



Species mixture effects in northern red oak–eastern white pine stands in Maine, USA



Justin Waskiewicz^{a,*}, Laura Kenefic^b, Aaron Weiskittel^a, Robert Seymour^a

^aThe University of Maine, School of Forest Resources, 5755 Nutting Hall, Orono, ME 04469, United States

^bUS Forest Service, Northern Research Station, 686 Government Rd., Bradley, ME 04411, United States

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ABSTRACT

Growth and yield studies of mixed-species stands lack generality, though mixture effects appear to be most likely in stands of species with contrasting traits and/or with vertical stratification. The northern red oak (*Quercus rubra* L.) – eastern white pine (*Pinus strobus* L.) forest type of the US Northeast is dominated by species of intermediate shade tolerance, often with a spatially heterogeneous lower canopy of shade-tolerant red maple (*Acer rubrum* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). We examined neighborhood scale plots (0.02 ha) with variable mixtures of these species and a range of age structure (44–140 years mean age) in southern Maine. Linear mixed effects regression was used to model canopy surface area, stem biomass growth, and stem biomass yield across gradients of composition. With stocking, age, and site quality held constant, more species-diverse plots had denser canopies and faster growth, but lower yield than compositionally simpler plots. For a variety of age structures, mixtures of oak and pine produced more canopy surface area and more stem biomass growth than would be expected if inter-specific competition were equal to intraspecific, and more than would be expected on plots dominated by one species or the other. Lower canopy red maple and hemlock contributed to higher plot-level values of all variables in mixed plots, but there was no evidence to suggest that any species contributed to stocking without displacing other species to some degree. This study demonstrates that white pine and red oak, along with other species, can grow in fine-scale mixtures in a variety of even- and two-aged structures without sacrificing productivity, and in some conditions enhancing it.

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1. Introduction

Complex stands containing several species and cohorts are common in temperate forests of northeastern North America, and their importance is likely to increase with the greater prevalence of partial cutting practices (Kittredge et al., 2003) and explicit management emphases on maintaining and enhancing complexity (Knoke et al., 2008; Puettmann et al., 2009). When two or more tree species occur together, there is potential for interactions which may be advantageous or detrimental relative to pure stands in terms of total productivity per unit area. Where mixture components differ greatly in stature, crown or root structure, shade tolerance, photosynthetic efficiency, phenology, or other traits, the potential for enhanced productivity is greatest, due to complementary resource use (competitive reduction; Kelty, 1992). With sufficient levels of competitive reduction, or in cases of active facilitation between species, the potential exists for overyielding (underyielding if species interfere with each other), a condition in which a mixture's aggregate content may exceed (or fall short

of) the expectation based on compositional proportions (Pretzsch, 2009). Overyielding appears as a convex curvature of predicted productivity over species proportions. If a mixture yields more than the most productive component species in monoculture, the pattern is called transgressive overyielding (Fig. 1, I).

The null hypothesis in studies of mixture effects is that yield or any other metric of aggregated output (e.g. growth rate, canopy density) is a linear combination of component species, without interaction terms. The mixed-stand literature contains many studies failing to reject this null hypothesis, including both natural and planted stands, and combinations of species both with similar traits (e.g. Chen and Klinka, 2003; Garber and Maguire, 2004) and seemingly complementary traits (e.g. Smith and Long, 1992; Montigny and Nigh, 2007). Underyielding interactions have also been found in some studies, especially but not always where component species have similar developmental patterns and/or shade tolerance (e.g. Chen et al., 2003; Cavard et al., 2010). An intriguing minority of studies have found overyielding in mixtures, often but not exclusively with species of complementary shade tolerances (e.g. Brown, 1992; Frivold and Frank, 2002).

In many studies of species mixtures, a pure condition is not represented for one of the components (often an emergent or lower

* Corresponding author. Tel.: +1 207 581 2841.

E-mail address: justin.waskiewicz@maine.edu (J. Waskiewicz).

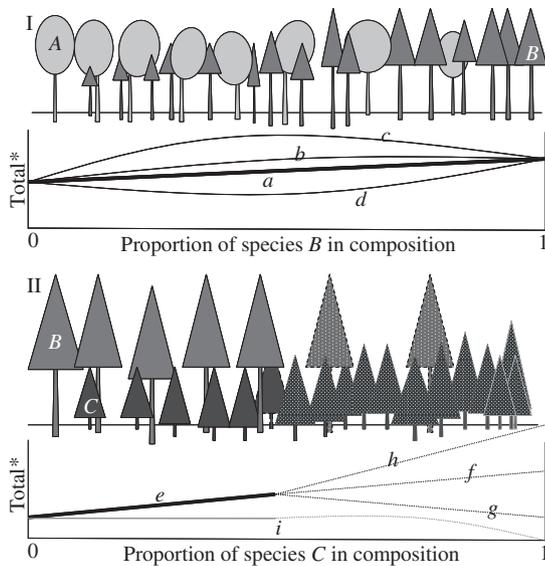


Fig. 1. Potential relationships between total canopy area, biomass yield, or growth rate (Total*) and given species' proportion of composition. In I, bold line *a* illustrates the null hypothesis of linear substitution between species A and B. Lines *b*, *c*, and *d* illustrate overyielding, transgressive overyielding, and underyielding, respectively. II illustrates interpretive difficulties with species that do not span the full possible range of composition: a positive linear relationship, *e*, for proportions of species C that only reach to 0.5 in data may be associated with neutral, positive, or negative mixture effects over the whole potential span (*f*, *g*, and *h*, respectively). An “additive” pattern for such species would be indicated by the nature of line *i*, representing the value for non-C species. If *i* has non-negative slope over the data range, C may be “additive,” in that its presence has no effect on the other species to at least some level.

canopy member), which changes the issue at question from one of substitution to that of additivity – completing the observational analogy to the two experimental mixture designs described by Kelty and Cameron (1995; Fig. 1, II). Additivity occurs when one component has no effect on some attribute (density, growth, yield, etc.) of the matrix. The phenomenon was first described by Enright (1982), studying emergent Klinki-pine (*Araucaria hunsteinii* K. Schumm.) among hardwoods in New Guinea, where the presence of the former had no relationship to the density (basal area) of the latter. In other studies, emergent trees in Chile and Japan have also been found to be additive to their surroundings (Aiba et al., 2007 and Donoso and Lusk, 2007, respectively). Additivity may also occur with lower canopy trees; in boreal mixedwoods, MacPherson et al. (2001) found that stands with white spruce (*Picea glauca* (Moench) Voss) growing beneath quaking aspen (*Populus tremuloides* Michx.) had roughly 10% higher growth and yield than pure aspen stands, while there was no significant correlation between the aspen component's growth and the density of spruce. In New England, lower-canopy eastern hemlock (*Tsuga canadensis* (L.) Carr) has been reported as additive to overstory hardwoods (mostly northern red oak (*Quercus rubra* L.); Kelty, 1989) because hardwood growth and yield was found to be the same with or without the hemlock component. The additivity phenomenon seems to be common only with vertically stratified stands, though there has been some debate about whether the underlying cause is structure-, size-, or age-related (see Midgley et al., 2002 and Lusk et al., 2003).

In highly complex stands, not only species proportions, but also cohort proportions may vary, along with density and microsite quality. All of these variables must be considered in an observational study (Vilà et al., 2003; Long and Shaw 2010). Density is particularly important, as several studies have shown that this factor can affect structural development in mixtures (Garber and Maguire, 2004; Amoroso and Turnblom, 2006), and it typically correlates with higher growth and yield regardless of composition. Where

comparisons are made among stands or neighborhoods of varying stem density and/or age, an expression of stocking such as relative density index (RDI; Long and Daniel, 1990) is an appropriate medium, provided that the index accounts for inherent differences in maximum stocking potential among component species (e.g., Woodall et al., 2005; Ducey and Knapp, 2010). Inclusion of such covariates in growth models, however, complicates assessment of additivity, because that phenomenon essentially depends on an increase of total stocking simultaneous with an increase in the additive species' proportion.

Controlled experiments to study mixture effects have been carried out in Europe, the tropics, and the Pacific Northwest (e.g., Brown, 1992; Menalled et al., 1998; Montigny and Nigh, 2007), but no experimental studies involving species common to northeastern North America exist. The abundance of potential species and cohort combinations limits the practicality of experimental analysis with these species groups, leading researchers in this area to rely on observational studies of naturally heterogeneous stands (Bravo et al., 2001). Kelty (1989), for example, compared embedded patches of hardwood-hemlock mixture with the pure hardwood matrix in two heterogeneous stands in southern New England, treating the two patch types as being conceptually two intermixed stands with irregular boundaries.

Stands composed primarily of northern red oak and eastern white pine (*Pinus strobus* L.) in mixture with red maple (*Acer rubrum* L.) and eastern hemlock are common, especially on private lands in southern and central New England in the US Northeast, where they have important timber, wildlife, and recreational values (McWilliams et al., 2005). These stands have developed horizontally heterogeneous combinations of vertically stratified elements (Smith et al., 1997), resulting from a history of partial disturbance. A matrix of shade-intolerant to intermediate hardwoods (mostly red oak), initially established as advance regeneration beneath old-field pine stands, now dominates over patches of shade-tolerant species (mostly hemlock and red maple) and surrounds individuals and groups of pre-disturbance residual pines and oaks (Cline and Lockard, 1925; Smith et al., 1997). The various combinations of tree stature, shade tolerance, and age make these stands ideally suited for study of potential mixture effects.

This study focused on the neighborhood scale within red oak – white pine dominated mixed stands, where we sought to determine: (1) whether gradients of species diversity or composition correlated with plot-level crown surface area (CSA), stem biomass growth rate (BGR), or stem biomass yield (BIO); (2) if mixture effects generating over- (or under-) yielding of canopy surface, growth, or yield occurred between major species; and (3) if additivity was evident for any of the observed species. Default hypotheses were: (1) that diversity and composition indices are unimportant to predicting CSA, BIO, or BGR when relative density, age, and site quality are accounted for; (2) that species' contributions to CSA, BGR, or BIO are proportional to their contribution to total relative density regardless of other species' presence; and (3) that all species' proportions have a significant negative linear correlation with other species' density.

2. Methods

2.1. Study site

This study was conducted at the Massabesic Experimental Forest (MEF, 43°30'N, 70°30'W), a US Forest Service, Northern Research Station property in York County, Maine, dominated by the eastern white pine – northern red oak – red maple forest cover type (Society of American Foresters type 20; Baldwin and Ward, 1980). Soils are coarse textured loam and sand, generally Aquic

and Typic Haplorthods (Brayton, Colton, Croghan, Hermon, Naumburg, and Skerry series) formed from till of glaciated uplands and glacio-fluvial deposits, are generally well drained and are moderately deep (~150 cm; Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2012). Data collection was concentrated in areas typed as pine-oak (basal area >25% combined white pine and red oak) by Dibble et al. (2004). Other common tree species in the study areas included: red maple, eastern hemlock, white oak (*Q. alba* L.), paper birch (*Betula papyrifera* Marsh.), and black oak (*Q. velutina* Lam.), with scattered individuals and small groups of other species. Red and black oak were combined for analysis.

We collected data in six parcels (administrative units), three in each of the MEF's northern and southern units. MEF parcels differ in their history and their average structure and composition, though all are former agricultural lands abandoned in the 19th century, and all were exposed to an extensive wildfire of patchy intensity, which burned across this area of Maine in fall 1947 (McConkey and Smith, 1958). Salvage harvesting and windstorms in 1950 and 1954 reduced the overall stocking of the MEF by about 80%, though disturbance intensity varied considerably from point to point (McConkey and Smith, 1958). Northern parcels had a higher density of trees originating before the fire ("pre-fire" cohorts) than southern parcels, but all were two-(or more) aged at a large scale. Individuals and patches of pre-fire relicts, which ranged from 65 to over 200 years old at breast height, were imbedded in a matrix of post-fire origin trees, 45–60 years old, depending on species and whether seed or vegetative origin. Patches of overtopped hemlock were common in all but one parcel, and all parcels were heterogeneous, so that composition and age structure both varied from point to point at a fine scale.

2.2. Data collection

In summer 2007, we established 121 plots on points randomly selected from groups representing the range of overstory composition and age structure encountered in an earlier preliminary survey (Fig. 2). Plots were 8.0 m in radius (0.02 ha), but to capture information about the location and dimensions of adjacent trees likely to be competitively relevant to those inside the plots, we also recorded measurements on all trees within a 2.3 m² ha⁻¹ angle gauge sweep of any tree inside a plot.

For each tree, we recorded species, diameter (at 1.37 m, with 0.1 cm precision, using a steel diameter tape), and location (polar coordinates from plot center, in 1° and 0.01-m increments, using a hand compass and Haglof Vertex III rangefinder/hypsometer). Within and adjacent to each plot, upper canopy trees (emergent, dominant or codominant canopy position, designated relative to surrounding tree stature and without consideration of species or cohort; Helms, 1998), and a subset of lower canopy trees (10% randomly selected beyond a minimum of three per species per plot), were measured in more detail. On these detail-measured trees, total height, height to base of contiguous crown, and crown radii in cardinal directions were recorded (0.01 m increments, using Haglof and hand compass, with a clinometer to determine crown drip-line), and two perpendicular increment cores were extracted at 1.37 m. Pairs of cores were mounted side-by-side on wood backing, sanded to a minimum of 600-grit, and digitally scanned at 1600 dpi. We used Regent Instruments' WinDendro™ software to provide increment measurements (0.001 mm) between date marks that were manually assigned to the rings in each image – double-checking with a dissecting scope, sanding more finely, and re-scanning at higher resolutions when particularly narrow rings warranted. Cores were read back to the last discernable ring; if the pith was not included in the core, the approximate pith date was estimated (Applequist 1958; not possible for hollow trees). Mea-

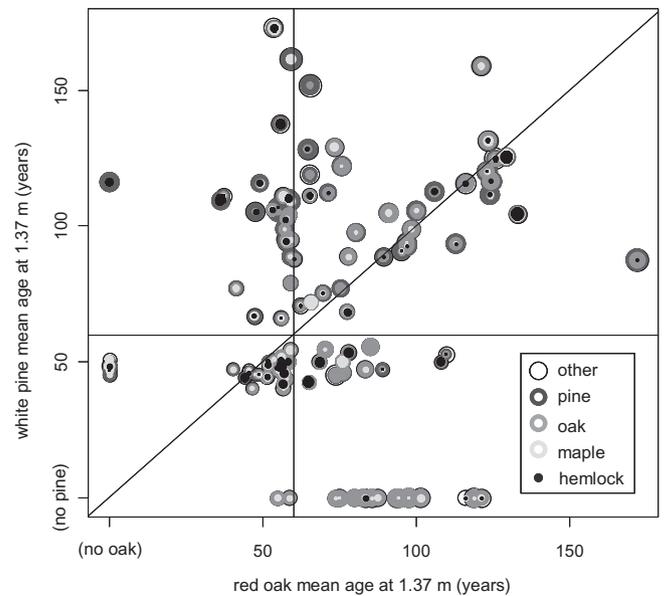


Fig. 2. Age structure and composition of plots in this study. Each plot in the study is represented as a circle of concentric grayscale. Total circle size (area) is proportional to plot-level mean age (AGEm) and each shade's area is proportional to its species share of relative density index (RDI). Horizontal and vertical lines are at 60 years, the pre-fire/post-fire cohort boundary. Thus, plots in the lower left section are composed of post-fire trees, plots in the upper left of post-fire oak and pre-fire pine, plots in the upper right of pre-fire trees of both species, and plots in the lower right contain pre-fire oak and post-fire pine. The diagonal line is 1:1, where pine and oak are of the same mean age. Maple and hemlock ages do not affect plot positions in this figure (these species were almost always of post-fire origin).

surements of the two cores per tree were combined by quadratic mean and scaled according to species-specific radial shrinkage factors given in the US Forest Service Wood Handbook (Forest Products Laboratory, 1999). Because only the second- and third-to-last rings were used in growth estimates, and because total age estimates were averaged at the plot level, with low precision guaranteed by inclusion of hollow or un-cored trees, cross-dating of cores was not conducted.

2.3. Data preparation

To generate a single site index (SI) value for each plot, where no one species/age/canopy position was always present, we used a generalized linear model fitting individual tree SI values (calculated for emergent, dominant, and codominant white pine, red oak, red maple, hemlock, and paper birch by the Carmean et al. (1989) equations) by species, with covariates and interaction terms found to be relevant (see online Supplemental materials). We then used model coefficients to calculate the expected SI value for codominant position, post-fire cohort white pine, age 50, at each plot.

We calculated stem volumes (m³) using Honer's (1967) volume equations for most species, and Schnur's (1937) volume table for white and black oak. The average annual volume growth rate (dm³ year⁻¹) from end of 2004 to end of 2006 (i.e.: the 2005 and 2006 growing seasons) was generated for measured trees by subtraction of projected past volumes, which were based on measured radial increments and estimated height increments for the period. Height increments were estimated using Carmean et al. (1989) growth curves, with an adjustment for lower-canopy trees based on the ratio of individual lower-canopy tree crown lengths to the plot average crown lengths of dominant and codominant trees. Sizes and ages of some trees in our study exceeded the dimensions and ages used in the published equations and tables; thus, a degree

of unavoidable extrapolation was necessary in our growth and yield estimation. The 2004–2006 growth period was chosen because measurements taken in 2007 would still be reasonably representative of conditions present at the beginning of the growth period (end of 2004 growing season) with respect to crown sizes and plot density. The period's individual-tree increments were consistent with longer-term averages – faster than the 5-year average and slower than the 10-year average, but not significantly different from either by a two-sample *t*-test ($n = 1864$, $p = 0.14$ and 0.38 , respectively). Because species vary in wood density, and therefore in volume growth relative to actual resource consumption, we converted volume to approximate biomass by multiplying each tree's volume by green specific gravity values (i.e., dry mass per unit green volume) in the US Forest Service Wood Handbook (Forest Products Laboratory, 1999).

We estimated height and crown dimensions and 2004–2006 growth for unmeasured trees (some individuals of lower canopy position, and some plot-adjacent trees of all crown classes) using non-linear mixed effects models modified from the literature (Bragg, 2001; Robinson and Wykoff, 2004; Ducey, 2009; Hann and Weiskittel, 2010). These incorporated measured diameter and surrounding conditions (basal area, basal area of larger stems, stems per hectare, SI) in fixed effects, and combinations of individual tree species, cohort, canopy position, parcel and plot in random effects (see online Supplemental materials), and all models were weighted by variance power functions of DBH (Pinheiro and Bates, 2000). The age of hollow trees and those not cored was estimated as the average for proximate members of the same species and cohort.

Given the measured or estimated crown dimensions (crown length and crown radius), we generated estimates of crown surface area (m^2), and crown volume (m^3) for each tree, modeling post-fire hardwood and softwood crowns by shapes approximating those used by Pretzsch (2009) for oak (*Quercus petraea* L.) and for spruce (*Picea abies* L.), with pre-fire cohort shapes modified to approximate the broader, flatter crowns typical of older specimens of most types (see online Supplemental materials).

From tree locations, crown dimensions, and shapes, we calculated plot-level crown surface area (CSA, $m^2 m^{-2}$) within the boundaries of the vertical column formed by each plot. This method included data gathered from trees with stems outside but crowns inside of the plot boundaries and excluded portions of crowns extending over plot boundaries from stems inside. Our adjustment for these overlapping crowns eliminated the edge effect that might otherwise bias canopy metrics (Nelson et al., 1998), and also provided more comprehensive quantification of the neighborhood conditions affecting the trees within plots. To estimate growth and yield at the plot level, we scaled each tree's

biomass and biomass growth by the proportion of modified crown volume and surface area lying inside plot boundaries (see online Supplemental materials). This method diminished the growth and yield contribution of large trees with overhanging crowns and incorporated a portion of trees overhanging from outside. The net effect of these methods on the plot-level stem biomass growth rate (BGR, $Mg ha^{-1} year^{-1}$) and stem biomass yield (BIO, $Mg ha^{-1}$) was no change in overall means, but a reduction in variability. We also calculated a weighted mean age (AGEm, years at 1.37 m) for each plot by scaling each tree's contribution to the average according to its within-plot modified crown volume.

For each species on each plot, we calculated the stand density index (SDI) by the metric summation method (Shaw, 2000): $\sum TPH_i (DBH_i/25)^{1.6}$, where TPH_i is the stem density (ha^{-1}) represented by the *i*th tree on a plot, and DBH_i is its diameter at 1.37 m. The SDI thus calculated for each species, per plot, was then divided by the theoretical 99th percentile maximum SDI of that species, estimated by Woodall et al.'s (2005) equation based on green specific gravity. The resulting relative density index (RDI, unitless) values were summed to produce a plot-level RDI having the desirable attribute of aggregating individual species' density contributions independent of the remaining composition (Ducey and Knapp, 2010).

2.4. Analysis

We used linear mixed effects regression in R (R Development Core Team, 2008) to model plot-level CSA, BGR, and BIO by independent variables that differed by objective, with total RDI, SI, and AGEm as covariates. Models were weighted by a variance power function (Pinheiro and Bates, 2000) of the dependent variable and were calculated with multi-level random effects, on the intercept term, of parcel-in-unit. We began with all covariates and all two-way interaction terms, and proceeded by backward elimination (Neter et al., 1996) until all model coefficients showed statistical significance (*t*-test, $\alpha = 0.05$). We used effective species richness ($DIV = e^{index}$; Erskine et al., 2006) derived from an RDI-based Shannon diversity index of five species categories (the four major species plus 'other') to evaluate relationships between diversity and dependent variables. We used another index, mean specific gravity ($SGm = BIO/volume$; Woodall et al., 2005), to evaluate the relationship between dependent variables and generalized composition, with high values of SGm representing oak-dominated plots and low values representing pine-dominated plots. For objective 2, we substituted individual species' proportions of RDI and their interaction terms as the independent variables. We examined statistically significant variable and interaction term coefficients to assess species effects, plotting

Table 1
Summary of attributes for independent variables relative density index (RDI), site index (SI), plot-level mean age (AGEm), plot-level mean specific gravity (SGm), effective species richness (DIV), and major species' composition, and for dependent variables plot-level canopy surface area (CSA), stem biomass growth rate (BGR), and stem biomass (BIO).

Variable	Units	Minimum	Maximum	Median	Mean	Standard deviation
RDI	Unitless	0.283	0.875	0.543	0.543	0.119
SI	m^a	14.6	23.2	18.9	18.7	1.81
AGEm	Years, at bh	44.3	139.7	72.5	76.2	22.3
SGm	$g cm^{-3}$	0.344	0.566	0.441	0.455	0.068
DIV	Unitless	1.01	4.80	2.67	2.73	0.85
Pine	Proportion of RDI	0	0.936	0.241	0.283	0.252
Oak	Proportion of RDI	0	0.999	0.425	0.416	0.286
Maple	Proportion of RDI	0	0.735	0.035	0.084	0.114
Hemlock	Proportion of RDI	0	0.580	0.003	0.074	0.127
CSA	$m^2 m^{-2}$	1.94	11.48	6.71	6.94	1.68
BGR	$Mg ha^{-1} year^{-1}$	1.13	4.39	2.53	2.50	0.60
BIO	$Mg ha^{-1}$	45.9	293.0	113.4	124.5	47.8

^a SI values are for white pine, 50 years old at breast height.

Table 2

Coefficients (standard errors beneath) for linear mixed effects models of plot-level crown surface area (CSA), stem biomass (BIO), and stem biomass growth rate (BGR) in mixed stands at the Massabec Experimental Forest, based on effective species richness (DIV, unitless), plot-level mean specific gravity (SGm, g cm⁻³, an index of composition), the covariates relative density index (RDI, unitless), white pine site index (SI, m at 50 years), and plot-level mean age (AGEm, yrs), and interaction terms. Bold font indicates significance at $p < 0.05$.

Dependent variable	Intercept	DIV	SGm	RDI	AGEm	SI	DIV * RDI	SGm * AGEm	RDI * AGEm	RDI * SI	AGEm * SI	Adj. R ² (fixed effects)	AIC
CSA (m ² m ⁻²)	-10.6 4.47	0.737 0.150		9.52 0.993	0.122 0.057	0.612 0.229					-0.0070 0.0030	0.29	437
BGR (Mg ha ⁻¹ year ⁻¹)	3.81 1.46	0.095 0.038		-4.18 2.69	-0.007 0.002	-0.179 0.081				0.437 0.148		0.50	154
BIO (Mg ha ⁻¹)	81.3 49.9	12.8 4.28		-87.7 87.0	-0.721 0.623	-8.44 2.54	-30.11 9.43			19.7 4.42	0.072 0.034	0.74	973
CSA	2.91 0.63			7.82 1.07								0.27	433
BGR	5.09 1.34		-3.51 0.530	-3.22 2.39	-0.007 0.002	-0.125 0.073				0.350 0.130		0.64	120
BIO	9.11 40.8		65.5 53.2	-200 68.4	0.877 0.408	-0.967 2.37		-2.35 0.726	1.84 0.480	14.3 4.80		0.88	929

curves or three-dimensional surfaces as necessary to examine changes across variation in species combinations. For objective 3, we used RDI as the dependent variable in the same model type, then non-subject species RDI, with subject species RDI proportion and proportion² terms as independent variables.

3. Results

3.1. Diversity and composition

Tree species diversity ranged widely among plots (Table 1); Shannon diversity index values ranged from 0.01 to 1.57 (mean 0.95), corresponding to DIV values of 1.01–4.80, out of a potential range of 1–5. All else being equal, more diverse plots (more and/or more evenly proportioned species present) contained more crown surface area and produced more stemwood biomass per year than less diverse plots. More diverse plots tended, however, to yield less total stem biomass, a relationship which diminished with lower RDI (Table 2).

When species composition was indexed by SGm (ranging from 0.34 for pure white pine to 0.56 for pure red oak, with slightly higher values occurring for plots containing white oak), it did not contribute to total plot-level CSA when RDI was accounted for – nor did SI or AGEm (Table 2). SGm was significantly correlated with stem biomass growth (BGR), which decreased with increasing hardwood dominance at any given AGEm, RDI or SI. SGm was indirectly correlated with stem biomass yield (BIO), through a negative interaction with AGEm, so that BIO increased with AGEm more steeply in increasingly softwood-dominated plots (SI and RDI were also positively correlated with BIO, regardless of composition).

Covariates were highly variable (Table 1) and, for the most part, only weakly correlated with each other (Fig. 3). Younger plots tended to have higher diversity (DIV) because there were few pre-fire cohort maple and hemlock. A positive relationship between SI and AGEm was likely due to lower pre-fire cohort abundance in southern parcels, which also tended to have lower SI (mean SI = 18.7 m). RDI for the plots in our sample averaged 0.54, just below the level of expected onset of self-thinning (Drew and Flewelling, 1979), and RDI tended to decline with higher SGm.

3.2. Species' interactions

Seventy-two plots (60%) were dominated (>50% of RDI) by one of the four major species (46, 24, 1, and 1 for oak, pine, maple and hemlock, respectively); the rest were mixtures with no one species dominant. A full span of compositional proportion, from zero to near 100% of RDI, was represented in the sample for pine

and oak, but maple and hemlock rarely constituted more than 40% of RDI (Table 1).

When species' proportions of RDI were entered as individual terms in a model predicting plot total CSA, each contributed significantly, both independently and through interaction terms (Table 3). This model fit more parsimoniously based on AIC (Akaike, 1973) than the models based on species DIV or SGm, in spite of the additional terms. SI and AGEm were again found to be unrelated to CSA, but CSA did increase significantly with RDI, and this increase was steeper with higher proportions of pine in the mixture (Fig. 4). Hemlock yielded more CSA per unit of composition than maple, which yielded more than pine or oak. Pine contributed more than oak to CSA at high RDI; the reverse was true at low RDI. At most levels of RDI, CSA was maximized in mixtures of pine and oak, relative to plots dominated by either alone (transgressive overyielding, Fig. 4). At average RDI, a 1:1 ratio of pine to oak (with 15% of remaining RDI divided among other species) was predicted to have 109% the maximum CSA for a 0:1 ratio at the same RDI. There was also a positive interaction between pine and hemlock, generating a overyielding in predicted CSA as RDI shifted from one to the other (Table 3). Whether pine-hemlock overyielding would be transgressive, or would even be consistent across a full span of proportions, could not be determined because hemlock composition exceeded 40% of RDI on few plots.

A model of BGR incorporating individual species proportions proved to be less parsimonious than one based on SGm (Table 3), but illuminated individual species interactions. BGR tended to increase with higher proportions of pine relative to oak, except at high SI or with young oak, where the two species were of nearly equal productivity. Our model of BGR showed a significant pine * AGEm interaction term – BGR declined less steeply with age as the proportion of pine increased. There was also a significant pine * oak interaction term, but its net effect on the BGR response surface was modified by the pine * AGEm term. Where pine and oak were of the same cohort, our model predicted a convex, transgressive overyield pattern (Fig. 5), reaching 100–106% of pine-dominated plot BGR at ratios of pine to oak, varying with AGEm (55–110 years), from 1.5:1 to 19:1 (15% of RDI in other species). Ratios producing peak growth shifted toward oak with increasing SI or decreasing RDI. Where pine was of an older cohort than oak, the overproduction pattern was reduced, and not transgressive except at high SI; where oak was older, the overproduction curve was more pronounced, and transgressive. Our model also indicated a significant interaction term between hemlock and maple (Table 3), though occurring within a limited span of total proportion of composition. This term generated an underyielding pattern where the two species occurred together, such that, where the species together constituted only 40% of RDI, total BGR where they were

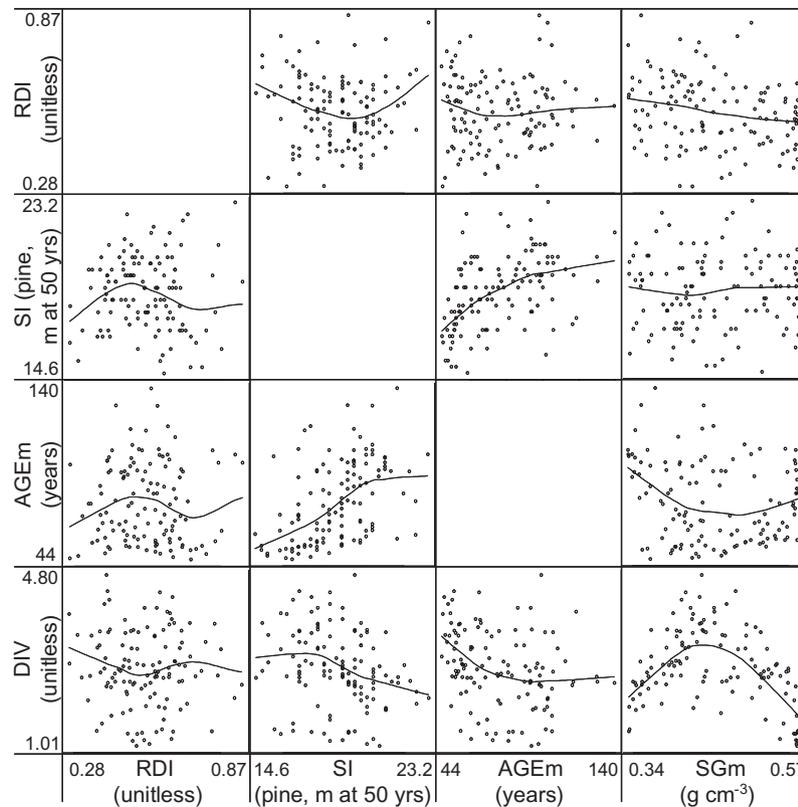


Fig. 3. Scatterplot matrix of covariates relative density index (RDI), site index (SI), and plot-level mean age (AGEm), with the variables effective species richness (DIV, fourth row) and plot-level mean specific gravity (SGm, an index of composition, fourth column). Axes span the range of their respective variables. Lines are loess smoother functions through datapoints (span = 2/3, degree = 1, evaluated at 50 points).

mixed 1:1 under post-fire oak was predicted to be only 92% of where maple made up all of the 40%.

A model predicting BIO, allowing distinct coefficients for the RDI proportions of each major species, fit more parsimoniously than the simpler models using only DIV or SGm (Table 3). Interaction terms between RDI and SI, AGEm, oak, and pine; between SI and oak, AGEm, and pine; and between maple and hemlock, made this model much more complicated than the models of CSA or BGR. We found no evidence of overyielding with any species pairs, though the maple * hemlock interaction term indicated underyielding where those species occurred together (Table 3). Pine was the higher-yielding member of the pine–oak pair, especially on poorer sites or denser plots, but mixture effects between these species were evident only when they differed in age, because a gradient of species proportion then generated a gradient of AGEm. Mixed plots tended to overyield where the pine component was post-fire and oak pre-fire, and to underyield when pine were pre-fire and oak post-fire (Fig. 6). Plots where maple and hemlock co-occurred had lower stem biomass than plots where either was singly dominant in the understory. Although these species rarely constituted more than a minority of total RDI, the effect was about 3 Mg ha⁻¹ less, or 97% (at a 1:1 mix of the two beneath 50% post-fire oak, 10% others) compared to a maple-dominated understory.

3.3. Additivity

The inclusion of RDI in the above models precluded the possibility of evaluating the hypothesis that total stocking may increase with increased proportion of a given species. Models predicting non-subject species RDI from SI, AGEm, subject species RDI proportion, proportion squared, and two-way interactions all retained significant coefficients for the subject species term, failing to reject the null hypothesis that the density of one species corresponds to

reductions in density of others (Table 4). The squared term remained only in the model for oak, interacting with AGEm in such a way that non-oak RDI declined non-linearly with increasing oak proportion, at high AGEm. Although the squared term and interaction terms were significant in this case, a model lacking them (i.e. a linear decline in non-oak RDI with increased oak) fit more parsimoniously based on AIC.

4. Discussion

4.1. Diversity and composition

Species diversity (DIV) on small plots in oak–pine stands correlated with both greater canopy density (CSA) and stem biomass growth rate (BGR), even when accounting for the density (RDI), potential productivity (SI) and age (AGEm) of the plots. Other recent studies have found that covariates such as these can render diversity a non-significant factor in predicting productivity or yield (Edgar and Burk, 2001; Vilà et al., 2003; Liang et al., 2007; Long and Shaw, 2010; and Jacob et al., 2010). One way this study differs is that each of the four main species contrasted with the others in shade tolerance, life form, or both, thus making niche separation and competitive reduction more likely (Kelty, 1992). We did find that more species-diverse plots generally had lower stem biomass yield (BIO), especially at high RDI. In this respect, our findings were more typical, but may be due to the nature of one of the species. Low-diversity, high-density plots were inevitably dominated by pre-fire cohort white pine, which were by far the largest members of the MEF forest. Achieving the same density values with higher diversity would necessarily mean replacing some of the pine with lower-yielding species. It is also important to note that BIO, unlike BGR, implicitly incorporates mortality over the course of stand development – though it cannot be assessed with our data, it is

Table 3

Coefficient values (and standard errors) for variables in linear mixed effects models of plot-level crown surface area (CSA), stem biomass (BIO), and stem biomass growth rate (BGR) in mixed stands at the Massabesic Experimental Forest based on species proportions of relative density index (RDI) and covariates total RDI, white pine site index (SI), and plot-level mean age (AGEm). Bold font indicates significance at $p < 0.05$.

	CSA (m ² m ⁻²)	BGR (Mg ha ⁻¹ year ⁻¹)	BIO (Mg ha ⁻¹)
Intercept	6.974 (1.798)	6.543 (1.595)	115.476 (37.071)
RDI (unitless)	-0.7800 (3.291)	-6.321 (2.716)	-225.011 (66.532)
SI (m at 50 year)		-0.370 (0.104)	-5.857 (2.425)
AGEm (year)		0.008 (0.008)	0.002 (0.202)
Pine ^a	-9.354 (2.884)	-0.417 (0.597)	-93.244 (24.040)
Oak	-5.722 (2.619)	-3.074 (1.311)	-93.563 (33.887)
Maple	3.968 (1.147)	0.908 (0.431)	35.716 (9.555)
Hemlock	4.242 (1.432)	1.272 (0.478)	17.625 (10.363)
RDI * SI		0.635 (0.176)	16.637 (4.270)
RDI * AGEm		-0.032 (0.016)	0.826 (0.412)
RDI * pine	14.272 (4.996)		109.391 (41.002)
RDI * oak	9.596 (4.722)		62.730 (30.582)
SI * oak		0.167 (0.073)	4.585 (1.936)
AGEm * pine		0.014 (0.007)	1.251 (0.194)
Pine * oak	4.344 (1.880)	1.366 (0.558)	
Pine * hemlock	11.940 (4.217)		
Maple * hemlock		-7.413 (3.108)	-178.426 (62.684)
Adj. R ² (fixed)	0.47	0.65	0.92
AIC	370	143	846

^a Variables given by species names are species' proportion of total plot RDI.

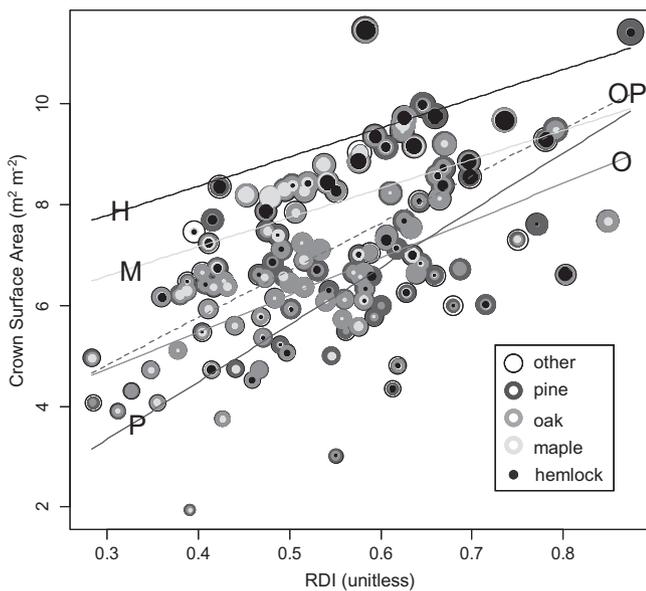


Fig. 4. Plot level crown surface area (CSA) as related to relative density index (RDI) and composition. Line H: modeled for RDI 40% hemlock, 55% pine and oak, 5% other species; M: 40% maple, same otherwise; P: 85% pine, 15% hemlock, maple, and other species; O: 85% oak, same otherwise; OP (dashed): 85% oak and pine, same otherwise. Total marker size is proportional to CSA and area of gray shades represents proportion of RDI by species. Line OP is higher than both lines O and P, indicating transgressive overyielding of CSA at all levels of RDI.

possible that high DIV plots had higher gross, but lower net growth than low DIV plots.

Species composition, expressed as a softwood-hardwood gradient (SGm), was negatively correlated with both BGR and BIO, but not related to CSA. Again, the great size and productivity of pre-fire cohort pines is likely to have been a factor, especially for BIO. Higher BGR, with unchanged CSA, in softwood-dominated plots implies that conifer canopies were more efficient at producing stemwood biomass, not just volume. Softwood species tend to have less wood in branches than hardwoods (Young et al., 1980), and oak, especially of the pre-fire cohort, often had very large branches unaccounted for in our analysis, so these findings might not hold with respect to total, rather than stem-only, biomass growth and yield.

4.2. Species interactions

It is generally believed that oak is an aggressive species that does not share space well with others, and especially poorly with conspecifics (Cline and Lockard, 1925; Kittredge, 1988). Our study findings were consistent with this perception – at higher densities (above 0.6 RDI), pine-dominated plots had more CSA than oak-dominated ones (Fig. 4). Interestingly, the CSA of plots where pine and oak were mixed exceeded that of plots dominated by either one species or the other, especially at moderate density. This transgressive mixture effect may be due to the vertical stratification that typically accompanied the combination of those two species (where pre-fire pine occurred above or post-fire pine below oak of either cohort).

Maple and hemlock contributed more to CSA per unit proportion of RDI than other species (Table 3), but neither occurred in high proportion on any plot (rarely more than half of RDI). Both of these species are considered shade tolerant, and both generally occurred in lower canopy positions, where lower efficiency would generate greater crown:stem ratios over time, leading to disproportionate canopy contribution relative to the stem-wise calculated RDI contribution. Extrapolation of this result to proportions of these species greater than ~0.5 is unwarranted, because crown:stem ratios of those species in such circumstances would likely differ as their average exposure to light would increase with greater proportional dominance.

Overyielding has been found to occur in mixtures of Scotch pine (*Pinus sylvestris* L.) and oaks (*Q. petraea* L. and *Q. pyrenaica* Willd.) in Europe (Río and Sterba, 2009; Perot and Picard, 2012), but this study is the first to document the phenomenon in the most common pine-oak mixture type – and one of the most common forest types – in northeastern North America. To provide a secondary test of this finding, we examined the subset of 57 plots having >75% of RDI in pine and oak, modeling BGR by SGm and covariates, as before, but including an SGm² term allowing a non-linear response. The coefficient of the squared term was significantly non-zero ($p = 0.0004$, t -test), generating a curve peaking at a SGm of 0.42 g cm⁻³. Competitive reduction between pine and oak is surprising given that the species in this case are of similar shade tolerance, but they do exhibit distinct differences in crown form and canopy position even when of the same age.

Though we found no interaction term between pine and oak in predicting stem biomass yield (BIO), RDI, SI and AGEm interacted

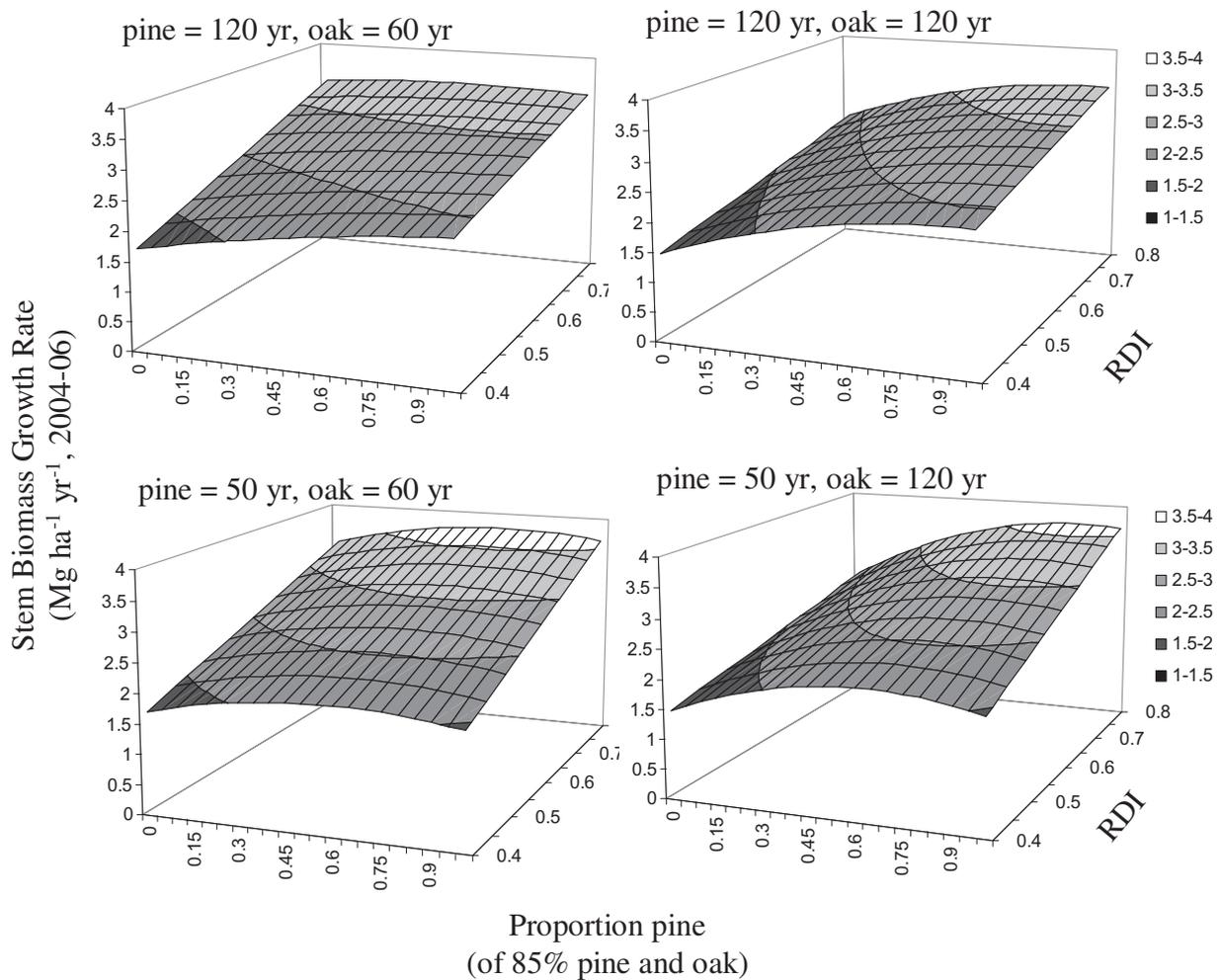


Fig. 5. Relationships between plot-level stem biomass growth rate, relative density index (RDI) and composition (proportion of RDI). Non-oak/pine composition is 15%, divided evenly between hemlock, maple, and other species, pine 50-year site index is 19 m, and plot-level mean age varies with composition, assuming ages at 1.37 m given above for pine and oak, 50 years for hemlock, and 55 years for maple. Convex curvature indicates overproduction.

with each species differently. Because changes in species proportion often meant changes in AGEm in our study, plots with young pine achieved maximum yield in mixture, though the location of the optimum-yielding proportion shifted toward pine at higher RDI or lower SI. This is consistent with white pine's known capacity for achieving maximum yields at high densities (Schlaegel, 1971) and the regional understanding of pine as a more productive species on poorer sites (Lancaster and Leak, 1978). White pine is also known for maintaining high growth rates over long time periods (Barrett et al., 1976) so pre-fire cohort pines in mixture were able to contribute far more than oak to BIO, regardless of the age of oak. This finding is similar to Fajvan and Seymour's (1999), where pine occurred in a matrix of red spruce (*Picea rubens* Sarg.) and hemlock, and pine proportion was linearly related to total volume yield. However, the underproduction we found for pre-fire pine with post-fire oak was unexpected, given that in such a mixture, the pine typically emerged 5–10 m or more above the oak canopy. We suspect that such emergent pine behave more like the hoop-pine (*Araucaria cunninghamii* D. Don.) from Enright's (1982) study of emergent trees than the additive *A. hunsteinii* – i.e. their dense and vertically deep crowns exist partially within and not exclusively above the B stratum in this case, and cast more shade than sparsely foliated species. The weaker and in some cases negative mixture effects for yield require further explanation, in light of the stronger mixture effects found for growth. Either the current

growth of our plots does not match past growth, or past mortality has been higher in mixed than pure plots.

4.3. Additivity

RDI was related to composition, but we found no evidence for additivity (Table 4). Total RDI was greater in stands with larger proportions of hemlock, but non-hemlock density declined with the overall increase; it must be that the decline is less than substitutional, so hemlock is semi-additive, adding more to total density than it displaces, at least up to the level of composition occurring in this study. This finding differs from that of Kelty (1989), whose study showed patches of lower canopy hemlock were additive beneath red oak-dominated overstories, and MacPherson et al. (2001), who found no correlation between lower canopy white spruce density and that of overstory aspen. This study's stands had greater within-plot species diversity and age structure complexity, and we used RDI rather than BA to quantify density. Because a finding of additivity was anticipated for hemlock, we tested further alternative hypotheses accommodating additivity for this species, including using BA instead of RDI, and confining analysis to a subset of plots with oak-dominated overstories. We did not find evidence for hemlock additivity in our data under any approach. This study's larger, edge-adjusted plots reduced variability, especially for large-crowned trees (which overlap more on

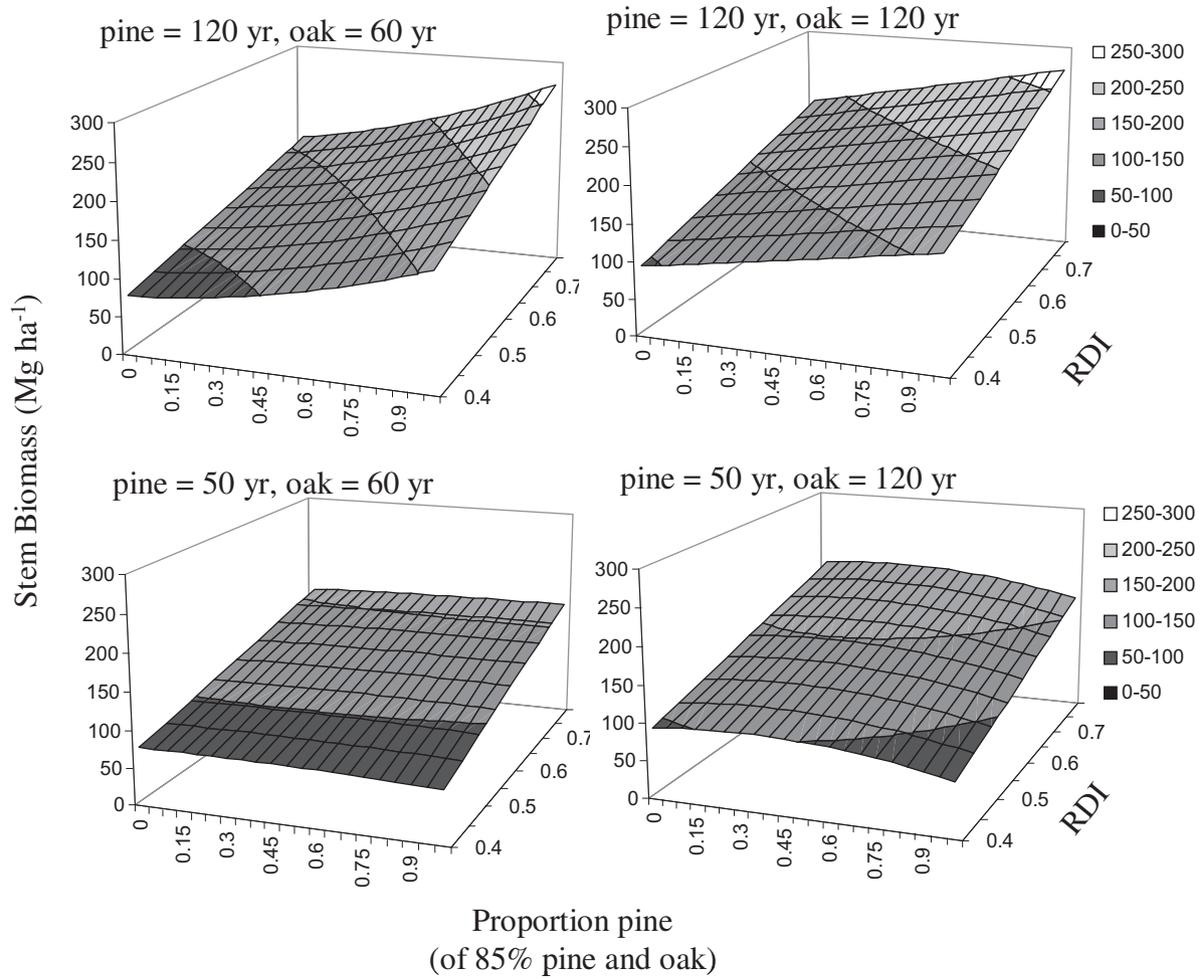


Fig. 6. Plot-level stem biomass yield related to relative density index (RDI) and composition (proportion of RDI). Non-oak/pine composition is 15%, divided evenly between hemlock, maple, and other species, pine 50-year site index is 19 m, and plot-level mean age varies with composition, assuming ages at 1.37 m given above for pine and oak, 50 years for hemlock, and 55 years for maple. Convex curvature indicates overyielding, and concave curvature underyielding.

Table 4

Coefficients (and standard errors) of linear mixed effects models predicting relative density index (RDI, unitless) of non-subject species from subject species proportion of RDI and plot-level mean age (AGEm, years). Bold font indicates significance at $p < 0.05$.

Dependent variable	Intercept	Subject spp. proportion ^a	AGEm	AGEm * subject spp.	Subject spp. proportion ²	AGEm * proportion ²
Total RDI	0.664 (0.113)	-0.551 (0.176)	0.00156 (0.00059)			
Non-oak RDI	0.549 (0.073)	-1.023 (0.231)	-0.000568 (0.000872)	0.00619 (0.00273)	0.478 (0.171)	-0.00573 (0.00202)
Non-pine RDI	0.410 (0.047)	-0.448 (0.022)	0.000926 (0.000364)			
Non-maple RDI	0.426 (0.071)	-0.653 (0.074)	0.00153 (0.00057)			
Non-hemlock RDI	0.326 (0.069)	-0.235 (0.063)	0.00202 (0.00053)			

^a Total RDI model based on plot-level mean specific gravity (SGm, an index of composition), not proportion of a given subject species.

small plots). Without this variability reduction, the statistically significant negative trends in non-hemlock density over hemlock proportion might have been hidden.

4.4. Limitations

Density, age, composition, and vertical structure all interact in mixed stands (Chen and Klinka, 2003; Garber and Maguire, 2004; Amoroso and Turnblom, 2006). The metrics used to summarize composition and age variables in this study necessarily simplify these factors. For example, plots with a mean age of 100 may

consist of either a single cohort originating at the turn of the century, a two-cohort combination of pre-fire trees originating in the 19th century mixed with others from after the 1947 fire, or a mixture of multiple cohorts. AGEm is a function of the proportion of trees in pre-fire cohorts and the age of those cohorts, so it cannot be interpreted as having developmental meaning – plots with a current AGEm of 50 should not be expected to become like the plots of AGEm 100, even if their species composition is identical. Vertical structure is also confounded with composition and age. For example, as the proportion of oak increases, the canopy status of post-fire pine changes, forming a lower stratum rather than a

side-by-side canopy partner; pre-fire pine, on the other hand, has the opposite vertical structural relationship at the same compositional proportions. A model examining the effect of a change in oak proportion of composition, or plot AGEm, is necessarily also examining the effect of changes in vertical structure.

5. Conclusions

For a variety of age structures, mixtures of oak and pine are capable of producing more canopy surface area and more current annual stem biomass increment than would be expected if interspecific competition were equal to intraspecific, and more than can be produced by monocultures of either species. This transgressive overyielding pattern has been documented in relatively few forest types, and it has important implications for managing these species. This study demonstrates that red oak and white pine can grow together in intimate even- and two-aged mixtures without sacrificing productivity. Thinning operations in established mixtures should aim to maintain intimate mixture of these species, with pine increasingly favored on poorer sites and older stands. Up to at least 40% stocking in red maple or, especially, hemlock appears to increase canopy surface area and biomass production even further, though it is unclear if pure stands of these typically subordinate species would be more productive than the mixtures. We found no evidence for a completely additive pattern for any species, but plots with hemlock were more densely stocked, with a decline in non-hemlock species' contribution to stocking less than the increase in hemlock's contribution.

Stands dominated by northern red oak and eastern white pine are an important part of the New England landscape, providing timber, wildlife habitat, and aesthetic values within one of the most densely populated regions of North America. Public opinion and policies increasingly demand management approaches that maintain complexity in both species composition and age structure, providing for non-timber ecosystem services as well as wood products. Within the range of conditions we encountered in this study, silvicultural treatments aimed at maintaining pine in mixture with oak of equal or greater age may be more productive than those maintaining a monoculture of either, and two-storied structures with maple or hemlock under pine and/or oak will be more productive than single-storied structures. Production and some biodiversity concerns may thus be addressed simultaneously.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.02.027>.

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