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Differential success of oak and red maple regeneration in oak and pine stands on intermediate-quality sites in northern Lower Michigan

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Abstract

Red pine (*Pinus resinosa* Ait.) was the most abundant species in the overstory on intermediate-quality sites in north central Lower Michigan prior to the lumbering era of the late 1800s. Northern red oak (*Quercus rubra* L.) stands that replaced portions of the presettlement pinery are maturing. However, these sites are not returning to the former species composition due to greater abundance of red maple (*Acer rubrum* L.) and white pine (*Pinus strobus* L.) and a lack of oak and red pine regeneration. Our primary objective was to compare the effects of pine and oak cover types on natural oak and red maple regeneration. We measured oak and red maple regeneration in 2001, 10 years after initial application of canopy cover and understory treatments in natural oak stands and red pine plantations on comparable sites. Oak shelterwoods harvested to 25% canopy cover contained significantly more oak seedlings (∼60 cm height) than all other treatments, a majority of which were located in understory treatment plots, where red maple regeneration was mechanically removed. In agreement with other research in oak-dominated stands, these results suggest that light shelterwoods with understory control may be the most viable means of recruiting oaks. Lack of oak regeneration that was progressing toward the canopy in the oak stands compared to the pine stands suggested that, even with understory control after shelterwood cutting, oak may not compete as well in the understory of oak as in pine stands. In contrast, red maple dominated the understory of oak stands, but exhibited poor development and was significantly less abundant in the pine stands. Oak regeneration was also less dense in the pine stands, but free to grow. Factors in the red pine plantations studied, such as increased litter depth, few seed sources, and decreased availability of soil moisture and nitrogen are likely to have reduced the germination and competitive ability of understory red maple stems, thereby benefiting the growth of oak seedlings having lesser shade tolerance. The differential success of oak and red maple regeneration observed in the red pine stands on intermediate-quality sites has led us to suggest that restoration

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of beneficial oak and pine interactions and a shift in focus from regenerating oak beneath oak to regenerating oak beneath pine may be warranted.

Keywords: Oak regeneration; Red maple; Red pine; Northern Lower Michigan; Competition; Forest succession; Restoration

1. Introduction

Classical successional theory emphasized predictable sequences of species over time and stable endpoints, including predictable transitions from pine- to oak-dominated communities and the eventual development of stable, climax oak forests (Clements, 1916; Weaver and Clements, 1929; Odum, 1959). More recently, it has been suggested that the concepts of ecosystem stability and movement of forests toward a successional climax may not hold for many ecosystems (DeAngelis and Waterhouse, 1987; O'Neill, 2001). The predictability of deterministic pathways has also been questioned (Botkin, 1979). In contrast to a classical, unidirectional pathway of succession, Thoreau described reciprocal replacement of oak and pine in 19th century New England (Whitney and Davis, 1986; Abrams, 2001). The presence of oak stands on sites previously dominated by pine, the current development of pine beneath oak stands, and advanced oak regeneration under pine canopies has suggested a possible cyclic relationship between these species (Crow, 1988; Sarnecki, 1990; Johnson, 1992).

It is likely that millions of acres of existing oak forest in eastern North America originated as advanced regeneration beneath a pine canopy (Lorimer, 1992). On intermediate-quality sites in northern Lower Michigan, late 19th century lumbering of the red and white pine resource and subsequent wildfires resulted in an increase of three primary cover types: aspen, oak, and jack pine (Whitney, 1987). Red maple and oak were cited as understory species in 56 and 67%, respectively, of Government Land Office (GLO) surveyor line descriptions in the pine/pine–oak presettlement forest type (Whitney, 1986). Oak became dominant on many sites following the pine-lumbering era and wildfires that burned through an abundance of slash on vast areas of cutover land. The resulting dominance of oak has been attributed less to the removal of the pine stands, and more to the fires that followed (Whitney, 1987). However, prior to the catastrophic fires associated with the lumbering era, certain characteristics of mature pine stands may have influenced the relative abundance and competitive position of understory oak and red maple. Differences in the physiological response to conditions beneath a dense pine canopy may have decreased competitors of oak sufficiently for oak to develop well-established root systems, which would, therefore, have enabled oak to respond with greater vigor than red maple following the removal of the pine overstory and reccurring intense fires.

During the 1930s, the Civilian Conservation Corps reforested the stump fields of northern Michigan with pine, most of which was red pine. This was followed by another wave of red pine plantation establishment in the 1950s and 1960s (MDNR, 2004). As in the presettlement pine forest, oak is a common component of the regeneration layer in many of these pine plantations, particularly after thinning (Sarnecki, 1990).

As they have matured, pine plantations have become a cornerstone for the Michigan softwood forest products industry. Similarly, stands of northern red and white oak have become a prominent resource for the hardwood forest products industry, as well as serving as a critical source of mast and browse for prominent game species, such as wild turkey and white-tailed deer. Due to the dual importance of oak for sustaining profitable industries based on game and hardwood forest products, managers in Michigan and elsewhere have been frustrated for many years by the inability to reliably regenerate northern red oak on sites, where oak is the dominant component of the overstory and maple is a competitor. In the Lake States, as in the southeast (e.g., Cook et al., 1998; Ross et al., 1986), oak regeneration on the low end of the site-quality spectrum has not been particularly problematic. Regeneration of northern pin oak (*Quercus ellipsoidalis* Hill) in communities associated with jack pine (*Pinus banksiana* Lamb.) has been relatively successful along the outwash plain. However, regeneration of northern red oak stands on intermediate site-quality kamic ridges or high site-quality moraines has been notoriously unsuccessful.

The multiple values of oak species and the lack of dependable oak regeneration success on the better sites with aggressive competition have stimulated two decades of field research and examination of several lines of evidence on the causes of, and solutions for, this oak regeneration problem (e.g., Crow, 1988). By the 1980s and early 1990s, increased competition between oak seedlings and species that were either more shade tolerant or faster growing than oak had been forwarded as an explanation for widespread regeneration failures in stands dominated by mature oaks (Lorimer, 1994). It was also hypothesized that several decades of fire exclusion resulting from active efforts to protect the recovering forest resource had resulted in an increase in the dominance of several shade-tolerant or fast-growing competitors, all of which were less tolerant of fire than oak (Abrams, 1992). The hypothesis that an increase in the abundance of several important competitors of oak may be the underlying and pervasive cause for regeneration failures across the eastern U.S. has resulted in a strong research focus on techniques for reducing either the abundance or aggressive height growth of these competitors.

Promising techniques for regenerating even-aged, oak-dominated stands include inhibiting the development of shade-intolerant competitors through the shelterwood method of reproduction (Loftis, 1990) and various means of shade-tolerant understory competitor control, such as prescribed burning (Barnes and VanLear, 1998). However, testing of these techniques is incomplete across all regions of the eastern U.S., where oak regeneration failures are occurring. Further, long-term verification that these techniques will eventually produce fully stocked, mature oak stands is lacking.

One decade after initial establishment of treatments in 1991, the objectives of this research were to: (1) test the hypothesis that the relative success of natural oak and red maple regeneration differs between oak and pine cover types; (2) compare the natural regeneration of oak and red maple in clear-cuts, 25% cover shelterwoods, 75% cover shelterwoods, and uncut controls; (3) determine the effects of herb-layer, shrub-layer, and litter removal treatments applied within overstory treatments on natural regeneration of oak and red maple.

2. Methods

Study sites were located on state forestland in Crawford and Roscommon Counties, Michigan within the Grayling Outwash Plain of the Highplains Subsection of the northern Lower Peninsula (Albert, 1995). The soils on these sites were formed in pitted outwash and have an intermediate site index (17–18 m at age 50) for northern red oak. Soil pits excavated within each site provided evidence that the soil physical and chemical properties of the natural oak stands and red pine plantations were comparable (Kim et al., 1996). Analysis of "witness" tree records for these intermediate-quality sites in Crawford and Roscommon counties (Whitney, 1987) has indicated that overstory species composition prior the lumbering era included: 41% red pine (*Pinus resinosa*), 19% white pine (*Pinus strobus*), 18% jack pine (*P. banksiana*), 13% *Quercus* spp., 5% *Populus* spp., and only 0.4% red maple (*Acer rubrum*).

Three natural oak stands and three red pine plantations were studied. Counts of annual rings on stumps following treatment implementation indicated the oak stands were 88–100 years old, and the pine plantations were 59–75 years old in 1991 (Buckley et al., 1998). Canopy structure in oak stands was comprised of three main strata. Red maple occupied the subcanopy but was subordinate to northern red oak, and white pine was present in a suppressed sapling layer beneath both red maple and oak. Scattered white oak (*Quercus alba* L.) grew as co-dominants and very few overstory red pines were present in the oak stands. The canopy in each red pine plantation contained a few scattered red oak, white oak, and red maple. Overstory red maple density was approximately two to three times greater in the oak than in the pine stands. However, red maple in the pine stands were generally larger in size with vigorous crowns located in the canopy.

In 1991, each of the six stands was subdivided into four $66\ \text{m} \times 66\ \text{m}$ (0.44 ha) plots receiving four canopy treatments at random: clear-cut, 25% canopy cover, 75% canopy cover, and uncut (control). Each block (either oak or pine) of four overstory plots measured 1.74 ha in area. In order to reflect the original target levels of canopy cover, the partial cutting treatments will be hereafter labeled according to canopy cover levels just after completion of treatments. It is important to note, however, that canopy cover increased between the time of treatment implementation in 1991 and sampling in 2001. Plots originally harvested to 25 and 75% canopy cover averaged 50 and 90% canopy cover, respectively, in 2001. All partial overstory removal treatments were accomplished by thinning from below in both oak and pine stands, and red maple and suppressed pine were assigned the highest priority as trees to be cut. As a result, most red maple and red pine in the main canopy layer, but in a subordinate position to the taller oaks and pines, were removed. Prior to treatment, relatively few red maple with a dbh greater than 2.54 cm and a crown located below the main canopy occurred in the middlestory. Those middlestory red maples that were present prior to treatment were either cut or knocked down during logging. Advanced red maple regeneration below 2.54 cm dbh was present prior to harvesting and persisted after harvesting was complete. Overstory treatments were further subdivided into four 15 m × 15 m (0.02 ha) understory subplots receiving a control and three treatments at random: shrub-layer removal (all vegetation 25 cm in height up to stems 2.54 cm dbh—predominantly red maple seedlings and bracken fern), herb-layer removal (all vegetation <25 cm in height—predominantly *Vaccinium* spp., *Gaylussacia baccata* (Wang) Koch, *Carex pensylvanica* Lam., and other graminoid species), and removal of litter in small (1 m^2) subplots. Shrub- and herb-layer removal were accomplished by hand over the entire 15 m × 15 m (0.02 ha) area of understory plots assigned these treatments. Litter removal was implemented in 1991 to accomplish an objective of a related study of artificial regeneration on these sites (Buckley et al., 1998), and consisted of removing litter in 1 m^2 square patches centered on spots reserved for planting. Removal of litter from the entire 0.02 ha plot was not feasible due to the large number of herb, shrub, and tree seedling stems that would be damaged, particularly bracken fern fronds. This vegetation also trapped litter and entangled the rake as litter was being removed. As a result, litter was removed from 36 patches, each measuring 1 m^2 in area, which comprised 16% of the entire understory plot area. All understory treatments were implemented in 1991, repeated in 1992 and maintained intermittantly between 1992 and 2001. An 18 m buffer was left between the outside edges of understory treatment plots and the borders of overstory treatment plots in order to reduce edge effects.

In July of 2001, density of oak, red maple, and other natural regeneration was measured according to three size classes: <25 cm in height, 25 cm in height—2.54 cm dbh, and >2.54–10 cm dbh. One-meter square quadrats and 2 and 4 m diameter circular plots were used for sampling each respective size class. Four sampling points were systematically established at four equally spaced planting spots formerly used in the related study of artificial regeneration (Buckley et al., 1998) within each 15 m × 15 m understory treatment subplot. Quadrats and circular plots were nested and centered at each of the four points within each understory treatment subplot. Thus, all 15 m × 15 m subplots for all understory treatments and controls were sampled in the same way for natural regeneration using the same number (four) and size (1 m^2, 2 m diameter, and 4 m diameter) of plots. In litter removal plots, 1 m^2 square sampling plots for small natural regeneration corresponded exactly with the 1 m^2 patches, where litter was removed. Although 1 m^2 litter removal patches also fell within the center of the larger 2 and 4 m diameter regeneration plots used to sample medium and large natural regeneration, litter removal did not impact the entire area contained within these plots.

The experimental design was developed with the intent of using analysis of variance to evaluate treatment effects. All F tests were conducted at the $\alpha = 0.05$ level. Pair-wise comparisons between canopy cover and understory treatments were conducted using Tukey's honestly significant difference (HSD). Separate analyses with reduced models were conducted within types of canopy composition when overall ANOVA indicated significant canopy composition × canopy cover interactions. The overall ANOVA model used to investigate effects of oak and pine stands, canopy cover, and understory treatments was:

$$Y_{i(j)kl} = \mu + \beta_j + \tau_{i(j)} + \gamma_k + \lambda_l + \beta\gamma_{jk} + \beta\lambda_{jl} + \gamma\tau_{i(j)k} + \lambda\tau_{i(j)l} + \gamma\lambda_{kl} + \beta\gamma\lambda_{jkl} + \varepsilon_{i(j)kl}$$

where μ is the overall mean, β_j the canopy composition, $\tau_{i(j)}$ the block (canopy composition), γ_k the canopy cover, λ_1 the understory treatment, $\beta\gamma_{jk}$ the canopy composition × canopy cover, $\beta\lambda_{jl}$ the canopy composition × understory treatment, $\gamma\tau_{i(j)k}$ the canopy cover × block (canopy composition), $\lambda\tau_{i(j)l}$ the understory treatment × block (canopy composition), $\gamma\lambda_{kl}$ the canopy cover × understory treatment, $\beta\gamma\lambda_{jkl}$ the canopy composition × canopy cover × understory treatment, and $\varepsilon_{i(j)kl}$ is the error term consisting of the interaction $\tau\gamma\lambda_{i(j)kl}$; $i = 1, 2, 3$; $j = 1, 2$; $k = 1, 2, 3, 4$; $l = 1, 2, 3, 4$.

The primary focus of this study was to compare regeneration of the oak genus as a whole relative to regeneration of a primary competitor red maple. Due to this focus and the occurrence of some plots with no stems of either white oak or northern red oak, tallies of northern red oak and white oak stems were pooled prior to statistical analyses.

Table 1
Stems per hectare by species of regeneration, size class, and cover type

Regeneration	Size class	Oak stands	Pine stands
Red maple	Small[a]	33100a[b] (5300)[c]	4000b (1300)
	Medium	17888a (1783)	1782b (1050)
	Large	2435a (476)	31b (25)
Oak	Small	19100a (2100)	4600b (1100)
	Medium	10599a (1528)	2451b (414)
	Large	175a (96)[d]	111a (48)[e]

[a] Small: <25 cm height; medium: 25 cm height–2.54 cm dbh; large: >2.54–10 cm dbh.
[b] Across cover types, means within a given size class with the same letters are not significantly different at the alpha = 0.05 level.
[c] 1 standard error is given in parentheses.
[d] All stems incorporated in this mean originated as sprouts from three stumps.
[e] All stems incorporated in this mean are independent genets.

3. Results

Northern red oak and white pine were the most abundant species in their respective genera in the regeneration layer of both oak and pine stands. Northern red oak comprised 85% of all oak regeneration in oak stands and 90% of all oak regeneration in pine stands. The abundance of northern red oak relative to white oak regeneration was consistent with the relative abundance of these species in the overstory. White pine accounted for 98% of the pine regeneration in oak stands and 51% of the pine regeneration in the red pine stands. Overall, density of white pine regeneration was low relative to northern red oak and red maple regeneration.

Red maple regeneration was significantly less abundant in pine than oak stands within all canopy cover treatments and in all size classes (Table 1). All of the large red maple saplings (>2.54–10 cm dbh) in the pine stands were sprouts from two red maple stumps. Except for stump sprouts, none of the red maple stems in the pine stands exceeded 85 cm in height. In contrast, individual red maple stems in clear-cuts and plots thinned to 25% cover in oak stands ranged up to 8 m in height. Oak regeneration 2.54 cm dbh and below was also significantly less abundant in pine than oak stands (Table 1). However, oak stems 2.54 cm dbh and below outnumbered red maple stems of the same size in the pine stands, and there was little difference in the density of oak stems >2.54 cm dbh between the pine and oak stands. All of the large (>2.54–10 cm dbh) oak saplings documented in oak stands (Table 1) were represented by three coppice clumps that bordered sampling locations, and each oak clump was overtopped by red maple. Oak stems >2.54 cm dbh in the pine stands (Table 1) were all independent genets and free to grow.

In the oak stands, the shelterwood treatments and controls contained significantly more small oak seedlings (<25 cm height) than clear-cuts (Table 2). The 75% cover treatment in the oak stands had the highest mean density of small oak seedlings (Table 2), but this mean did not differ significantly from the means for the 25% cover treatment and the uncut controls. The density of medium oak stems 25 cm in height—2.54 cm dbh was significantly greater in the 25% canopy cover treatment than in the control and other treatments in the oak stands (Table 2). Large oak stems (>2.54–10 cm dbh) were restricted to the clear-cut and 25% cover treatments, but differences in large oak stem density across overstory treatments in the oak stands were not statistically significant (Table 2). Small red maple seedling density was significantly greater in uncut oak plots than in clear-cuts and 25% cover plots, and not significantly different from density in plots originally thinned to 75% canopy cover (Table 2). Red maple stem density in the medium (25 cm height–2.54 cm dbh) size class did not differ significantly across overstory treatments in the oak stands (Table 2). Large (>2.54–10 cm dbh) red maple sapling density was significantly greater in clear-cuts and plots originally thinned to 25% canopy

Table 2
Stems per hectare by cover type, species of regeneration, size class, and canopy cover treatment

Cover	Regeneration	Size class	CC[a]	25%	75%	UC
Oak stands	RM	Small[b]	4400b (1200)	10000b (1600)	44000ab (10290)	74000a (5500)
		Medium	9422a (2069)	23491a (2387)	22473a (3661)	16101a (4488)
		Large	4615a (1178)	3661a (1035)	1273ab (430)	127b (95)
	Oak	Small	6900a (1700)	22300b (4500)	25400b (3700)	21900b (4200)
		Medium	10504b (1241)	23555a (3501)	6430b (1050)	1783b (637)
		Large	364a (232)	299a (264)	0a	0a
Pine stands	RM	Small	208a (208)	1875a (877)	4166a (2876)	10000a (3756)
		Medium	66a (66)	5902a (4045)	796a (403)	332a (268)
		Large	0a	133a (102)	0a	0a
	Oak	Small	1500a (1100)	1300a (600)	5200a (1600)	10600a (3100)
		Medium	1592a (700)	4297a (1178)	2196a (668)	1655a (477)
		Large	67a (45)	266a (197)	33a (33)	67a (67)

Means with the same letter are not significantly different across canopy cover treatments at the alpha = 0.05 level.
[a] CC: clear-cut; 25%: thinned to 25% canopy cover; 75%: thinned to 75% canopy cover; UC: uncut.
[b] Size classes, significance, and standard error as in Table 1.

cover than in the uncut plots in the oak stands (Table 2).

Differences were not statistically significant in the pine stands (Table 2), but overstory pine plots thinned to 25% canopy cover had the greatest mean density of oak regeneration 25 cm and greater in height. This distribution resembles the more substantial and statistically significant pattern across canopy cover treatments in the oak stands (Table 2).

Stem density of red maple regeneration also varied across pine replicates. Nearly, all of the red maple 25 cm and greater in height in the pine stands was located in one replicate. Therefore, there were no statistical differences in red maple density among canopy cover treatments in the pine stands (Table 2). Density of red maple <25 cm in height was greatest in uncut plots, while density of red maple 25 cm and greater in height was greatest in plots originally thinned to 25% canopy cover. Thus, patterns in size class and density relative to levels of canopy removal were similar for oak and red maple, with one important exception. Independent red maple stems had not grown into the largest size class in the pine stands, while oak stems were present in the largest size class in all canopy cover treatments and even the uncut control in the pine stands.

There were no statistically significant differences in oak and red maple density across understory treatments. However, the following trends across treatment combinations were noted. In the oak stands, the greatest number of oak stems 25 cm and greater in height occurred in the 25% canopy cover/shrub removal treatment combination (Table 3). In addition, herb-layer removal plots tended to contain less oak regeneration than the shrub-layer removal plots in both shelterwood treatments in the oak stands (Table 3). In contrast, in the pine shelterwoods, density of oak stems tended to be greater in the herb-layer removal treatments than in the shrub-layer removal treatments (Table 3).

Due to the removal of litter in 1 m^2 patches in the litter removal treatment, it is important to note that many medium and large seedlings in the larger 2 and 4 m diameter plots were not impacted at all by litter removal. However, the 1 m^2 subplots used for litter removal coincided with the 1 m^2 plots used to sample small stems <25 cm in height. Although the differences were not statistically significant, density of small red maple stems was 5–15 times greater in these litter removal plots than in the remaining understory treatments within the 75% cover treatment in the pine stands (Table 3). On the other hand, 0 small red maple seedlings occurred in the litter removal treatment within the 25% cover treatment in the pine stands (Table 3). Litter-layer removal treatments also had the highest small oak stem density within the 75% cover treatment in the pine stands, but the differences in density were not as substantial as those in red maple.

Table 3
Stems per hectare by species of regeneration and size class within cover type/shelterwood/understory treatment combinations[a]

Cover	Regeneration	Size class	C	L	H	S
25% Oak cover	RM	Small	**11167**	11167	8333	9500
		Medium	25465	24934	20160	23343
		Large	6499	4509	3846	0
	Oak	Small	39167	12500	18333	19167
		Medium	19099	24404	17772	**32892**
		Large	133	0	133	0
25% Pine cover	RM	Small	3333	0	2500	1667
		Medium	16446	3979	1857	1326
		Large	133	398	0	0
	Oak	Small	2500	0	833	1667
		Medium	3448	2653	**9019**	2122
		Large	133	133	796	0
75% Oak cover	RM	Small	35833	31667	58333	50833
		Medium	18038	30770	18568	22547
		Large	928	1459	2785	0
	Oak	Small	35833	28333	11667	25833
		Medium	7958	6897	3448	7427
		Large	0	133	0	0
75% Pine cover	RM	Small	2500	**12500**	833	833
		Medium	1592	1592	0	0
		Large	0	0	0	0
	Oak	Small	3333	8333	3333	5833
		Medium	2122	1857	3979	796
		Large	0	0	133	0

Bold values indicate noteworthy values.
[a] C: control; L: litter-layer removal within 1 m^2 plots; H: herb-layer removal; S: shrub-layer removal.

Average stem height was fairly consistent in the small (<25 cm) and large (>2.54–10 cm dbh) size classes, but the medium size class (25 cm height–2.54 cm dbh) exhibited some variability across overstory/understory treatment combinations. In the oak shelterwoods, where the red maple was not mechanically removed, oak regeneration was overtopped by two layers of red maple regeneration. Red maple within the medium size class overtopped oak (Table 4) in addition to the layer of red maple within the largest size class. One understory plot in the pine shelterwoods thinned to 25% canopy cover contained medium-sized red maple regeneration. In this plot, red maple was slightly taller than oak. In the pine shelterwoods thinned to 75% canopy cover, oak regeneration was consistently taller than red maple in every understory treatment, while red maple was consistently taller than oak regeneration in oak shelterwoods (Table 4).

4. Discussion

In the oak stands, the vigorous response of red maple sprouts and independent seedlings to canopy

Table 4
Average height of single stem regeneration 25 cm height–2.54 cm dbh within shelterwood/cover type/understory treatment combinations

Cover	Regeneration	C[a]	L	H	S
25% Oak cover	RM	185	131	200	68
	Oak	53	63	82	54
25% Pine cover	RM	50	–	–	–
	Oak	44	55	52	37
75% Oak cover	RM	139	121	165	54
	Oak	66	34	30	34
75% Pine cover	RM	28	28	–	–
	Oak	65	51	57	125

[a] Understory treatments as in Table 3.

removal treatments clearly impeded the progress of co-occurring oak regeneration toward the canopy. In the plots thinned to 25% oak canopy cover, oak stems that were either present at the time of treatment, or established after treatments were applied in 1991, were overtopped by red maple by the time of sampling in 2001. The only exception to this occurred in the understory plots receiving shrub-layer removal, which included removal of red maple regeneration. Although differences were not statistically significant, mechanical removal of understory red maple in shrub-layer removal plots appears to have increased oak density, which suggests that understory control may be beneficial while oak regeneration is becoming established. Application of treatments that only target red maple, however, can be logistically difficult and expensive. Chemical treatment of red maple stumps and mechanical or mechanical and chemical treatment of red maple saplings are intensive and expensive tasks. A combination of prescribed fire and shelterwood cutting has shown promise in the southeast as a technique for favoring oak sprouts over red maple sprouts (Brose and VanLear, 1998). Oak reproduction is top-killed by fire in addition to red maple, however, and previous research suggests that oak stems need to be at least 1.27 cm in basal diameter before they are top-killed in order to obtain oak sprouts that are competitive (Sander, 1971). Several decades are often required to accumulate high densities of well-established oak reproduction (Lorimer, 1994; Larsen and Johnson, 1998), over which time red maple would often dominate the regeneration cohort if left uncontrolled and thus, limit the development of oak seedling size and mass.

The trend in the density of large oak stems across the oak and red pine cover types must be interpreted cautiously, but suggests that reduced red maple recruitment in the pine stands may have contributed to greater density of large oak stems. Differences in density of large oak stems between cover types were not statistically significant (Table 1), but it is necessary to take the origin of these stems into account. Stump sprouting only affected the tallies of stems in the largest (>2.54–10 cm dbh) size class, but substantially impacted the overall density of oak stems in the largest size class in the oak stands. The mean of 175 large oak stems in the oak stands was calculated from three stump sprouts that will likely self-thin to one to three individuals per stump, whereas the mean of 111 large oak stems in the pine stands was calculated from independent genets.

The result that red maple was significantly less abundant in pine than in oak stands on comparable, intermediate-quality sites suggests that factors in the red pine plantations and physiological limitations in red maple may have reduced the ability of red maple to colonize the understory of red pine plantations. Observations of the regeneration layer in many other red pine plantations in the study region before, during, and after this study confirm that low abundance of red maple regeneration in the understory of unthinned red pine plantations is not restricted to the three red pine plantations studied. The larger regeneration size classes are of particular interest in predicting future stand composition. The greater proportional decrease in red maple stems from the small to medium and large size classes than that exhibited by oak in the pine stands (Tables 1 and 2) suggests that survival of red maple into larger size classes is less likely in the pine than oak stands. Further, it is possible that factors beyond red maple seed sources are responsible for the significantly lower density of red maple regeneration in all size classes in the pine than oak stands (Table 1). The lack of significant differences in the density of both red maple and oak in all size classes across overstory treatments in the pine stands (Table 2) could have resulted from low power due to having a rather low number of replicate stands representing each cover type.

Several factors could have contributed to poor red maple regeneration in pine stands, including insufficient seed sources, litter depth, seedbed pH, and the availability of soil moisture and nutrients. There were far fewer reproductively mature red maple within the pine than within the oak stands, which likely affected the local abundance of red maple seed produced and subsequent establishment of red maple seedlings and saplings. By design, the number of reproductively mature stems of other species is quite limited in successful plantings of pine monocultures. As a result, low abundance of reproductively mature red maple is not unique to the three red pine plantations studied. The removal of most of the red maple seed source and other stems in the partial cutting and clear-cutting treatments in the oak stands resulted in release of red maple advanced reproduction that had already become established prior to treatment, and also new reproduction. In the pine stands, a few overstory red maple with crowns adequate for seed production remained following treatment implementation in 1991. Thus, although parent trees necessary for red maple recruitment beneath pine were not abundant, they were present. Further, at the scale of multiple stands, red maple seed sources and seedlings tend to have a ubiquitous distribution on similar parent materials in the region. Therefore, it is plausible that some amount of red maple seed produced by sources in surrounding stands dispersed into the pine and oak stands studied.

The deep litter layers in the red pine plantations studied may have been an additional important factor resulting in significantly less recruitment of red maple in red pine plantations than the oak stands on these intermediate-quality sites. Litter depths were measured in all plots in 1991 for a related study, and litter depths in uncut and 75% cover plots within the red pine stands typically measured 5–6 cm. Red maple samaras are among the lightest maple fruits and are efficiently wind-dispersed. On average, cleaned red maple seeds are 183 times lighter than northern red oak acorns (Schopmeyer, 1974). The light weight of red maple seeds that promotes wind dispersal also translates into small amounts of seed reserves. The limited stored reserves in red maple seeds may have frequently resulted in failure of red maple seedling radicles to penetrate the 5–6 cm litter layer in pine stands in order to reach mineral soil and secure sufficient soil moisture during dry periods. No evidence suggests mechanisms other than the physical environment facilitate red maple seed dispersal into deep litter layers. The result that density of small red maple stems was 5–15 times greater in litter removal plots than in the remaining understory treatments within the 75% cover treatment in the pine stands (Table 3) provides some evidence that thick litter in pine stands may reduce establishment or survival of red maple seedlings. However, these differences were not statistically significant, and the litter removal treatment within the 25% cover treatment in the pine stands had 0 small red maple seedlings (Table 3). Patterns in medium and large red maple cannot be interpreted with respect to litter removal because many of these stems did not fall within the 1 m^2 litter patches, where litter was removed. It is important to note that observations in additional stands within the study region have indicated excellent red maple recruitment and survival in pine plantations on high-quality sites, and sites with high water tables. Thus, the influence of the litter layer on red maple seedling survival may be stronger on intermediate-quality sites, such as those studied than on better sites that have greater nutrient and/or soil moisture levels.

The density of mature oak in the red pine plantations investigated was also very low, but acorns are well-dispersed over the landscape by multiple animal dispersal vectors. Squirrels and other small mammals move acorns tens of meters from seed-bearing trees, and blue jays disperse acorns over several kilometers (Darley-Hill and Johnson, 1981, Barnes et al., 1998). It has been demonstrated that blue jays preferentially cache acorns in forested habitats with relatively open understory structure, such as that in the red pine stands studied (Johnson et al., 1997). Further, extensive cacheing of acorns by European jays and abundant regeneration of oak in mature pine stands has been described in Germany and Spain (Mosandl and Kleinert, 1998; Gomez, 2003).

Although blue jays may be important dispersal vectors for oak, the proximity and abundance of oak seed sources may influence the density of acorns cached in a given stand. Thus, differences in the density of oak regeneration between the pine replicates may have been due to differences in the abundance and proximity of oak seed sources. Similar spatial effects are likely prevalent across the landscape of northern Lower Michigan. It is possible that oak seed source proximity has been affected by the preference of certain sites for planting red pine. Early pine plantations, such as those in the study area were not established on the kamic ridges within the outwash plain, where desirable regeneration of oak and aspen was abundant, but instead reforestation efforts focused on the stump fields that did not convert to deciduous species in the more frost-prone areas (Whitney, 1987). The second wave of plantations was concentrated on higher quality sites (MDNR, 2004). These latter plantations were often established within northern hardwood communities, where the distance to an oak-dominated stand would generally have been even greater than the former plantations.

Analysis of soils in oak stands converted to red pine has indicated that increased acidity may accompany conversion to red pine (Udvig, 1986). It could be suggested that variation in pH effected the differential success in oak and red maple regeneration between oak and red pine stands. Red maple, however, occurs on soils with a wide range of soil pH levels (Walters and Yawney, 1990), and pH of the A/E and Bw horizons did not differ significantly between the oak and pine stands in 1991 (Kim et al., 1996). Additional effects of overstory composition on soil nutrient dynamics may have impacted regeneration. In 1991 and 1992, net nitrogen mineralization was two to three times greater in oak than in pine stands. Despite these differences, N-concentrations, N-content, and N-use efficiency of oak seedlings did not differ between the oak and red pine stands (Kim et al., 1996). N-use efficiency was not analyzed for red maple seedlings, but it is likely that they benefited from greater nitrogen mineralization in the oak stands.

In addition to red maple seed sources, red pine litter, and potential effects of red pine on soil chemical properties, competition for soil moisture may have been greater between mature red pine and red maple seedlings in the pine stands than between mature oak and red maple seedlings in the oak stands. Volumetric soil moisture measurements obtained at the center of all understory plots in 1991 and 1992 suggested 2–4% less soil moisture in pine shelterwoods and uncut plots than in oak shelterwoods and uncut plots (Buckley et al., 1998). Overall, mean volumetric soil moisture values calculated over replicates, overstory treatments, and understory treatments in oak and red pine stands were, respectively, 11.07 and 9.25% in 1991 and 9.73 and 7.79% in 1992 (Buckley et al., 1998). These differences were not significant at the $\alpha = 0.05$ level in either year, although the p-values for the 1991 and 1992 analyses were 0.080 and 0.055, respectively. Working on sandy soils in Michigan, Urie (1959) found that soil moisture depletion was greater in red pine than in oak stands from mid-April to mid-August. Soil moisture depletion by red pine also began several weeks earlier than oak budbreak and the start of moisture depletion by oak in the spring (Urie, 1959). Anderson et al. (1969) suggested that the herb-layer response to canopy reduction in Lake States pine forests is more dependent on moisture than light, indicating that overstory pines may substantially impact the availability of soil moisture for understory regeneration. Greater basal area in pine than oak plots thinned to equal levels of canopy cover and greater depletion of soil moisture by mature red pine than mature oak may have resulted in lesser availability of soil moisture in the pine than in the oak stands.

It can be argued that lesser availability of soil moisture in the pine than oak stands could have negative effects on the regeneration of both oak and red maple. However, oak species and red maple differ in their soil moisture requirements. Red maple tends to have a dual tolerance of both wet and dry site conditions, but exhibits a threshold of tolerance to the driest of sites (Walters and Yawney, 1990). In Michigan, red maple occurs in both deciduous swamp and dry-mesic pine or oak–pine forests. It can be dominant in the bottomlands, but is generally restricted to a subordinate competitive position on upland sites (Barnes and Wagner, 1981). Upland oak species have multiple adaptations to drought (Abrams, 1990), and have been demonstrated to maintain high rates of photosynthesis during drought conditions (Reich and Hinckley, 1980). Thus, northern red oak and white oak could be more tolerant of the relatively dry understories of red pine plantations than red maple. This difference between oak and red maple may be most pronounced in microsites with thick pine litter, which would reduce the ability of red maple first-year seedling roots to colonize the moist humus layer and mineral soil.

The drought tolerance of juvenile oak and the absence of mid-story red maple could have enabled the slower growing and less shade-tolerant oak reproduction to become well-established. Thus, oak may have been well-positioned to utilize a rapid increase in resources, such as light and moisture when pine basal area was reduced during the implementation of treatments. Again, it should be noted that the effects of a pine overstory on soil moisture and understory species composition are likely to be most prevalent on poor and intermediate-quality sites. Red maple regeneration is often abundant in pine plantations on sites with abundant soil moisture.

Apart from potential negative effects on red maple, mature pines provide three additional benefits for oak regeneration. Measurements of photosynthetically active radiation (PAR) obtained at the center of all understory plots in 1992 revealed that given percentages of red pine canopy cover transmit more PAR to the understory than equal percentages of oak canopy cover (Buckley et al., 1999). The second benefit that oak reproduction derives from mature pines is year-round frost protection. Late spring frosts, which coincide with the first flush of oak growth are common in the study region, and late spring frosts have been documented on the study sites in multiple years over the past decade (Buckley et al., 1998). Finally, greater levels of ectomycorrhizae (ECM) that are beneficial to oak seedlings may be associated with pine as opposed to oak cover types. Previous research on these sites suggested that specific ECM may have contributed to significantly larger root-collar diameter on oak seedlings in pine stands than in oak stands. The difference could not be explained by overall ECM, but seemed to be associated with a 10% greater abundance of Type III ECM (''shiny white with abundant interconnected filaments and rhizomorphs'') in the pine than in the oak stands (Zhou et al., 1998).

The effects of fire suppression on species composition within the oak stands was a probable factor in increased density of red maple in the oak stands as suggested by a number of studies (Lorimer, 1985; Crow, 1988; Reich et al., 1990; Abrams, 1992). However, it is quite likely that fire is not the sole factor that provides oak an advantage against competitive species like red maple. Wildland fire may work synergistically with other factors, such as stand composition. Greater negative impacts of prescribed fires on red maple regeneration have been documented in stands with greater fuel loading (Huddle and Pallardy, 1996). Similarly, previous research on these study sites indicated that the continuity and chemical composition of red pine fine fuels were found to produce greater temperatures and residence time of prescribed fires, thereby having a greater negative effect on understory red maple in pine than in oak stands (Hartman, 2003). The latter result was unanticipated considering the fact that related fire behavior outputs, such as heat per unit area are generally predicted using the same fuel model for representing the understory of oak and long-needled pine stands (Anderson, 1982).

A complex silvicultural conundrum is created when overtopping red maple prevents oak regeneration from becoming well-established. Small, poorly developed oak stems cannot produce sprouts that will successfully compete with sprouts from much larger red maple. This scenario necessitates an approach that puts oak regeneration in a more competitive position relative to red maple prior to using prescribed fire. The observed beneficial interactions between oak regeneration and mature pines have led us to suggest that on intermediate-quality sites, reintroduction of disturbances, such as fire may not be as beneficial in the absence of interactions between oak regeneration and mature pine similar to those that enabled oak to become well-established in the past. Attempting to arrest succession from oak to red maple is difficult and expensive. Rather than focusing on regenerating oak beneath oak, regenerating oak beneath pine would capitalize on the beneficial interactions between oaks, pines, and red maple that appear to accompany transitions from mature pine to oak on intermediate sites.

5. Management implications

Pine pulpwood sells for more than oak pulpwood and oak sawlogs are worth more than pine. Oak trees provide mast while pine stands provide cover. In terms of the monetary value of the timber, the value of red pine and oak change relative to size because pine is more valuable than oak in a young stand and mature oaks are more valuable than mature pine. Similarly, an oak–pine site provides habitat for different species of wildlife as succession continues. In the northern forest, several wildlife species have a diet, wherein oak mast is essential, including black bear, white-tailed deer, raccoon, wild turkey, and blue-jay, all of which have populations that are currently sustaining themselves (Marquis et al., 1976; Healy, 1997; Pfannmuller, 1991; Rogers and Lindquist, 1991). However, populations of 26 species associated with mixed-mesic pine forests in Michigan have declined more than 50%, including the Black-throated Green, Yellow-rumped and Blackburnian Warblers, Fisher, and both Redback and Spotted Salamanders (MDNR, 2004). In view of both timber and wildlife implications, it would be most appropriate to incorporate pine into oak management in a way that would increase overall timber value and wildlife habitat, while ensuring greater long-term sustainability of oak sawtimber and wildlife species dependant on oak mast.

The clumped age class distribution of red pine has added to the difficulty of management decisions for red pine plantations on federal and state forests in northern Michigan. Past techniques for planting red pine have focused on monoculture plantation management. As these plantations began to mature, negative opinions of red pine developed due to the lack of understory diversity in homogenous, very dense stands prior to thinning. Thus, red pine stands were perceived and misinterpreted as ‘‘biological deserts’’ (Dickmann, 1993). Consequently, very few red pine have been planted in recent decades. This social effect combined with the lack of natural red pine regeneration has left the sustainability of the red pine resource, ecological niche, and profitable market in question. However, recent developments in management policy in the region are promising for future red pine sustainability. Utilizing a technique that classifies sites based on understory plant species (Burger and Kotar, 2003), the Michigan Department of Natural Resources (2004) found that intermediate-quality sites that are often represented by a maple-leaved viburnum or witch hazel shrub component were best for red pine restoration when evaluating the social, economic, and biological aspects of planting red pine on various sites. Red maple is often a substantial competitor on these types of sites, and based on our results, red pine restoration on similar sites may have negative impacts on red maple regeneration and beneficial long-term effects on oak regeneration.

In the southeast, evenly distributed mixtures of even-aged oak and pine have been difficult to attain due to faster growth rates of pine. Instead, Clatterbuck (1989) suggested a two-aged technique for regenerating oak beneath pine that is similar to a European practice for regenerating oaks beneath Norway spruce or European Larch (Penistan, 1974). Future planning on how to alternate oak and pine rotations in the Lake States seems appropriate, whether at the scale of stands or large groups within stands. This type of management would facilitate the cyclic nature of oak and pine dominance that was observed in presettlement New England by Thoreau (Whitney and Davis, 1986; Abrams, 2001) and described through more recent research of second-growth forests in the Lake States (Crow, 1988; Sarnecki, 1990; Johnson, 1992). With respect to silviculture and restoration of the mixed pine–oak stand type, it may be most practical to continue initiating the process with artificial red pine regeneration due to difficulties in naturally regenerating red pine as opposed to white pine and the ease of planting pine as opposed to hardwoods. There are several positive outcomes that could result from using red pine as a nurse species for regenerating oak. In addition to providing an opportunity to restore past interactions and habitats within the mixed pine–oak forest type, planting red pine on sites where an oak seed source is left scattered or in groups would provide an opportunity to balance the age class distribution of red pine through plantations that could be socially, economically, and biologically acceptable. Instead of repeated oak shelterwood burning, prescribed fire could be utilized for regenerating oak beneath pine by providing additional red maple control before planting and after thinning pine. This type of management would capitalize on the volume growth lost had regeneration been setback repeatedly over a period of time in which pine could have been regenerating, eliminate the possibility of damaging valuable oak sawtimber through repeated shelterwood burning, and potentially more closely replicate natural successional processes. In addition to these positive outcomes, we feel the most important result of restoring red pine to sites currently dominated by oak may be greater long-term sustainability of northern red oak as a component on intermediate-quality sites, where red maple is a competitor.

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