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Morphological acclimation and growth of ash (*Fraxinus pennsylvanica* Marsh.) advance regeneration following overstory harvesting in a Mississippi River floodplain forest

Alexander Sinz[a], Emile S. Gardiner[b,*], Brian Roy Lockhart[b], Ray A. Souter[b]

[a] Albert Gerst Strasse 1, 07407 Keilhau, Germany
[b] USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776, USA

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ABSTRACT

Stand-level growth responses and plant-level patterns of biomass accumulation and distribution were examined to learn how stand structure influences morphological acclimation and growth of green ash (*Fraxinus pennsylvanica* Marsh.) advance regeneration following overstory harvesting. Nine, 20-ha plots that received clearcut harvesting (100% basal area removal), partial harvesting (50% basal area removal), or no harvesting (control) were sampled to measure height, root-collar diameter, leaf, stem and root biomass, and leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) of ash regeneration. Six years after treatment, plot-level analyses indicated that ash growth was greatest in plots receiving clearcut harvesting, and least in control plots. Examination of LMR, SMR and RMR revealed that this growth response was not associated with acclimation that altered plant morphology. Total biomass ranged 275-fold among sampled plants, and much of this variation was accounted for by measurements of stand leaf area index (LAI). Along the gradient of stand LAI, values greater than 2 inhibited biomass accumulation. Stand LAI values less than 1.5 promoted ash biomass accumulation which reached a maximum where LAI values approached 0.7 and tapered above or below this value. Our findings indicate that green ash regeneration can be managed beneath light canopy cover, and the ability of seedlings to establish and persist beneath closed canopies and vigorously respond to release without having to endure prolonged morphological acclimation provides flexibility in developing regeneration protocols.

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1. Introduction

Certain tree species endemic to broadleaf forests of the northern temperate zone can exhibit a regeneration strategy that involves seed germination and accrual of established seedlings in the understory of closed-canopy stands (Carvell and Tryon, 1961; Hara, 1987; Streng et al., 1989; Marks and Gardescu, 1998; Houle, 1991; McClure et al., 2000; Szwagrzyk et al., 2001). This “seedling bank” strategy can ensure a persistent source of advance regeneration for sporadic mast producers, and can maintain regeneration in a favorable position to respond to canopy disturbance (Oliver and Larson, 1996; Marks and Gardescu, 1998). Foresters working in temperate broadleaf forests regularly manage these processes to accomplish natural regeneration of several species, notably oaks (*Quercus* spp.) and beeches (*Fagus* spp.) (Crow, 1988; Loftis, 1990; Collet et al., 2001; Harmer and Morgan, 2007; Madsen and Hahn, 2008). Critical to management is that advance regeneration comprising the seedling bank must be capable of persisting several years in the shaded understory, and must also possess the ability to acclimate and quickly favor height growth in response to a regeneration harvest.

Ash (*Fraxinus* spp.) species are commonly found as overstory trees in deciduous forests throughout the northern temperate zone where they are favored for their silvical characteristics and valued timber quality (Schlesinger, 1990; Kerr and Cahalan, 2004; Nakamura et al., 2007). Where ash is an overstory component of deciduous forests, workers regularly document established cohorts of ash advance regeneration in the forest understory (Tapper, 1992; Emborg, 1998; Frey et al., 2007; Nakamura et al., 2007). These observations suggest that several ash congeners of the northern temperate zone share a common regeneration strategy on forested sites, a strategy that involves formation of a seedling bank. As with other species that mast irregularly (Frey et al., 2007), advance regeneration that persists in the understory provides the various ash species with an opportunity to quickly respond to canopy disturbance. Rapid height growth and vigorous development of ash advance regeneration out of the seedling bank have been observed in response to natural disturbance and disturbance resulting from

* Corresponding author. Tel.: +1 662 686 3184; fax: +1 662 686 3195.
E-mail address: egardiner@fs.fed.us (E.S. Gardiner).

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regeneration harvesting (Wardle, 1959; Johnson, 1975; Tapper, 1993; Marigo et al., 2000).

Though an established seedling bank is usually necessary to successfully regenerate ash in broadleaf stands (Thurston et al., 1992; Liptzin and Ashton, 1999; Miller and Kochenderfer, 1998), the presence of advance regeneration does not necessarily assure successful regeneration. Herbivory, for example, is a concern in some European forests because it can suppress European ash (*F. excelsior* L.) advance regeneration potentially limiting its competitive response to release (Modrý et al., 2004; Kupferschmid and Bugmann, 2008). Where herbivory is not a significant issue, insufficient light availability is a factor that has been implicated as potentially limiting the growth response of ash regeneration following canopy disturbance (Madsen and Hahn, 2008; Collet et al., 2008). Vigorous height growth of ash released by harvesting has been linked to relatively low residual stand basal areas (Oliver et al., 2005), and light availability as determined by the partial canopy is likely a prominent driver of the ash growth response (Petriţan et al., 2009). In any case, little is known about the mechanisms of morphological acclimation that support rapid development of ash advance regeneration released from the seedling bank by canopy disturbance, or the degree to which stand structure determines morphology and growth of ash advance regeneration.

To gain an understanding of how ash advance regeneration acclimates morphologically to compete for resources made available by canopy disturbance, and the extent to which stand characteristics determine the morphological response, we investigated biomass accumulation of green ash (*F. pennsylvanica* Marsh.) advance regeneration following overstory harvesting in a floodplain forest of the Mississippi River. Objectives in pursuing this research were to: (1) assess stand-level response in height and root-collar diameter by ash regeneration to residual overstory conditions produced by stand harvesting; (2) identify whole-plant patterns of biomass distribution associated with the growth response of ash regeneration following overstory disturbance; and (3) describe biomass accumulation and distribution for ash regeneration relative to leaf area index of harvested stands.

2. Methods

2.1. Species

Green ash is endemic to North America where it is widely distributed throughout the central and eastern United States and parts of Canada (Kennedy, 1990). It is found most abundantly and exhibits highest productivity on alluvial soils of floodplains in the southern United States (Kennedy, 1990). While green ash trees are considered shade intolerant, seedlings are classified as shade tolerant and may exist in a seedling bank in the understory of bottomland hardwood forest for several years (Kennedy, 1990). Like other ash congeners, overstory disturbance is needed to promote the development of advance green ash seedlings into higher canopy positions (Oliver et al., 2005).

2.2. Study site

The study was established in a mature bottomland hardwood forest located on Pittman Island, Issaquena County, Mississippi. Pittman Island is adjacent and west of the Mississippi River in the Lower Mississippi Alluvial Valley (32°55′50″N; 91°09′07″W). The site is in a humid, subtropical region of the Northern Temperate Zone with hot summers and moderate winters. Mean annual temperature between 1991 and 2001 was about 18 °C with a July average of 28 °C and a January average of 7 °C at the nearby (≈15 km) Lake Providence, Louisiana weather station (National Climatic Data Center, 2007). Mean annual rainfall during this same period exceeded 1500 mm, with winter and spring months receiving about 50% more precipitation than summer and fall months (National Climatic Data Center, 2007).

Topography of the island is characterized by alternating ridge and swale (a long, narrow depression between ridges) features created by sediment deposition and erosion from the migrating Mississippi River channel. The study site is routinely inundated by floodwater from the river, particularly during the late winter and spring months when snowmelt occurs in northerly areas of the drainage basin. Because soils on Pittman Island are alluvial in origin, they have not been completely delineated and mapped by series. However, predominant soil series of the floodplain ridges on which this study occurred include Commerce (fine-silty, mixed, superactive, nonacid, thermic Fluvaquentic Endoaquepts), Robinsonville (coarse-loamy, mixed, superactive, nonacid, thermic Typic Udifluvents), and Bowdre (clayey over loamy, smectitic, thermic Fluvaquentic Hapludolls) (Wynn et al., 1961). Reaction of the surface horizon typically ranges between a pH of 6.1 and 7.8 for the Commerce series, 6.6 and 7.8 for the Robinsonville series and 5.6 and 7.3 for the Bowdre series (Wynn et al., 1961). Samples collected through our research revealed that surface soil texture on the study site averaged 4% sand, 28% silt and 68% clay.

At the initiation of this research, vegetative cover on the site was a mature, mixed bottomland hardwood forest. Overstory composition and the majority of stand basal area was comprised of sugarberry (*Celtis laevigata* Willd.), sweet pecan (*Carya illinoensis* (Wang) K. Koch), boxelder (*Acer negundo* L.), American elm (*Ulmus americana* L.), Nuttall oak (*Q. nuttallii* Palm.) and green ash. Forbes, woody and herbaceous vines, and tree seedlings, including green ash, predominated the understory flora (Kellum et al., 1999; Lockhart, 1998).

2.3. Experimental design

In 1995, 3 replicates of 3, 20-ha treatment plots were delineated on the study site. Each treatment plot was assigned 1 of 3 treatment levels that included 100% harvest of the basal area (clearcut), a nominal goal of 50% harvest of the basal area (partial cut), and a non-harvested control. Treatment plots were harvested with felling machinery and logs were bucked on the plot then skidded to a loading deck. Following the harvest of plots receiving 100% basal area removal, residual stems >5 cm (2 in.) dbh were felled with a chainsaw. All harvesting occurred in Winter 1995/1996.

2.4. Sampling procedures

Six-years after treatment application (Summer 2001), we initiated sampling efforts to quantify growth and morphology of green ash regeneration relative to the three stand conditions following harvest treatments. Transect lines (about 440 m long spaced 50 m apart) were systematically established through each treatment plot to locate green ash regeneration. A random starting point was chosen and transects were walked and searched for green ash regeneration. Ash regeneration had to meet certain age, morphological and site conditions to be marked and given a unique identification number for use in this study. We included only regeneration that was apparently established prior to the harvest or the year of the harvest. To meet this criterion, plants had to exhibit flush scars on the stem consistent with a minimum age of 6 years. Plants had to be single stemmed and free of significant insect, disease or herbivore damage. Further, plants had to be established on a topographic ridge in the floodplain so that variability associated with the effects of soil and hydroperiod on seedling growth would be minimal. Locating and marking plants that met these criteria continued until 75 individuals were tagged in each treatment plot.

Table 1
Stand characteristics (mean ± standard error) on a Mississippi River floodplain site 6 years after overstory harvesting, Pittman Island, MS, 2001.

Variable	Control	Partial harvest	Clearcut
Trees (ha^{-1})	575 ± 22	393 ± 48	802 ± 113
Average dbh (cm)	19.0 ± 0.8	18.9 ± 0.9	4.2 ± 0.1
Canopy tree dbh (cm)[a]	37.6 ± 1.4	30.2 ± 1.7	6.1 ± 0.3
Basal area ($m^2\ ha^{-1}$)	25.3 ± 1.5	16.4 ± 2.5	1.3 ± 0.2
Average height (m)	13.5 ± 0.4	13.3 ± 0.5	4.4 ± 0.1
Canopy tree height (m)	24.5 ± 0.5	21.2 ± 0.8	7.0 ± 0.2
Leaf area index	3.0 ± 0.15	1.8 ± 0.11	0.4 ± 0.06
Understory vegetation ($kg\ ha^{-1}$)	590 ± 79	2060 ± 718	3998 ± 1039

[a] The five tallest trees in each sample plot were sampled as canopy trees.

From the pool of 75 tagged stems in each treatment plot, 25 individuals (225 total plants) were randomly selected for the measurement of height (cm) and root-collar diameter (mm). Of the 25 plants sampled for height and diameter in each treatment plot, 5 individuals were randomly selected for intensive morphology sampling. The 45 plants selected for morphology sampling were excavated from soil with hand tools then dissected into leaf, stem and root tissues. All tissues were cleaned in the laboratory then dried at 70 °C to a constant weight.

A cross-section of stem tissue immediately above the apparent root-collar was collected from each of the 45 plants sampled for morphology. The stem cross-section was prepared for ring analysis to determine plant age, stem diameter at the time of the overstory harvest, and stem diameter at sampling. Plant age was determined by counting the number of annual rings in the stem section with the aid of a Nikon 102 dissecting microscope and a video monitor. Two perpendicular measurements of stem diameter were collected with a vernier caliper at the outer edge of the ring from the 1995 growing season (overstory harvest followed this growing season), and inside the bark at the outer edge of the ring from the 2001 growing season (season in which sample plants were harvested).

To quantify the impact of harvesting practices on residual stand structure and the resulting understory environment, stand variables including stand density, tree height, diameter at breast height (dbh), basal area, canopy height, and leaf area index (LAI) were measured near the excavation pit of each sample seedling. Stand density, tree height and dbh were measured in 0.04-ha (0.1-ac) circular plots centered over each excavation pit. All trees with a dbh > 2.54 cm (1 in.) were sampled by species. LAI was measured with a Nikon CoolPix 950 digital camera and fish-eye converter lens positioned 0.8 m above seedling excavation pits. Canopy images were collected in the early morning and late afternoon under cloud free skies, and analyzed with HemiView 2.1 Canopy Analysis Software to compute LAI. Understory vegetation was quantified by harvesting all vegetation in 3, 1 m × 1 m sample frames randomly located in each treatment plot. Harvested vegetation was dried and weighed then values were converted to $kg\ ha^{-1}$ for reporting.

2.5. Data analyses

Data analyses were conducted to address the response by green ash regeneration at the plot-level and at the plant-level. The plot-level approach, which addressed objective 1 of this research, was used to identify how height and root-collar diameter of green ash regeneration responded within the harvested experimental units. Mean heights and root-collar diameters for green ash regeneration were calculated from the 25 observations collected in each treatment plot. Plot means were transformed with the logarithmic transformation then analyzed with Analysis of Variance procedures to test for harvest treatment effects on sixth-year height and root-collar diameter of green ash regeneration. A height/root-collar diameter ratio was also computed for each plant, and plot means for this variable were analyzed as described for height and root-collar diameter. These tests were conducted with SAS software (Version 9.1) according to a Completely Randomized Design, and means of significant treatment effects were separated with Duncan's multiple range test. All statistical tests were conducted at an alpha level of 0.05.

While the Analysis of Variance approach addressed plot-level treatment effects on green ash height, root-collar diameter, and height/root-collar diameter ratio, it could not reveal morphological mechanisms of acclimation expressed by green ash (objective 2), or how individual green ash stems responded to localized environmental conditions created by the overstory harvests (objective 3). Therefore, we conducted more detailed regression analyses of plant-level morphology and the morphological responses to environmental variables measured at each sample plant location. These analyses explored relationships between green ash morphology variables and overstory LAI. Root mass, stem mass, leaf mass, and total plant mass were plotted against LAI to determine trends in response. The relationship between total biomass accumulation and stand LAI was quantified with a segmented polynomial model that proposed a quadratic regime for low stand LAI and a linear regime for high stand LAI.

Root mass ratio (RMR = root mass/total plant mass), stem mass ratio (SMR = stem mass/total plant mass), and leaf mass ratio (LMR = leaf mass/total plant mass) were calculated from measured values of root mass, stem mass and leaf mass. Prior to conducting detailed examination of biomass distribution patterns, it was important to determine if sample plant height or mass influenced green ash morphology. This determination was made by conducting simple linear regression analyses with plant height and total biomass as independent variables and LMR, SMR, and RMR as dependent variables. A significant relationship between height or total biomass and any of these ratios would be indication that plant size plays a role in determining how green ash accumulated biomass. Simple linear regressions were also conducted between stand LAI and LMR, SMR, and RMR to determine the effect of stand structure on morphology of regeneration. Because examination of stem cross sections revealed that 8 of the 45 plants intensively sampled for morphology had established on the site a year or more after the harvest, these 8 plants were removed from all analyses.

3. Results

3.1. Plot-level response

Overstory harvesting created three distinct stand conditions on the study site that were perpetuated 6 years after treatment (Table 1). Relative to unharvested control plots, the clearcut treatment reduced mean stand basal area by 95%, lowered mean LAI by 87% and increased biomass of understory vegetation by more than 575%. It should be noted that stems and associated basal area reported for the clearcut treatment in Table 1 are attributed to ingrowth of regeneration rather than stems left residual to the harvest. Partial harvesting decreased mean stand basal area by 35%,

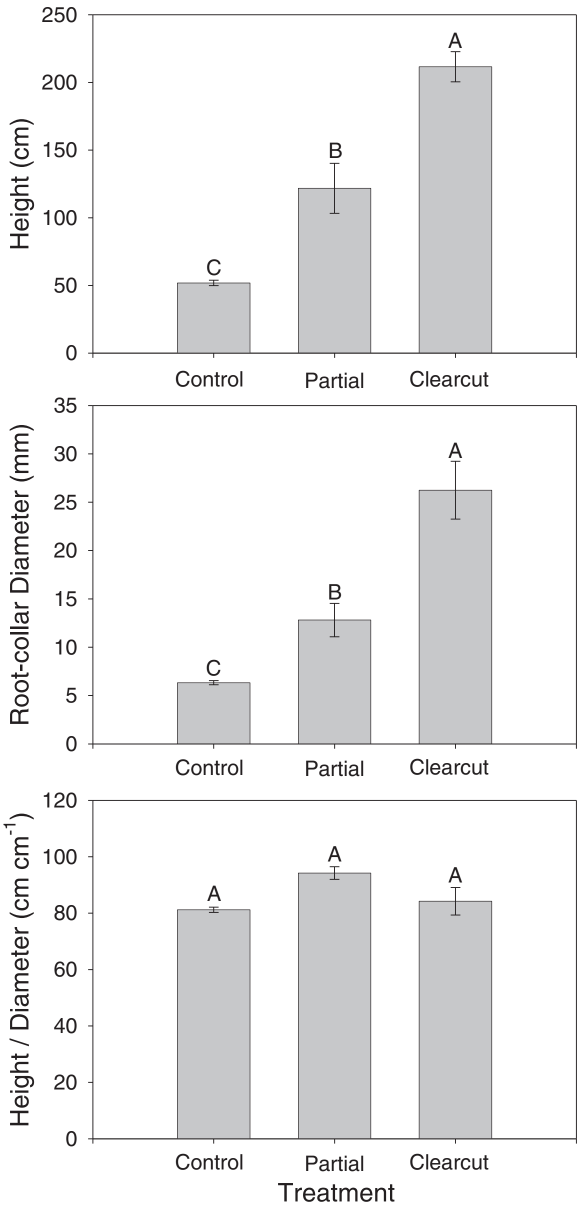

Fig. 1. Stand-level response in height, root-collar diameter and height/diameter ratio for green ash natural regeneration 6 years after overstory harvesting. Bars represent plot means, error bars are ± the standard error, and different letters above error bars signify a difference between treatment means at the 0.05 probability level.

lowered mean LAI 40%, and increased biomass of understory vegetation by 250% compared to control plots (Table 1). While advance regeneration contributed to the treatment responses observed for understory biomass, increases were primarily driven by forbs, herbaceous vines, and woody vines that rose in importance following stand disturbance (Kellum et al., 1999).

Growth of ash regeneration showed a positive response to overstory harvesting with significant increases in mean heights and root-collar diameters (Fig. 1). Greatest heights were found in clearcut plots where ash regeneration averaged more than 4 times the height of regeneration growing in control plots ($P > F = 0.0002$) (Fig. 1). Regeneration established in partially harvested plots was more than twice the height of that in controls (Fig. 1). Root-collar diameters patterned similarly to heights as the largest stem diameters were found in clearcut plots, and the smallest were found in unharvested controls ($P > F = 0.0003$) (Fig. 1).

While regeneration showed a strong height and root-collar response to overstory harvesting, stand treatments appeared to have little effect on how stems partitioned growth. The height/diameter ratio averaged 87 cm cm^{-1} across the study site, remaining consistent between all three levels of canopy harvest ($P > F = 0.0701$) (Fig. 1).

3.2. Plant-level response

Ash regeneration excavated for morphological analysis ranged between 6- and 10-years-old. Examination of stem cross-sections also revealed that these seedlings had an average root-collar diameter of 1.7 mm prior to treatment application. Six years after stand harvesting, total biomass ranged 1228 g with the smallest plant weighing 4.5 g and the largest plant weighing 1232.2 g. Leaf tissue was the smallest component of total plant biomass ranging between 0.9 and 178.7 g. Stem biomass varied between 1.9 and 622.0 g, while root biomass measured between 1.6 and 431.5 g among the sampled plants.

Sample plants excavated in this study ranged 259 cm in height, but proportional distribution of biomass remained similar across this range. LMR, SMR and RMR remained relatively constant for all plant heights observed in this study (Fig. 2). Likewise, regression analysis conducted for LMR, SMR, RMR and total biomass revealed that biomass distribution by ash regeneration was not influenced by plant size ($P > F = 0.5282$) (Fig. 3). In other words, accumulation of leaf, stem, and root biomass relative to total plant biomass remained constant within the range of harvested plants. Collectively, Figs. 2 and 3 illustrate that sample plant size was not a confounding factor influencing proportional distribution of biomass in this study.

LAI values corresponding to each sample plant location in the broadleaf stand ranged from 0.11 to 4.15. Though green ash seedlings exhibited long-term persistence in the understory at high stand LAI values, trends in the data suggest that the greatest potential for biomass accumulation occurred where stand LAI was low (Fig. 4). Our data indicates that stand LAI values of 2 or more substantially limited green ash biomass accumulation. In contrast, a sharp increase in the potential for biomass accumulation occurred below a stand LAI value of 1.5 (Fig. 4). Segmented polynomial regression, with quadratic and linear segments, supported a distinct threshold of biomass accumulation consistent with these LAI values.

Proportional accumulation of leaf and stem biomass did not vary within the range of stand LAI values observed in this study (Fig. 5). Regardless of stand LAI, green ash regeneration maintained about 16% of total biomass in leaf tissue and about 50% of total biomass in stem tissue. The remaining 34% of total biomass was maintained in the root system. Proportional accumulation of root biomass showed a statistical dependence on stand LAI ($\Pr > F = 0.0389$), but this trend was weak with a model slope of −0.016 and LAI accounting for less than 12% of the variation observed for RMR ($r^2 = 0.1163$) (Fig. 5).

4. Discussion

4.1. Regeneration response to canopy disturbance

The first objective of our work was to assess stand-level response in height and root-collar diameter by green ash natural regeneration released by overstory harvesting. Silvicultural practices for release are regularly applied by foresters managing broadleaf stands, and response of advance regeneration to various overstory treatments has been well documented for a wide range of broadleaf species throughout the temperate zone (Loftis,

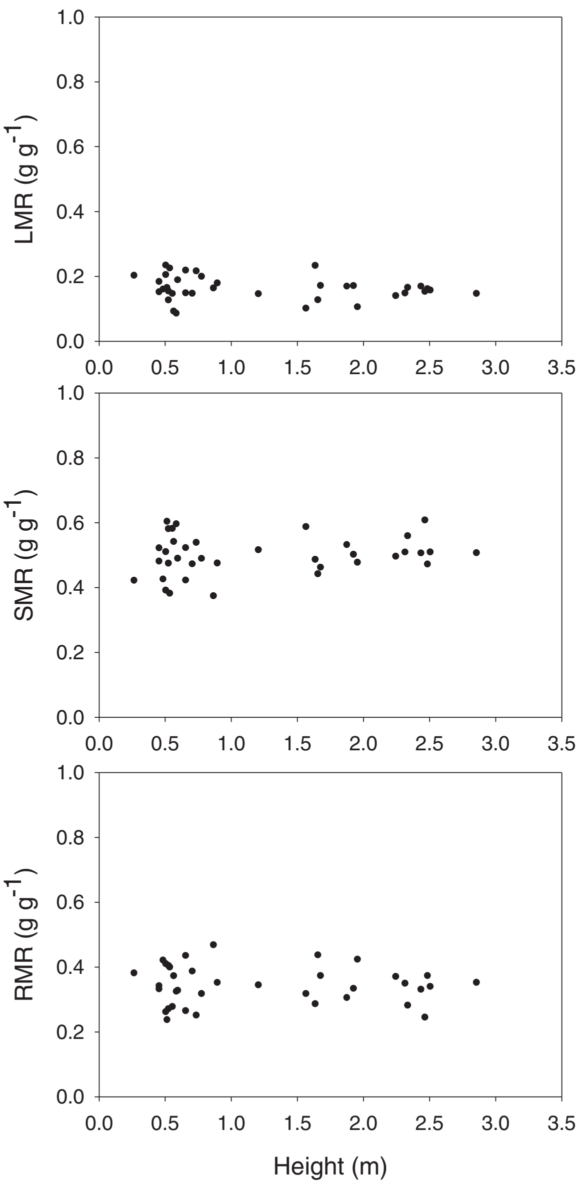

Fig. 2. Leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) relative to stem height of green ash natural regeneration 6 years after overstory harvesting.

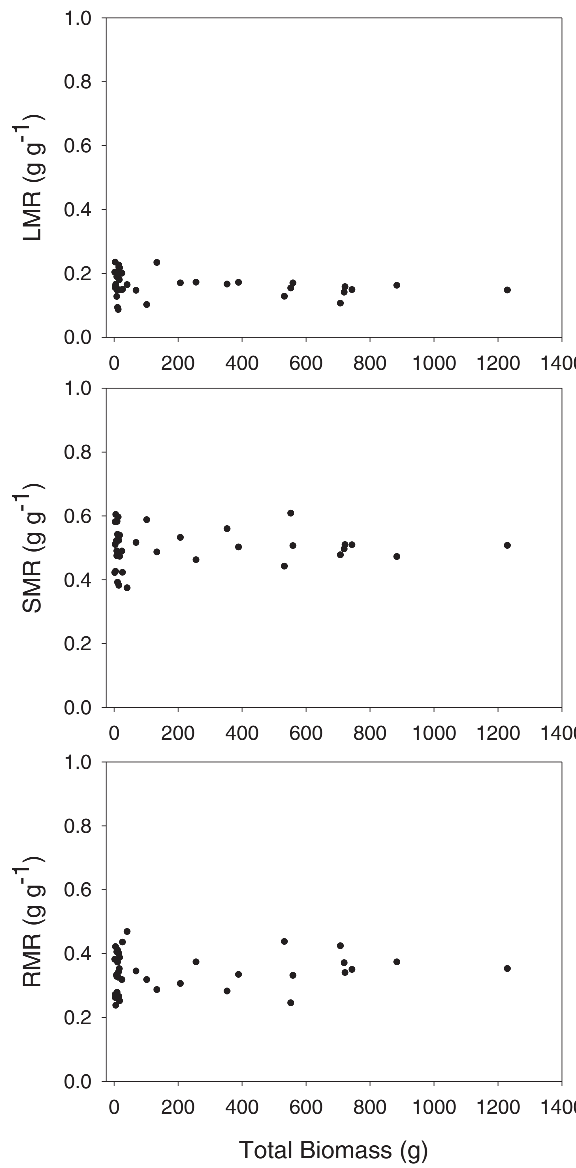

Fig. 3. Leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) relative to biomass accumulation by green ash natural regeneration 6 years after overstory harvesting.

1990; Suh and Lee, 1998; Collet et al., 2001; Fei et al., 2005; Harmer and Morgan, 2007). In line with our expectations, advance ash regeneration responded to overstory harvesting with substantial stem height and root-collar diameter development as compared to regeneration established in plots where the overstory remained intact. Six years after harvest, height and root-collar diameter growth of regeneration established beneath partially harvested canopies responded vigorously, but ash development was greatest under the highest level of canopy disturbance. The growth response to overstory harvesting appeared to be largely determined by the amount of overstory removed, with the intact overstory of control plots suppressing height and diameter growth of established ash regeneration.

Another component of the growth response to overstory disturbance involves the proportional growth of stem height and root-collar diameter. Work conducted in other broadleaf stands has demonstrated that stand structure, through its influence on resource availability, can influence shoot growth such that the plant favors either height or diameter growth over the other. This prioritization of growth can be observed in the height/root-collar diameter ratio of the stem. Petriţan et al. (2009), who studied European beech (*Fagus sylvatica* L.), sycamore maple (*Acer pseudoplatanus* L.) and European ash, illustrated that each of these species favored height growth over diameter growth as light availability in the forest understory decreased. The findings by Petriţan et al. (2009) support earlier observations made on several other broadleaf species (Thadani and Ashton, 1995; Dignan et al., 1998; Ricard et al., 2003), but proportional height and diameter growth of green ash regeneration examined in this study was not influenced by overstory harvesting. Height/root-collar diameter ratios were relatively fixed regardless of whether regeneration developed under the full overstory of control plots, the thin overstory of partially harvested plots, or the open environment of clearcut plots. Thus, our results indicate that the level of overstory harvest strongly controlled the growth rate of green ash regeneration, but appeared inconsequential to how stem growth was prioritized at the stand level.

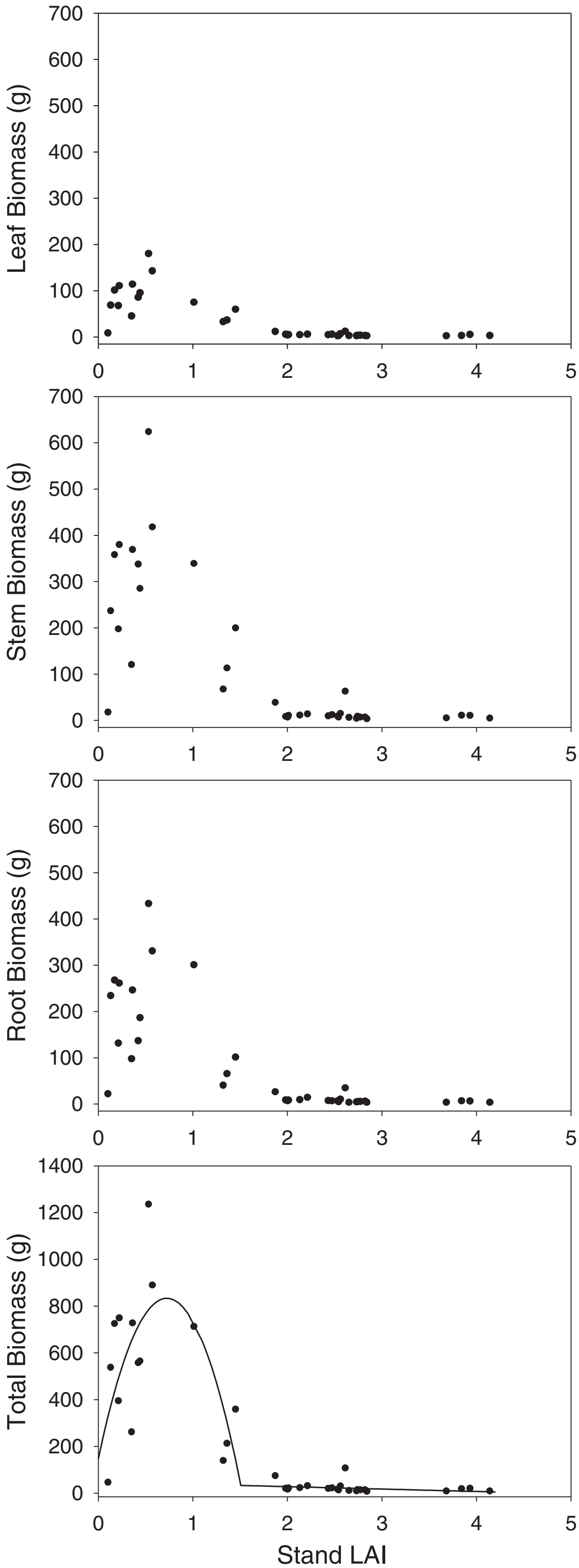

Fig. 4. Leaf, stem, root and total biomass of green ash natural regeneration relative to stand leaf area index (LAI) 6 years after overstory harvesting.

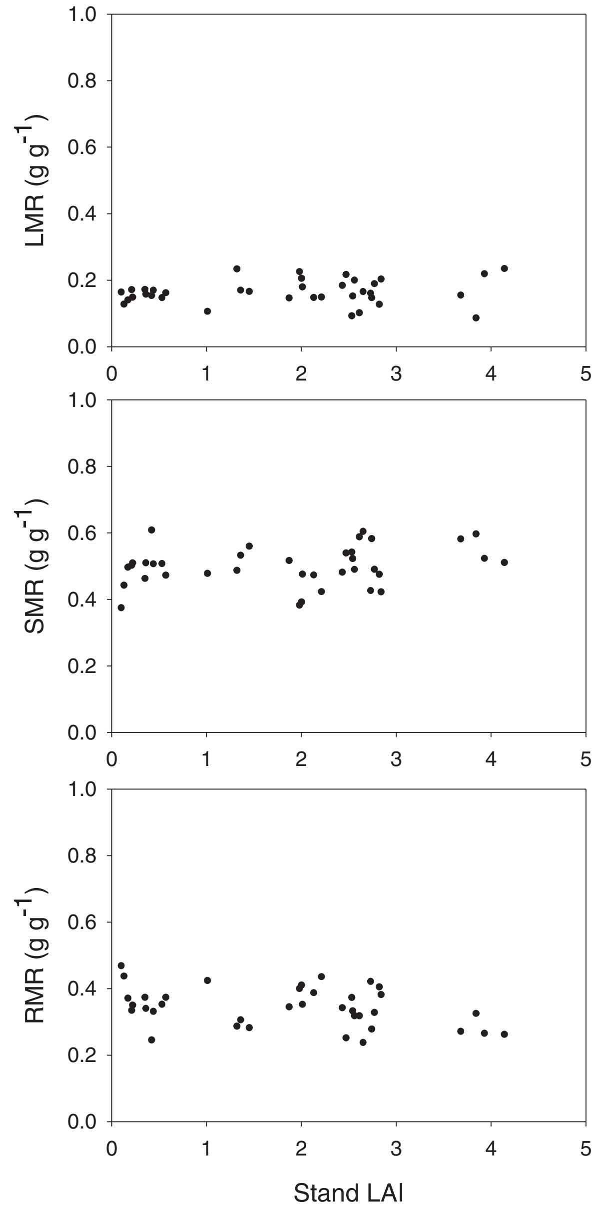

Fig. 5. Leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) relative to stand leaf area index (LAI) 6 years after overstory harvesting.

4.2. Morphological variation associated with growth

Stand-level findings for height, root-collar diameter and height/root-collar diameter ratio discussed above raise the question of how green ash regeneration acclimates morphologically to support the observed growth response to overstory disturbance. Attributing morphological responses to environmental factors that influence plant growth can, however, be problematical because proportional biomass accumulation in leaf, stem, and root tissues can often vary with plant size (Rice and Bazzaz, 1989; McConnaughay and Coleman, 1999; Wright and McConnaughay, 2002). For temperate broadleaf species, increasing seedling and sapling heights or total mass can be accompanied by shifts in allometric relationships including decreases in LMR (Walters et al., 1993; Niinemets, 1998; Curt et al., 2005), increases in SMR (Walters et al., 1993; Niinemets, 1998) and decreases in root/shoot ratio (Cao and Ohkubo, 1998; Niinemets, 1998). Therefore, analysis of treatment effects on biomass distribution patterns must take into account the potential confounding factor of plant size.

Contrary to the above discussion on other temperate broadleaf species, the growth response observed for green ash was not accompanied by shifts in proportional biomass accumulation. LMR, SMR, and RMR, as illustrated in Figs. 2 and 3, remained constant over the 259 cm range of height and 1228 g range of total biomass observed in this study. While others have observed similar isometric responses to plant size, reported cases have usually involved experimentation on plants occupying relatively small ranges in size (Van Hees and Clerkx, 2003). In our experiment, proportional accumulation of biomass within plants remained relatively static even though height ranged more than 10-fold and total biomass ranged 275-fold among the sampled plants. This finding, supported by Figs. 2 and 3, provides evidence that green ash regeneration maintains a fixed morphology relative to size through seedling and sapling development, and prioritization of biomass accumulation to above- or below-ground tissues does not drive early height or biomass growth.

4.3. Biomass accumulation and distribution relative to stand LAI

Development of advance regeneration in temperate broadleaf forests is often linked to the influence of the prevailing stand structure on resource availability in the understory (Crow, 1992; Agestam et al., 2003; Oliver et al., 2005; Dobrowolska, 2008). Stand LAI, as measured in this study, provides an index of stand structure that may integrate availability of critical understory resources such as light and moisture, and account for resource availability more directly than other measures such as stand basal area. We found green ash regeneration surviving beneath a wide range in stand LAI across the study site, and stand LAI explained a significant amount of the observed variation in total biomass accumulation by ash regeneration. Little biomass accumulation occurred beneath the densest overstory canopies where stand LAI values exceeded 2. Regeneration was able to increase biomass accumulation when stand LAI decreased below this threshold value and showed maximum accumulation when stand LAI values neared 0.7. However, additional canopy thinning failed to improve the understory environment for green ash regeneration as biomass accumulation decreased when stand LAI values dipped below 0.7. We speculate this decrease resulted from competition exerted by rank vegetation that developed beneath sparse overstory cover.

The pattern of biomass accumulation along the stand LAI gradient provides evidence that stand structure could be optimized to maximize growth of green ash regeneration. Paquette et al. (2006), who conducted a meta-analysis of underplanted seedling survival and growth, found evidence for such a response to stand density among several studies conducted in temperate deciduous forests. According to their findings, height growth of underplanted seedlings (primarily oaks) in temperate deciduous forests tended to be greatest where shelterwoods provided moderate canopy cover (50–75% canopy cover) (Paquette et al., 2006). Other research conducted on underplanted green ash and white ash (*Fraxinus americana* L.) seedlings, however, reported best growth beneath canopies more open than identified in the Paquette et al. (2006) study (Truax et al., 2000; Parker et al., 2008). Our findings were more in line with these reports on underplanted ash seedlings, as green ash natural regeneration clearly demonstrated superior biomass accumulation beneath sparse overstory cover.

The non-linear response of total biomass accumulation observed in this study also suggests that factors limiting this process, e.g. light, nutrient or moisture stress, shifted in relative importance as stand structure changed along the stand LAI gradient. If this were the case, then it would be expected that the change in total biomass accumulation would be accompanied by a change in proportional biomass accumulation within the seedling. This is because understory resource availability can drive proportional biomass accumulation within seedlings to favor morphological acclimation that enhances acquisition of a limiting resource. This has been observed for other temperate species grown under controlled environments. For example, Naidu and DeLucia (1997), who raised northern red oak (*Q. rubra* L.) seedlings in pots beneath various levels of canopy cover, observed an increase in total seedling biomass when plants were moved from beneath a full overstory to a canopy gap. This increase in biomass accumulation was driven by a disproportionate increase in root biomass which they attributed to higher moisture demand in the more open environment of the gap. Ammer (2003) observed similar shifts in seedling morphology for European beech and pedunculate oak (*Q. robur* L.) raised beneath various densities of shade cloth, demonstrating increases in root/shoot ratio as seedling size increased under high light availability.

Much of our knowledge concerning biomass accumulation and distribution by regeneration relative to stand structure is based on work with artificial regeneration, because studies on whole-plant biomass distribution for natural regeneration in temperate forests are not readily available. Reports from work on artificial regeneration led us to expect a change in proportional biomass accumulation along the stand LAI gradient. However, Fig. 5 illustrates that the response in green ash biomass distribution over the range of stand LAI in this study was largely isometric. Above-ground distribution of biomass (LMR and SMR) was not influenced by canopy cover, and stand LAI accounted for less than 12% of the variation in below-ground biomass distribution (RMR). These findings, drawn from evidence in Fig. 5, indicate that stand structure has little influence on the proportional biomass accumulation in green ash seedlings and saplings. Thus, the growth response by green ash regeneration following canopy disturbance does not appear to involve morphological mechanisms of acclimation at the plant level as seen for other temperate broadleaf species, particularly artificial regeneration.

5. Management implications

While ash species are important in broadleaf forests throughout the northern temperate zone, our knowledge of how their seedlings and saplings acclimate and grow following stand disturbance is limited. This study quantified the stand-level response of height and root-collar diameter growth by green ash advance regeneration following overstory harvesting; examined plant-level patterns of morphological acclimation associated with the growth response of ash regeneration following stand disturbance; and, described biomass accumulation and distribution for ash regeneration relative to stand LAI in a bottomland hardwood forests on the floodplain of the Mississippi River. Several silvicultural implications can be drawn from our findings.

First, we confirmed that green ash regeneration can establish and persist for several years beneath a full canopy of mixed, broadleaf species. We also confirmed that established natural regeneration can respond with vigorous growth following overstory disturbance. These findings are in line with observations made on the regeneration strategies of other disturbance-dependent species that mast sporadically. Because ash regeneration can be accrued in an understory seedling bank, and this advance regeneration can respond vigorously to overstory removal, managers have an opportunity to develop seedlings into larger size classes and also have flexibility concerning the timing of regeneration harvests.

Next, green ash regeneration exhibited the potential for vigorous growth upon release, and this growth response was not associated with a change in proportional biomass accumulation within the plant. In other words, height and diameter growth following release were not dependent upon prioritization of biomass accumulation to either above- or below-ground tissues. This is in contrast to other temperate species that must undergo significant morphological acclimation to support increased function when released to high light environments. The ability to maintain a static pattern of biomass accumulation beneath a wide range in understory environments may provide green ash with a competitive strategy for responding to stand disturbance.

Finally, stand LAI explained a significant amount of the observed variation in total biomass accumulation by ash regeneration. We were able to identify a threshold stand LAI value of 2, above which green ash showed minimal biomass accumulation. Additionally, regeneration grew best under a sparse overstory canopy (stand LAI $\approx$ 0.7). These findings indicate that retention of light canopy cover during the regeneration phase could be used to manage green ash regeneration and temporarily maintain structure in the stand that would perhaps benefit other management objectives.

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References

Agestam, E., Ekö, P.-M., Nilsson, U., Welander, N.T., 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. For. Ecol. Manage. 176, 61–73.

Ammer, C., 2003. Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changes in the R/FR-ratio of radiation. Ann. For. Sci. 60, 163–171.

Cao, K.-F., Ohkubo, T., 1998. Allometry, root/shoot ratio and root architecture in understory saplings of deciduous dicotyledonous trees in central Japan. Ecol. Res. 13, 217–227.

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

Collet, C., Lanter, O., Pardos, M., 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Ann. For. Sci. 58, 127–134.

Collet, C., Piboule, A., Leroy, O., Frochot, H., 2008. Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. Forestry 81, 135–150.

Crow, T.R., 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91, 192–200.

Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) – a review. For. Sci. 34, 19–40.

Curt, T., Coll, L., Prévosto, B., Balandier, P., Kunstler, G., 2005. Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition. Ann. For. Sci. 62, 51–60.

Dignan, P., King, M., Saveneh, A., Walters, M., 1998. The regeneration of *Eucalyptus regnans* F. Muell. under retained overwood: seedling growth and density. For. Ecol. Manage. 102, 1–7.

Dobrowolska, D., 2008. Effect of stand density on oak regeneration in flood plain forests in Lower Silesia, Poland. Forestry 81, 511–523.

Emborg, J., 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. For. Ecol. Manage. 106, 83–95.

Fei, S., Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2005. Forest regeneration composition and development in upland, mixed-oak forests. Tree Physiol. 25, 1495–1500.

Frey, B.R., Ashton, M.S., McKenna, J.J., Ellum, D., Finkral, A., 2007. Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. For. Ecol. Manage. 245, 54–63.

Hara, M., 1987. Analysis of seedling banks of a climax beech forest: ecological importance of seedling sprouts. Vegetatio 71, 67–74.

Harmer, R., Morgan, G., 2007. Development of *Quercus robur* advance regeneration following canopy reduction in an oak woodland. Forestry 80, 137–149.

Houle, G., 1991. Regenerative traits of tree species in a deciduous forest of northeastern North America. Holarctic Ecol. 14, 142–151.

Johnson, R.L., 1975. Natural regeneration and development of Nuttall oak and associated species. In: USDA Forest Service Research Paper SO-104, 12 p.

Kellum, J.E., Sundell, E., Lockhart, B.R., 1999. Composition and diversity of ground flora three years following clearcutting and selection cutting in a bottomland hardwood ecosystem. In: Haywood, J.D. (Ed.), Proceedings of the Tenth Biennial Southern Silvicultural Research Conference. USDA Forest Service, General Technical Report SRS-30, pp. 107–113.

Kennedy Jr., H.E., 1990. *Fraxinus pennsylvanica* Marsh. – Green Ash. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, pp. 348–354.

Kerr, G., Cahalan, C., 2004. A review of site factors affecting the early growth of ash (*Fraxinus excelsior* L.). For. Ecol. Manage. 188, 225–234.

Kupferschmid, A.D., Bugmann, H., 2008. Ungulate browsing in winter reduces the growth of *Fraxinus* and *Acer* saplings in subsequent unbrowsed years. Plant Ecol. 198, 121–134.

Liptzin, D., Ashton, P.M.S., 1999. Early-successional dynamics of single-aged mixed hardwood stands in a southern New England forest, USA. For. Ecol. Manage. 116, 141–150.

Lockhart, B.R., 1998. Riverfront hardwood regeneration 1-year following complete and partial overstory harvesting. In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference. USDA Forest Service, General Technical Report SRS-20, pp. 269–271.

Loftis, D.L., 1990. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. For. Sci. 36, 908–916.

Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest managed by close to nature principles – a gap cutting based experiment. Can. J. For. Res. 38, 1716–1729.

Marigo, G., Peltier, J.-P., Girel, J., Pautou, G., 2000. Success in the demographic expansion of *Fraxinus excelsior* L. Trees 15, 1–13.

Marks, P.L., Gardescu, S., 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. J. Tor. Bot. Soc. 125, 287–296.

McClure, J.W., Lee, T.D., Leak, W.B., 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manage. 127, 181–189.

McConnaughay, K.D.M., Coleman, J.S., 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology 80, 2581–2593.

Miller, G.W., Kochenderfer, J.N., 1998. Maintaining species diversity in the central Appalachians. J. For. 96 (7), 28–33.

Modrý, M., Hubený, D., Rejšek, K., 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. For. Ecol. Manage. 188, 185–195.

Naidu, S.L., DeLucia, E.H., 1997. Growth, allocation and water relations of shade-grown *Quercus rubra* L. saplings exposed to a late-season canopy gap. Ann. Bot. 80, 335–344.

Nakamura, F., Shin, N., Inahara, S., 2007. Shifting mosaic in maintaining diversity of floodplain tree species in the northern temperate zone of Japan. For. Ecol. Manage. 241, 28–38.

National Climatic Data Center, 2007. http://cdo.ncdc.noaa.gov/ancsum/ACS.

Niinemets, Ü., 1998. Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap-understory continuum: interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. Int. J. Plant Sci. 159, 318–330.

Oliver, C.D., Burkhardt, E.C., Skojac, D.A., 2005. The increasing scarcity of red oaks in Mississippi River floodplain forests: influence of the residual overstory. For. Ecol. Manage. 210, 393–414.

Oliver, C.S., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley & Sons, Inc, New York, 520 pp.

Paquette, A., Bouchard, A., Cogliastro, A., 2006. Survival and growth of under-planted trees: a meta-analysis across four biomes. Ecol. Appl. 16, 1575–1589.

Parker, W.C., Elliott, K.A., Dey, D.C., Boysen, E., 2008. Restoring southern Ontario forests by managing succession in conifer plantations. For. Chron. 84, 83–94.

Petriţan, A.M., Lüpke, B.v., Petriţan, I.C., 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. Eur. J. For. Res. 128, 61–74.

Ricard, J.P., Messier, C., Delagrange, S., Beaudet, M., 2003. Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. Ann. For. Sci. 60, 749–756.

Rice, S.A., Bazzaz, F.A., 1989. Quantification of plasticity of plant traits in response to light intensity: comparing phenotypes at a common weight. Oecologia 78, 502–507.

Schlesinger, R.C., 1990. *Fraxinus americana* L. – white ash. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, pp. 333–338.

Streng, D.R., Glitzenstein, J.S., Harcombe, P.A., 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecol. Mono. 59, 177–204.

Suh, M.H., Lee, D.K., 1998. Stand structure and regeneration of *Quercus mongolica* forests in Korea. For. Ecol. Manage. 106, 27–34.

Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J., 2001. Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. For. Ecol. Manage. 141, 237–250.

Tapper, P.-G., 1992. Demography of persistent juveniles in *Fraxinus excelsior*. Ecography 15, 385–392.

Tapper, P.-G., 1993. The replacement of *Alnus glutinosa* by *Fraxinus excelsior* during succession related to regenerative differences. Ecography 16, 212–218.

Thadani, R., Ashton, P.M.S., 1995. Regeneration of banj oak (*Quercus leucotrichophora* A. Camus) in the central Himalaya. For. Ecol. Manage. 78, 217–224.
Thurston, S.W., Krasny, M.E., Martin, C.W., Fahey, T.J., 1992. Effect of site characteristics and 1st- and 2nd-year seedling densities on forest development in a northern hardwood forest. Can. J. For. Res. 22, 1860–1868.
Truax, B., Lambert, F., Gagnon, D., 2000. Herbicide-free plantations of oaks and ashes along a gradient of open to forested mesic environments. For. Ecol. Manage. 137, 155–169.
Van Hees, A.F.M., Clerkx, A.P.P.M., 2003. Shading and root–shoot relations in saplings of silver birch, pedunculate oak and beech. For. Ecol. Manage. 176, 439–448.
Walters, M.B., Kruger, E.L., Reich, P.B., 1993. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. Oecologia 96, 219–231.
Wardle, P., 1959. The regeneration of *Fraxinus excelsior* in woods with a field layer of *Mercurialis perennis*. J. Ecol. 47, 483–497.
Wright, S.D., McConnaughay, K.D.M., 2002. Interpreting phenotypic plasticity: the importance of ontogeny. Plant Species Biol. 17, 119–131.
Wynn Jr., A.H., Morris Jr., W.M., Scott, F.T., Walton, L.B., 1961. Soil survey of Issaquena County, Mississippi. In: USDA, Soil Conservation Service Series 1959, No. 2.