Eur J Forest Res (2015) 134:281–291
DOI 10.1007/s10342-014-0850-2

ORIGINAL PAPER

Effects of species composition, management intensity, and shade tolerance on vertical distribution of leaf area index in juvenile stands in Maine, USA

Andrew S. Nelson · Robert G. Wagner · Aaron R. Weiskittel · Michael R. Saunders

Received: 24 May 2014 / Revised: 8 September 2014 / Accepted: 20 October 2014 / Published online: 2 November 2014

Abstract Leaf area index (LAI) affects forest-atmosphere fluxes and light interception rates and thus influences forest productivity. Early silvicultural treatments affect LAI partitioning among species of different shade tolerance in natural stands due to changes in composition and structure. We examined effects of species compositional objectives (conifer, hardwood, and mixedwood) and management intensity (low: thinning and/or release to 2,500 crop trees ha^{-1}, medium: thinning and/or release plus planting to 2,500 crop trees ha^{-1}, and a second year of vegetation control) on LAI and its vertical distribution in different shade tolerance groups over a 7-year period. Hardwood LAI increased by 242 and 318 % in the low and medium hardwood treatments, respectively, compared to a 123 % increase in the untreated control. Thinning possibly increased resource availability for upper stratum shade intolerant hardwoods, while also increasing light penetration through the canopy for midstory shade tolerant hardwoods. Conifer treatments substantially reduce overtopping hardwood LAI, facilitating an increase in conifer LAI by 281 and 378 % in the low and medium treatments, respectively. The height from the canopy base where LAI peaked increased between 29 and 80 % in the low mixedwood and medium hardwood treatments from pre-treatment through 7 years post-treatment. Comparatively, LAI at the peak increased by 16 and 36 % in the low and medium conifer treatments, respectively, with a minimal change in the height of the LAI peak. These contrasting responses were likely due to slower conifer reaction following treatment than hardwoods and stacking of conifer foliage within the middle portion of the canopy.

Keywords Hardwood · Conifer · Mixedwood · Weibull distribution · Thinning · Release · Acadian forest

Introduction

Leaf area index (LAI; one-sided leaf area per unit of ground area) represents the exchange surface between plant canopies and the atmosphere (Jarvis and Leverenz 1983). Rates of water and carbon fluxes and light interception depend on the amount of LAI and affect net photosynthesis and plant productivity (Waring 1983). The relationships between LAI and productivity have been well studied across many different forest types (Jarvis and Leverenz 1983; Leverenz and Hinckley 1990; Bolstad et al. 2001), where LAI has been found to explain 80–90 % of the variation in aboveground net primary productivity in the USA (Gholz 1982; Fassnacht and Gower 1997). The strong relationship between these two variables has been used to estimate productivity at scales of individual trees (Seymour and Kenefic 2002), stands (Vose and Allen 1988), and entire landscapes (Ruimy et al. 1994). In addition, the

---

Communicated by Christian Ammer.

A. S. Nelson (✉) · R. G. Wagner · A. R. Weiskittel
School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME 04469-5755, USA
e-mail: nelsona@uamont.edu

Present Address:
A. S. Nelson
Arkansas Forest Resources Center, Division of Agriculture, University of Arkansas, P.O. Box 3468, Monticello, AR 71656, USA

M. R. Saunders
Department of Forestry and Natural Resources, Purdue University, 715 W. State St., West Lafayette, IN 47907-2061, USA

relationship is a fundamental component of many process-based growth and physiological models (Landsberg 2003; Medlyn et al. 2003).

These models and many large-scale examinations of LAI-productivity relationships make simplifying assumptions about canopy structure (Ruimy et al. 1994; Medlyn et al. 2003). They are based on a generalized model of LAI development, which suggests that LAI increases exponentially after disturbances that remove a portion of the canopy or in young stands from establishment until crown closure, followed by a plateau or decline in LAI after crown closure (Waring and Running 1998). These idealized patterns of LAI development are common in single species or single stratum stands, but cannot be applied to mixed stands or multi-strata stands as variation in shade tolerance among species affects the amount and distribution of LAI within the different canopy layers (Oker-Blom et al. 1989).

Total LAI production and vertical LAI distribution often vary among stands with different species composition, horizontal structures, and ages (Brown and Parker 1994; Vose et al. 1995). Shade intolerant species inherently minimize self-shading by developing multi-layered crowns with steep leaf angles (Horn 1971; Valladares and Niinemets 2007). Light not intercepted by a shade intolerant upper stratum may be captured by lower strata shade tolerant species because of their ability to survive in low-light conditions (Lieffers and Stadt 1994). In contrast, when shade tolerant species dominate an upper stratum, the development of lower strata may be limited because these species capture most of the available light by developing denser crowns (Canham et al. 1994). The result is often a more equal distribution of LAI throughout the vertical canopy length when shade intolerant species are in the upper stratum, while the majority of LAI is allocated to the upper canopy when the upper stratum is dominated by shade tolerant species. These contrasting patterns have implications for forest dynamics, succession, and overall stand productivity.

Disturbances, such as early silvicultural treatments applied to manipulate species composition and reallocate resource availability, affect total LAI production and vertical distribution due to changes in composition and stand structure (Forrester et al. 2013). Species exhibit inherent differences in leaf area responses to changing environmental conditions. For example, shade tolerant species often respond more slowly to increased light availability than shade intolerant species (Wagner et al. 2011), possibly because shade tolerant species heavily invest carbohydrates in leaf area and partition less carbohydrates to woody tissue (Valladares and Niinemets 2008). Shade intolerant species, comparatively, partition a greater amount of carbohydrates to woody tissue to quickly build branch structure, maintain dominance, and avoid suppression (Niinemets 1998), which often results in a faster growth reaction of shade intolerant species after a disturbance.

Across much of north-temperate and boreal North America, stand replacing disturbances often result in forests composed of rapidly growing shade intolerant species in an upper canopy stratum, with intermediate shade tolerant and shade tolerant species growing in the lower strata either as advance regeneration (e.g., following clear-cutting, blowdown, or insect defoliation) or as newly established individuals (e.g., following fire) (Seymour 1995; Brassard and Chen 2006). Stands can be shifted in different trajectories early in development to favor species of different shade tolerances while altering forest structure (Olson et al. 2012).

The goal of this study was to investigate temporal changes in canopy LAI of juvenile stands in response to a range of early silvicultural interventions designed to shift species composition to hardwood, conifer, or conifer–hardwood mixedwood at two intensities of management (low: release and/or thinning, and medium: release and/or thinning plus enrichment planting of white spruce [*Picea glauca* (Moench) Voss] and four hybrid poplar clones (three *Populus deltoides* × *Populus nigra* clones and one *Populus nigra* × *Populus maximowiczii* clone), and a second year of vegetation control). Specific objectives included quantifying treatment effects over a 7-year period on: (1) total LAI production within the stands, (2) LAI partitioning among species shade tolerance groups (shade intolerant hardwood, shade tolerant hardwood, and intermediate shade tolerant and shade tolerant conifers), (3) vertical distribution of LAI through the canopy for the entire stand, and (4) vertical distribution of LAI by shade tolerance group.

We expected that: (1) when young stands start with similar species composition and total LAI, hardwood treatments that thinned upper stratum shade intolerant hardwood species would exhibit the greatest expansion in LAI due to the dominance of rapidly growing trees, followed by mixedwood treatments that retained a smaller proportion of shade intolerant hardwood species in the upper stratum while releasing and thinning advance regeneration conifers, and lastly, the conifer treatments where most of the upper and middle strata hardwood trees were removed, (2) greater management intensity, which included additional vegetation control, would initially reduce LAI more than treatments only applied once, but would exhibit a more rapid expansion in LAI due to less competition, (3) the vertical canopy length of shade intolerant species would increase the most in response to treatment due to vigorous growth and partitioning of more LAI to upper portions of the canopy to capture light, and (4) the upward expansion of LAI in conifer species following release would be less than hardwood species due to greater shade tolerance and ability to vertically stack LAI due to multiple foliage cohorts.

Methods

Study site

This study used data from the Silvicultural Intensity and Composition (SIComp) experiment located on the Penobscot Experiment Forest (PEF) in eastern Maine, USA (44°49′N, 68°38′W). Forests at the PEF are classified as the Acadian forest type (Braun 1950), which is a transitional forest type between the eastern hardwood forests to the south and conifer-dominated boreal forests to the north. The 30-year (1951–1980) mean annual temperature at Bangor, ME, USA ($\sim$16 km from the site) was 6.6 °C, with an average low of −7.0 °C in February and average high of 20.0 °C in July. Precipitation averages 1,060 mm year^{-1}, of which 48 % occurs between May and October. Annual snowfall averages 2,390 mm, and the frost-free period in the region is between 140 and 160 days year^{-1}.

The SIComp experiment site was clear-cut harvested in 1995. The site regenerated naturally to a mix of hardwood species, including trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), and advance regeneration conifer species, including balsam fir [*Abies balsamifera* (L.) Mill.], red spruce (*Picea rubens* Sarg.), white spruce, and eastern white pine (*Pinus strobus* L.).

Experimental design and measurements

Factorial treatment combinations of two management intensities (low and medium) and three species compositional objectives (hardwood, conifer, and mixedwood) were applied in 2004, 9 years after harvest, plus a hardwood-dominated untreated control (Nelson et al. 2013). The experiment was a restricted-randomized design, where conifer and mixedwood treatments were restricted to areas with adequate conifer stocking. In the low hardwood treatment, overstory hardwood trees were thinned to 2,500 crop trees ha^{-1} (2 × 2 m spacing), while the low conifer treatment released conifer advance regeneration by cutting most of the hardwood overstory and thinning conifer advance regeneration to 2,500 crop trees ha^{-1}. The low mixedwood treatment was a combination of overstory hardwood thinning, conifer release, and conifer thinning to 2,500 crop trees ha^{-1}, where 67 % of crop trees were conifers, and 33 % were hardwood trees. The medium intensity treatments had the same objectives of hardwood thinning, conifer release, and conifer thinning to 2,500 crop trees ha^{-1}, but 50 % of the crop trees were planted, plus competing vegetation around crop trees was controlled for 2 consecutive years. Enrichment planting consisted of 100 % white spruce in the medium conifer treatment, 67 % white spruce and 33 % hybrid poplar in the medium mixedwood treatment, and 100 % hybrid poplar in the medium hardwood treatment.

In each treatment, non-crop tree vegetation was controlled within a 1-m radius around all crop trees using manual and chemical control methods. Hardwood vegetation around conifer crop trees were treated with a basal bark application of 20 % triclopyr ester mixed with bark oil. Hardwood vegetation around hardwood crop trees were controlled with motorized brushsaw to avoid herbicide flashback. Conifer vegetation around conifer crop trees were removed with motorized brushsaws. In the medium intensity treatments, a second year of shrub and hardwood control was applied with triclopyr and brushsaws, and a 3 % glyphosate foliar spot-treatment to control herbaceous vegetation. White spruce 2–0 half-sib container seedlings were planted within the center of a 2 × 2 m crop tree growing space cell with a pottiputki. Hybrid poplar cuttings were planted by hand within the center of a 2 × 2 m crop tree growing space cell. All planted seedlings/cuttings were planted to ensure that 50 % of the crop trees were planted. Mean pre-treatment basal area ranged from 5.48 m^2 ha^{-1} (low conifer) to 8.26 m^2 ha^{-1} (low hardwood) (Table 1).

The seven treatments (six treatments plus untreated control) were replicated four times across the site as 0.09-ha square treatment plots (30 × 30 m) with a 0.04-ha square measurement plot nested in the center (20 × 20 m). Five 16 m^2 (radius = 2.257 m) circular subplots (four centered on the measurement plot corners and one at the plot center) were established and measured prior to treatment in 2004 (year 0), and 1, 2, 5, and 7 years after treatment to track stand-level changes in structure and composition. For each tree, DBH was measured and trees were identified by species. In addition, DBH, total height (HT), and crown length (CL; HT minus the height to the base of the live crown, excluding epicormic branches) were measured on all crop trees in the 0.04-ha measurement plots in the same years. Crop tree data were not used to examine stand-level LAI since trees that established following treatment and trees outside the 1-m treatment radius around each crop tree were not removed. Crop tree measurements were used only to develop HT and CL models to predict these variables for all trees in the 16-m^2 subplots.

Analytical approach

To estimate stand LAI in each subplot, it was necessary to first estimate individual tree leaf area. Tree leaf area of

Table 1 Summary stand-level statistics for each of the seven treatments in the study

Treatment	Basal area (m^2 ha^{-1})			Hardwood stem density ≥1.37 m tall (1,000 stems ha^{-1})			Conifer stem density ≥1.37 m tall (1,000 stems ha^{-1})			Conifer stem density <1.37 m tall (1,000 stems ha^{-1})		
	Pre-trt	2 years post-trt	7 years post-trt	Pre-trt	2 years post-trt	7 years post-trt	Pre-trt	2 years post-trt	7 years post-trt	Pre-trt	2 years post-trt	7 years post-trt
Untreated control	6.06	8.77	19.16	15.25	12.91	12.53	1.04	1.25	1.81	2.38	2.01	1.77
Low conifer	5.48	2.21	10.59	16.16	1.59	3.41	1.47	2.12	3.97	2.94	2.16	1.45
Low mixedwood	5.68	3.14	11.75	14.06	1.22	3.00	1.28	2.12	4.47	4.53	3.14	3.58
Low hardwood	8.26	5.41	14.74	17.12	4.47	10.78	0.59	0.29	0.87	2.97	2.51	2.19
Medium conifer	5.64	0.82	7.00	15.19	0.72	3.47	0.97	1.72	5.28	3.91	3.75	1.85
Medium mixedwood	6.26	2.35	9.57	14.03	1.19	3.69	0.87	1.44	3.22	2.97	2.53	1.31
Medium hardwood	6.38	2.95	12.80	13.69	3.82	7.44	0.19	0.00	0.37	1.61	1.34	1.30

Total basal area (m^2 ha^{-1}), hardwood stem density (1,000 stems ha^{-1}) of trees ≥1.37 m tall, conifer stem density (1,000 stems ha^{-1}) of trees ≥1.37 m tall, and conifer stem density (1,000 stems ha^{-1}) of trees <1.37 m tall in three measurement periods are shown: prior to treatment (pre-trt), 2, and 7 years post-treatment

hardwood species was estimated using models developed from destructively sampled trees across all the treatments at the study site (Nelson et al. 2014). Tree leaf area of conifer species was estimated using models developed by Weiskittel et al. (2009). Estimates of HT or CL in addition to DBH were required to predict individual tree leaf area. Therefore, HT and CL were estimated from models developed from the crop tree measurements, with DBH as the sole predictor in two-parameter power functions ($HT = \beta_0 DBH^{\beta_1}$; $CL = \beta_0 DBH^{\beta_1}$), where β_0 and β_1 were parameters estimated for each species with maximum likelihood.

Leaf area was summed for all trees in each subplot and divided by the subplot area (16 m^2) to estimate total stand LAI. The number of trees ha^{-1} is presented in Table 1. Species were then divided into three shade tolerance groups based on their silvical characteristics (Burns and Honkala 1990a, b). The groups included: shade intolerant hardwood [aspen sp., birch sp., cherry sp. (*Prunus*)], shade tolerant and intermediate tolerant hardwood species [maple sp., ash sp. (*Fraxinus*), northern red oak (*Quercus rubra* L.), American beech (*Fagus grandifolia* Ehrh.), American basswood (*Tilia Americana* L.), and yellow birch (*Betula alleghaniensis* Britton)], and shade tolerant and intermediate tolerant conifer species (balsam fir, spruce sp., eastern hemlock, and eastern white pine). There were no shade intolerant conifer species at the site. Individual tree leaf area was estimated for each tree in the subplots by shade tolerance group using the leaf area models, then summed by group, and divided by the subplot area to estimate LAI. Leaf areas of uncommon hardwood species were estimated with the hardwood models for the same genus or within the same shade tolerance group. Analysis of variance (ANOVA) was used to test for treatment, year, and treatment × year differences in total LAI and LAI by shade tolerance group, accounting for treatment plot and subplot nested within treatment plot as random effects. Significance was assessed at $\alpha = 0.05$. Homogeneity of variance was examined using graphs of residuals versus observed data, and normality was examined with qq-plots. These analyses found that data transformation was unnecessary.

Vertical distribution of canopy LAI was estimated by first dividing each individual tree vertical crown into 20-cm vertical segments from the base of the crown to the top of the tree. The amount of leaf area in each segment was estimated with species-specific, individual tree, right-truncated Weibull distribution models (Weiskittel et al. 2009; Nelson et al. 2014). These distribution models predict the amount of leaf area at any height above the base of the live crown. Next, the vertical length of each subplot's canopy was defined using the HT of the tallest tree (upper canopy limit height) and the height to the base of the live crown of the shortest tree (lower canopy limit height). The subplot vertical canopy length was then divided into 20-cm sections. Numerous different canopy partitions were tested, and 20-cm sections were optimal for obtaining model convergence and realistic parameter estimates. The height from the ground to the midpoint of each of the 20-cm individual crown segment and the height from the ground of each vertical total canopy section were used to assign the estimated leaf area in each tree crown segment to one of the total canopy sections. Leaf area in each of the 20-cm subplot canopy sections was then summed and divided by the subplot area to estimate LAI for each vertical canopy section.

Trees in each subplot were classified into one of the three shade tolerance groups, and then, the right-truncated Weibull distribution models were used to estimate leaf area for 20 cm tall individual tree crown segments for trees within each shade tolerance group. The vertical canopy length (HT of the tallest tree and height to the base of the live crown of the smallest tree) was defined for each shade tolerance group and split into 20-cm sections. The height from the ground to the midpoint of each of the 20-cm individual crown segment and the height from the ground of each vertical total canopy section were used to assign the estimated leaf area in each tree crown section to one of the 20-cm total canopy sections by shade tolerance group. Leaf area in each of the 20-cm subplot shade tolerance canopy sections was summed and divided by the subplot area to estimate LAI for each vertical canopy section.

For both the entire stand canopy and for each shade tolerance group, LAI in each of the 20-cm vertical stand canopy sections was used to fit vertical canopy LAI distributions for each subplot. Three distributions were compared (right-truncated Weibull, Johnson's Sb, and 4-parameter beta). These distributions were selected since they had previously been used to model vertical leaf area distribution (Maguire and Bennett 1996; Jerez et al. 2005; Weiskittel et al. 2009; Nelson et al. 2014). Distribution parameters were estimated using maximum likelihood and an expectation/maximization algorithm modified from Robinson (2004) to account for cross-correlation between parameters that arises when multiple parameters are estimated simultaneously. Goodness-of-fit among the three distributions was compared by calculating the root mean square error (RMSE) and mean absolute error (MAE) for each treatment × year combination. Preliminary analysis found that the Weibull distribution had the lowest RMSE and MAE among treatment × year combinations and therefore used for all further analyses. The right-truncated Weibull distribution was defined as (Karian and Dudewicz 2011):

$$p(X) = \left(\frac{1}{\eta}\right)^{\beta} \beta X^{(\beta-1)} \mathrm{e}^{-\left((X/\eta)^{\beta}-(\gamma/\eta)^{\beta}\right)}$$

where $p(X)$ is the probability density of LAI, X is the absolute height from the canopy base (m) of LAI (where the canopy base was defined as the height to the base of the live crown of the shortest tree in each subplot), η is the Weibull scale parameter, β is the Weibull shape parameter, and γ is the Weibull truncation point.

Table 2 Total stand leaf area index (LAI) prior to treatment, 1, 2, 5, and 7 years after treatments were applied

Treatment	Years since treatment				
	Pre-trt	1	2	5	7
Untreated control	1.91 a	3.30 a	2.97 a	5.75 a	6.45 a
Low conifer	2.04 a	1.04 bc	1.48 b	3.32 bc	4.62 ab
Low mixedwood	2.03 a	1.06 bc	1.46 b	4.01 bc	4.73 ab
Low hardwood	2.67 a	1.34 b	1.65 b	4.82 ab	5.55 ab
Medium conifer	2.00 a	0.43 c	0.92 b	2.69 c	3.53 b
Medium mixedwood	2.26 a	0.71 bc	1.08 b	3.43 bc	3.82 b
Medium hardwood	1.92 a	0.89 bc	1.08 b	3.61 bc	4.12 b
Standard error between treatments	0.50	0.26	0.30	0.59	0.72

LAI is shown for all seven treatments, plus the between treatment standard error within each measurement period. The same letters within a column indicate values not significantly different at $\alpha = 0.05$ level

To explore differences in vertical LAI distribution among treatment × year combinations, ANOVA models were fit for the Weibull shape and scale parameters with treatment, year, and treatment × year as fixed effects, and treatment plot and subplot within treatment plot as random effects. ANOVA models were fit for the entire canopy and for each shade tolerance group. Significance was assessed at the $\alpha = 0.05$ level. Homogeneity of variance was examined using graphs of residuals versus observed data, and normality was examined with qq-plots. These analyses showed that data transformation was unnecessary. All analyses were performed in R version 3.0 (R Core Team 2013).

Results

Total LAI within the stands

Total LAI did not differ among plots prior to treatment ($p > 0.95$), ranging from 1.91 ± 0.50 (mean ± SE) in the untreated control to 2.67 ± 0.50 in the low hardwood treatment. LAI was reduced by all treatments in the second year post-treatment, but LAI increased again and eventually surpassed pre-treatment values by the seventh year post-treatment. By the seventh year after treatment, LAI was not significantly different among the species compositional objectives ($p > 0.62$) or between the management intensities ($p > 0.94$). The only difference was that the medium intensity treatments had a substantially lower LAI than the untreated control ranging from 36 % less to 45 % less in the medium hardwood and medium conifer treatments, respectively (Table 2). Overall, total LAI ranked from highest to lowest 7 years after treatment

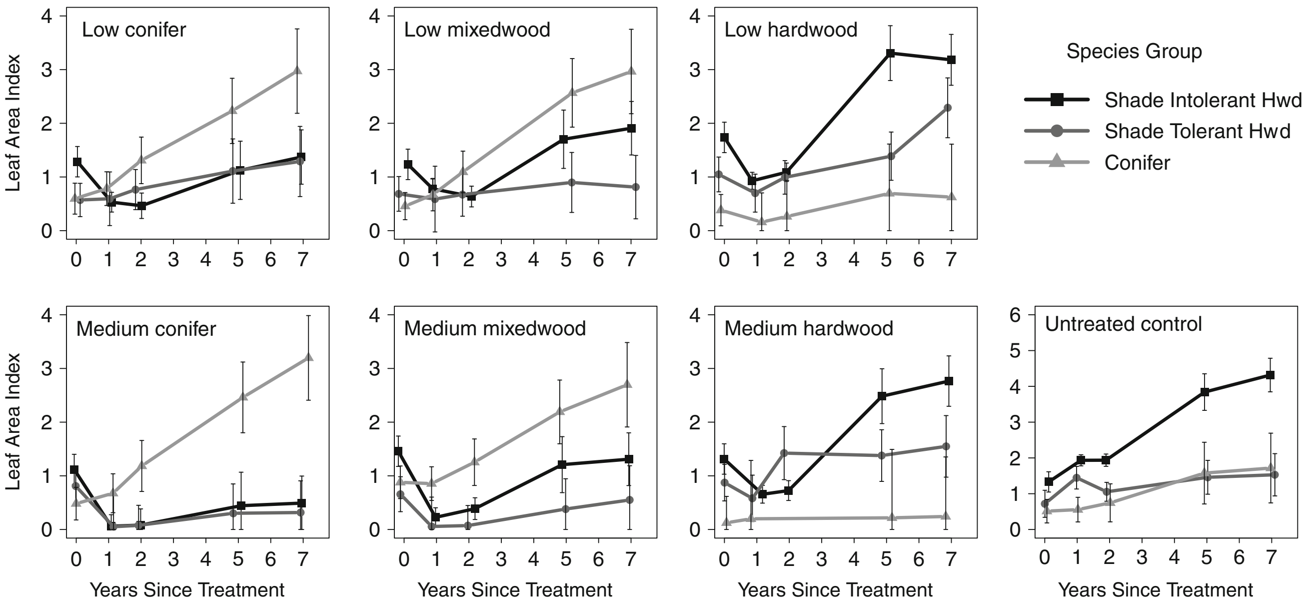

Fig. 1 Change in leaf area index by shade tolerance species group (shade intolerant hardwood, shade tolerant hardwood, and conifer) from pre-treatment (year 0) through 7 years post-treatment in stands shifted to different species compositional objectives (conifer, mixedwood, and hardwood) with two management intensities (low: release and/or thinning, and medium: release and/or thinning plus enrichment planting of white spruce and hybrid poplar, and a second year of vegetation control)

in the following order: untreated control > low hardwood > low mixedwood > low conifer > medium hardwood > medium mixedwood > medium conifer.

Total LAI partitioning among shade tolerance groups

Shade intolerant hardwood species had the greatest proportion of LAI in all treatments prior to manipulation, ranging from 46 to 57 % of the total LAI in the medium conifer and medium hardwood treatments, respectively (Fig. 1). The conifer and mixedwood treatments that focused on promoting conifer species resulted in substantial declines in shade intolerant hardwood LAI ($p < 0.01$), where in the second year post-treatment inventory, shade intolerant LAI ranged from 6 to 23 % of the total LAI in the medium conifer and low mixedwood treatments, respectively. The combination of herbicide application and cutting of shade intolerant hardwood species in the conifer treatments maintained a low proportion of shade intolerant hardwood LAI through the seventh year, while promoting an increase in conifer LAI. For instance, 62 % of the pre-treatment LAI was in shade intolerant hardwood species in the low conifer treatment, while after 7 years, 64 % of the LAI was conifer species. The majority of LAI in the mixedwood treatments was also shifted to conifer species 7 years after treatment where the proportion of conifer LAI increased from 22 % prior to treatment to 54 % 7 years after treatment in the low mixedwood.

Vertical distribution of LAI

Weibull shape and scale parameters differed among treatment × year combinations when all species were combined ($p \leq 0.01$) (Table 3). In addition, the treatments influenced both the amount of LAI that occurred at the peak from the base of the canopy and the distance from the canopy base where LAI peaked (Fig. 2). Prior to treatment, the amount of LAI at the vertical peak ranged from 0.87 in the untreated control to 1.14 in the low hardwood. All treatments initially reduced the amount of LAI at the vertical peak, and by 7 years after treatment, peak LAI ranged from 0.87 in the medium mixedwood to 1.33 in the medium conifer treatment. Bigger differences among treatments were observed for the height from the canopy base where LAI peaked. The change in the height where LAI peak was most pronounced in the hardwood treatments (low: +2.12 m, medium: +2.17 m) and the medium conifer treatment (−1.15 m). A lower response was found in the low conifer (+0.66 m), low mixedwood (+0.74 m), and medium mixedwood treatments (+0.87 m) between pre-treatment and 7 years post-treatment.

Vertical LAI partitioning among shade tolerance groups

The vertical distribution of shade intolerant hardwood LAI changed the most over the measurement period among shade tolerance groups, with a substantial increase in the

Table 3 ANOVA model p values and random effect standard deviations (SDs) testing for treatment, year, and treatment × year differences in right-truncated Weibull distribution shape and scale parameters

Factor	Weibull shape				Weibull scale			
	All species	Shade intolerant hardwood	Shade tolerant hardwood	Conifer	All species	Shade intolerant hardwood	Shade tolerant hardwood	Conifer
Treatment	<0.01	<0.01	0.03	0.01	<0.01	<0.01	<0.01	0.45
Year	<0.01	<0.01	0.11	<0.01	<0.01	<0.01	0.02	0.28
Treatment × year	0.04	0.09	0.33	0.57	0.01	<0.01	0.68	0.08
Plot random effect SD	<0.01	0.14	0.16	<0.01	<0.01	<0.01	0.09	<0.01
Subplot/plot random effect SD	0.08	<0.01	0.04	0.11	0.22	0.27	0.13	0.43

Models were fit for all species combined and for each of the three shade tolerance groups (shade intolerant hardwood, shade tolerant hardwood, and conifer species). The random effects were plot and subplot within plot (subplot/plot)

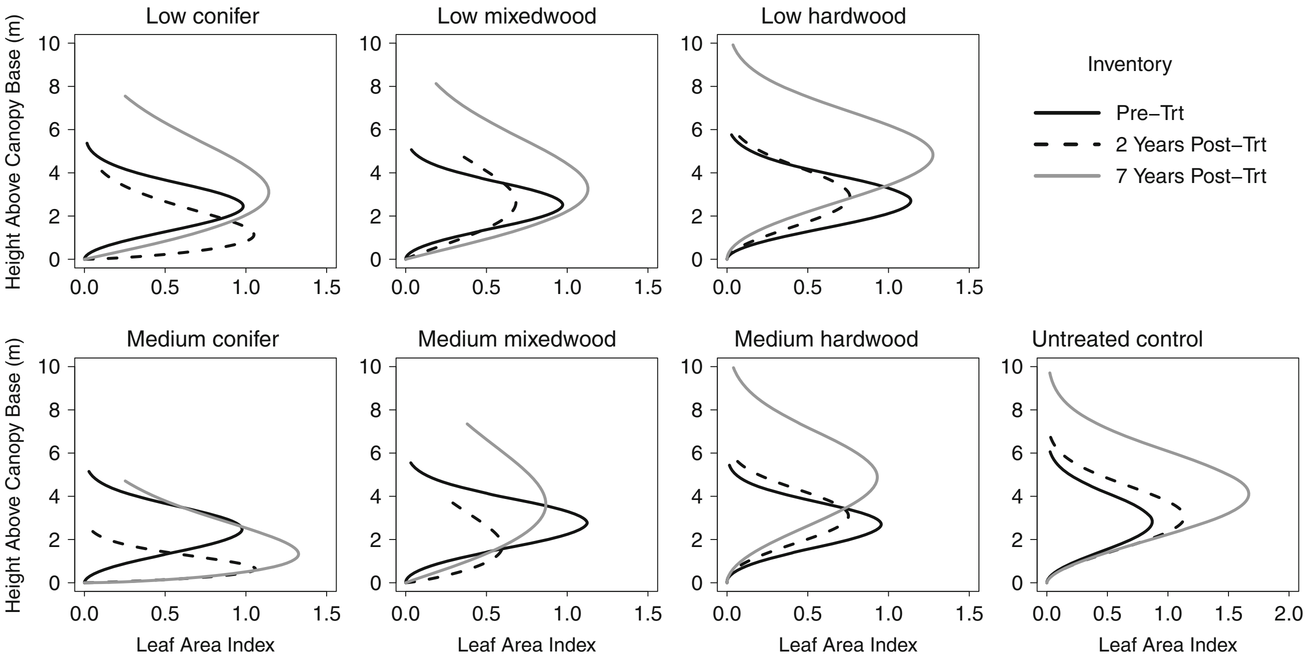

Fig. 2 Vertical distribution of canopy leaf area index prior to treatment (pre-trt), 2 and 7 years after treatment in stands shifted to different species compositional objectives (conifer, mixedwood, and hardwood) with two management intensities (low: release and/or thinning, and medium: release and/or thinning plus enrichment planting of white spruce and hybrid poplar, and a second year of vegetation control). Vertical leaf area index was fit with right-truncated Weibull distributions. *Curves* represent Weibull distributions with mean parameters by treatment estimated with ANOVA

height above the canopy base where LAI peaked between pre-treatment and 7 years post-treatment, except in the medium conifer treatment. For instance, in the low hardwood and medium hardwood treatments, respectively, the height of the LAI peak increased by 1.72 and 2.26 m (Fig. 3), while the amount of LAI at the peak increased by only 0.04 and 0.07 between pre-treatment and 7 years after treatment (Fig. 4). The change in height where LAI peaked above the canopy base was less pronounced for the shade tolerant hardwood and conifer species groups. The major change in conifer vertical LAI distribution was a substantial increase in the amount of LAI at the peak, ranging from 0.46 to 1.64 in the medium mixedwood and medium conifer treatments, respectively, between pre-treatment and 7 years after treatment (Fig. 4).

Discussion

All the plots in the study started with similar canopy structures composed of shade intolerant hardwood species vertically stratified over shade tolerant hardwood and

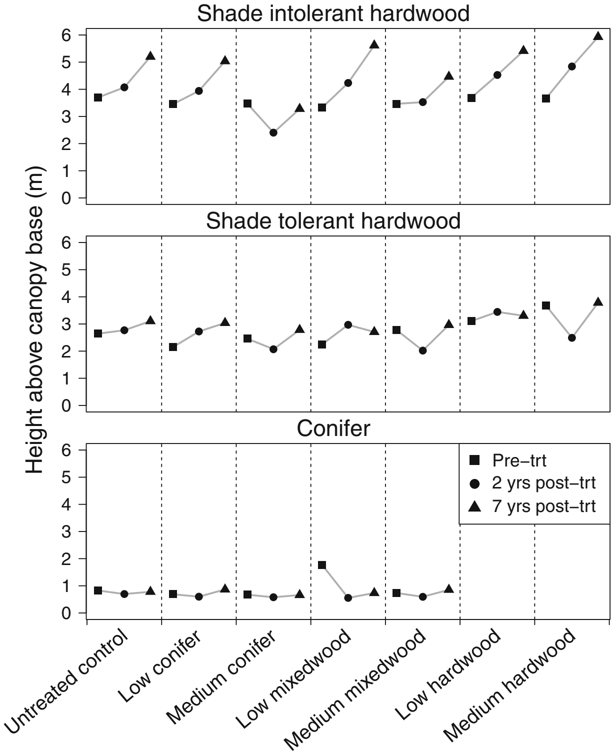

Fig. 3 Height from the base of the canopy where leaf area index peaked for shade intolerant hardwood, shade tolerant hardwood, and conifer species prior to treatment, 2, and 7 years after treatment. The treatments were a combination of species compositional objectives (conifer, mixedwood, and hardwood) at two management intensities (low: release and/or thinning, and medium: release and/or thinning plus enrichment planting of white spruce and hybrid poplar, and second year of vegetation control). Vertical distributions of leaf area index were modeled with Weibull distributions, where parameters were least-square mean estimates by treatment

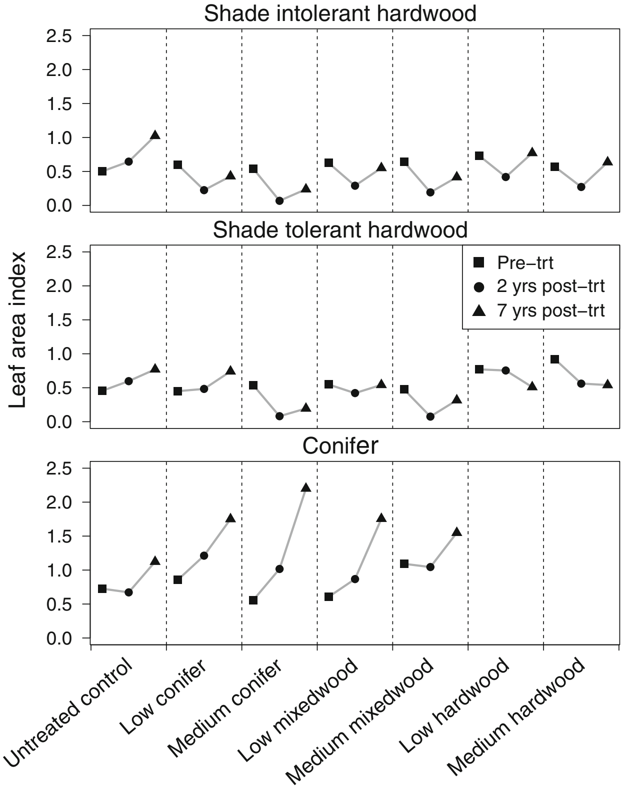

Fig. 4 Leaf area index at the height from the base of the canopy where leaf area index peaked for shade intolerant hardwood, shade tolerant hardwood, and conifer species prior to treatment, 2, and 7 years after treatment. The treatments were a combination of species compositional objectives (conifer, mixedwood, and hardwood) at two management intensities (low: release and/or thinning, and medium: release and/or thinning plus enrichment planting of white spruce and hybrid poplar, and second year of vegetation control). Vertical distributions of leaf area index were modeled with Weibull distributions, where parameters were least-square mean estimates by treatment

conifer species. Shifting stands to conifer, mixedwood, or hardwood composition strongly affected total LAI development and vertical LAI distribution. The results suggest that the treatment differences in LAI were due to the initial treatment objectives and the different responses of species shade tolerance groups to altered stand structure. Response to management intensity, however, was less pronounced across all three compositional objectives.

Total LAI response to treatment

LAI of young, single stratum stands often increases exponentially before reaching a maximum following crown closure (Waring and Running 1998). We hypothesized a similar pattern would occur in the untreated control since shade intolerant hardwood species dominated the upper strata, which would rapidly approach crown closure. Instead, total LAI was still increasing 14 years (stands were 7 years old when treatments were applied) after stand initiation (Table 2), primarily from increases in shade intolerant hardwood LAI. Even though shade tolerant hardwood and conifer species can persist in low-light conditions by capturing scattered sunflecks (Lieffers and Stadt 1994), these species contributed little to changes in LAI (Fig. 1). By age 14, the shade intolerant hardwood stratum was differentiating and self-thinning (Nelson et al. 2013), yet the increases in LAI suggest dominant and codominant trees' LAI production far exceeded the LAI losses from density-dependent mortality. This pattern may have occurred because LAI of trees that died contributed little to overall stand LAI since they were being shaded and likely had small crowns, while LAI of dominant and codominant trees was rapidly expanding because of greater resource availability.

The dominance of shade intolerant hardwood LAI in plots with hardwood compositional objectives 7 years after treatment was expected, since the treatments removed the less vigorous trees, poorly formed trees, and trees infected with hypoxylon canker [*Hypoxylon mammatum* (Wahl.) Mill.]. This removal created additional growing space for expansion of residual tree leaf area. Similar responses have been found with other shade intolerant species, including shining gum [*Eucalyptus nitens* (H. Deane & Maiden) Maiden] (Medhurst and Beadle 2001) thinned to different densities. Early in stand development is the optimal time to thin shade intolerant stands to increase LAI, since as stands mature, LAI tends to vary little with respect to stand density (Jack and Long 1991), due to short life spans and reduced vigor with age. Even though LAI in both the hardwood treatments and untreated control were dominated by shade intolerant species, thinning the upper stratum stimulated an increase in shade tolerant hardwood LAI that occupied the middle stratum. This increase was likely due to increased light penetration through the upper stratum. Similar patterns have been found in unmanaged northern hardwood stands composed of shade tolerant species following overstory disturbance (Canham et al. 1990).

The rapid expansion in conifer LAI following release from shade intolerant and shade tolerant hardwood LAI was likely caused by increased light and other resource availability to residual conifer trees. Similar patterns have been found for aboveground biomass production of shade tolerant conifers (Olson et al. 2012; Nelson et al. 2013) due to morphological changes associated with greater resource availability including increased terminal and lateral growth (Messier et al. 1999). Hardwood LAI was not completely removed in the conifer treatments and exhibited a gradual increase over the 7-year observation period. This increase was likely due to a combination of small hardwood trees missed by the treatments, stems that sprouted from cut stumps, and new individuals that established in gaps not occupied by conifers (Nelson et al. 2013). Therefore, hardwood species are likely to continue to contribute to total LAI in the future, but at a much lower proportion than in the hardwood treatments. Hardwood LAI was intentionally retained in the mixedwood treatments primarily as scattered shade intolerant trees in the upper stratum. LAI of conifer and shade tolerant hardwood species in the mixedwood treatments is likely to continue to increase and may develop into the upper canopy.

More LAI was retained in the low than the medium intensity treatments across all three compositional objectives, resulting in greater overall LAI 7 years after treatment. Similar results were found when monospecific shining gum stands were thinned to different densities (Medhurst and Beadle 2001). Comparatively, relative LAI between the second and seventh years after treatment increased more in the medium intensity treatments than the low intensity treatments for all of the compositional objectives. For instance, LAI increased by 488 % in the medium conifer treatment and 247 % in the low conifer treatment. These differences may be explained by greater net photosynthesis and carbon allocation to crown development (foliage + support structures) of residual trees in the medium intensity treatments because of lower competition for light, water, and nutrients, which often allows for greater resource capture (Pothier and Margolis 1991).

Vertical distribution of LAI response to treatment

Vertical canopy length differed more among the compositional objectives than management intensities. The shade intolerant upper canopy stratum exhibited the greatest increase in vertical canopy length among the species groups, rapidly expanding upwards, while maintaining a similar distribution of LAI within the canopy. This increase in vertical canopy length was expected since upper canopy layers experienced no overhead competition and could continue to increase in height. Shade intolerant hardwood species can also have foliage at lower portions of the crown (Nelson et al. 2014), because of limited self-shading from above associated with multi-layered crown structures (Horn 1971). Therefore, hardwood treatments that intentionally retained shade intolerant species had the greatest increase in vertical canopy length. More shade intolerant hardwood LAI was removed in the conifer and mixedwood treatments, and hence, the vertical canopy length increased to ~8 m compared to ~10 m in the hardwood and untreated control treatments. Balsam fir was the dominant shade tolerant conifer species across the site and the most prevalent conifer species in the conifer and mixedwood treatments following treatment. Balsam fir inherently exhibits slower growth than shade intolerant hardwood species even in open-growing conditions possibly because of lower photosynthetic capacity (Pothier and Prévost 2002). The shift to slower growing conifer species and their inherent slower growth rates are possible reason for the slower expansion of the vertical canopy length in the conifer and mixedwood treatments.

The height from the canopy base where LAI peaks is a surrogate measure for the canopy region of maximum light interception and is the most photosynthetically productive portion of the canopy (Ellsworth and Reich 1993). The finding that LAI peaked in the middle third of the canopy across all treatment and age combinations correspond to similar patterns found for individual tree crowns across a range of hardwood and conifer species with different tolerances to shade (Weiskittel et al. 2009; Nelson et al. 2014). The peak of LAI in the middle of the canopy has also been found in mature southern Appalachian hardwood forests (Vose et al. 1995), suggesting this is a pattern that continues through time following crown closure. Most LAI is partitioned to the middle of the canopy because the top of the canopy is usually composed of newly formed branches, which tend to have less leaf area per branch than larger branches lower in the canopy (Nelson et al. 2014). In addition, LAI tends to be less in lower portions of the canopy because of shading from above and reduced light availability.

The species shade tolerance groups showed distinct responses in vertical LAI distribution to the treatments. The height above the canopy base where LAI peaked was greater in the low mixedwood and medium hardwood treatments compared to the low hardwood and untreated control likely because of reduced competition in the upper canopy that allowed for greater canopy expansion. The height from the canopy base where LAI peaked was less consistent for shade tolerant hardwood species across treatments, likely because they were not typically species selected as crop trees and they occupied untreated areas outside the 1-m radius treatment zone around each crop tree. The lack of response for conifer species in the height where LAI peaked, but the substantial increase in LAI at the peak, shows a contrasting response to density management than the hardwood species. Instead of building a taller vertical canopy and moving the peak in LAI upwards, conifer species partitioned more LAI horizontally to fill in the available growing space. Similar patterns have been found in other conifer species, where mature western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] trees partitioned leaf area further from the stem at increasing distance from the top of the tree to the base of the crown (Kershaw and Maguire 1996).

Acknowledgments Funding for this study was provided by the Northeastern States Research Cooperative, the Cooperative Forestry Research Unit, and Henry Saunders'—Chair at the University of Maine. We thank Derek Brockmann and Vance Brown, as well as the other technicians who assisted with data collection and implementing treatments for the SIComp experiment.

Conflict of interest The authors declare that they have no conflict of interest.

References

Bolstad PV, Vose JM, McNulty SG (2001) Forest productivity, leaf area, and terrain in southern Appalachian deciduous forests. For Sci 47:419–427

Brassard BW, Chen HY (2006) Stand structural dynamics of North American boreal forests. Crit Rev Plant Sci 25:115–137. doi:10.1080/07352680500348857

Braun EL (1950) Deciduous forests of Eastern North America. Hafner, New York

Brown MJ, Parker GG (1994) Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Can J For Res 24:1694–1703. doi:10.1139/x94-219

Burns RM, Honkala BH (1990a) Silvics of North America, conifers, vol 1. Agriculture handbook 654. US Department of Agriculture Forest Service, Washington, DC

Burns RM, Honkala BH (1990b) Silvics of North America, hardwoods, vol 2. Agriculture handbook 654. US Department of Agriculture Forest Service, Washington, DC

Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can J For Res 20:620–631. doi:10.1139/x90-084

Canham CD, Finzi AC, Pacala SW, Burbank DH (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can J For Res 24:337–349. doi:10.1139/x94-046

Ellsworth D, Reich P (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169–178. doi:10.1007/BF00317729

Fassnacht K, Gower ST (1997) Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can J For Res 27:1058–1067. doi:10.1139/x97-058

Forrester DI, Collopy JJ, Beadle CL, Baker TG (2013) Effect of thinning, pruning and nitrogen fertiliser application on light interception and light-use efficiency in a young *Eucalyptus nitens* plantation. For Ecol Manag 288:21–30. doi:10.1016/j.foreco.2011.11.024

Gholz HL (1982) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63:469–481. doi:10.2307/1938964

Horn HS (1971) The adaptive geometry of trees. Princeton University Press, Princeton

Jack SB, Long JN (1991) Response of leaf area index to density for two contrasting tree species. Can J For Res 21:1760–1764. doi:10.1139/x91-243

Jarvis PG, Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OS, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology IV. Springer, Berlin, pp 233–280

Jerez M, Dean TJ, Cao QV, Roberts SD (2005) Describing leaf area distribution in loblolly pine trees with Johnson's Sb function. For Sci 51:93–101

Karian ZA, Dudewicz EJ (2011) Handbook of fitting statistical distributions with R. CRC, Boca Raton

Kershaw JA Jr, Maguire DA (1996) Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: horizontal distribution of foliage within branches. Can J For Res 26:128–142

Landsberg J (2003) Physiology in forest models: history and the future. For Biom Model Inf Sci 1:49–63

Leverenz J, Hinckley T (1990) Shoot structure, leaf area index and productivity of evergreen conifer stands. Tree Physiol 6:135–149. doi:10.1093/treephys/6.2.135

Lieffers VJ, Stadt KJ (1994) Growth of understorey *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstorey light transmission. Can J For Res 24:1193–1198. doi:10.1139/x94-157

Maguire DA, Bennett WS (1996) Patterns in vertical distribution of foliage in young coastal Douglas-fir. Can J For Res 26:1991–2005

Medhurst JL, Beadle CL (2001) Crown structure and leaf area index development in thinned and unthinned *Eucalyptus nitens* plantations. Tree Physiol 21:989–999. doi:10.1093/treephys/21.12-13.989

Medlyn B, Barrett D, Landsberg J, Sands P, Clement R (2003) Conversion of canopy intercepted radiation to photosynthate: a review of modelling approaches for regional scales. Funct Plant Biol 30:153–169. doi:10.1071/FP02088

Messier C, Doucet R, Ruel JC, Claveau Y, Kelly C, Lechowicz MJ (1999) Functional ecology of advance regeneration in relation to light in boreal forests. Can J For Res 29:812–823. doi:10.1139/cjfr-29-6-812

Nelson AS, Wagner RG, Saunders MR, Weiskittel AR (2013) Influence of management intensity on the productivity of early successional Acadian stands in eastern Maine. Forestry 86:79–89. doi:10.1093/forestry/cps064

Nelson A, Weiskittel A, Wagner R (2014) Development of branch, crown, and vertical distribution leaf area models for contrasting hardwood species in Maine, USA. Trees 28:17–30. doi:10.1007/s00468-013-0926-5

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. doi:10.1086/297553

Oker-Blom P, Pukkala T, Kuuluvainen T (1989) Relationship between radiation interception and photosynthesis in forest canopies: effect of stand structure and latitude. Ecol Model 49:73–87. doi:10.1016/0304-3800(89)90044-6

Olson MG, Wagner RG, Brissette JC (2012) Forty years of spruce-fir stand development following herbicide application and precommercial thinning in central Maine, USA. Can J For Res 42:1–11. doi:10.1139/x11-132

Pothier D, Margolis A (1991) Analysis of growth and light interception of balsam fir and white birch saplings following precommercial thinning. Ann For Sci 48:123–132. doi:10.1051/forest:19910201

Pothier D, Prévost M (2002) Photosynthetic light response and growth analysis of competitive regeneration after partial cutting in a boreal mixed stand. Trees 16:365–373. doi:10.1007/s00468-001-0158-y

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Robinson AP (2004) Preserving correlation while modelling diameter distributions. Can J For Res 34:221–232. doi:10.1139/x03-191

Ruimy A, Saugier B, Dedieu G (1994) Methodology for the estimation of terrestrial net primary production from remotely sensed data. J Geophys Res Atmos 99:5263–5283. doi:10.1029/93JD03221

Seymour RS (1995) The Northeastern Region. In: Barrett JW (ed) Regional silviculture of the United States, 3rd edn. Wiley, New York, pp 31–80

Seymour RS, Kenefic LS (2002) Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands. Can J For Res 32:2032–2042. doi:10.1139/x02-120

Valladares F, Niinemets U (2007) The architecture of plant crowns: from design rules to light capture and performance. In: Pugnaire F, Valladares F (eds) Function plant ecology. Taylor and Francis, New York, pp 101–149

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Annu Rev Ecol Evol Syst 39:237. doi:10.1146/annurev.ecolsys.39.110707.173506

Vose JM, Allen HL (1988) Leaf area, stemwood growth, and nutrition relationships in loblolly pine. For Sci 34:547–563

Vose JM, Clinton BD, Sullivan NH, Bolstad PV (1995) Vertical leaf area distribution, light transmittance, and application of the Beer–Lambert Law in four mature hardwood stands in the southern Appalachians. Can J For Res 25:1036–1043. doi:10.1139/x95-113

Wagner S, Fischer H, Huth F (2011) Canopy effects on vegetation caused by harvesting and regeneration treatments. Eur J For Res 130:17–40. doi:10.1007/s10342-010-0378-z

Waring R (1983) Estimating forest growth and efficiency in relation to canopy leaf area. Adv Ecol Res 13:327–354. doi:10.1016/S0065-2504(08)60111-7

Waring RH, Running SW (1998) Forest ecosystems: analysis at multiple scales, 2nd edn. Academic Press, San Diego

Weiskittel AR, Kershaw JA Jr, Hofmeyer PV, Seymour RS (2009) Species differences in total and vertical distribution of branch- and tree-level leaf area for the five primary conifer species in Maine, USA. For Ecol Manag 258:1695–1703. doi:10.1016/j.foreco.2009.07.035