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Light availability influences root carbohydrates, and potentially vigor, in white oak advance regeneration

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Abstract

Oaks (*Quercus* spp.) are experiencing recurring regeneration failures associated with pervasive mid- and under-story strata of shade tolerant species in intact, undisturbed forests. Where oak regeneration occurs, inadequate vertical height and depleted root carbohydrate stores impede the ability of regenerating oaks to respond when light does become available. A variety of silvicultural techniques have been developed to increase the penetration of diffuse light, enhancing the light environment on the forest floor, and thereby increasing the likelihood of regenerating oaks to successfully respond to increased light transmittance. We measured shoot and root characteristics, and root soluble non-structural carbohydrate concentrations of white oak (*Q. alba* L.) advance regeneration exposed to enhanced light intensities associated with a mid-story removal and a clearcut, and compared white oak regeneration vigor to untreated controls.

Root diameter and soluble non-structural carbohydrates increased with increasing light availability. Our data suggest that white oak responds to increases in light transmittance by building below-ground biomass and carbohydrates in the root system prior to an above-ground response. Our study shows that white oak regeneration vigor increases with only modest increases in light. In the absence of other pressures, enhancing the light environment to the forest floor should contribute to successful regeneration of this species.

Keywords: *Quercus*; White oak; Seedling vigor; Silviculture

1. Introduction

Oaks (*Quercus* spp.) dominate hardwood forests throughout much of eastern North America (Clark, 1992), and are exceedingly important both ecologically (Rogers et al., 1993) and economically (Lockhart et al., 2000). Intermittent disturbances, both natural and anthropogenic, have been critical to the formation and maintenance of these forests (Abrams and Nowacki, 1992). Fire, herbivory, pathogens, grazing, and harvesting have all played a role in the disturbance regimes forming today's forests (Abrams and Nowacki, 1992; Clark, 1992). Loss of these intermittent disturbances with contemporary land management practices has resulted in declining oak dominance, with concurrent increases in more invasive species (Clark, 1992; Abrams, 2003). The standing volume of oak is decreasing (Spencer and Kingsley, 1991), and the standing volume of competing species such as red maple (*Acer rubrum* L.) is increasing (Clark, 1992). The result is that oaks are being lost from intermediate and high quality sites where they once dominated (Carvell, 1979).

Members of the genus *Quercus* are intermediate in shade tolerance (Dey and Parker, 1996), and white oak (*Q. alba* L.) is one of the more shade tolerant oak species (Abrams, 2003). While this is an advantage over shade intolerant species such as yellow-poplar (*Liriodendron tulipifera* L.) under an intact canopy, even white oak cannot persist in the densely shaded under-story of intact upland forests for extended periods of time (Lorimer, 1983). Oaks also have a conservative growth strategy, favoring root growth over shoot growth. This strategy allows for the perpetuation of seedling sprouts in the under-story of intact forests through recurrent shoot dieback and subsequent resprouting (Hodges and Gardiner, 1992). This conservative growth strategy, coupled with its relative shade intolerance, suggest that as a group oaks are disturbance-dependent, and

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rely on increases in diffuse and direct light levels generated by disruption of the mid-story and canopy (Dey and Parker, 1996).

Oak survival and regeneration success on upland sites is considered proportional to the size of advance regeneration (i.e., saplings and seedlings) (Sander, 1972; Loftis, 1990). Successful advancement of oak regeneration into dominant crown positions after disturbance depends on its ability to maintain competitive height growth. Vigor, or the ability to respond to a release, historically has been related to height or stem growth (Waring et al., 1980). If the advance oak regeneration present at the time of disturbance is not of sufficient vigor when released, regeneration fails and loss of oak will result (Sander, 1972). Under intact canopies, northern red oak (*Q. rubra* L.) advance regeneration rarely reaches a height that allows it to be competitive (Loftis, 1992; Kaelke et al. (2001)). While height or stem growth of advance oak regeneration is one indicator of vigor, top dieback and the resprouting exhibited by oaks confounds this relationship due to the wide array of root ages and carbohydrate concentrations associated with existent stems (Hodges and Gardiner, 1992). A more complete knowledge of the ability of advance oak regeneration to respond to release is critical to developing silvicultural approaches aimed at oak recruitment.

The development of a pervasive mid- and under-story stratum in intact forests populated by shade tolerant species has been postulated as a factor affecting oak regeneration (Lorimer et al., 1994). Sugar maple (*A. saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and red maple are believed to have invaded sites that they did not occupy historically (Abrams, 1998). In the Cumberland Plateau region of the eastern US, red and sugar maple dominate the mid-story and under-story, creating densely shaded conditions at the forest floor (Barton and Gleeson, 1996; Arthur et al., 1998).

Removal of mid and under-story vegetation to enhance regeneration has been evaluated in northern red and cherrybark oaks (*Q. pagoda* Raf.) (Loftis, 1983; Lorimer et al., 1994; Lockhart et al., 2000), and results suggest that the observed increases in growth could potentially lead to more positive responses in the event of full canopy removal. Mid-story removal is designed to increase diffuse light levels to a point at which oak can achieve a positive carbon balance and attain positive height growth, while preventing excessive direct sunlight from reaching the forest floor, thereby hindering the growth of shade intolerant competitors such as yellow-poplar and black cherry (*Prunus serotina* Ehrh.) (Loftis, 1983). The increase in diffuse light allows advance oak regeneration to increase vigor prior to complete canopy removal, improving its competitive advantage (Loftis, 1983).

In woody plants carbohydrates are quantitatively the dominant constituent. They are direct products of photosynthesis and play critical roles in the synthesis of organic compounds and in energy storage. Carbohydrate concentrations vary temporally and are species-specific and tissue-specific (Kramer and Kozlowski, 1979), and have been used as a physiological indicator of a variety of growth and response traits. In oak, carbohydrates have been shown to change in response to disturbance (Kruger and Reich, 1997; Adams and Rieske, 2001, 2003). Kruger and Reich (1997) found an increase in whole plant total non-structural carbohydrate content of northern red oak after two successive prescribed fires. Increases in foliar soluble non-structural carbohydrate concentrations of white oak regeneration were noted 1 year after a prescribed fire, which corresponded with enhanced seedling vigor (Adams and Rieske, 2001, 2003). These observed increases were in response to prescribed fire, and may differ from responses to other types of disturbances.

Carbohydrate reserves in root systems of advance oak regeneration, and the extent to which they fluctuate in response to changing environmental conditions, is not fully understood. No studies to date have used root carbohydrate levels (soluble or total non-structural) to quantify oak seedling vigor (the ability to respond to release), or to predict potential growth response. Our study focuses on root characteristics and soluble non-structural carbohydrates of advance white oak regeneration as a first response variable to a cultural treatment aimed at increased size. We measured root characteristics of white oak regeneration growing under intact canopies, and assessed regeneration response to increasing light using two silvicultural treatments: a mid-story removal and a clearcut.

2. Methods

2.1. Study sites

Study sites were located on Berea College Forest (Madison County, KY) in the Knobs physiographic region of the Cumberland Plateau. Soils in the region are primarily silt loams consisting of four series (Shelocta, Captina, Rockcastle, and Weikert series). Our study sites were on soils mainly of the Shelocta series, which consist of deep well drained soils that are strongly acidic.

Four sites (Fentruss Spur, Horse Cove, Pigg House, and Water Plant) containing numerous cohorts of white oak regeneration, the majority of which were <30 cm tall, were selected. The site index at each site was measured by taking an increment core of seven dominant trees per site and obtaining an approximate age from the core. Site indices were determined using upland oak site index curves (Schnur, 1937), and ranged from 22.2 to 23.8 m (mean 23 m). The mid-story (intermediate and overtopped crown classes) and under-story (advance regeneration and saplings) was dominated by red maple, sugar maple, American beech, and minor components of other species. Prior to our site treatments, basal areas ranged from 32.3–35.1 m^2.

At each site a 0.2 ha area was evenly divided into two plots, surrounded by an 8 m buffer to minimize edge effects. In February 2004 a mid-story removal was implemented in one plot at each site. This involved removal of approximately 20% of the total stand basal area. Stand basal area calculations included all stems 2.5 cm and greater. The mid-story removal was accomplished by felling trees with a chainsaw starting with the 2.5 cm size class and moving up through diameter classes until the 20% removal target was achieved. To facilitate sampling, all slash was removed. Stumps were immediately sprayed with glyphosate (100% Roundup Pro®, Monsanto, St. Louis) to prevent resprouting. The remaining control plot at each site was left undisturbed. At Fentruss Spur only, a commercial clearcut was performed in November 2003, in addition to the mid-story removal. After the clearcut, all remaining stems >2.5 cm in diameter were cut and sprayed with triclopyr (Garlon 4®, Dow AgroSciences, Indianapolis) to prevent sprouting.

2.2. Regeneration Sampling

Pre- and post-treatment, white oak advance regeneration were sampled to measure root soluble non-structural carbohydrate concentration relative to growth characteristics, root age, and light availability. Prior to treatment installation (January 2004), 30 advance regeneration were destructively sampled from each study site ($N = 120$). In January 2005, approximately 12 months following the mid-story removal, 17 white oak advance regeneration were extracted from the mid-story removal and control treatments at each site ($N = 68$ per treatment), and 33 white oak advance regeneration were extracted from the clearcut. Regeneration were excavated using a hand trowel to ensure intact root systems, labeled, stored on ice and transported to the laboratory, where they were processed within 4 h.

In the laboratory, seedling tops and roots were severed. Height, basal diameter, and number of internodes (growth flushes), were measured for all seedling tops. Total height was measured from the root collar to the base of the terminal bud. Basal diameter was measured using a digital caliper at the root collar and was the average of two perpendicular measurements. All internodes or growth flushes were measured between bud scale scars.

Roots were washed and weighed. Root diameter was measured 2.5 cm below the root collar at two perpendicular locations using a digital caliper. Root length was measured from the root collar to the tip of the main root. After measuring, the root was cut 2.5 cm below the root collar, and growth rings were counted with a hand lens to determine root age. The 2.5 cm root section was flash frozen in liquid nitrogen, and immediately placed in a −20 °C freezer for storage. The remaining section of the root was again weighed, dried in a 50 °C oven for 10 days, and re-weighed. Moisture content was determined and was applied to obtain a dry weight for the entire root system.

Based on our samples, regeneration were classified into two groups: 'true seedlings,' which had roots and tops of the same age, and 'seedling sprouts,' which were advance regeneration that had experienced top dieback and had a top age that did not coincide with the root age. Regeneration was further grouped into the following age categories based on root age: 1–4, 5–7, 8–10, and ≥11 years in the 2004 sampling. Because of the limited sample size in 2005, the 1–4 and 5–7 years categories were combined.

Following measurements, root samples were lyophilized (Virtis Freezmobile, 12SL, Gradiner, NY) for 10 days, and ground with a 20 mesh screen in a Wiley Mill (Arthur H. Thomas Co., Philadelphia, PA). Before being ground, samples were stored in glass dessicators to prevent reabsorption of moisture into freeze-dried tissue. Ground root samples were then stored at −20 °C for later analysis of root carbohydrates. Root soluble non-structural carbohydrate concentrations were analyzed colorimetrically with an anthrone/thiourea reagent (Quarmby and Allen, 1989), and were used as an indicator of root status and regeneration vigor.

2.3. Statistical analysis

A multivariate analysis of variance (MANOVA, SAS, 2000) was used to determine if overall seedling vigor was affected by our canopy treatments (mid-story removal, clearcut, and intact canopy), using seedling height, root collar diameter, number of internodes, and root diameter, root length, root mass, and root soluble carbohydrates as our measures of seedling vigor, and the Wilkes Lambda test statistic to determine significance. A multivariate analysis of variance was also performed on each site individually (Fentruss Spur, Horse Cove, Pigg House, and Water Plant) to assess overall seedling fitness by site.

Additionally we used ANOVA to test root and shoot characteristics individually to assess which characteristics affected seedling vigor. A univariate analysis (ANOVA) was performed using sites as blocks, mid-story removal, control and clearcut as treatments and individual regeneration as replicates. This univariate analysis (Proc GLM) used each component of the multivariate model as a dependent variable, root age as a covariate, and canopy treatment as the independent variable. The univariate approach was performed twice, once across all sites to determine treatment effect and secondly using site as an additional independent variable when significant treatment effects were evident. Treatment effects (mid-story removal vs. control) were assessed separately for each site using a *t*-test at the $P < 0.05$ level; clearcut was not included since it was implemented at only one site. To determine differences in root soluble non-structural carbohydrate concentration, a fixed effects analysis of variance was used with site, treatment (mid-story removal, clearcut, and intact canopy) and age as main effects. Bartlett's Test for equality of variances was used to ensure the assumption of equal variances. Multiple comparison tests were then performed on each type of regeneration (true seedlings and seedling sprouts) and all site treatments (intact canopy, mid-story removal, and clearcut). Least significant difference (LSD) was used to detect pairwise differences in root soluble non-structural carbohydrate concentration between canopy treatments.

3. Results

3.1. Root and shoot characteristics

The multivariate analysis indicated that white oak regeneration responded to a mid-story removal with an overall increase in seedling vigor (seedling height, basal diameter, number of internodes, and root diameter, length, mass, and carbohydrates) ($F_{21,750} = 6.71$, $P < 0.0001$). Associated with this increase in seedling vigor, there was also a significant site effect ($F_{21,750} = 3.53$, $P < 0.0001$) and a significant site x treatment interaction ($F_{42,1228} = 2.13$, $P < 0.0001$). Seedling vigor increased significantly at Fentruss Spur ($F_{7,25} = 9.81$,

$P < 0.0001$), Horse Cove ($F_{7,25} = 5.04$, $P = 0.001$), and Water Plant ($F_{7,25} = 42.14$, $P < 0.0001$), but only marginally at Pigg House ($F_{7,24} = 2.31$, $P = 0.06$). Further analysis using a univariate approach across all sites showed significant treatment effects on total seedling height, basal diameter, number of internodes, root diameter, and root soluble carbohydrates, but no treatment effect on root length or root mass across all sites (Table 1). Site significantly affected seedling height and basal diameter ($F_{3,279} = 7.46$, $P < 0.0001$, and $F_{3,279} = 6.16$, $P = 0.0005$, respectively), with a site × treatment interaction for seedling height ($F_{6,279} = 4.92$, $P < 0.0001$). There was a marginally significant site effect on root diameter ($F_{3,279} = 2.44$, $P = 0.07$) and root length ($F_{3,279} = 2.25$, $P = 0.08$), but root mass did not vary with site. There was also a moderately significant site × treatment interaction for root diameter ($F_{6,279} = 2.06$, $P = 0.06$), but not for root length, root mass, or basal diameter.

Some differences in seedling growth parameters were evident at each site. At Fentruss Spur (Table 2A), which was the only site with a clearcut, pre-treatment seedlings were significantly taller than any of our treatments, which did not differ. Regeneration growing in full sun (clearcut treatment) had significantly greater seedling basal diameter and root diameter than did seedlings growing under an intact canopy or mid-story removal (Table 2A). Horse Cove had the fewest detectable physical differences in seedling response. Seedling basal diameter was the only parameter that differed, and was greatest on seedlings growing under the mid-story removal (Table 2B). At Pigg House (Table 2C), regeneration under the mid-story removal had less height growth, fewer internodes, and less root length than did regeneration under the intact canopy. Root mass was greater than the pre-treatment seedlings, but did not differ from control seedlings growing under an intact canopy. The observed differences in root parameters at Pigg House may be due, in part, to differences in regeneration age; seedlings sampled from plots in both the mid-story removal and the intact canopies were significantly older than those sampled from our pre-treatment plots. At Water Plant (Table 2D), regeneration did not respond positively to the mid-story removal. Seedling height was lower under the treatment canopy than under the intact canopy or in the pre-treatment seedlings, but again, this response may be complicated by differences in root age.

3.2. Root carbohydrates

Root soluble non-structural concentrations increased across all sites in response to the increasing light levels associated with a mid-story removal (Table 3). At Fentruss Spur and Horse Cove, root carbohydrates in advance regeneration increased in response to a mid-story removal, while the other two sites showed no increase relative to the intact canopy (Table 3). There was no significant site × treatment interaction. Oak regeneration growing at Fentruss Spur under the full sun that resulted from a clearcut had greater root soluble non-structural carbohydrate concentrations than those growing under the mid-story removal or the intact canopies (Table 3).

Root carbohydrate concentrations in regenerating white oak growing under an intact canopy was ~5%, but varied among sites. Pre-treatment regeneration at Water Plant contained greater root carbohydrates than did regeneration at Horse Cove (Table 3). The remaining sites were intermediate, and did not differ. Post-treatment root carbohydrates of regeneration at both Pigg House and Water Plant were greater than at Horse Cove. There was no difference between the 2004 pre-treatment and 2005 untreated controls, with the exception of regeneration growing at Pigg House, which had higher soluble non-structural carbohydrate concentrations in the untreated controls than in the pre-treatment regeneration (Table 3).

Root soluble non-structural carbohydrate concentration was inversely proportional to root age ($F_{3,114} = 3.85$, $P = 0.01$) (Fig. 1), which ranged from 1 to >11 years. Regeneration with 1–4-year-old roots contained significantly greater carbohydrates than did regeneration with >8-year-old roots. In the younger, 1–7-year-old age class, root carbohydrates did not change in response to a mid-story removal or a clearcut (Fig. 2). In the 8–10 years old age class, root carbohydrates increased in response to increasing light (mid-story removal $F_{1,52} = 9.77$, $P = 0.003$, and clearcut $F_{1,41} = 7.91$, $P = 0.008$). The ≥11 years old age class responded similarly (mid-story removal $F_{1,25} = 5.39$, $P = 0.03$, and clearcut $F_{1,22} = 7.33$, $P = 0.01$). There was

Table 1
Characteristics (mean ± S.E.) of regenerating white oak (*Quercus alba* L.) across four sites in central Kentucky prior to silvicultural treatments and 1 year post-treatment

Seedling parameter	Pre-treatment ($N = 119$)	Mid-story removal ($N = 68$)	Intact canopy ($N = 68$)	Clearcut (full sun) ($N = 33$)	F_{df}/P
Seedling					
Height (cm)	26.24 ± 0.76b	25.52 ± 0.94b	30.81 ± 1.17a	20.71 ± 1.04c	$F_{3,282} = 10.76/<0.0001$
Diameter (mm)	4.25 ± 0.11c	4.68 ± 0.19ab	4.47 ± 0.15ab	5.18 ± 0.21a	$F_{3,282} = 5.28/0.002$
Number of internodes	6.53 ± 0.19ac	6.99 ± 0.31b	7.64 ± 0.3abc	6.09 ± 0.35c	$F_{3,282} = 5.04/0.002$
Root					
Length (cm)	30.52 ± 0.84a	30.42 ± 1.25a	31 ± 1.35a	25.36 ± 1.08a	$F_{3,278} = 0.46/0.71$
Mass (g)	9.35 ± 0.67a	13.16 ± 2.75a	10.13 ± 1.79a	10.71 ± 0.79a	$F_{3,278} = 0.53/0.66$
Diameter (mm)	8.28 ± 0.21b	8.31 ± 0.44b	7.89 ± 0.25b	9.98 ± 0.35a	$F_{3,278} = 4.66/0.003$
Age (years)	7.7 ± 0.23b	8.86 ± 0.67ab	9.32 ± 0.44a	8.94 ± 0.43ab	$F_{3,278} = 3.65/0.01$
SNC[a] (%)	5.27 ± 0.13c	5.93 ± 0.17b	5.22 ± 0.17c	6.68 ± 0.40a	$F_{3,272} = 9.56/<0.0001$

Means within rows followed by the same letter do not differ.
[a] Soluble non-structural carbohydrates.

Table 2
Physical characteristics (mean ± S.E.) of regenerating white oak (*Q. alba* L.) on four sites in central Kentucky prior to silvicultural treatments and 1 year post-treatment

Seedling parameter	Site treatment				
	Pre-treatment ($N = 30$)	Full sun (clearcut) ($N = 33$)	Mid-story removal ($N = 17$)	Intact canopy (control) ($N = 17$)	F_{df}/P
(A) Fentruss Spur (site index 22)					
Seedling					
Height (cm)	25.98 ± 1.48 a	21.05 ± 1.01 b	21.31 ± 1.37 b	22.71 ± 1.41 ab	$F_{3,94} = 3.34/0.02$
Diameter (mm)	4.26 ± 0.22 b	5.18 ± 0.22 a	4.13 ± 0.29 b	4.10 ± 0.30 b	$F_{3,94} = 5.15/0.002$
Number of internodes	6.60 ± 0.38 a	6.00 ± 0.40 a	6.10 ± 0.56 a	6.50 ± 0.57 a	$F_{3,95} = 0.43/0.73$
Root					
Length (cm)	31.50 ± 1.67 a	25.36 ± 1.48 b	28.91 ± 2.00 ab	28.70 ± 2.06 ab	$F_{3,94} = 2.87/0.04$
Mass (g)	11.30 ± 1.33 a	10.71 ± 2.83 a	12.86 ± 3.83 a	6.34 ± 3.94 a	$F_{3,94} = 0.69/0.56$
Diameter (mm)	8.60 ± 0.41 b	9.98 ± 0.50 a	8.01 ± 0.67 b	7.54 ± 0.69 b	$F_{3,94} = 3.75/0.01$
Age (years)	7.53 ± 0.66 a	8.94 ± 0.63 a	9.31 ± 0.89 a	8.24 ± 0.87 a	$F_{3,92} = 1.18/0.32$

Seedling parameter	Site treatment			
	Pre-treatment ($N = 30$)	Mid-story removal ($N = 17$)	Intact canopy (control) ($N = 17$)	F_{df}/P
(B) Horse Cove (site index 22)				
Seedling				
Height (cm)	29.32 ± 1.50 a	24.23 ± 1.82 a	33.47 ± 1.77 a	$F_{2,59} = 1.95/0.15$
Diameter (mm)	4.38 ± 0.22 b	5.37 ± 0.29 a	4.45 ± 0.29 b	$F_{2,60} = 4.65/0.01$
Number of internodes	7.10 ± 0.39 a	8.18 ± 0.54 a	8.00 ± 0.52 a	$F_{2,59} = 0.94/0.40$
Root				
Length (cm)	30.60 ± 1.7 a	32.88 ± 2.79 a	29.48 ± 2.79 a	$F_{2,60} = 0.50/0.61$
Mass (g)	8.50 ± 1.35 a	13.66 ± 5.67 a	14.37 ± 5.67 a	$F_{2,60} = 0.79/0.46$
Diameter (Mm)	7.80 ± 0.42 a	8.59 ± 0.61 a	7.88 ± 0.61 a	$F_{2,60} = 0.78/0.46$
Age (years)	8.62 ± 0.72 a	8.94 ± 0.96 a	10.56 ± 0.96 a	$F_{2,58} = 1.36/0.26$
(C) Pigg House (site index 23.8)				
Seedling				
Height (cm)	22.88 ± 1.48 c	28.73 ± 2.13 b	39.06 ± 2.13 a	$F_{2,61} = 15.1/<0.001$
Diameter (mm)	4.39 ± 0.22 b	5.06 ± 0.43 ab	5.38 ± 0.43 a	$F_{2,61} = 2.45/0.09$
Number of internodes	6.30 ± 0.38 b	7.20 ± 0.61 ab	8.80 ± 0.61 a	$F_{2,61} = 5.61/0.006$
Root				
Length (cm)	30.30 ± 1.67 b	31.23 ± 2.83 b	38.67 ± 2.92 a	$F_{2,60} = 3.55/0.04$
Mass (g)	8.50 ± 1.33 b	20.09 ± 4.75 a	13.70 ± 4.75 ab	$F_{2,61} = 3.39/0.04$
Diameter (mm)	8.30 ± 0.41 a	9.91 ± 0.86 a	9.09 ± 0.86 a	$F_{2,61} = 1.83/0.17$
Age (years)	7.13 ± 0.71 b	11.25 ± 0.97 a	10.71 ± 0.95 a	$F_{2,60} = 7.69/0.001$
(D) Site: Water Plant (site index 23.5)				
Seedling				
Height (cm)	26.90 ± 1.48 ab	23.83 ± 1.98 b	30.56 ± 2.04 a	$F_{2,60} = 2.80/0.07$
Diameter (mm)	4.26 ± 0.22 a	4.19 ± 0.25 a	3.98 ± 0.25 a	$F_{2,60} = 0.24/0.79$
Number of internodes	5.90 ± 0.38 b	6.60 ± 0.57 ab	7.50 ± 0.59 a	$F_{2,60} = 3.03/0.06$
Root				
Length (cm)	27.70 ± 1.67 a	28.75 ± 1.83 a	27.42 ± 1.88 a	$F_{2,60} = 0.10/0.91$
Mass (g)	9.10 ± 1.33 a	6.03 ± 0.874 a	5.85 ± 0.90 a	$F_{2,60} = 1.46/0.24$
Diameter (mm)	8.50 ± 0.41 a	6.77 ± 0.38 b	7.01 ± 0.39 b	$F_{2,60} = 4.33, 0.02$
Age (years)	7.53 ± 0.42 a	6.12 ± 0.56 b	7.75 ± 0.58 a	$F_{2,60} = 2.65/0.08$

Means within rows followed by the same letter do not differ.

no difference in soluble non-structural carbohydrate concentration in the mid-story removal or clearcut in 8–10 years old regeneration, or regeneration ≥11 years (Fig. 2).

4. Discussion

White oak advance regeneration showed only minor initial changes in above-ground growth in response to the changing light regime associated with a mid-story removal and a clearcut, and root diameter was the only below-ground physical parameter we measured that showed a response to our treatments. However, striking differences were evident in root soluble non-structural carbohydrates in white oak advance regeneration with the changing light regime 1 year after treatment. Soluble non-structural carbohydrates in regenerating white oak roots were greatest following full canopy removal, intermediate in the mid-story removal, and lowest in regeneration growing under an intact canopy. Similar responses

Table 3
Root soluble non-structural carbohydrates (mean% ± S.E.) of regenerating white oak (*Q. alba* L.) on four sites in central Kentucky prior to silvicultural treatments and 1 year post-treatment

Root soluble non-structural carbohydrates (%)	Pre-treatment (N = 119)	Mid-story removal (N = 68)	Intact canopy (N = 68)	Clearcut (full sun) (N = 33)	F_{df}/P
All sites	5.27 ± 0.13c	5.93 ± 0.17b	5.22 ± 0.17c	6.68 ± 0.40 a	$F_{3,272}$ = 9.56/<0.0001
Fentruss Spur	5.49 ± 0.24 ABb	6.15 ± 0.41 Aa	5.14 ± 0.41 ABb	6.68 ± 0.32 a	$F_{3,89}$ = 4.16/0.0008
Horse Cove	4.87 ± 0.25 Bab	5.50 ± 0.28 Aa	4.41 ± 0.27 Bb	–	$F_{2,58}$ = 4.39/0.02
Pigg House	4.93 ± 0.24 ABb	6.17 ± 0.29 Aa	5.73 ± 0.29 Aa	–	$F_{2,61}$ = 8.51/0.0005
Water Plant	5.49 ± 0.24 Aa	5.88 ± 0.45 Aa	5.65 ± 0.46 Aa	–	$F_{2,55}$ = 0.07/0.94
F_{df}/P	$F_{3,111}$ = 3.29/0.02	$F_{3,63}$ = 0.78/0.51	$F_{3,62}$ = 3.80/0.02	–	–

Means within columns followed by the same upper case letter, and means within rows followed by the same lower case letter, do not differ.

to changing growth environments are exhibited by other species (Chapin et al., 1990). This buildup of root carbohydrates may be especially important in woody plants such as oaks, which rely on sprout production from dormant buds following a disturbance (Chapin et al., 1990; Hodges and Gardiner, 1992). We believe that the increase in soluble root carbohydrates of our regeneration subjected to a mid-story removal is an indicator of the potential usefulness of this treatment.

A delay in above-ground biomass accumulation associated with a mid-story removal has been documented in cherrybark oak (Janzen and Hodges, 1987; Deen et al., 1993; Lockhart et al., 2000), and could be attributed to the hydraulic structure in younger seedlings, which may be inadequate for the increased demand for resources that results from a release (Lockhart et al., 2000; Mencuccini, 2003). Additionally, the lag in above-ground biomass accumulation found in these studies may be due in part to the time required for seedling acclimation with respect to bud break phenology under the altered light environment (Mcgee, 1975, 1976). The older root systems in our study contained lower soluble carbohydrates, which may indicate less vigor compared to younger seedlings of the same size. The inverse relationship between soluble non-structural carbohydrate concentrations and root age suggest that older seedlings, growing under intact canopies, may be less competitive upon release. Subsequent growth measurements on our test seedlings will demonstrate whether the observed increases in root soluble non-structural carbohydrates can be converted to future gains in biomass.

Our understanding of the availability of carbohydrates for remobilization in different portions of woody plant root systems is rudimentary (Chapin et al., 1990). We analyzed whole-root soluble non-structural carbohydrates, but the amount of carbohydrate available for biomass production is unknown. In cherrybark oak, the current year's photosynthate (soluble carbohydrates) is mobilized and stored in the current year's root growth ring (Lockhart et al., 2003), suggesting that carbohydrates available for growth may be much less than the total amount sequestered in the root system (Ziegler, 1964). If carbohydrates stored in 'dead cells' of woody plants are unavailable for mobilization (Ziegler, 1964), carbohydrates in growth rings beyond the current year may not be available for use by growing tissue (Chapin et al., 1990; Ziegler, 1964). If only current year photosynthate is available for growth, the decrease in carbohydrate content with root age may negatively affect the release of older root systems. The distinction between available and unavailable carbohydrates should be investigated further if we are to fully understand the use of these carbohydrate reserves for future growth.

The increase in soluble non-structural carbohydrates of regenerating white oak we measured adds credence to the hypothesis regarding the conservative growth strategy of oaks (Hodges and Gardiner, 1992). The bias toward producing root carbohydrates rather than above-ground biomass corroborates this hypothesis, but also suggests that the vigor of white oak regeneration does increase with light availability. However, similar studies of northern red and cherrybark oaks suggest that it may take years for seedling size to be sufficient to take advantage of a complete canopy removal (Loftis, 1983; Janzen

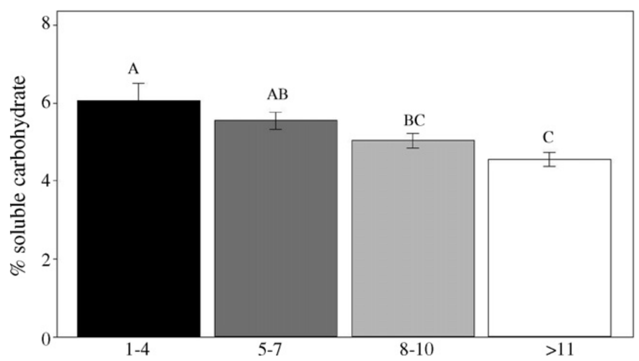

Fig. 1. Root soluble non-structural carbohydrates (%) by root age class in white oak advance regeneration growing under an intact canopy across all sites. Letters represent significant differences at the $P \leq 0.05$ level (LSD).

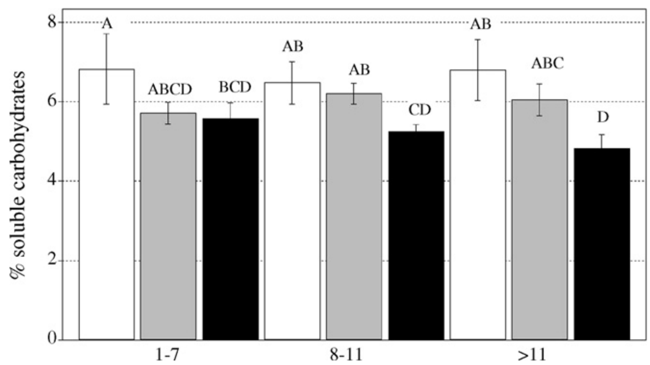

Fig. 2. Effects of root age and light availability (clearcut (□), mid-story removal (▩), and intact canopy (■)) on root soluble non-structural carbohydrate (%) of white oak advance regeneration. Letters represent significant differences at the $P \leq 0.05$ level (LSD).

and Hodges, 1987; Deen et al., 1993; Lockhart et al., 2000). Our observed increase in overall seedling vigor (dominated by an increase in root carbohydrates) is encouraging, and has implications for developing management strategies to enhance white oak regeneration.

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References

Abrams, M.D., Nowacki, G.J., 1992. Historical variation in fire, oak recruitment and post-logging accelerated succession in central Pennsylvania. J. Torr. Bot. Soc. 119, 19–25.

Abrams, M.D., 1998. The red maple paradox: what explains the widespread expansion of red maple in eastern forests? Bioscience 48, 355–364.

Abrams, M.D., 2003. Where has all the white oak gone? Bioscience 53, 927–938.

Adams, A.S., Rieske, L.K., 2001. Herbivory and fire influence white oak (*Quercus alba* L.) seedling vigor. Forest Sci. 47, 331–337.

Adams, A.S., Rieske, L.K., 2003. Prescribed fire affects white oak seedling phytochemistry: implications for insect herbivory. For. Ecol. Manage. 176, 37–47.

Arthur, M., Parateley, R., Blankenship, B., 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. J. Torr. Bot. Soc. 125, 225–236.

Barton, A.M., Gleeson, S.K., 1996. Ecophysiology of seedlings of oaks and red maple across a topographic gradient in eastern Kentucky. Forest Sci. 42, 335–342.

Carvell, K.L., 1979. Factors affecting the abundance, vigor and growth response of understory oak seedlings. In: Proceedings of Regenerating Oaks in Upland Hardwood Forests—1979 John S. Wright Forestry Conference, Purdue University, Lafayette, IN, pp. 23–26.

Chapin III, S., Shulze, E., Mooney, H., 1990. The ecology and economics of storage in plants. Annu. Rev. Ecol. Syst. 21, 423–447.

Clark, F.B., 1992. An historical perspective of oak regeneration. In: Loftis, D.L., Mcgee, C. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. USDA Gen. Tech. Rep. SE-84, pp. 250–263.

Deen, R.T., Hodges, J.D., Janzen, G.C., 1993. The influence of midstory–understory control treatments on regeneration of red oak species following clearcutting. In: Brissette, J.C. (Ed.), Proceedings of the Seventh Biennial Southern Silviculture Research Conference. USDA Gen. Tech. Rep. SO-93, pp. 117–121.

Dey, D., Parker, W., 1996. Regeneration of red oak (*Quercus rubra* L.) using shelterwood systems: ecophysiology, silviculture, and management recommendations. Ontario Ministry of Natural Resources Forest Research Information Paper No. 126, 59 pp.

Hodges, J.D., Gardiner, E.S., 1992. Ecology and physiology of oak regeneration. In: Loftis, D.L., Mcgee, C. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. USDA Gen. Tech. Rep. SE-84, pp. 54–65.

Janzen, G.C., Hodges, J.D., 1987. Influence of midstory and understory vegetation removal on the establishment and development of oak regeneration. In: Shoulders, E. (Ed.), Proceedings of the Third Biennial Southern Silviculture Research Conference. USDA Gen. Tech. Rep. SE-42, pp. 455–461.

Kaelke, C.M., Kruger, E.L., Reich, P.B., 2001. Trade-offs in seedling survival, growth and physiology among hardwood species of contrasting successional status along a light-availability gradient. Can. J. For. Res. 31, 1602–1616.

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic, New York.

Kruger, E.L., Reich, P.B., 1997. Responses of hardwood regeneration to fire in mesic forest openings. III. Whole plant growth, biomass distribution, and nitrogen and carbohydrate relations. Can. J. For. Res. 27, 1841–1850.

Lockhart, B.R., Hodges, J.D., Gardiner, E.S., 2000. Response of advance cherrybark oak reproduction to mid-story removal and shoot clipping. Southern J. Appl. For. 24, 45–50.

Lockhart, B.R., Hodges, J.D., Gardiner, E.S., Ezell, A., 2003. Photosynthate distribution patterns in cherrybark oak seedling sprouts. Tree Physiol. 23, 1137–1146.

Loftis, D.L., 1983. Regenerating red oak on productive sites in the southern Appalachians: a research approach. In: Jones, E. (Ed.), Proceedings of the Second Biennial SouthernSilviculture Conference. USDA Gen. Tech Rep. SE-024, pp. 144–150.

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

Loftis, D.L., 1992. Regenerating northern red oak on high quality sites in the southern Appalachians. In: Loftis, D.L., Mcgee, C. (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. USDA Gen. Tech. Rep. SE-84, pp. 202–210.

Lorimer, C.G., 1983. Eighty-year development of northern red oak after partial cutting in a mixed-species Wisconsin forest. Forest Sci. 29, 371–383.

Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82, 227–237.

Mcgee, C.E., 1975. Change in forest canopy affects phenology and development of northern red and scarlet oak seedlings. Forest Sci. 21, 175–179.

Mcgee, C.E., 1976. Differences in budbreak between shade-grown and open-grown oak seedlings. Forest Sci. 22, 484–486.

Mencuccini, M., 2003. The ecological significance of long-distance water transport: Short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell Environ. 26, 163–182.

Quarmby, C., Allen, S.E., 1989. Organic constituents. In: Allen, S.E. (Ed.), Chemical Analysis of Ecological Materials. Wiley, New York, pp. 160–201.

Rogers, R., Johnson, P., Loftis, D.L., 1993. An overview of oak silviculture in the United States: the past, present and future. Ann. For. Sci. 50, 535–542.

Sander, I.L., 1972. Size of advance reproduction: key to growth following harvest cutting. USDA Forest Service Res. Pap. NC-79, 1972, 6 pp.

SAS Institute, 2000. SAS Software Version 8. SAS, Cary, NC.

Schnur, G.L., 1937. Yield, stand, and volume tables for even-aged upland oak forests. USFS Gen. Tech. Bull. 560, 88.

Spencer, J.S., Kingsley, N.P., 1991. The oak resource in the Upper Midwest: an overview. In: Proceedings of the Oak Resource in the Upper Midwest Conference. Publ. no. NR-BU-5663-3, St. Paul, pp. 11–17.

Waring, R.H., Thies, W.G., Muscato, D., 1980. Stem growth per unit leaf area: a measure of tree vigor. Forest Sci. 26, 112–117.

Ziegler, H., 1964. Storage mobilization and distribution of reserve material in trees. In: Zimmmerman, M.H. (Ed.), The Formation of Wood in Forest Trees. Academic, New York, pp. 307–320.