the design of MOFEP certainly is not the most efficient for examining the influence of environmental factors on oak regeneration. Rather, a more efficient design would include a random selection of treated stands replicated by ELT, stand-level site index, or some other representation of site quality. But MOFEP was designed to examine the cumulative effects of commonly used silvicultural practices for sustaining oak ecosystems and how they affect plant and animal communities at large scales. Here, scale must explicitly be considered as most animals use large areas of contiguous forest for both food and cover. For many species of songbirds, mammals, and herptiles, the impacts of harvesting are not confined to the treated stands. Some plant distributions may be affected by harvesting in adjacent or nearby stands, particularly those that rely on seed dispersal by wind or animals. The cumulative effects of silvicultural practices cannot be evaluated at landscape scales by examining a random selection of treated stands. Some of these landscape-level effects of silvicultural practices on forest fauna at the MOFEP study sites have been discussed elsewhere (Gram et al., 2003; Kabrick et al., 2004; Renken et al., 2004).

Our findings suggest that ELTs provide a suitable framework for examining oak regeneration. This was not unexpected because many of the abiotic factors used to define ELTs have been shown to influence oak regeneration success (Carvell and Tryon, 1961). Because ELTs are defined by multiple factors including vegetation, they have the added advantage of accounting for differences in the composition of the competitors of oaks. Ecological classification schemes also offer the advantage of being a part of an internationally recognized framework used in Europe and North America to systematically classify forest land at multiple scales in an ecologically meaningful way. In North America, this framework has been used to classify the USA to the subsection level (Keys et al., 1995) and many state and federal agencies have used this framework to identify land type associations, ELTs, and phases of ELTs (Hix, 1988; Van Kley, 1993; McNabb et al., 1999; Dolan and Parker, 2005). Larsen and Johnson (1998) suggested that this framework should be examined for its utility for understanding and predicting oak regeneration success. Our study shows that ecological classification provides a useful way for partitioning landscapes into ELTs for examining oak regeneration dynamics at stand scales. These scales are most relevant to forest managers operationally implementing regeneration practices.

5. Conclusion

Red oak group species appeared to be regenerating successfully only in stands harvested with clearcutting and that white oak group species were regenerating with clearcutting and with the combination of group and single-tree selection. This suggests that the single-tree selection method or a combination of the single-tree and group selection as practiced in this study will cause a compositional shift from a mix of white oak and red oak group species to a composition predominately comprising the white oak group. The regeneration process for the red oak group species in our study was strongly influenced by the long-lasting effects of site quality and pre-harvest stand conditions which can vary considerably within forested landscapes. On low-quality sites, red oak reproduction was more abundant prior to harvesting and increased more rapidly after harvesting than on high quality-sites. An ecological framework is valuable for partitioning the landscape into finer-scale land units each having a similar propensity to (1) accumulate red oak reproduction in advance of harvesting and (2) respond to various regeneration methods differently. The framework provides a mechanism for purposefully designing long-term replicated experiments to quantify red oak regeneration dynamics and to more systematically determine the factors associated with successes and failures. This framework was less important for understanding regeneration dynamics for species of the white oak group.

Acknowledgments

We thank the staff of the Missouri Department of Conservation for data collection and other assistance and Dr. Mark Ellersieck of the University of Missouri for assistance with the analyses. We also thank two anonymous reviewers who provided many helpful suggestions for improving the manuscript. Funding for this study was provided by the Missouri Department of Conservation and the USDA Forest Service Northern Research Station.

References

Beck, D.E., Hooper, R.M., 1986. Development of southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. 10, 168–172.

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. 23, 133–138.

Brookshire, B.L., Jensen, R., Dey, D.C. 1997. The Missouri Ozark Forest Ecosystem Project: Past, present, and future. In: Brookshire, B.L., Shifley, S.R. (Eds.), Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An experimental Approach to Landscape Research, Gen. Tech. Rep. NC-193, St. Louis, MO, June 3–5, 1997. USDA Forest Service, North Central Research Station, St. Paul, MN, pp. 1–25.

Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28, 331–339.

Brose, P.H., Van Lear, D.H., Keyser, P.D., 1999. A Shelterwood-Burn Technique for regenerating productive upland oak sites in the Piedmont region. South. J. Appl. For. 16, 158–163.

Brose, P.H., Schuler, T.M., Ward, J.S. 2006. Responses of oak and other hardwood regeneration to prescribed fire: What we know as of 2005. In: Dickinson, M.B. (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference, Gen. Tech. Rep. NRS-P-1, Columbus, OH., November 15–17, 2005. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp. 123–135.

Burns, R.M., Honkala, B.M. (tech. cords)., 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. USDA, Forest Service, Washington, DC, vol. 2, 877 p.

Carvell, K.L., Tryon, E.H., 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. For. Sci. 7, 98–105.

Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., Russell, W.E., 1997. National hierarchical framework of ecological units. In: Boyce, M.S., Haney, A. (Eds.), Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources. Yale University Press, New Haven, CT.

Dey, D.C., Johnson, P.S., Garrett, H.E., 1996. Modeling the regeneration of oak stands in the Missouri Ozark Highlands. Can. J. For. Res. 26, 573–583.

Dolan, B.J., Parker, G.R., 2005. Ecosystem classification in a flat, highly fragmented region of Indiana, USA. Forest Ecol. Manage. 219, 109–131.

Grabner, J.K., 2002. Patterns in upland forest vegetation in relation to geology, topography, and soils: An approach to ecological land classification in the southeast Missouri Ozarks. M.S. thesis, University of Missouri-Columbia. 137 p.

Gram, W.K., Porneluzi, P.A., Clawson, R.L., Faaborg, J., Richter, S.C., 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. Cons. Bio. 17, 1324–1337.

Guldin, J.M., Baker, J.B., 1989. Uneven-aged silviculture, southern style. J. For. 96, 22–26.

Hardin, J.W., Leopold, D.J., White, F.M., 2001. Harlow and Harrar's Textbook of Dendrology, 9th ed. McGraw Hill, Boston, 534 p.

Helms, J.A. (Ed.), 1998. The Dictionary of Forestry. The Society of American Foresters, Bethesda, MD, p. 210.

Hilt, D.E., 1985. Species composition of young Central Hardwood stands that develop after clearcutting. In: Dawson, J.O., Majerus, K.A. (Eds.), Proceedings of the 5th Central Hardwood Forest Conference, University of Illinois, Champaign-Urbana, pp. 11–14.

Hix, D.M., 1988. Multifactor classification and analysis of upland hardwood forest ecosystems of the Kickapoo River Watershed, Southwestern Wisconsin. Can. J. For. Res. 18, 1405–1415.

Hodges, J.D., Gardiner, E.S., 1993. Ecology and physiology of oak regeneration. In: Loftis, D.L., McGee, C.E. (Eds.) Oak Regeneration: Serious Problems, Practical Recommendations, Gen. Tech. Rep. SE-84, Knoxville, TN, September 8–10, 1992. USDA Forest Service, Southeastern Experiment Station, Asheville, NC, pp. 54–65.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.

Johnson, P.S., 1992. Oak overstory/reproduction relations in two xeric ecosystems in Michigan. For. Ecol. Manage. 48, 233–248.

Johnson, P.S., Jacobs, R.D., Martin, A.J., Godel, E.D., 1989. Regenerating northern red oak: three successful case histories. North. J. Appl. For. 6, 174–178.

Johnson, P.S., Shifley, S.R., Rogers, R., 2002. The Ecology and Silviculture of Oaks. CABI Publishing, New York, 503 p.

Kabrick, J., Meinert, D., Nigh, T., Gorlinsky, B.J., 2000. Physical environment of the Missouri Ozark Forest Ecosystem Project sites. In: Shifley, S.R., Brookshire, B.L. (Eds.), Missouri Ozark Forest Ecosystem Project: Site History, Soils, Landforms, Woody and Herbaceous Vegetation, Down Wood, and Inventory Methods for the Landscape Experiment, Gen. Tech. Rep. NC-208, USDA Forest Service, North Central Research Station, St. Paul, MN, pp. 41–70.

Kabrick, J.M., Jensen, R.G., Shifley, S.R., Larsen, D.R., 2002. Woody vegetation following even-aged, uneven-aged, and no-harvest treatments on the Missouri Ozark Forest Ecosystem Project Sites. In: Shifley, S.R., Kabrick, J.M. (Eds.), Proceedings of the Second Missouri Ozark Forest Ecosystem Project symposium, Gen. Tech. Rep. NC-227, St. Louis, MO, October 17–18, 2000. USDA Forest Service, North Central Research Station, St. Paul, MN, pp. 84–101.

Kabrick, J.M., Renken, R.B., Kurzejeski, E.W., Jensen, R.G., Gram, W.K., Clawson, R.L., Porneluzi, P.A., Faaborg, J., Fantz, D.K., Grabner, J., Johanson, M., 2004. The Missouri Ozark Forest Ecosystem Project: Findings from ten years of evaluating management effects on forest systems. In: Yaussy, D.A.; Hix, D.M.; Long, R.P.; Goebel, P.C. (Eds.), Proceedings of the 14th Central Hardwood Forest Conference; Wooster, OH, March 16–19, 2004. Gen. Tech. Rep. NE-316, USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 484–496.

Keys Jr., J., Carpenter, C.A., Hooks, S.L., Koenig, F.G., McNab, W.H., Russell, W.E., Smith, M.L., 1995. Ecological units of the eastern United States—first approximation (map and booklet of map unit tables). Technical Publication R8-TP21. U.S. Department of Agriculture, Forest Service, Atlanta, GA.

Larsen, D.R., Johnson, P.S., 1998. Linking the ecology of natural oak regeneration to silviculture. For. Ecol. Manage. 106, 1–7.

Larsen, D.R., Loewenstein, E.F., Johnson, P.S., 1999. Sustaining recruitment of oak reproduction in uneven-aged stands in the Ozark Highlands, Gen. Tech. Rep. NC-203, USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, 11 p.

Law, J.R., Lorimer, C.G., 1989. Managing uneven-aged stands. Central Hardwood Note 6.08., USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN. 6 p.

Loftis, D.L., 1983. Regenerating southern Appalachian mixed hardwood stands with the shelterwood method. South. J. Appl. For. 7, 212–217.

Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. 36, 917–929.

Loftis, D.L., McGee, C.E. (Eds.), 1993. Oak Regeneration: Serious Problems, Practical Recommendations. Symposium Proceedings, Gen. Tech. Rep. SE-84, Knoxville, TN, September 8–10, 1992. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC, 319 p.

Lorimer, C.G., 1993. Causes of the oak regeneration problem. In: Loftis, D.L., and McGee, C.E. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations, Gen. Tech. Rep. SE-84, Knoxville, TN, September 8–10, 1992. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC, pp. 14–39.

McNabb, W.H., Browning, S.A., Simon, S.A., Fouts, P.E., 1999. An unconventional approach to ecosystem unit classification in western North Carolina, USA. For. Ecol. Manage. 114, 405–420.

Meinert, D., Nigh, T., Kabrick, J., 1997. Landforms, geology and soils of the MOFEP study area. In: Brookshire, B.L., Shifley, S.R. (Eds.), Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An Experimental Approach to Landscape Research, Gen. Tech. Rep. NC-193, St. Louis, MO, June 3–5, 1997. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, pp. 56–68.

Nigh, T., Buck, C., Grabner, J., Kabrick, J., Meinert, D., 2000. Ecological Classification System for the Current River Hills Subsection. Missouri Department of Conservation Publication, Jefferson City, MO, 84 p.

Renken, R.B., Gram, W.K., Fantz, D.K., Richter, S.C., Miller, T.J., Ricke, K.B., Russell, B., Wang, X., 2004. Effects of forest management on amphibians and reptiles in Missouri Ozark forests. Cons. Bio. 18, 174–188.

Roach, B.A., Gingrich, S.F., 1968. Even-Aged Silviculture for Upland Central Hardwoods, 335. USDA Forest Service Agriculture Handbook, 39 p.

Sander, I.L., 1972. Size of Oak Advance Reproduction: Key to Growth Following Harvest Cutting. Res. Pap. NC-79, USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, 6 p.

Sander, I.L., Johnson, P.S., Rogers, R., 1984. Evaluating Oak Advance Reproduction in the Missouri Ozarks. Res. Pap. NC-251. USDA Forest Service, North Central Experiment Station, St. Paul, MN, 11 p.

Schlesinger, R.C., Sander, I.L., Davidson, K.R., 1993. Oak regeneration potential increased by shelterwood treatments. North. J. Appl. For. 10, 149–153.

Sheriff, S.L., He, Z., 1997. The experimental design of the Missouri Ozark Forest Ecosystem Project. In: Brookshire, B.L., Shifley, S.R. (Eds.), Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An Experimental Approach to Landscape Research, Gen. Tech. Rep. NC-193, St. Louis, MO, June 3–5, 1997. USDA Forest Service, North Central Research Station, St. Paul, MN, pp. 26–40.

Spetich, M.A. (Ed.), 2004. Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. Gen. Tech. Rep. SRS-73, Fayetteville, AR, October 7–10, 2002. USDA Forest Service, Southern Research Station, Asheville, NC. 311 p.

Steel, R.G.D., Torrie, J.H., Dickey, D.A., 1997. Principles and Procedures of Statistics: A Biometrical Approach, third ed. McGraw-Hill Companies, Inc., New York, 666 p.

Van Kley, J.E., 1993. Ecological classification of the Hoosier National Forest. Dissertation, Purdue University, West Lafayette, IN.

Weigel, D.R., Johnson, P.S., 1998. Planting Northern Red Oak in the Ozark Highlands: A Shelterwood Prescription. Gen. Tech. Brief TB-NC-6.

Weigel, D.R., Van Sambeek, J.W., Michler, C.H. (Eds.), 2005. Proceedings of the 9th Workshop on Seedling Physiology and Growth Problems in Oak Plantings, Gen. Tech. Rep. NC-262, West Lafayette, Indiana, October 18–20, 2004. USDA Forest Service, North Central Research Station, St. Paul, MN. 28p.