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EFFECTS OF FIRE AND THINNING ON GROWTH, MYCORRHIZAL COLONIZATION, AND LEAF ANATOMY OF BLACK OAK AND RED MAPLE SEEDLINGS

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ABSTRACT.—Prescribed fire and/or thinning may improve oak seedling reproduction in forests and limit competitors such as red maple due to altered light or soil-moisture conditions. Because both leaf and root development may be affected by these disturbances, differences in biomass, mycorrhizal colonization, and leaf anatomy between seedlings of black oak (*Quercus velutina*, an ectomycorrhizal species) and red maple (*Acer rubrum*, an endomycorrhizal species) were described and quantified. In spring 2001, four treatments were initiated at Zaleski State Forest, Vinton County, OH: undisturbed control (C); basal area thinned by 29 percent (T); site exposed to prescribed burn (B); or thinned plus burned (T+B). In June and August 2001, four seedlings (two oak, two maple) from six plots per treatment were excavated from three subsites with different moisture levels (two mesic, two intermediate, two xeric; 48 seedlings per species per collection date). Roots were prepared chemically for mycorrhizal analysis; leaf sections were embedded in epoxy resin and examined microscopically. Biomass measurements of all seedling parts were quantified. Endomycorrhizal colonization of maple roots was not affected by treatments. Oak short roots were predominantly ectomycorrhizal; endomycorrhizal structures were observed primarily in June (T+B). In oak leaves, blade thickness and starch grains in chloroplasts (August) were greater in T and T+B than in C or B. Maple leaves, while thinner than oak, had thicker leaf blades in all disturbance treatments compared to C, but less starch in chloroplasts (August). By August, treatments positively affected leaf parameters in oak (leaf area, mass, specific leaf mass) and maple (leaf number, area, mass) probably due to increased light and/or altered soil conditions. Oak seedlings grown on sites with thinning and burning as management tools may gain a competitive advantage by forming both mycorrhizal types early in the season (i.e., additional nutrient uptake) and through increased starch production in leaves late in the season that would improve seedling growth and carbon transfer to roots.

Since the early 20th century, the composition and structure of Appalachian mixed-oak forests has been shifting from oak-dominant to mesophytic dominant species. Many attribute this shift to changes in cutting practices and to an aggressive suppression of fire beginning in the 1920s. Currently, the mid- and understory of these forests contain a high proportion of shade-tolerant mesic species, e.g., red maple (Lorimer 1984), that exhibit low resistance to fire (Abrams 1992) and fewer of the less shade-tolerant oak, e.g., black oak. Written accounts at the time of European settlement (ca. 1800) in southern Ohio suggest that Native Americans used fire to manage forest composition and structure (Hutchinson and others 2003). Oak is drought-tolerant and fire-adapted, with a large root system that resprouts after repeated burnings (Abrams 1996, Brose and others 2001). Oak regeneration on xeric sites is successful, but failures are common on high-quality mesic sites (Abrams and Downs 1990). Fire may reduce understory vegetation and thereby reduce competition; overstory thinning would result in increased light for oak.

Mycorrhizae are symbiotic associations of tree fine roots and certain soil fungi. Oak species are classified as ectomycorrhizal (possessing an external fungal mantle and Hartig net hyphae between cortical cells) while maples are classified as endomycorrhizal (with vesicles, arbuscules, and/or hyphal coils in cortical cells) (Smith and Read 1997). Both types of mycorrhizae generally benefit seedling establishment or growth through increased nutrient uptake and improved water relations in the roots (Allen 1991). The effects of fire on rhizosphere processes such as mycorrhizal associations are scarce and generally limited to coniferous ecosystems (Mah and others 2001).

Improved light conditions in the forest due to disturbances such as thinning or burning generally increase photosynthesis in leaves; photosynthates due to increased carbon fixation can be observed

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microscopically as starch grains in leaf chloroplasts. Reich and Abrams (1990) reported that fire enhanced photosynthesis of *Quercus ellipsoidalis* seedlings. Similarly, Musselman and Gatherum (1969) observed that photosynthesis increased by 50 percent in red oak seedlings grown at 31 percent of full sunlight compared to those grown at 8 percent. Photosynthate allocation to mycorrhizae that is used for fungal growth has been considered a "cost" to the plant (Jones and others 1991). However, light-enhanced photosynthesis may support both mycorrhizal colonization (with no additional cost) and increased seedling growth to improve oak competitiveness and survival. Characterizing seedling biomass, mycorrhizal colonization of fine roots, and leaf anatomy (leaf thickness, starch in leaves) after thinning and burning of forest sites will help us better understand seedling growth and physiology following such treatments. In this study we compare and quantify first-year effects of burning and thinning on growth parameters, mycorrhizal colonization, and foliar anatomy in red maple and black oak seedlings.

Study Area

Zaleski State Forest is a study area within the Ohio Hills site of the U.S. Joint Fire Science National Fire and Fire Surrogates project. Located within the unglaciated Allegheny Plateau, the site has a highly dissected topography with elevations ranging from 200 to 300 m and slopes of 10 to 40 percent. The forest is dominated by strongly acidic (pH=3.6) loamy soils (ultisol: Hapludults) with a C:N ratio of about 20 (Ralph E.J. Boerner, 2003, Ohio State University, pers. commun.). The study area is about 80 ha and is divided into four 20-ha treatment units corresponding to undisturbed control (C), basal area thinned by 29 percent (T), site exposed to prescribed burn (B), and site thinned and burned (T+B). Within each treatment area, ten 50- by 20-m plots were established across a range of moisture conditions (three xeric, four intermediate, and three mesic) determined with an integrated moisture index (IMI) (Iverson and others 1997). In all, 40 vegetation plots were generated.

On the T and T+B sites, the average initial basal area was 27.1 m^2ha^{-1}. A commercial thinning from below to 18.6 m^2ha^{-1} basal area was conducted during the winter of 2000; low-intensity surface burns were conducted on 4 April 2001. Air temperature was measured at 25 cm from forest floor with stainless steel temperature probes and logged every 2 seconds with buried data loggers. Maximum air temperatures during the burns ranged from 42.2 to 414.6°C in the T+B unit and 63.8 to 397°C in the B unit.[1]

Methods

Seedling Collection

In June and August 2001, two black oak and two red maple seedlings randomly selected from two mesic, two intermediate, and two xeric plots from each of the four treatments (C, T, B, T+B) were excavated (48 seedlings per species per collection). Seedlings were predominantly 1.0 cohort or older. Root systems with accompanying soil were placed in sealed plastic bags in coolers and transported the same day to the USDA Forest Service laboratory at Delaware, OH. Seedling root systems were washed free of soil before processing.

Seedling Growth and Biomass

Seedling height, taproot length, and stem and root-collar diameters were measured. Roots were separated into tap and first-order laterals, and leaves and first-order laterals were counted. Leaf area was estimated using a calibrated LI-3100 Area Meter.[2] Short roots from each seedling were placed in vials containing FAA (formalin-acetic acid-alcohol) for mycorrhizal assessment. Representative short roots and leaf-blade segments (2 mm^2) were placed in 3-percent glutaraldehyde to process for microscopical

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[1]Iverson, L.R.; Prasad, A.M.; Hutchinson, T.F.; Rebbeck, J.; Yaussy, D. Fire and thinning in an Ohio oak forest: grid-point analysis of the fire behavior, environmental conditions, and tree regeneration across a topographic moisture gradient. In preparation.

[2]The use of trade, firm, or corporation names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

analysis. Following growth measurements and tissue sampling, tissue of each seedling was separated into leaves, stem, and roots, oven-dried at 70°C to constant mass (g dry weight), and weighed. The root/shoot ratio and specific leaf mass (g m^{-2}) of each seedling were calculated.

Mycorrhizal Analysis

Red maple. Fine roots were cleared in 10-percent KOH and stained with trypan blue (Phillips and Hayman 1970). Endomycorrhizal structures (hyphal coils, vesicles, arbuscules) were observed under a stereomicroscope, and colonization of maple roots systems was calculated using the grid-line intersect method (Giovannetti and Mosse 1980) using 1-cm intersects marked in a petri dish. Forty-three intersects per root system were evaluated by recording the presence or absence of mycorrhizal structures.

Black oak. Root tips from each root system were inspected microscopically for a fungal mantle or Hartig net (ectomycorrhizal structures). Oak short roots with no obvious fungal mantle were cleared and stained (as for maple roots) to determine whether endomycorrhizal structures were present. Quantification of oak root mycorrhizal colonization was conducted by direct counts of entire root systems (Grand and Harvey 1982) and rating each tip as ectomycorrhizal, endomycorrhizal, or nonmycorrhizal. The proportion of short roots that were mycorrhizal was then expressed as percent ectomycorrhizal tips only or percent ectomycorrhizal plus endomycorrhizal tips.

Leaf Microscopy

Leaf-blade segments from each treatment combination fixed in 3-percent glutaraldehyde were post-fixed in 2-percent osmium tetroxide, dehydrated in a graded ethanol series, and infiltrated with PolyBed-Araldite epoxy resin. Resin-embedded leaf cross sections were photographed under an Olympus BH light microscope, and leaf thickness at three positions per blade was measured for three leaf blades per treatment. Leaf segments were ultrathin-sectioned and examined with a JEOL JEM-1010 transmission electron microscope; leaf mesophyll cells were photographed and two starch grains in chloroplasts from five mesophyll cells in each of three blades per treatment were measured (length x width of 30 grains per treatment).

Statistical Analysis

The effects of treatment, IMI, and their interactions on percent mycorrhizal colonization, leaf thickness, taproot length, number of first order laterals, shoot height, seedling diameter, root-collar diameter, leaf number, area, and biomass, stem biomass, root dry biomass, root/shoot ratio, and specific leaf mass were tested as a two factor ANOVA using SAS General Linear Model analysis (SAS Institute 1999). Effects were considered significant if $p \leq 0.05$.

Results

Seedling Growth and Biomass

Growth and biomass data from red maple and black oak seedlings collected in June (2 months after prescribed fire) showed no significant differences due to treatment or IMI (soil moisture) (data not shown). Although not always statistically significant at $p \leq 0.05$, black oak and red maple seedlings harvested from T, B, and T+B plots in August were more massive than the C seedlings (table 1). In red maple, leaf area per seedling was greater by 106, 180, and 247 percent on B, T, and T+B plots, respectively, compared to controls ($p = 0.02$). Leaf mass ($p = 0.03$), and leaf number ($p = 0.03$) was substantially greater in all treatments relative to controls. Root-collar diameter of maple seedlings from xeric plots were 1.6 times larger than that of seedlings from intermediate or mesic plots ($p = 0.01$). No other significant effects associated with IMI were detected. Borderline significant treatment effects were detected for root collar diameter ($p = 0.06$) of maples. In black oak, total leaf area per seedling was greater by 39, 175, and 140 percent in T, B and T+B plots, respectively ($p = 0.014$), compared to C. Leaf mass did not differ between seedlings from C and T plots, but did increase by 170 percent in B and T+B oak seedlings compared to controls ($p = 0.007$). Specific leaf mass was nearly 20 percent greater in oak seedlings from T and T+B plots relative to controls ($p = 0.05$). Root mass showed borderline significance ($p = 0.06$), as control roots had 53 to 75 percent less mass than roots in all other treatments. IMI had no significant effect on oak growth or biomass measurements, and no significant interaction between IMI and treatments was detected for either species.

Table 1.—Mean (± std error)[a] of the growth and biomass of black oak and red maple seedlings four months after prescribed fires and/or overstory thinning at Zaleski State Forest, Vinton County, OH

	Treatment			
Growth parameter	Control	Burn	Thin	Thin+Burn
			Black oak	
Shoot height, *cm*	18.24 ± 2.36	15.60 ± 2.40	14.03 ± 2.36	14.03 ± 2.36
Stem diameter, *mm*	2.65 ± 0.19	3.10 ± 0.20	2.68 ± 0.19	2.92 ± 0.19
Root collar diameter, *mm*	3.02 ± 0.35	5.59 ± 0.35	4.52 ± 0.35	4.57 ± 0.35
Leaf number	4.25 ± 0.47	4.92 ± 0.47	3.58 ± 0.47	4.91 ± 0.47
Leaf area, cm^2	53.52 ± 26.29 a	146.88 ± 26.29 b	74.28 ± 26.29 a	128.37 ± 26.29 b
Leaf mass, *g*	0.27 ± 0.10 a	0.72 ± 0.10 b	0.46 ± 0.10 a	0.75 ± 0.10 b
Specific leaf mass, $g\ m^{-2}$	4.96 ± 0.24 a	5.08 ± 0.24 a	5.96 ± 0.24 b	5.86 ± 0.24 b
Stem mass, *g*	0.51 ± 0.17	0.72 ± 0.17	0.62 ± 0.17	0.60 ± 0.17
Root mass, *g*	0.83 ± 0.33	3.24 ± 0.33	2.39 ± 0.33	1.75 ± 0.33
Taproot length, *cm*	23.03 ± 1.83	22.96 ± 1.83	25.45 ± 1.83	19.70 ± 1.83
First-order lateral roots, *no.*	29.00 ± 4.19	32.92 ± 4.19	27.83 ± 4.19	25.75 ± 4.19
Root:shoot ratio	1.12 ± 0.44	2.57 ± 0.44	2.13 ± 0.44	1.42 ± 0.44
Plant mass, *g*	1.61 ± 0.53	4.74 ± 0.53	3.48 ± 0.53	3.20 ± 0.53
			Red Maple	
Shoot height, *cm*	9.89 ± 0.88	8.32 ± 0.88	12.38 ± 0.88	11.20 ± 0.88
Stem diameter, *mm*	1.55 ± 0.19	1.67 ± 0.19	1.84 ± 0.19	2.06 ± 0.19
Root collar diameter, *mm*	1.53 ± 0.29	2.47 ± 0.29	2.25 ± 0.29	2.90 ± 0.29
Leaf number	4.08 ± 0.62 a	7.08 ± 0.62 b	8.75 ± 0.62 b	11.33 ± 0.62 c
Leaf area, cm^2	18.78 ± 6.82 a	38.64 ± 6.82 ab	52.72 ± 6.82 bc	65.24 ± 6.82 c
Leaf mass, *g*	0.08 ± 0.03 a	0.16 ± 0.03 a	0.23 ± 0.03 ab	0.27 ± 0.030 b
Specific leaf mass, $g\ m^{-2}$	4.57 ± 0.03	4.10 ± 0.03	4.38 ± 0.03	4.10 ± 0.03
Stem mass, *g*	0.09 ± 0.03	0.14 ± 0.03	0.21 ± 0.03	0.15 ± 0.03
Root mass, *g*	0.15 ± 0.21	0.48 ± 0.21	0.78 ± 0.21	0.58 ± 0.21
Taproot length, *cm*	16.97 ± 2.70	19.08 ± 2.70	22.14 ± 2.70	18.83 ± 2.70
First-order lateral roots, *no.*	23.83 ± 2.78	24.58 ± 2.78	29.25 ± 2.78	23.50 ± 2.78
Root:shoot ratio	0.86 ± 0.46	1.74 ± 0.46	1.44 ± 0.46	1.48 ± 0.46
Plant mass, *g*	0.32 ± 0.27	0.78 ± 0.27	1.21 ± 0.27	0.99 ± 0.27

[a]Least square means ± 1 standard error presented; means followed by a different letter (across a row) significantly different at $p \leq 0.05$.

Mycorrhizal Assessment of Roots

Red Maple. Endomycorrhizal colonization was extensive in maple roots for all treatments (table 2). Percent colonization was significantly greater in the T+B treatment in August compared to T or B alone, but it was not significantly different from the control. The greatest percent increase in infection from June to August (14.2) was in T+B, possibly due to increased light and less competing vegetation. Hyphal coils in cortical cells were the most common endomycorrhizal structure, though vesicles and arbuscules also were present.

Black Oak. Ectomycorrhizal short roots displayed numerous morphotypes (examples: brown smooth, brown fuzzy, black), but these were not identified by species. Roots appearing nonmycorrhizal that were cleared and stained with trypan blue often contained hyphal coils and vesicles (endomycorrhizal structures) that were indistinguishable from those observed in red maple roots. Percent mycorrhizal colonization (table

Table 2.—Mean percent (± 1 std error)[a] ectomycorrhizal (EM) and endomycorrhizal (VA) colonization in red maple and black oak seedling roots from undisturbed soil (Control) or exposed to treatments (Thin; Burn; Thin+Burn)

	Red maple		Black oak			
Treatment	June (VA)	August (VA)	June (EM)	June (EM+VA)	August (EM)	August (EM+VA)
Control	61.6 ± 3.8	69.2 ± 3.2 ab	69.1 ± 4.6 a	72.0 ± 3.9 a	54.4 ± 4.6 ab	54.4 ± 4.2a
Thin	59.3 ± 3.8	62.8 ± 3.2 b	44.8 ± 4.6 b	46.2 ± 3.9 b	60.9 ± 4.6 a	61.2 ± 4.2a
Burn	69.1 ± 4.1	64.4 ± 3.2 b	53.4 ± 4.6 b	54.0 ± 3.9 b	50.2 ± 4.6 ab	50.9 ± 4.2a
Thin+Burn	61.8 ± 3.8	76.0 ± 3.2 a	48.3 ± 4.6 b	67.9 ± 3.9 a	46.6 ± 4.6 b	50.5 ± 4.2a

[a]Means followed by different letters within a column significantly different at p d≤0.05.

Table 3.—Mean (± 1 std error)[a] leaf thickness (µm) of red maple and black oak seedlings grown in control soil or exposed to treatments

	Red maple		Black oak	
Treatment	June	August	June	August
Control	108.0 ± 3.3 a	114.8 ± 3.2 a	155.2 ± 3.8 bc	129.3 ± 4.2 c
Thin	120.0 ± 3.3 b	126.9 ± 3.2 b	162.0 ± 3.8 ac	141.8 ± 4.2 b
Burn	118.4 ± 3.3 b	130.5 ± 3.2 b	148.3 ± 3.8 b	128.0 ± 4.2 c
Thin+Burn	118.8 ± 3.3 b	131.6 ± 3.2 b	169.3 ± 3.8 a	155.6 ± 4.2 a

[a] Means followed by different letters within a column significantly different at p d≤0.05.

2) was quantified for ectomycorrhizal (EM) tips only and for the combination of EM plus endomycorrhizal (VA) tips. In June, the percentage of EM tips was highest in control roots, i.e., undisturbed soil had greater early season EM colonization. However, with the addition of VA tips, percent colonization in T+B increased to the level of the control. By August, there was no treatment difference in percent colonization when EM+VA tips were quantified, nor was there an effect attributable to treatment in EM tips alone (table 2) because no treatment differed significantly from the control. It is interesting that ectomycorrhizal colonization between June and August increased in the T treatment (44.8 to 60.9 percent) while the percentage in other treatments decreased. Soil moisture (IMI) did not significantly affect mycorrhizal colonization.

Leaf Anatomy

Leaf thickness was greater in black oak than red maple for each treatment (table 3). Red maple leaves were thicker in August than in June for each comparable treatment, whereas black oak leaves were thinner in August compared with those in June. Black oak leaves were thicker in T and T+B treatments (table 3) due to thicker mesophyll layers (spongy mesophyll plus palisade cells). In August, the percentage of leaf thickness due to mesophyll layers (n = 12 measurements per treatment) were: C, 72.8; B, 73.1; T, 80.8; T+B, 78.0. All disturbance treatments resulted in thicker red maple leaves (table 3) compared to controls due to less air space in mesophyll area in the latter (i.e., more tightly packed cells and thinner mesophyll).

Soil moisture index (IMI) did not affect thickness of red maple leaves (table 4). Leaves from black oak seedlings growing in the xeric site (June and August) and intermediate site (August) were thicker than those from the mesic site (table 4). Black oak leaves from the mesic site had a slightly thinner mesophyll cell layer and elongated (rather than rounded) upper epidermal cells that accounted for the overall thinner leaves.

In June, starch grains were found in chloroplasts from all leaves of both tree species. By August, starch grains in chloroplasts of black oak leaves were larger and more abundant in the T and T+B treatments (fig. 1) than in the C or B treatment (fig. 2). Measurement (LxW) of starch grains quantified the larger size in the T and T+B for black oak and in the T treatment for red maple (table 5). Differences in frequency of starch in mesophyll cells in August also were observed: 47 percent of maple mesophyll cells versus 29 percent of oak cells examined had no starch grains present. Although 91 percent of leaf mesophyll cells

Table 4.—Effect of soil moisture (IMI, integrated moisture index[a]) on mean thickness (± 1 std error)[b] (¼m) of red maple and black oak leaves

IMI	Red maple		Black oak	
	June	August	June	August
Xeric	112.2 ±2.9	123.6 ± 2.8	170.9 ± 3.4 a	145.5 ± 3.7 a
Intermediate	117.0 ±2.9	129.7 ±2.8	157.6 ± 3.4 b	143.0 ± 3.7 a
Mesic	119.7 ±2.9	124.6 ±2.8	147.6 ± 3.4 c	127.6 ± 3.7 b

[a]Iverson and others 1997.
[b]Means followed by different letters within a column significantly different at p d≤0.05.

from oak seedlings grown in the T or T+B contained abundant starch grains, maple leaves from these same treatments had about equal numbers of cells with and without starch grains. In C and B treatments, there were no starch grains in 69 and 41 percent, respectively, of mesophyll cells from leaves of sampled oak seedlings. In red maple leaves from the same treatments, 63 and 37 percent of examined mesophyll cells had no starch grains.

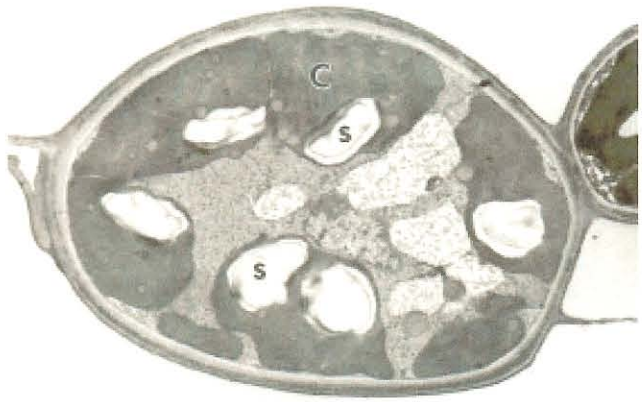

Figure 1.—Spongy mesophyll cell from black oak seedling, B+T treatment, August collection. Large starch grains (S) were observed in chloroplasts (C).

Discussion

Forest disturbance due to burning, thinning or both increased foliar area and mass in red maple and black oak seedlings, probably by increasing the amount of light in the understory. Light increased from 8.7 percent open sky in C plots to 17.8 in T, 14.5 in T+B, and 11.8 in B plots (Todd Hutchinson, 2001, Northeastern Research Station, pers. commun.).

Thicker leaf blades in black oak (T and T+B) were due to increased mesophyll thickness. In other studies, increased leaf-blade thickness in *Quercus petraea* (sessile oak) (Igboanugo 1992) and in black oak (Ashton and Berlyn 1992) was attributed to increased mesophyll thickness. Of the three oak species they examined, black oak was the most drought-tolerant, had the greatest anatomical plasticity, and the highest photosynthetic rates under different light conditions (Ashton and Berlyn 1992). They also reported that thicker anatomical dimensions promote higher water-use efficiency and lower evapotranspirational demands under higher light conditions. This led Ashton and Berlyn to conclude that black oak is sufficiently flexible to adapt to heterogeneous environments and to compete in drought-prone environments.

The abundant starch grains observed in leaf chloroplasts of black oak in August probably is due to high photosynthesis, as reported for black oak (Ashton and Berlyn 1992). Late-season starch production may benefit shoot growth (observed in August) and, although not directly measured in our study, may result in greater transfer of carbohydrate to roots (belowground biomass investment). Growth stimulation of black oak by inoculation with ectomycorrhizal fungi was demonstrated by Daughtridge and others (1986), and additional root carbohydrate might favor mycorrhizal colonization.

The extensive endomycorrhizal colonization of red maple in our study (59 to 76 percent) was similar to or higher than that reported for sugar maple by Cooke and others (1992), Klironomos (1995), and DeBellis and others (2002). Much of the herbaceous vegetation in the understory is classified as endomycorrhizal (Brundrett and Kendrick 1988); therefore, a high level of soil inoculum may account for the high colonization levels in our study. A lack of treatment effect due to thinning on endomycorrhizal colonization also was observed by DeBellis and others (2002): selective cutting had

Table 5.—Mean (± 1 std error) starch grain dimensions (when present[1]) within leaf mesophyll cells of red maple and black oak seedlings (samples collected in August 2001, about 4 months after a dormant-season prescribed fire)

Species	Treatment	Length	Width
		μm	
Black oak	Control	1.03 ± 0.08	0.45 ± 0.06
	Thin	1.64 ± 0.08	0.84 ± 0.09
	Burn	1.30 ± 0.10	0.61 ± 0.07
	Thin+Burn	2.09 ± 0.06	0.77 ± 0.05
Red Maple	Control	1.43 ± 0.18	0.36 ± 0.02
	Thin	1.84 ± 0.12	0.47 ± 0.03
	Burn	1.31 ± 0.08	0.38 ± 0.04
	Thin+Burn	1.26 ± 0.07	0.51 ± 0.07

[1]Five mesophyll cells per leaf were randomly chosen for measurement of starch grains.

no negative effect on mycorrhizal community structure because of the rapid regeneration of mycorrhizal hosts and minor levels of soil disruption. Klironomos (1995) reported that soil type can affect variability in endomycorrhizal structures; hyphal coils, the most common endomycorrhizal structure observed in our study, also was the most common structure found in sugar maple roots by Klironomos in podzolic (acidic) soil.

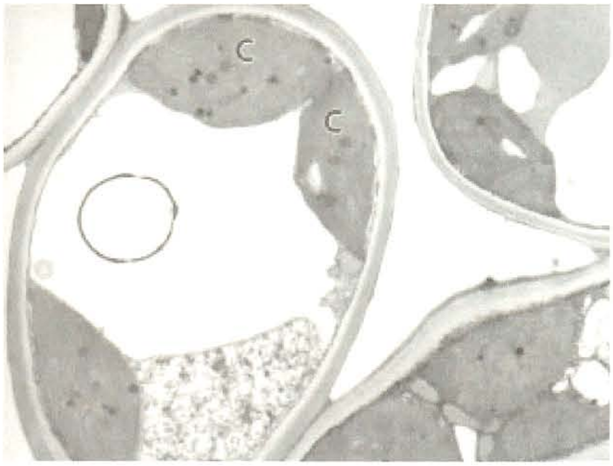

Figure 2.—Spongy mesophyll cells from black oak seedling, B treatment, August collection. Chloroplasts (C) had few starch grains.

Oak species generally are considered as ectomycorrhizal (Dickie and others 2001); however, we observed both ectomycorrhizal and endomycorrhizal associations on black oak roots. Endomycorrhizal associations on predominantly ectomycorrhizal oak roots have been reported (Grand 1969, Watson and others 1990, Dickie and others 2001), especially in extremely wet or dry soils (Watson and others 1990). Endomycorrhizal infection of predominantly ectomycorrhizal host plants might be increased in the presence of abundant endomycorrhizal hosts (Smith and others 1998, Dickie and others 2001), as occurred in the understory at Zaleski State Forest. The percentage of endomycorrhizal colonization of black oak roots decreased in August. Ectomycorrhizal fungi might be able to displace endomycorrhizal fungi (Lodge and Wentworth 1990, Chen and others 2000), and this likely occurred in our late-season sampling across all treatments. Additional research is needed to determine whether there is a functional significance (e.g., increased nutrient uptake) with respect to the dual mycorrhizal colonization of black oak roots. In *Salix repens* (a dual mycorrhizal plant), the endomycorrhizal association was beneficial over the short term (increased P uptake), though the ectomycorrhizal association benefited growth over the long term (van der Heijden 2001).

Thinning and/or burning favorably affected oak seedling leaf area and mass, leaf thickness, the presence of leaf starch in August, and possibly ectomycorrhizal colonization, probably due to an increase in the amount of light reaching the forest floor. The flexibility of oak roots in mycorrhiza formation (colonization by both endo- and ectomycorrhizae) might explain a portion of its success in resource-limiting or dry sites. Continuing to monitor stand management using thinning and burning prescriptions will provide additional data on oak competitiveness over the long term in mixed hardwood forests.

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