Silvicultural effects on environmental conditions and resulting aboveground productivity and carbon sequestration of northeastern mixedwood forests

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- Individual tree leaf area models were developed for common early successional hardwood species in the Northeast.
- Tree leaf area models were combined with long-term inventory data to examine temporal changes in stand leaf area index in response to different silvicultural treatments.
- Individual tree light capture and light-use efficiency of white spruce were compared between plantations and natural stands.

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http://www.nsrcforest.org

Project Summary

Early successional forests in Maine comprise nearly 12% of all forestlands in the state, yet their response to different intensities of silviculture are poorly understood. One way to understand the mechanisms driving silvicultural responses is to quantify resource capture and resource-use efficiency of individual trees and stands. Therefore, the goal of this project was to explore resource capture and resource-use efficiency of trees and stands in the SIComp experiment on the Penobscot Experimental Forest in eastern Maine. SIComp consists of factorial treatment combinations of silvicultural intensity and species compositional objectives. The distinct developmental trajectories provide an ideal setting to explore mechanistic drivers on forest productivity in the region. First we developed individual tree leaf area models for common early successional species in the region. We found that species differed considerably in the amount of leaf area they produce and how the leaf area was partitioned within their crowns. These models were then linked with SIComp inventory data to examine temporal changes in stand leaf area index (LAI) in response to the contrasting silvicultural treatments. Although LAI was reduced considerably in all treatments, LAI approached pre-treatment values seven years after treatment but shifted LAI to different species groups. LAI in both the conifer-dominated and mixedwood stands was shifted to conifer species and shade tolerant hardwood species, while LAI in hardwood-dominated treatments remained in shade intolerant hardwood species. Treatments also affected the vertical partitioning of LAI though the canopy, with the most rapid upward partitioning occurring in shade intolerant species. In contrast, conifer species allocated LAI laterally even after release. Last, we explored how contrasting growing conditions (plantations vs. natural stands) affected light capture and light-use efficiency of individual white spruce trees. For the average sized tree, trees in plantations absorb substantially more light than trees in natural stands due to lower neighborhood competition. In comparison, the efficiency that captured light was converted to aboveground biomass was greater in natural stands than in plantations, likely due to the moderate shade tolerance of white spruce. Overall, the results from this project provide initial findings to better understand the coexistence of multiple species in early successional stands in Maine that may assist in the refining silvicultural prescriptions and modeling efforts.

Background and Justification

- Aboveground productivity of forests is a product of resource availability, resource capture, and the efficiency that captured resources are converted into biomass increment (Binkley et al. 2002).
- Light capture is often indirectly estimated with leaf area, which reflects a tree's and stand's investment in light harvesting materials.
- Light capture and light-use efficiency can be directly assessed using light-intercept models, providing a mechanistic understanding of how trees respond to neighborhood growing conditions
- Examining patterns in light capture and use efficiency in response to silviculture provides a broader understanding of the underlying processes affecting growth and may assist in refining growth and yield models.

Methods: Individual Tree Leaf Area Models

Mean ± standard deviation (range) of attributes of the trees sampled for leaf area modeling by species. The number of trees (n), diameter at breast height (DBH; cm), total height (HT; m), crown length (CL; m), total leaf area (CLA; m^2), and crown width (CW; m) are shown for the 9 species in the investigation.

Species	n	DBH (cm)	HT (m)	CL (m)	CLA (m^2)	CW (m)
Red maple	12	3.3 ± 2.8 (0.5 - 10.4)	4.79 ± 2.83 (1.65-10.40)	3.62 ± 2.25 (1.17-8.15)	10.05 ± 23.55 (0.16 - 75.53)	1.73 ± 1.30 (0.14 - 5.12)
Paper birch	14	2.1 ± 2.0 (0.5 - 8.4)	3.81 ± 2.29 (1.55 - 9.55)	2.83 ± 1.91 (1.09 - 8.15)	4.12 ± 9.43 (0.08 - 35.82)	1.22 ± 0.59 (0.51 - 2.64)
Gray birch	14	1.9 ± 1.8 (0.6 - 6.9)	3.70 ± 2.56 (1.66 - 11.09)	2.89 ± 1.76 (1.21 - 6.90)	2.60 ± 4.31 (0.28 - 13.96)	1.20 ± 0.46 (0.43 - 2.06)
Bigtooth aspen	17	5.8 ± 3.2 (1.1-13.1)	7.65 ± 3.09 (1.87 - 13.00)	4.37 ± 2.46 (0.71 - 10.50)	13.63 ± 31.86 (0.02 - 91.46)	2.14 ± 0.98 (0.69 - 4.08)
Trembling aspen	14	5.9 ± 2.7 (2.6 - 12.0)	8.10 ± 2.50 (4.77 - 12.18)	4.92 ± 2.40 (1.11 - 9.56)	8.97 ± 13.21 (0.90 - 52.36)	2.24 ± 1.24 (0.94 - 5.71)
Hybrid poplar D51	5	4.3 ± 2.4 (1.4 - 7.5)	5.48 ± 2.37 (2.75 - 8.80)	5.00 ± 2.26 (2.40 - 8.30)	6.12 ± 5.58 (0.74 - 14.65)	1.74 ± 0.76 (1.02 - 2.99)
Hybrid poplar DN10	5	5.4 ± 3.6 (2.3 - 10.9)	6.75 ± 2.74 (4.15 - 10.85)	5.64 ± 2.83 (4.00 - 10.65)	9.84 ± 10.42 (1.26 - 26.20)	1.88 ± 0.74 (0.99 - 2.86)
Hybrid poplar DN70	5	4.5 ± 3.0 (0.7 - 8.7)	5.37 ± 2.44 (1.86 - 8.70)	4.28 ± 1.95 (1.79 - 6.80)	6.40 ± 6.09 (0.26 - 15.37)	1.85 ± 0.94 (0.42 - 2.86)
Hybrid poplar NM6	5	7.4 ± 4.0 (3.0 - 13.6)	8.26 ± 2.59 (4.65 - 11.90)	7.47 ± 3.44 (2.30 - 11.80)	21.18 ± 23.11 (3.60 - 60.70)	3.05 ± 1.15 (2.02 - 4.92)

- Trees were sampled from the SIComp experiment on the Penobscot Experimental Forest in eastern Maine in summer 2011
- Trees were cut at the base and branches were subsampled to develop branch-level projected leaf area models
- Branch models were used to predict leaf area of all branches within a tree and summed to obtain total leaf area estimates
- Nonlinear regression was used to fit total tree leaf area models by species

Results: Branch Leaf Area Models

Branch leaf area model parameter estimates, and standard error (SE) of parameter estimates. R^2 and residual standard error are shown to demonstrate the fit of the models. All model parameters were significant at the $\alpha = 0.05$ level, except the a_3 parameter for gray birch and bigtooth aspen.

	a_1		a_2		a_3		Fit Statistics	
Species	Estimate	SE	Estimate	SE	Estimate	SE	R^2	Residual standard error (m^2)
Red maple	2.6617	0.3181	1.4633	0.0705	1.0071	0.1633	0.856	0.1161
Paper birch	2.1353	0.0659	1.1522	0.0138	1.0434	0.0814	0.993	0.0343
Gray birch	2.7095	0.4281	1.4448	0.1391	1.2263	0.6846	0.351	0.1413
Bigtooth aspen	2.2666	0.3880	1.6631	0.1480	1.1684	0.7253	0.427	0.3324
Trembling aspen	1.6989	0.0987	2.0463	0.1285	0.9313	0.1759	0.837	0.2915
Hybrid poplar D51	2.3637	0.3623	1.3883	0.0493	2.9704	0.3554	0.651	0.1215
Hybrid poplar DN10	2.3346	0.0774	1.3451	0.0275	3.0329	0.1704	0.967	0.0393
Hybrid poplar DN70	2.6195	0.1322	1.5353	0.0470	2.8007	0.3870	0.862	0.0440
Hybrid poplar NM6	1.9782	0.0976	1.5532	0.0611	2.0932	0.2321	0.941	0.2084

A nonlinear function with the form $BLA = BD^{a_1} RBT^{a_2 - 1} e^{-a_3 RFS^{a_2}}$ best fit the observed data for all species with R^2 ranging from 0.35 for gray birch to 0.97 for for the DN10 hybrid poplar clone. The variables were as follows: BD - branch diameter, RBT - relative height of the branch tip, RFS - relative height of the start of the foliage along the branch, and $a_{1\text{-}3}$ were estimated parameters

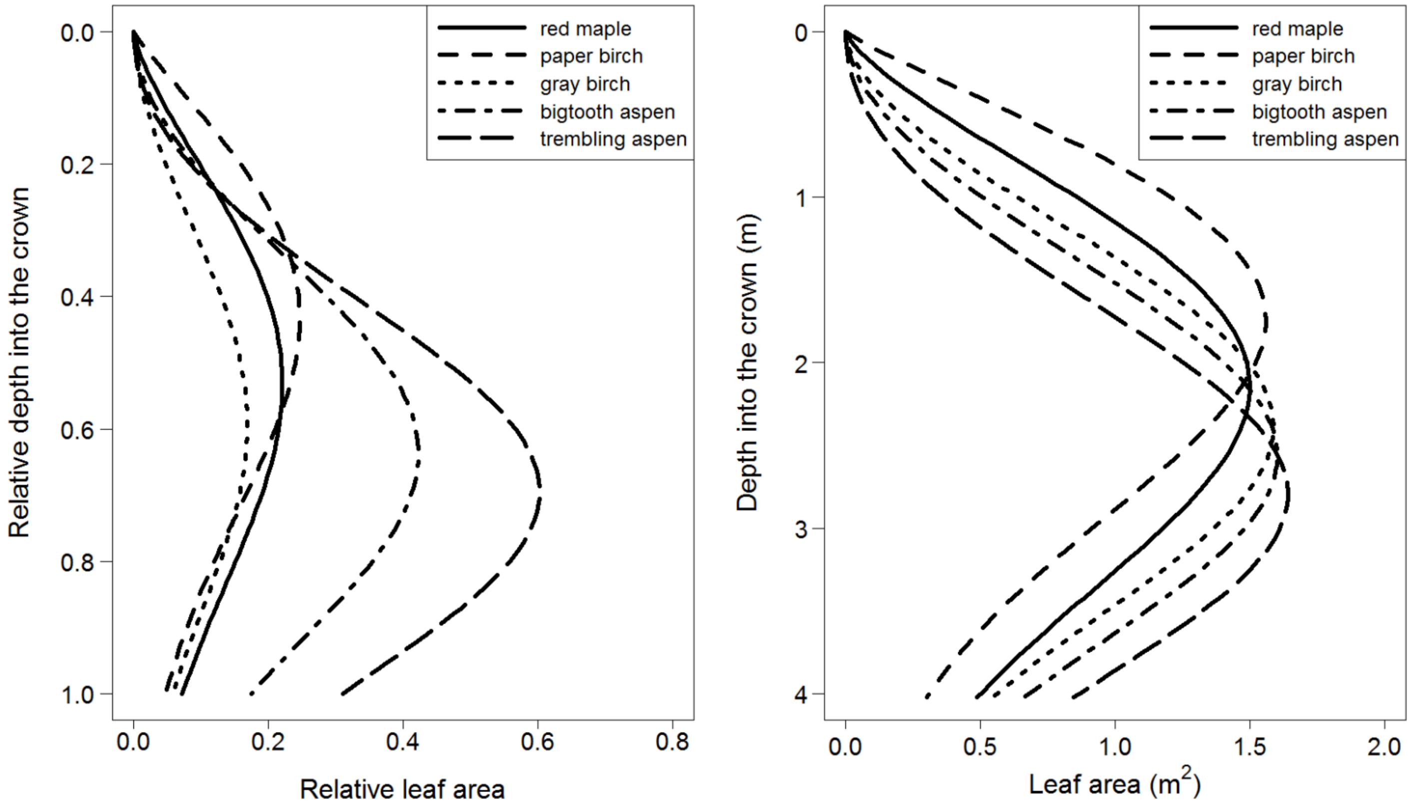
Results: Tree Leaf Area Models

Tree-level leaf area parameter estimates and standard error of parameters. R^2 and residual standard error are shown to demonstrate the fit of the models. All parameters were significant at the α = 0.05 level except gray birch b_1 and b_3.

	b_1		b_2		b_3		Fit Statistics	
Species	Estimate	SE	Estimate	SE	Estimate	SE	R^2	Residual standard error (m^2)
Red maple	0.1172	0.0343	1.7104	0.1192	1.6918	0.1902	0.985	0.165
Paper birch	0.7569	0.0684	2.2520	0.0424	-0.8978	0.1277	0.999	0.105
Gray birch	0.2076	0.1457	1.0639	0.2500	2.3032	1.2665	0.853	0.166
Bigtooth aspen	0.5260	0.2055	2.2374	0.1766	-1.0232	0.1767	0.961	0.609
Trembling aspen	0.3118	0.1094	2.0394	0.1514	-0.5766	0.1641	0.947	0.303
Hybrid poplar	0.1959	0.0629	1.8913	0.1068	0.4643	0.1573	0.912	0.483

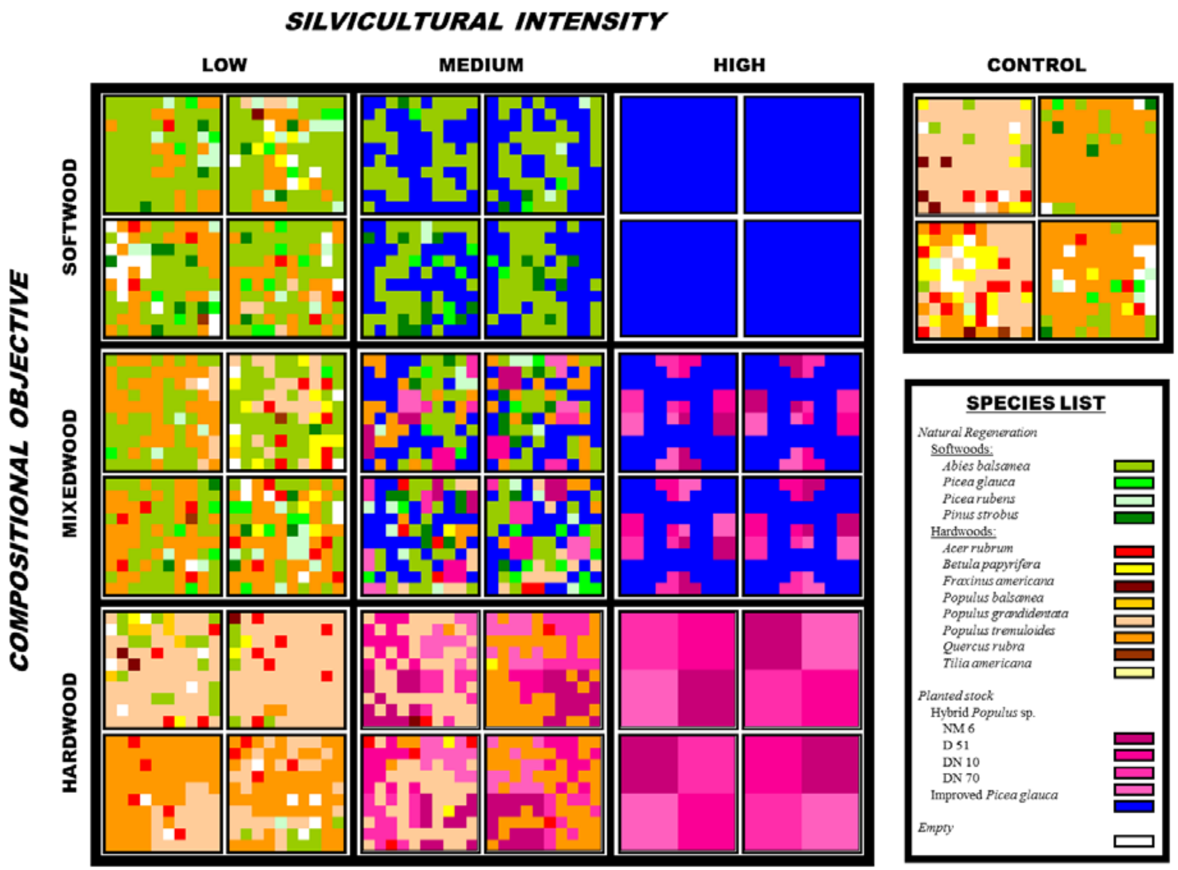
A nonlinear function with the form $CLA = b_1 DBH^{b_2} e^{b_3(\frac{DBH}{CL})}$ best fit the observed data for all species with R^2 ranging from 0.85 for gray birch to 0.99 for for paper birch. Hybrid poplar trees were combined in a single model due to the low sample size. The variables were as follows: DBH – diameter at breast height (1.37 m), CL – crown length, and $b_{1\text{-}3}$ were estimated parameters

Results: Vertical Leaf Area Models



Vertical distribution of leaf area within tree crowns was best fit with a right truncated Weibull distribution. Standardized across species, relative leaf area peaked at ½ to 2/3 of the relative depth into the crown from the top of the tree. For the averaged sized tree, leaf area peaked highest in the crown for paper birch and lowest in the crown for trembling aspen

Methods: Stand Leaf Area Index



- Leaf area index was estimated for trees in the SIComp experiment on the Penobscot Experimental Forest using the individual tree leaf area models developed for trees at the site.
- SIComp was designed to explore the effects of factorial combinations of silvicultural intensity and species compositional objectives in early successional stands.
- We used eight years of long-term inventory data and individual tree leaf area models to examine how treatments affected stand productivity

Methods: Stand Leaf Area Index

- Leaf area was summed for all trees within each plot to estimate leaf area index
- Leaf area index was then calculated separately for three broad species groups: shade intolerant hardwoods, shade tolerant hardwoods, and conifers.
- Vertical distribution of canopy leaf area index was estimated using the right-truncated Weibull distribution models developed for individual trees.
- New right-truncated Weibull distribution models were then fit for each treatment plot and measurement year for (a) all trees combined, and (b) for the individual species groups.

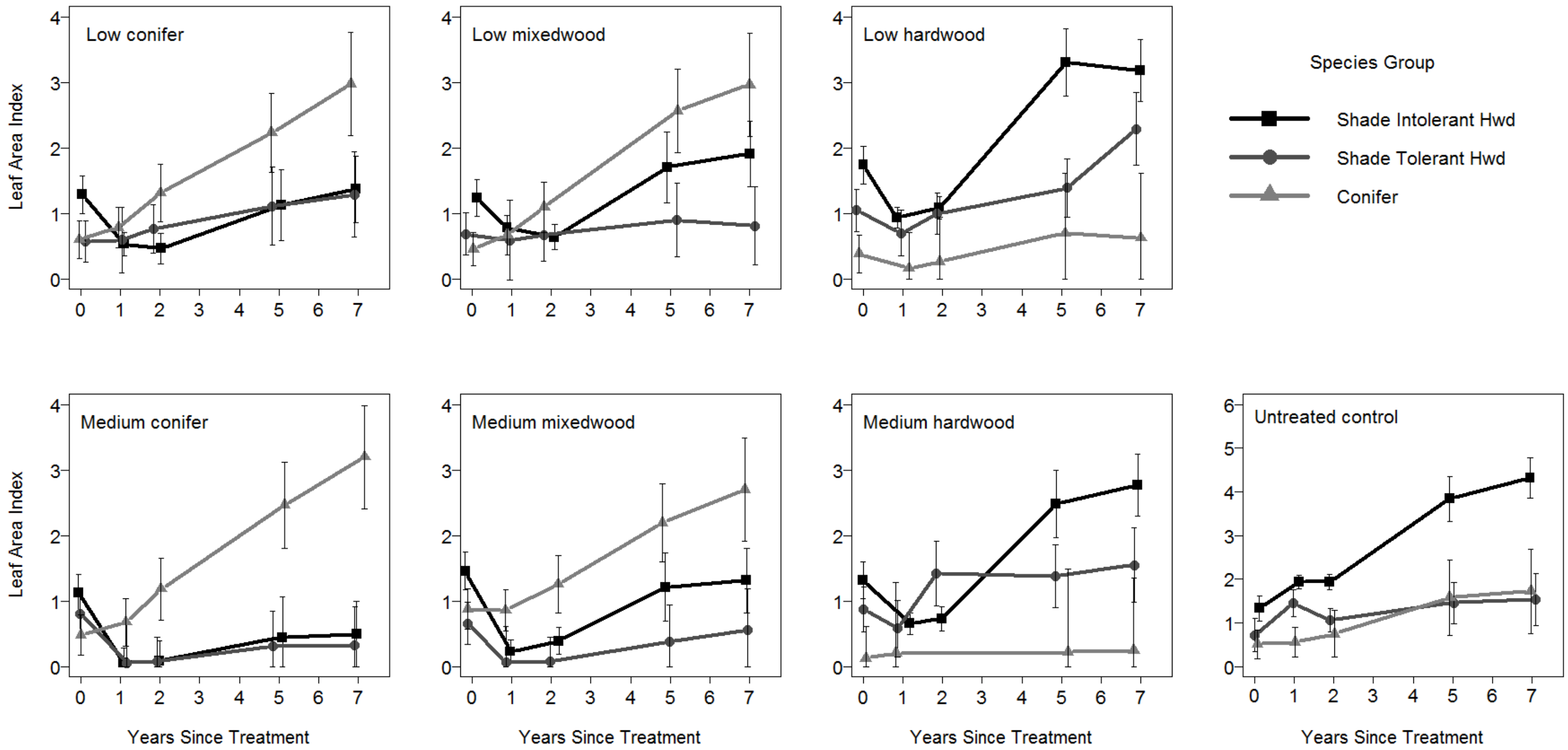
Results: Stand Leaf Area Index

Total stand leaf area index (LAI) prior to treatment, one, two, five, and seven years after treatments were applied. 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 α = 0.05 level.

	Years Since Treatment				
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

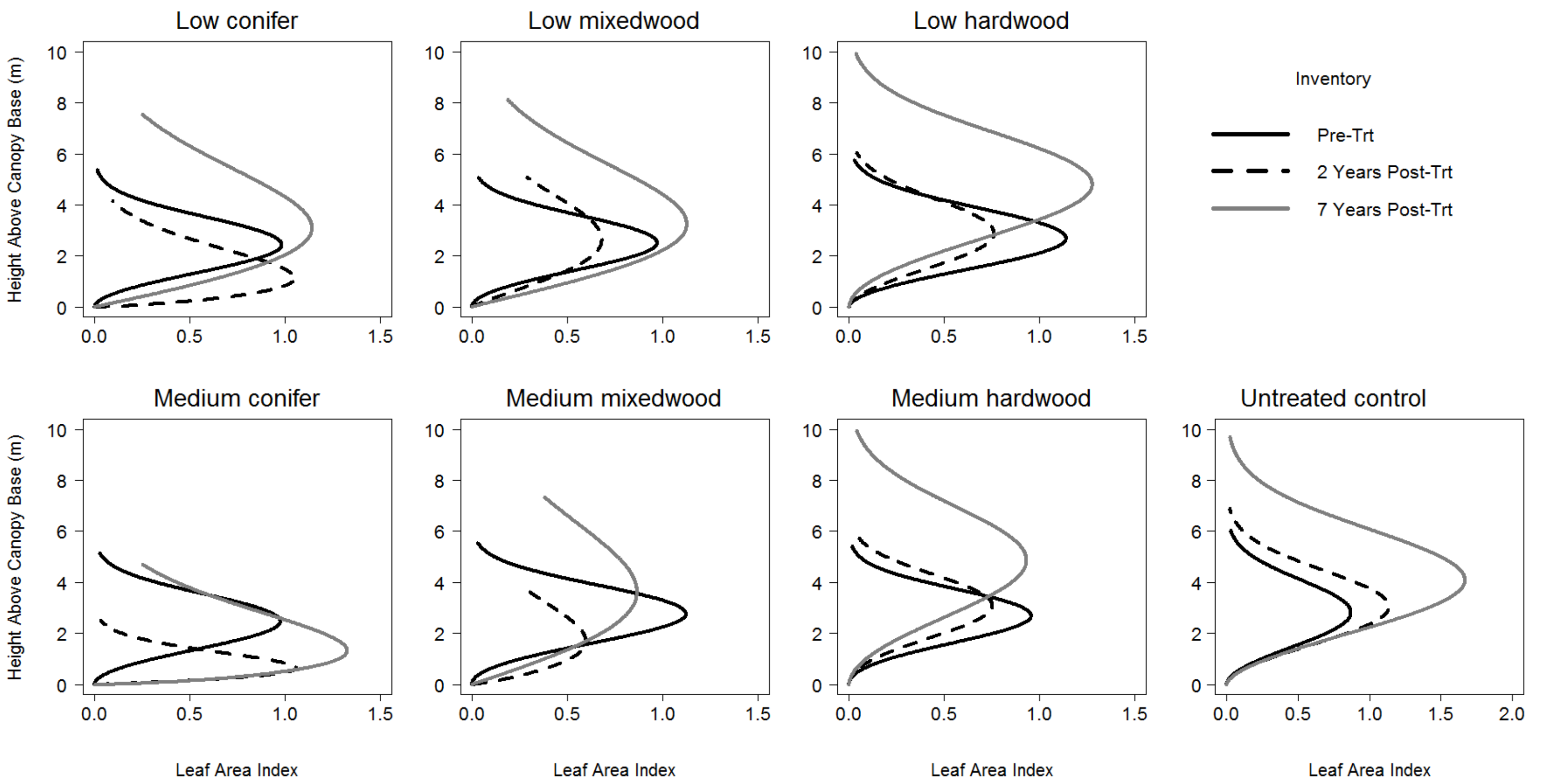
- Total leaf area index (LAI) did not differ between treatments before any manipulation.
- LAI was reduced in all treatments, but increased and eventually surpassed pre-treatment values seven years after treatment.
- Seven years post-treatment, LAI was not different between compositional objectives or between silvicultural intensities, except LAI in the medium intensity treatments was substantially lower than the untreated control

Results: Stand Leaf Area Index



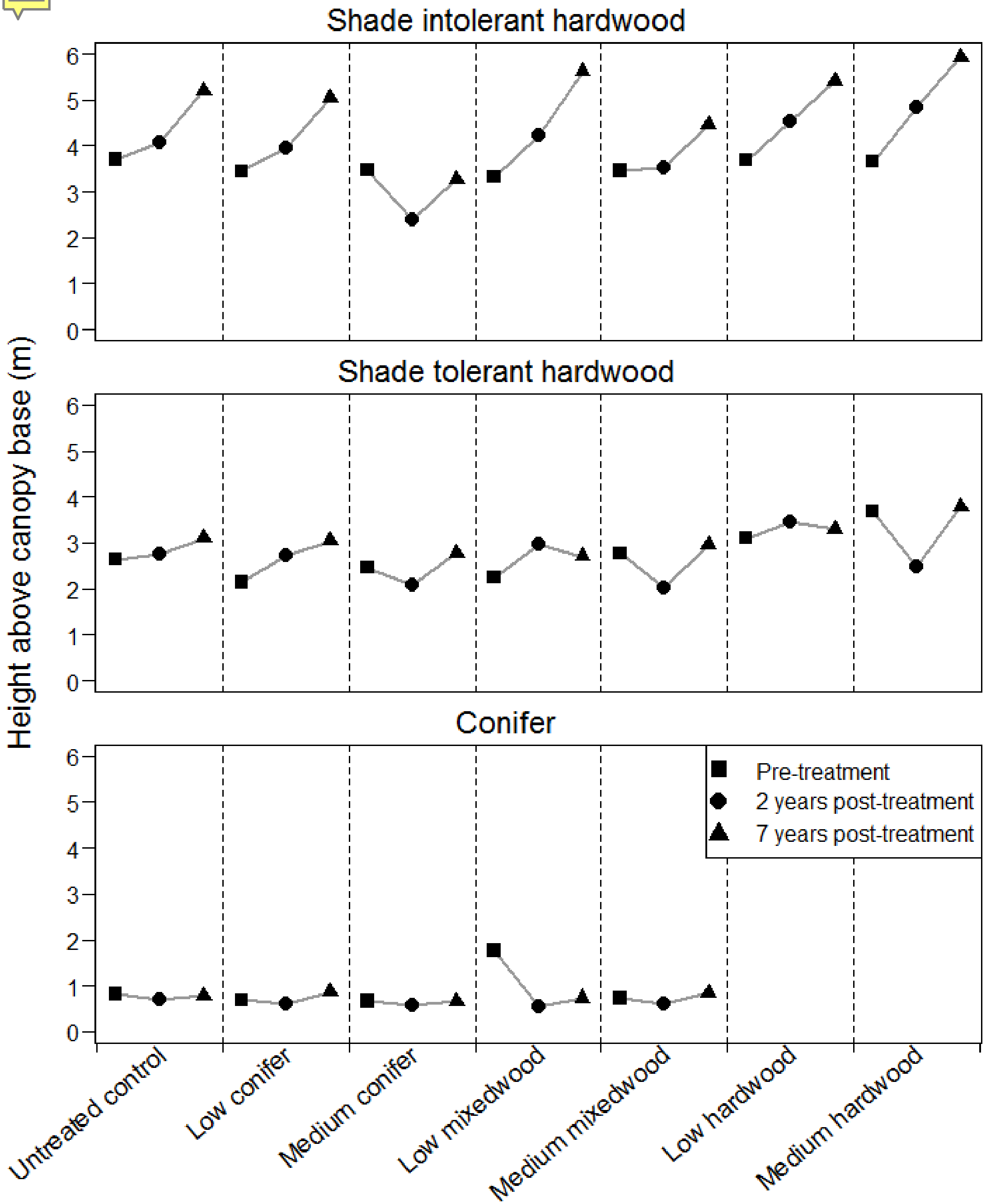
- LAI was greatest for shade intolerant hardwood species in all treatments before manipulation.
- Conifer and mixedwood treatments maintained low shade intolerant LAI, while promoting increased conifer LAI.

Results: Stand Leaf Area Index



- The treatments influenced both the amount of LAI that occurred where LAI peaked within the canopy, but also the distance from the canopy base where LAI peaked.
- The change in height where LAI peaked was greatest in the hardwood treatments, and less for the conifer and mixedwood treatments.

Results: Stand Leaf Area Index

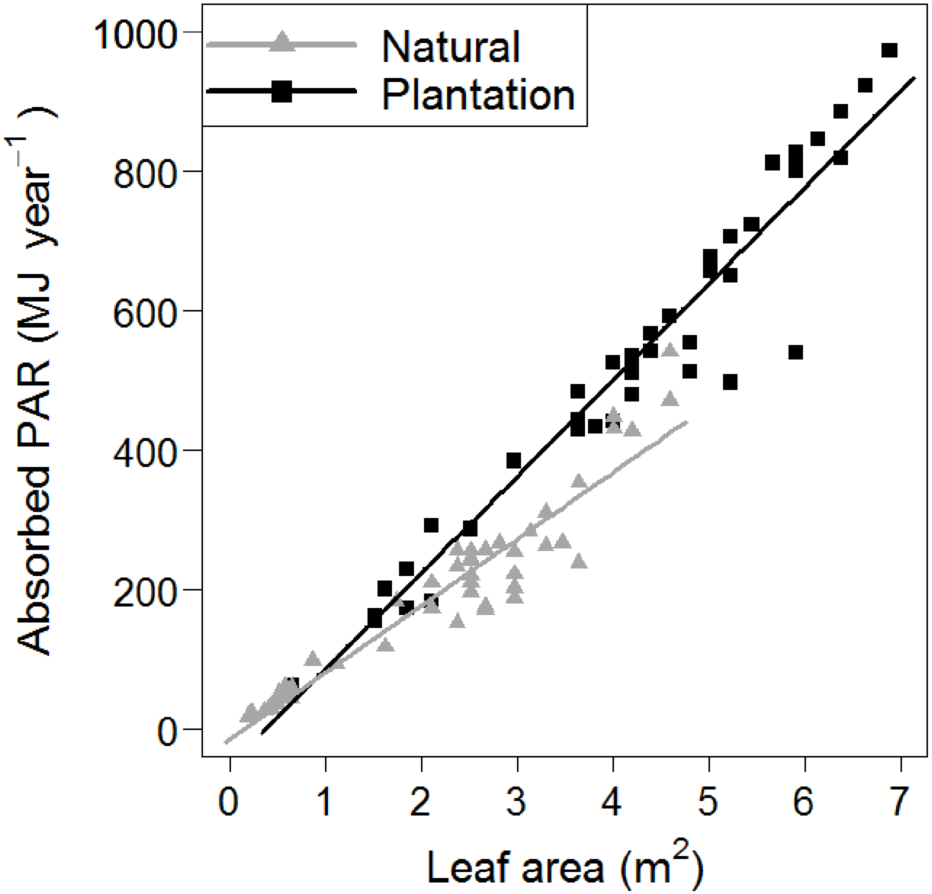


- The vertical distribution of shade intolerant hardwood LAI changed the most after treatment among the species groups, with a substantial increase in the height above the canopy base where LAI peaked.
- The change in height where LAI peaked was much less pronounced in the shade tolerant hardwoods and conifers in all treatment combinations, even treatments that removed overtopping shade intolerant hardwood LAI

Methods: White Spruce Light-Use Efficiency

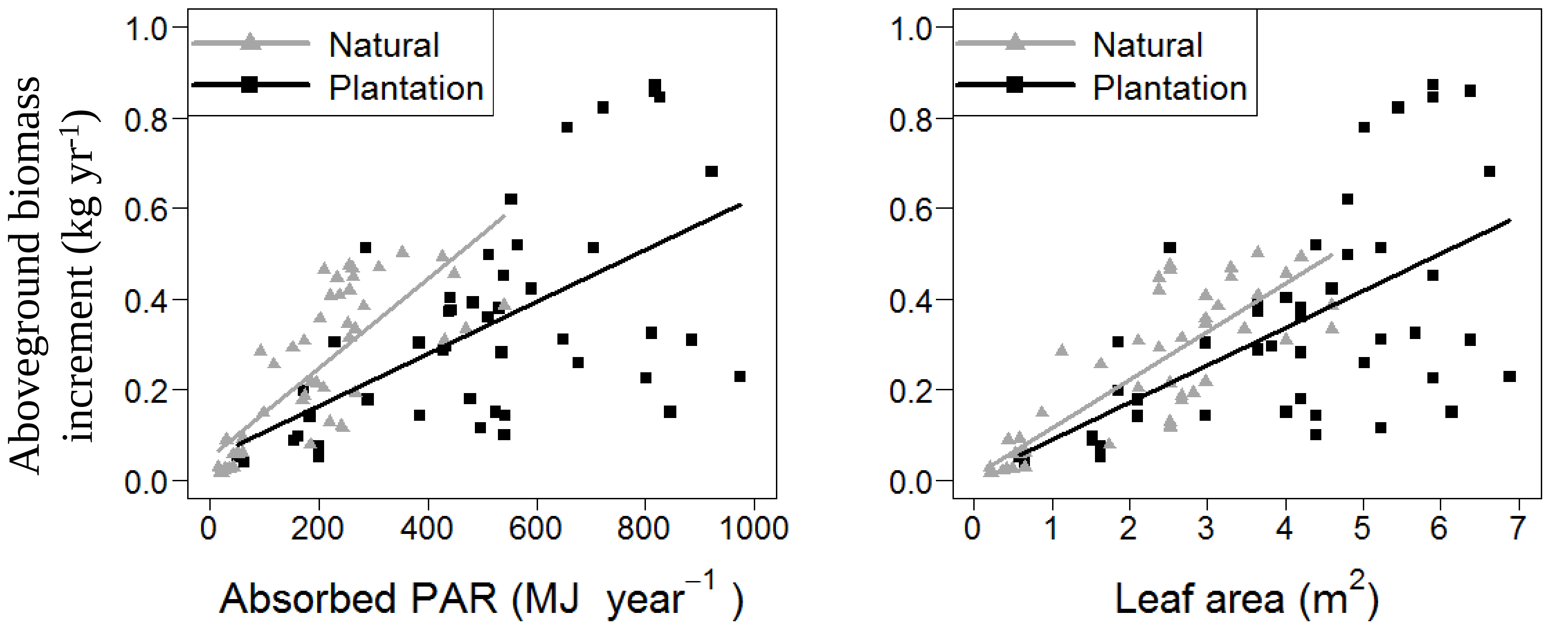
- The study was conducted on the SIComp experiment on the Penobscot experimental forest.
- Trees were selected from treatments with contrasting growing conditions: (a) white spruce enrichment planting in stands shifted to conifer and mixedwood dominance, and (b) white spruce planted in pure and mixed plantations with hybrid poplar trees.
- All trees within a 6 m radius of the focal white spruce tree were identified to species, stem mapped, and their size was measured (stem diameter, height, crown width, crown length).
- MAESTRA, an individual tree light capture model, was used to estimate the amount of light captured by each individual white spruce tree throughout the growing season by accounting for the shading by neighboring trees.
- Analysis of covariance was used to explore the effects of distance-weighted competition and tree size on light capture and use efficiency across the treatments.

Results: White Spruce Light-Use Efficiency



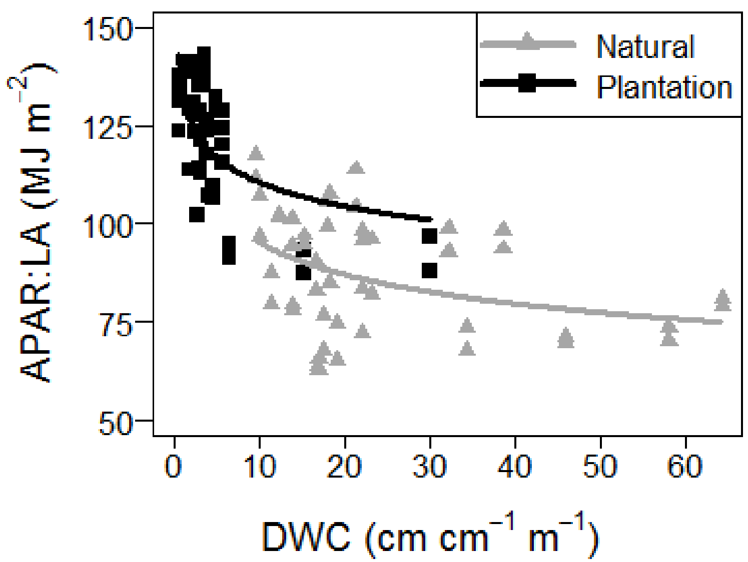
- Tree light capture increased linearly with tree size (represented by leaf area), but the slopes were different between the two growing conditions.
- At the mean leaf area of 3.1 m^2 $tree^{-1}$, APAR was 33% greater in plantations due to less neighborhood light competition.

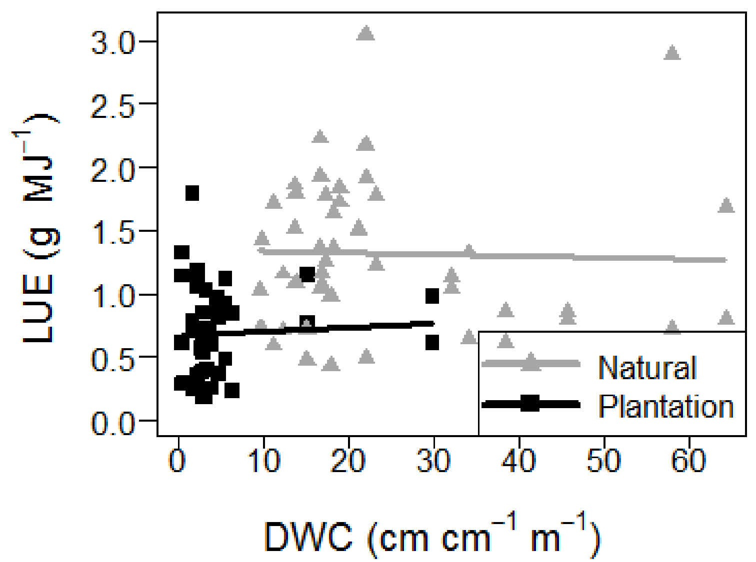
Results: White Spruce Light-Use Efficiency



- Aboveground biomass increment was positively related to APAR and leaf area, with slopes that differed by growing condition.
- At the mean APAR of 350 MJ tree^{-1}, biomass increment was 48% greater in natural stands, suggesting greater efficiency of converting captured light into biomass.

Results: White Spruce Light-Use Efficiency





- The ratio of captured light (APAR) to the amount of leaf area (LA) slightly decreased as competition increased suggesting white spruce maintains a similar leaf area across a broad range of light conditions.
- Light use efficiency (LUE) was not related to competition, possibly because the stands had yet to reach crown closure where differentiation in LUE often occurs.

Implications and applications in the Northern Forest region

- Our results demonstrate:
  - Early successional hardwood species differ considerably in their strategies for producing leaf area and partitioning leaf area within their crowns.
  - These different leaf area strategies among species allow for coexistence in mixed-species stands.
  - When scaled to a stand-level, these different strategies help explain some of the underlying effects of silvicultural treatments on aboveground productivity.
  - White spruce trees growing on contrasting environments differ considerably in light capture and light-use efficiency, with trees growing in natural stands exhibiting greater efficiency of converting captured light into biomass than plantation trees.

Future directions

- Expand individual tree leaf area models to more species common on Northeastern forests, especially shade tolerant hardwood species. This will provide a better understanding of species differences in light capture and coexistence.

- Assess light-use efficiency of white spruce trees in different treatments once trees begin to interact aboveground after crown closure. Then, a better understanding of the effects of pure- versus mixed-species forests on light capture and efficiency can be assessed.

- Explore the effects of belowground resource availability on light capture and light-use efficiency.

List of products

Peer-reviewed publications

- Nelson, A.S., Wagner, R.G., Day, M.E., Fernandez, I.J., Weiskittel, A.R., and Saunders, M.R. *In Review*. Effects of contrasting growing conditions on aboveground net primary productivity, light -use efficiency, and foliar $\delta^{13}C$ composition of juvenile white spruce trees. Trees - Structure and Function.
- Nelson, A.S., Wagner, R.G., Weiskittel, A.R., and Saunders, M.R. 2015. Effects of species composition, management intensity, and shade tolerance on vertical distribution of leaf area index in juvenile stands in Maine, U.S.A. European Journal of Forest Research 134: 281-291.
- Nelson, A.S., Weiskittel, A.R., and Wagner, R.G. 2014. Development of branch, crown, and vertical distribution leaf area models for contrasting hardwood species in Maine, U.S.A. Trees - Structure and Function 28(1): 17-30.

Other publications

- **Nelson, A.S.**, and Wagner, R.G. 2011. Influence of silvicultural intensity and species composition on the productivity of early successional stands in Maine. *In* Cooperative Forestry Research Unit 2011 Annual Report. *Edited by* B. Roth, Orono, ME. pp. 22-26.

List of products

Leveraged grants

- Wagner, R.G., Weiskittel, A.R., and Nelson, A.S. 2012-2014. Incorporating young hardwood stand responses to various levels of silviculture and stand composition into new CFRU growth & yield models. Cooperative Forestry Research Unit. $67,871.

Conference presentations

- Nelson, A.S., Weiskittel, A.R., Wagner, R.G., and Saunders, M.R. 2012. Vertical distribution and total tree leaf area equations of juvenile trees in eastern Maine. *Presented at:* Southern Mensurationist 2012 Annual Meeting. Jacksonville, FL.
- Nelson, A.S., Weiskittel, A.R., and Wagner, R.G. 2011. Crown and total biomass equations of young, naturally regenerated hardwood species in central Maine. *Presented at:* 15th Annual Northeastern Mensurationists Organization Meeting. Quebec City, Quebec, Canada.