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ARTICLE

Seedling growth responses to light and mineral N form are predicted by species ecologies and can help explain tree diversity

Michael B. Walters, John L. Willis, and Kurt W. Gottschalk

Abstract: Tree species distributions and diversity could be explained by rank changes in performance over multiple spatiotemporal resource gradients, i.e., resource partitioning. For 14 species planted in 45 harvest gap and closed canopy locations in a mesic northern hardwood forest community, Michigan, USA, we asked the following questions: (*i*) are species growth responses to light, nitrogen (N), or N form (ammonium vs. nitrate) related to their ecological distributions and phylogenies? and (*ii*) is there evidence of growth-based resource partitioning over measured resource gradients? Growth responses to the N form were consistent with both differences in uptake energy requirements between N forms and their availability through succession and across fertility gradients; height growth was negatively related to the species shade-tolerance score, especially in high light, i.e., shade-intolerant species responded to soil nitrate-N and shade-tolerant species responded to ammonium-N; fertile soil associated species responded to nitrate-N and infertile soil associated species to ammonium-N; and gymnosperms responded to ammonium-N and angiosperm responses varied. Modeled growth responses to resources showed only modest evidence for rank changes over resource gradients, with N contributing less to rank changes than light. Thus, growth responses to resources were accurately predicted by species ecology and (or) phylogeny; however, there was only modest support for the notion that growth-based resource partitioning underlies community-scale diversity in a northern hardwood forest.

Key words: height growth, shade tolerance, soil nitrogen, nitrate, ammonium, tree diversity.

Résumé : La distribution et la diversité des espèces d'arbre pourraient être expliquées par des changements de classe de performance selon de multiples gradients spatiotemporels de ressources, c'est-à-dire la répartition des ressources. Pour 14 espèces plantées à 45 endroits (trouée forestière ou couvert fermé) dans une communauté de feuillus nordiques établie sur une station mésique du Michigan, aux États-Unis, nous avons posé les questions suivantes : (*i*) est-ce que la réaction de croissance des espèces à la lumière, à l'azote (N) ou à la forme de N (ammonium ou nitrate) est reliée à leur distribution écologique et à leur phylogénie? et (*ii*) est-ce qu'il y a des signes de répartition des ressources fondée sur la croissance selon le gradient des ressources mesurées? La croissance en hauteur était négativement reliée au degré de tolérance à l'ombre des espèces, particulièrement en conditions de forte luminosité. En fonction des gradients de succession et de fertilité, la réaction de croissance à N était généralement cohérente avec la disponibilité des formes de N et des exigences énergétiques pour leur absorption : les espèces intolérantes à l'ombre réagissaient à N du sol sous forme de nitrate et les espèces tolérantes à l'ombre à N sous forme d'ammonium; les espèces associées aux stations fertiles réagissaient à N sous forme de nitrate et les espèces associées aux sols infertiles à N sous forme d'ammonium; les gymnospermes réagissaient à N sous forme d'ammonium alors que la réaction des angiospermes variait. La réaction modélisée de croissance aux ressources ne montrait que des signes modestes de changements de classe selon le gradient des ressources et N contribuait moins aux changements de classe que la lumière. Ainsi, la réaction de croissance aux ressources était prédite correctement par l'écologie et la phylogénie des espèces, mais il n'y avait qu'un appui modeste à la notion voulant que la répartition des ressources fondée sur la croissance soit à l'origine de la diversité à l'échelle de la communauté dans les forêts de feuillus nordiques. [Traduit par la Rédaction]

Mots-clés : croissance en hauteur, tolérance à l'ombre, azote du sol, nitrate, ammonium, diversité des arbres.

Introduction

A popular hypothesis proposed to explain tree diversity is that species have specialized regeneration niches and thus are able to coexist by partitioning complex environments (Grubb 1977). For trees, this hypothesis has mostly been examined as seedling (i.e., regeneration) light environment specialization at local community scales (i.e., the gap-partitioning hypothesis), with performance (e.g., growth) rank used as an index of specialization (Denslow 1980; Busing and White 1997; Schnitzer and Carson 2001; Coates et al. 2013). Studies testing the effects of multiple resources (e.g., light and soil resources) on rank changes in performance are less common, and most of these studies have focused on landscape-scale edaphic gradients rather than on community-scale soil resource variation (e.g., Schreeg et al. 2005; Van Couwenberghe et al. 2010; Lilles and Astrup 2012). However, both light and soil resources could vary broadly and orthogonally within forest communities resulting in far greater numbers of possible multiple-resource niches for species specialization than

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if species partitioned only light (Tilman 1985; Pacala and Tilman 1994).

In temperate forests, nitrogen (N) may exert a strong influence over both species diversity and distributions. In these ecosystems, N is considered to be the most common limiting nutrient (Vitousek and Howarth 1991), and both total mineral N and N forms (e.g., nitrate (NO_3^--N) and ammonium (NH_4^+-N)) are characterized by high spatiotemporal variability. Temporal variation in N is often associated with disturbance (an ephemeral increase in NO_3^--N availability; Jerabkova et al. 2011). Spatial variation in N at landscape scales is high among postglacial landforms (Zak et al. 1989; Walters and Reich 1997; Baribault et al. 2010) and also at much finer scales (1 m; Garten et al. (2007)). Given that temperate forest tree species are reported to vary in their growth responses to both N (Kobe 2007) and N forms (Marschner 2008), large spatiotemporal variation in N may help determine species distributions over both landscape-scale fertility gradients and within local forest communities (e.g., Frelich et al. 2003).

Among-species factors affecting N-form uptake capabilities are little explored. The lower energetic cost of assimilating ammonium (NH_4^+-N) than assimilating NO_3^--N (Chapin et al. 1987) may result in the seedlings of shade-tolerant tree species favoring NH_4^+-N uptake, whereas shade-intolerant species may be less discriminating given ample light energy and elevated NO_3^--N levels in their early successional regeneration niches. To our knowledge, this pattern has been examined (and confirmed) only for rainforest shrubs (Fredeen and Field 1992). Species more commonly found on less fertile soils may favor NH_4^+-N given that, with declining fertility, NO_3^--N availability declines more rapidly than NH_4^+-N (Walters and Reich 1997; Zak et al. 1989). Finally, given that NH_4^+-N is thought to dominate nitrogen uptake by conifers (Kronzucker et al. 1997), the N-form uptake could be constrained by phylogeny. However, reports of NO_3^--N uptake by conifers (Rothstein and Cregg 2005; Bow et al. 2010) cast some doubt on this notion.

In summary, the combination of spatiotemporal variation in light, N, N-form, and species-specific responses to variation in these resources could lead to growth-rank changes over multiple resource gradients. If it occurs, this pattern may help explain tree species diversity at community scales. Furthermore, associations of species-resource growth responses with shade tolerance, soil resource affinities, and phylogeny would have implications for predicting the basis for species distributions beyond specific forest communities, e.g., landscape-scale soil resource gradients.

In this report, we quantify height growth responses to light and soil N characteristics for planted seedlings of 14 tree species grown in harvest gaps and closed canopy locations in a mesic northern hardwood forest community, Michigan, USA. Specifically, we predict that (*i*) light and soil N characteristics will vary among harvest gaps and closed-canopy locations, (*ii*) tree seedling height growth will respond to variation in light and N form, and that these responses will vary among species, (*iii*) species responses to light and N form will be related to species differences in shade tolerance, soil fertility affinity, and phylogeny, and (*iv*) differences in species responses to community-scale variation in N forms and light will result in rank changes in growth among species.

Materials and methods

Our study site is a 16.7 ha mature northern hardwood forest on postglacial moraine topography in Emmet County, Michigan, USA (45°36′38.0″N, 84°53′40.6″W). Habitat type, a proxy for site nutrient and moisture regimes (Walters and Reich 1997; Burger and Kotar 2003), varies across the study site, with some areas classified as AFO (*Acer–Fagus–Osmorhiza*) and others as AFOCa (*Acer–Fagus–Osmorhiza–Caullophyllum*). AFOCa is the most mesic and nutrient-rich habitat class in the northern Lower Peninsula of Michigan, and AFO ranks second. These habitat classes typically support mesic northern hardwood forests dominated by sugar maple. Species composition at our site (% of basal area) is 79% sugar maple (*Acer saccharum* Marsh.), 9% basswood (*Tilia americana* L.), 7% white ash (*Fraxinus americana* L.), 5% American beech (*Fagus grandifolia* Ehrh.), and <1% other species.

We established 41 harvest gaps and four unharvested closed-canopy areas such that >30 m intact forest buffers were left between locations. Trees marked for removal in gaps ranged from single trees to multiple tree patches, leaving a postharvest gap area as large as 950 m^2. Marked trees were horse logged in the winter of 2006–2007. Single 10 m × 10 m plots were established centrally in each of the 45 locations. Fourteen of the 45 plots were unfenced, and the other 31 plots were fenced to exclude deer. Both fenced and unfenced plots were chosen to span the range of light environments and to be dispersed spatially within the stand. Sixteen 2 m × 2 m subplots with 0.5 m buffers between subplots were established as a square grid within each 10 m × 10 m plot. Of the 16 subplots, five were planted with first-year seedlings of 14 species in 2007, two were used for soil resource measurements (see further in Materials and methods), and nine were used for other components of the larger project. Planted tree species will be referred to by their common names throughout the paper (see Table 1 for Latin binomials). All species occur in the mixed hardwood–conifer forests of the Great Lakes region of North America. For most species, we planted 3- to 5-month-old seedlings. These were grown, from germination, as containerized seedlings in a 1:1 mixture of field soil and sand at the Michigan State University (MSU) Tree Research Center. Containerized seedlings were allowed to establish in a greenhouse and were then transferred outdoors to a lath house. Seedling roots were washed of soil before planting into experimental plots. For white ash and pin cherry (*Prunus pensylvanica* L. f.), first-year natural-origin seedlings were used. Most natural-origin seedlings established in the planted subplots, but some were transferred, bare root, from nearby areas. At least a single seedling per species was planted into each subplot of each plot. More were planted if seedlings were available. Seedling numbers varied among species due to variation in seed availability, germination, and early seedling survival. Seedling subplots were kept weeded of nontree vegetation starting in the middle of summer 2008, with removed vegetation left in the subplots. We also removed tree seedlings as needed to prevent crowding and competition among seedlings as they grew larger. Seedlings prioritized for removal were those that were (*i*) considered to compete for light with other individuals, (*ii*) without size bias relative to other seedlings of same species in the same subplot and (or) plot, and (*iii*) of the most abundant species among individuals considered competing.

Harvest gap size was estimated from tree bole to tree bole distances for residual gap-edge trees using the method of Runkle (1981). Resource availability characteristics that we measured were concentrations and net production rates of soil mineral N (in years 2007 and 2010), soil water (in years 2007 and 2010), and light availability (in years 2007, 2009, and 2010). Light availability was estimated as percentage (%) of open sky transmission from analyses of hemispherical photographs taken at 1.5–2 m above each subplot (n = 16 per plot) using Gap Light Analyzer version 2.0 software (Frazer et al. 1999). Incubations for determining soil N mineralization and nitrification rates were done using the pipe method (Raison et al. 1987) three times in 2007 (19 May – 16 June, 9 July – 8 August, and 24 August – 21 September) and once in 2010 (19 July – 19 August). For each sampling interval, four pairs of initial and incubated 5.08 cm (diameter) × 20 cm (depth) soil cores were taken in each of the two subplots randomly assigned for soil resource measurements per plot. Soil cores were combined and homogenized for each plot in the field, placed in a cooler, and transported to MSU for processing. There, soil water content was determined using one 20 g soil subsample, and another 20 g soil

Table 1. $Height_{@30\%light}$ (cm), $RGR_{ht@30\%light}$ ($cm \cdot cm^{-1} \cdot year^{-1}$), and $RDHt_{(8\%–12\%)}$ ($cm \cdot cm^{-1} \cdot (\%\ light)^{-1}$) (see Materials and methods for details on calculation) values are presented for each species. The extra variance explained is the percentage increase in adjusted R^2 from the addition of single soil N predictors (2007 measurements) to a model already including light as a predictor of seedling height. The soil resource characteristics shown are those that resulted in a decrease in AIC of >2.0 when added to the model, and Int. signifies that the soil response characteristic also included it's interaction with light.

Latin binomial	Common name	Shade tolerance	Soil fertility affinity	$Height_{@30\%light}$	$RGR_{ht@30\%light}$	$RDHt_{(8\%–12\%)}$	Soil response	Extra variance explained (%)
Prunus pensylvanica L. f.	Pin cherry	1.21	3.0	276.4	0.891	0.212	$[NH_4^+$-N], August	6
							N min., May	6
Populus grandidentata Michx.	Bigtooth aspen	1.21	2.8	102.1	0.902	0.300	None	—
Betula papyrifera Marshall	Paper birch	1.54	3.0	282.9	0.883	0.100	$[NO_3^-$-N], August	4
							$[NO_3^-$-N], mean	3
Fraxinus americana L.	White ash	2.46	4.0	94.9	0.791	0.058	$[NO_3^-$-N], May	17
							$[NO_3^-$-N], mean	12
							$[NO_3^-$-N], July	10
Quercus rubra L.	Northern red oak	2.75	2.22	64.9	0.726	0.064	$[NH_4^+$-N], August	3
							N min., July	2
Ulmus americana L.	American elm	3.14	5.0	142.1	0.928	0.076	Nitrif. (int), May	16
							$[NO_3^-$-N], mean	11
							$[NO_3^-$-N], May	7
							$[NO_3^-$-N], August	5
Pinus strobus L.	White pine	3.21	2.43	25.6	0.722	0.047	$[NH_4^+$-N], August	7
							N min., mean	6
Betula alleghaniensis Britton	Yellow birch	3.17	4.0	238.2	0.797	0.102	None	—
Acer rubrum L.	Red maple	3.44	2.72	85.8	0.733	0.091	N min., July	5
Picea glauca (Moench) Voss	White spruce	4.15	2.3	33.6	0.632	0.038	$[NH_4^+$-N] (int), August	12
Fagus grandifolia Ehrh.	American beech	4.75	3.9	35.1	0.352	0.023	none	—
Acer saccharum Marsh.	Sugar maple	4.76	4.1	47.2	0.615	0.039	$[NH_4^+$-N], July	20
							$[NH_4^+$-N], mean	19
							$[NH_4^+$-N], May	16
							Nitrif. (int), July	15
Tsuga canadensis (L.) Carrière	Eastern hemlock	4.83	3.5	15.6	0.569	0.067	None	—
Abies balsamea (L.) Mill.	Balsam fir	5.01	2.5	20.1	0.570	0.028	$[NH_4^+$-N] (int), August	19

Note: $RGR_{ht@30\%light}$, relative height growth rate; $RDHt_{(8\%–12\%)}$, relative difference in height percent increase in light; N min., N mineralization; Nitrif., N nitrification.

subsample was extracted with 50 mL 2 $mol \cdot L^{-1}$ KCl and analyzed colorimetrically for NH_4^+-N and NO_3^--N concentrations. Water content and NH_4^+-N and NO_3^--N concentrations were determined from the initial cores (i.e., 19 May 2007, 9 July 2007, and 24 August 2007 and 19 July 2010), and N mineralization and nitrification rates were determined from N differences between initial and incubated cores.

Diameter at the base of the main stem and total height were measured on planted seedlings in autumn 2008 and repeated in autumn 2010. Thus, seedlings were two years old with one full growing season in the experimental treatments and four years old with three full growing seasons when measured. Due to differences among species in the numbers planted and in survival, total seedling numbers for height measurements varied by species, ranging from 48 for bigtooth aspen to 806 for white ash, with a mean among species of 326. The mean number of seedlings per species per plot was 7.2. Each species had surviving seedlings in >35 of the 45 gap and (or) understory sites, except eastern hemlock (34), pin cherry (34), and bigtooth aspen (17).

All analyses were performed with JMP statistical software (JMP 9.0, SAS Institute, Cary, North Carolina). Plot (gap and closed-canopy locations) values were the experimental units for all analyses. Soil N and light data are plot means. For most analyses, we used total height at the end of the 2010 growing season. Species mean heights in low light at the end of the 2008 growing season ranged from 4 to 20 cm (Appendix A). They grew little in low light, so this range is likely similar to that for species mean heights when planted in 2007. We chose to use the 2010 total height because of the high degree of size similarity early in the experiment versus at the end of 2010 (15–300 cm) and because total height has intuitive appeal, high relevance to competitive advantage, and integrates seedlings full time in the treatments). We use seedling 2008–2010 relative height increment values in analyses with the shade-tolerance index so as to couch the relationship in a functional traits – shade tolerance context, which has been traditionally based on relative measures of growth (e.g., Walters and Reich 1999). We used the 75th quartile of seedling height rather than the mean because (*i*) the smaller seedlings tended to show signs of past damage or poor establishment and (*ii*) an upper quartile such as the 75th is representative of the more vigorous seedling pool that has the greatest probability of successfully competing and recruiting to adult tree status.

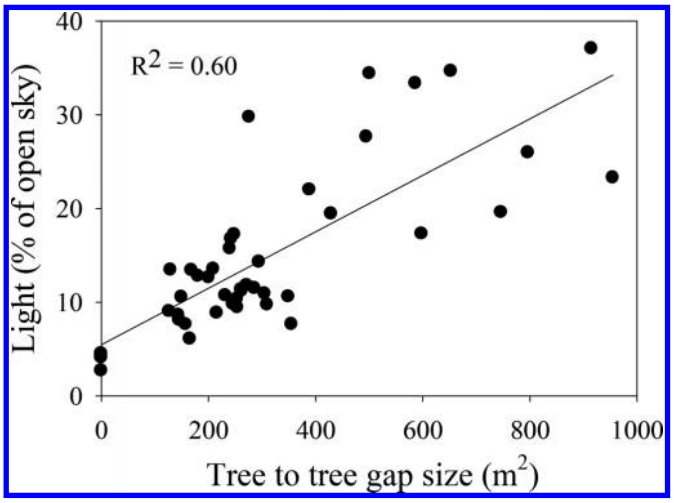
In preliminary analyses, we tested for height differences between fenced (deer excluded) and unfenced (deer not excluded) seedlings using a mixed least squares model with the nominal factor fenced vs. unfenced, the continuous factor light (log transformed to linearize), and their interactions. For the species that had significant fenced vs. unfenced main effects or interactions (pin cherry, bigtooth aspen, paper birch, American elm, and yellow birch), we only used seedlings from fenced plots and from unfenced closed-canopy plots for seedling height vs. resource analyses. All data were used for the other nine species. We included data from unfenced closed-canopy plots for all species because, in contrast to unfenced plots in gaps, there were no signs of deer herbivory (monitored bi-annually) on any of the seedlings through 2010. In this report, we do notreport deer effects on height growth because, by the end of our measurements in 2010, it was only the fastest growing, tallest species that had been browsed. Other shorter species could be impacted by deer if given more time to grow taller, so we defer these analyses for a future report.

For modeling seedling height by light availability, we used the three-parameter (θ_1, θ_2, and θ_3) mechanistic growth model (height = $\theta_1(1 - \theta_2^{(-\theta_3 \cdot \text{light})})$; Draper and Smith 1998) from JMP's model library. We chose the mechanistic growth model because it had high flexibility in fitting data that matched both our biological expectations and our scatter plot observations of height-growth responses to light, i.e., ranging from nearly linear to increasing to a saturating asymptote. We compared the mechanistic growth model with the Michaelis–Menten model, which is a two-parameter model that also accommodates asymptotic responses. However, the mechanistic growth model resulted in better fits and was better supported by Akaike's information criterion (AIC) scores (>2 units lower for most species). Thus, we used the mechanistic growth model to model the height vs. light data for all species. For each species, models were fit for both the 2008 height and the 2010 height using negative log likelihood loss functions to obtain maximum likelihood estimates using the Newton–Raphson optimization for iterative fitting (Appendix A). For the 2010 height data, models converged for all species. For the 2008 height data, neither the mechanistic growth model nor any other model (e.g., linear) converged for six of the species due to weak height-growth responses to light after one full growing season in the treatments. For these six species, flat lines representing the mean of the 75th percentile heights among harvest gaps are presented. We calculated pseudo-adjusted R^2 values for our nonlinear models as the square of the correlation between actual height values and nonlinear model prediction of height by light.

From our nonlinear height vs. light functions, we developed three species-level metrics for comparing height-growth performance. First, the height at 30% light ($\text{height}_{@30\%\text{light}}$, cm) is the regression estimate of 2010 height at 30% light. This metric was chosen to represent total height growth over the entire experiment in approximately the highest light levels where all species were present. Second, the relative height growth rate ($\text{RGR}_{\text{ht@30\%light}}$, $\text{cm}\cdot\text{cm}^{-1}\cdot\text{year}^{-1}$) is the difference between the log-transformed estimates of height at 30% light between 2010 and 2008 model fits divided by two (years). This metric represents the relative change in height over the last two years of the experiment. Third, the relative difference in height percent increase in light ($\text{RDHt}_{(8\%–12\%)}$) is the difference between log-transformed estimates of height predicted at 8% light and 12% light for 2010 model fits divided by 4 (percentage). This represents the responsiveness of height growth to increases in light over a range of (lower) light levels characteristic of small harvest gaps (Fig. 1).

The soil resource characteristics that we examined in relation to seedling height were concentrations of mineral N forms (i.e., [NO_3^--N] and [NH_4^+-N]) and water, and net N mineralization and nitrification rates, all expressed on a soil dry mass basis. For each measurement time in 2007 (n = 3) and its mean, we examined bivariate correlations of soil resources with the residuals of height vs. light models for each species. We added main effects and interactions for the resource–measurement time combination with the highest bivariate correlation for a given species to a stepwise multiple regression model of seedling height that already included light effects. Because light is first in the model, analyses are conservative for the effects of soil resources on growth when the soil resource and light covaried (see Results). In our stepwise models, added soil resource main effects and (or) interactions with light remained in the model if AIC decreased by >2.0 compared with models with light alone. For models already including light and one soil characteristic, additional soil resources were added using criteria described previously, but for no species did a second soil resource remain in the model. Adjusted R^2 values for the multiple regression and AIC values for the effects of light on height and the effects of light and a soil resource characteristic on height are reported from these stepwise analyses. Soil water was not significant in multiple regression models for any species, thus we do not present or discuss water data hereafter.

Fig. 1. The amount of light (% of open sky) above forest-floor vegetation (1.5 m height) vs. harvest gap size based on gap edge tree bole to tree bole distances (m^2).



We examined the relationships of shade tolerance, soil fertility affinities, and phylogeny with N-form responses for the nine species that responded to N form with nominal logistic regression (JMP, SAS Institute, Cary, North Carolina). The nominal response was NH_4^+-N vs. NO_3^--N and models were compared with uncertainty coefficients (R^2(U)) and $P > \chi^2$ values. For shade tolerance, we used the continuous index of Niinemets and Valladares (2006) (Table 1). A value for pin cherry was not reported, so based on other descriptions of its tolerance (e.g., Burns and Honkala 1990), we assigned it a value of 1.21, the same as for bigtooth aspen. For soil fertility affinity, we developed a continuous index from field-collected data on sapling associations with the habitat classes reported in Burger and Kotar (2003). The habitat classification system is vegetation-based (synecological coordinates ordination; Gutierrez-Espeleta 1996), with discreet classes collectively representing the range of soil fertility and moisture regimes found regionally on upland sites. In situ measurements of nitrogen and water availability have been found to be consistent with fertility and (or) moisture predictions of the system (Walters and Reich 1997). We estimated soil fertility affinity as the weighted mean of species sapling occurrence among the five well-drained habitat classes representing the soil fertility gradient in northern Lower Michigan. We assigned the habitat class of lowest fertility (PVCd) a value of 1, the second lowest a value of 2, etc., with the highest being 5. The weighting factor was the frequency of a species' occurrence among sites for a habitat class (1, <25% of sites within class; 2, >25% and <50% of sites, etc.). Thus, our soil fertility affinity index represents the average fertility where species occur (Table 1). Data were not reported for pin cherry, so based on reports of a broad soil resource distribution (Spurr 1956), we assigned pin cherry a soil fertility affinity index of 3.

To explore the effects of variation in soil N form and light on species rankings in height growth, we compared model predictions of height in response to different combinations of NO_3^--N, NH_4^+-N, and light. The values that we used were the 10th and 90th percentiles of mean 2007 values for NO_3^--N (1.10 and 8.74 $\mu g\cdot(g\ soil)^{-1}$) and NH_4^+-N, (4.19 and 9.64 $\mu g\cdot(g\ soil)^{-1}$), and for light, the 90th percentile (32.6%) and the mean of the lowest gap-light values with surviving bigtooth aspen and pin cherry (8.2%). Model predictions were compared using Spearman's rank correlation coefficients (ρ), with smaller values indicating greater changes in ranks.

Table 2. For each soil N characteristic, measurement date mean values (±SD) and Pearson correlations (*r*) with light (% open sky) are presented. In addition, for each N characteristic, Pearson correlations between-measurement dates are presented.

Characteristic	Month	*r* among dates	Mean values	*r* with light
[NO_3^--N]	May	May–July, 0.61***	2.32±1.70	0.05
	July	July–August, 0.61***	4.18±2.99	0.48***
	August	May–August, 0.41***	7.20±5.27	0.37*
[NH_4^+-N]	May	May–July, 0.59***	7.01±3.82	0.21
	July	July–August, 0.31*	6.10±3.12	0.44**
	August	May–August, 0.35*	6.69±2.27	0.28
N mineralization	May	May–July, –0.27ns	0.44±0.18	–0.10
	July	July–August, –0.06	0.39±0.14	0.33*
	August	May–August, 0.12ns	0.31±0.16	–0.18
N nitrification	May	May–July, 0.26ns	0.37±0.13	–0.13
	July	July–August, 0.46**	0.31±0.11	0.15
	August	May–August, 0.40**	0.24±0.13	–0.18

Note: Significance: ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Mean values for [NO_3^--N] and [NH_4^+-N] are presented in $\mu g \cdot g^{-1}$; mean values for N mineralization and N nitrification are presented in $\mu g \cdot g^{-1} \cdot day^{-1}$. Sample size = 45 for all correlations except those with May N characteristics (n = 42) as three gap samples were compromised for that sample date.

Results

Gap size, light, and soil resource availability

Light and soil resources varied broadly among gap and closed-canopy plots. Light availability ranged from 2.5% of open sky in undisturbed understory to ~35% in multitree 950 m² gaps (Fig. 1). For average 2007 values, [NO_3^--N] varied 30-fold; [NH_4^+-N], six-fold; N mineralization, 2.7-fold; and nitrification, six-fold among plots. Among the three 2007 soil measurement dates, light correlated positively with [NO_3^--N] in July and August, [NH_4^+-N] in July, and N mineralization in July (Table 2; Fig. 2, mean of the three dates), but overall, correlations between light and mineral N characteristics were weak. Furthermore, [NH_4^+-N] was not correlated with [NO_3^--N] for any measurement date or for 2007 means (data not shown). Collectively, these patterns indicate a considerable degree of orthogonal variation in [NO_3^--N], [NH_4^+-N], and light among gap and (or) understory plots. In contrast, both [NH_4^+-N] and [NO_3^--N] were correlated between measurement dates, with correlations particularly strong for [NO_3^--N] (Table 2).

Seedling responses to light and N

Seedling height responded to light for all species, and responses were highly species specific (Fig. 3). For example, at 30% light, total height varied by over an order of magnitude, and relative height growth rates varied 2.6-fold among species (Table 1; Appendix A). Diameter growth responses to light (data not shown) were similar in form and similar or weaker in strength compared with height responses for all species except for sugar maple and beech for which diameter responses were stronger (R^2 = 0.37 and R^2 = 0.46, respectively).

In addition to the effects of light, growth was predominantly affected by soil N-form concentrations. Among the soil resource variables tested, eight of the 14 species responded most strongly to either [NH_4^+-N] or [NO_3^--N], one species responded to N mineralization (red maple (*Acer rubrum* L.)), one species responded to nitrification (American elm), and four species did not respond to N (Table 1; Appendix A). Positive soil N × light interaction terms for American elm, white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) indicate that soil N impacts on height growth increase with light. For species affected by a soil N characteristic, an average of 11% more variation in growth was explained by N than by light alone.

Differences among species in height responses to light were strongly related to the shade-tolerance index. Compared with shade-tolerant species, shade-intolerant species had both greater height growth rates at higher light (30% of open sky light; Fig. 4*b*) and greater increases in height growth with increasing light at the lower light levels found in single tree gaps (8%–12%; Fig. 4*a*). Of the nine species that responded to either [NH_4^+-N] or [NO_3^--N] (Table 1), all four gymnosperms responded to [NH_4^+-N], whereas angiosperm responses varied (Fig. 5). Shade-intolerant angiosperms tended to respond to [NO_3^--N] and shade-tolerant species responded to [NH_4^+-N]. Among all species (including gymnosperms), the relationship between shade tolerance and [NH_4^+-N]

Fig. 2. Soil [NO_3^--N] and [NH_4^+-N] vs. amount of light (% open sky). Soil N data are means of the values obtained on the three 2007 measurement dates (n = 42 for each). Pearson correlation coefficients are r = 0.43 (P = 0.0037) for [NO_3^--N] and light and r = 0.40 (P = 0.0093) for [NH_4^+-N] and light.

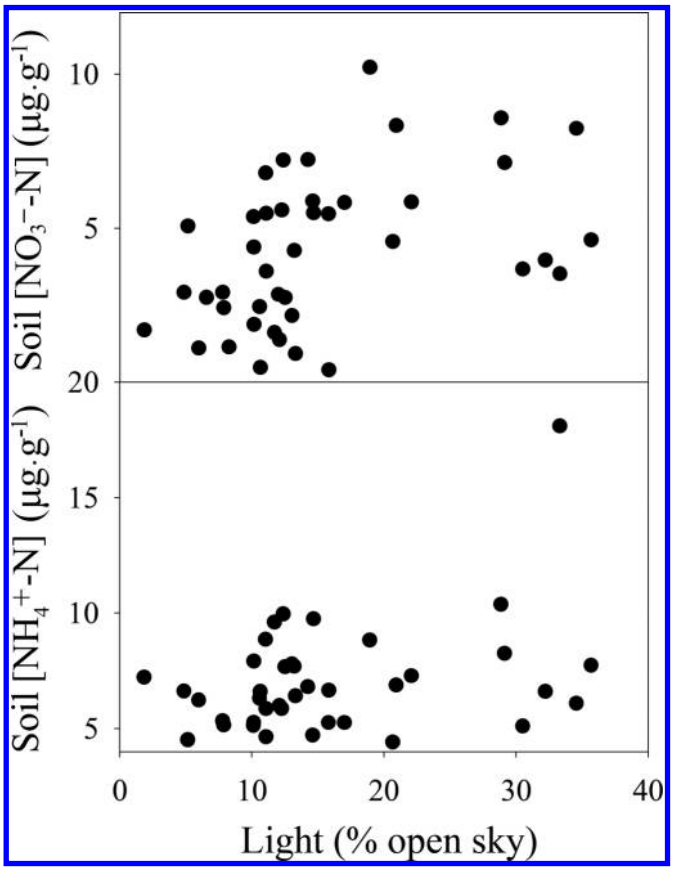
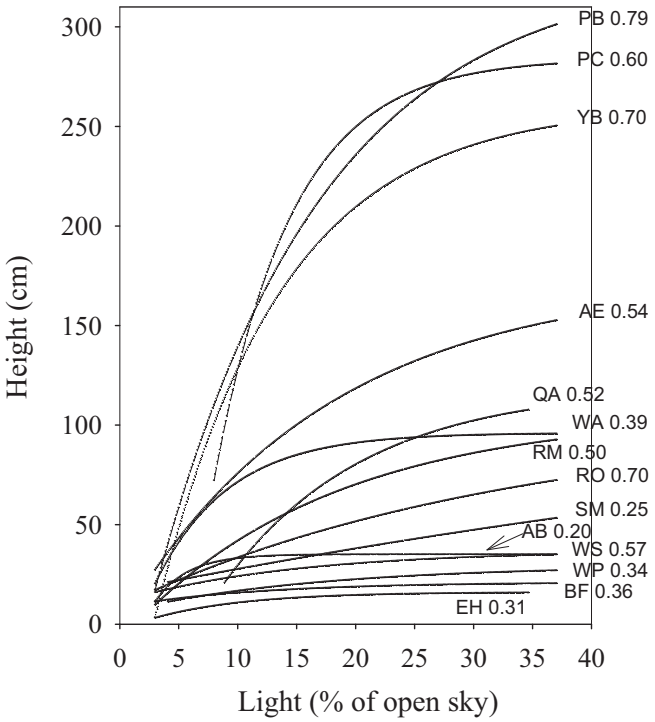


Fig. 3. Height growth responses (cm) vs. amount light (% of open sky). Species and pseudo-adjusted R^2 values associated with each curve are indicated. Individual species responses with raw data shown are in the first column of Fig. A1 of Appendix A. Species are indicated by their common name acronyms (Table 1).



vs. $[NO_3^-\text{-N}]$ response was weak (R^2(U) = 0.16, $P > \chi^2 = 0.181$), but excluding pin cherry strengthened it markedly (R^2(U) = 0.49, $P > \chi^2 = 0.022$). Species with lower soil fertility affinity indexes tended to respond to $[NH_4^+\text{-N}]$, whereas those associated with higher fertility sites tended to respond to $[NO_3^-\text{-N}]$ (R^2(U) = 0.34, $P > \chi^2 = 0.049$). Considering all species, the combination of shade tolerance and fertility affinity explained more variance in $[NH_4^+\text{-N}]$ vs. $[NO_3^-\text{-N}]$ response than either factor alone (R^2(U) = 0.65, $P > \chi^2 = 0.0236$), and both factors were important (fertility affinity, partial $P > \chi^2 = 0.017$; shade tolerance, partial $P > \chi^2 = 0.057$).

Modeled growth rank responses to variations in light and mineral N forms

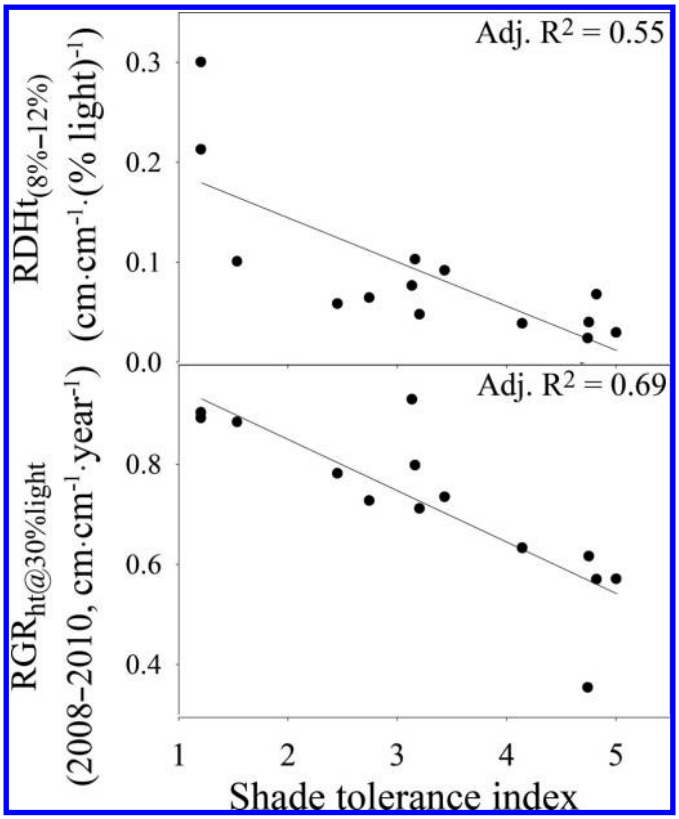
Model-estimated changes in species height rankings to variation in resources were modest. In all paired light–$[NO_3^-\text{-N}]$–$[NH_4^+\text{-N}]$ contrasts, Spearman's rank correlation coefficient values ranked from 0.80 to 0.96, with lower values indicating greater change in ranks (Fig. 6 and data not shown). For only one of the model contrasts incorporating mineral N-form effects (i.e., low light – high $[NO_3^-\text{-N}]$ – low $[NH_4^+\text{-N}]$ vs. high light – low $[NO_3^-\text{-N}]$ – high $[NH_4^+\text{-N}]$) were rank changes in height growth greater than for high light vs. low light alone.

Discussion

Light and soil resource variation and tree seedling growth responses

Our resource measurements indicated that light and soil mineral N forms varied broadly and orthogonally across 45 single- to multiple-tree harvest gaps and closed-canopy locations in a mesic northern hardwood forest community. This pattern results in a large multidimensional resource space that trees could partition via superior performance (i.e., specialization) on different subspaces (Pacala and Tilman 1994).

Fig. 4. The relative difference in height between 8% and 12% light in 2010 ($RDRHt_{(8\%–12\%)}$) and the relative height growth rate over two years (2008–2010) at 30% light ($RGRht_{@30\%light}$) vs. the shade-tolerance index (higher values indicate greater shade tolerance). Adjusted R^2 values are shown. Values used for this figure are from Table 1.



Height growth responded to soil N availability for 10 of the 14 mixed hardwood–conifer forest species that we planted. Lack of growth vs. N responses was not surprising for eastern hemlock and American beech, given they showed little growth at all, or for bigtooth aspen, which had low sample size. Only for yellow birch, whose growth responded strongly to light, was the lack of response to N surprising. The anomalous response of yellow birch could be related to its seedling establishment ecology, which is similar to similarly N-unresponsive eastern hemlock. For both of these closely co-occurring species (Kotar et al. 1999), an important seedling establishment substrate is nitrogen-poor decaying conifer wood (Marx and Walters 2006, 2008). It is possible that the nutrition of both species is dictated more by ectomycorrhizae, supported by both species, and associated organic sources of N than by the mineral N sources examined in this experiment.

For species that responded to N, the strongest response for eight of 10 species was to either $[NH_4^+\text{-N}]$ or $[NO_3^-\text{-N}]$. Perhaps soil N concentrations more closely reflect the root N availability environment for individual seedlings than net rates of production (i.e., mineralization and nitrification). The fate of mineralized N is uncertain and influenced by several processes (e.g., leaching, uptake) and competing uptake pools (other vegetation, microbes). For example, at a given constant N mineralization rate, increasing vegetation density would increase uptake of mineralized N, diminishing $[NH_4^+\text{-N}]$ and $[NO_3^-\text{-N}]$ and thus N availability to the individual plant.

The seedling height responses to N that we report require two caveats. First, our soil sampling effort was relatively modest with three sampling periods in 2007 and one in 2010. However, despite relatively large differences in the mean of plots values among

Fig. 5. Species responses to [NO_3^--N], [NH_4^+-N], and N mineralization versus their phylogeny (gymnosperm or angiosperm), soil fertility affinity, and shade tolerance. "None" indicates no response to soil N characteristics. The datum indicated by the arrow is for pin cherry. Nominal logistic regression results of [NO_3^--N] vs. [NH_4^+-N] responses to these characteristics are in Results.

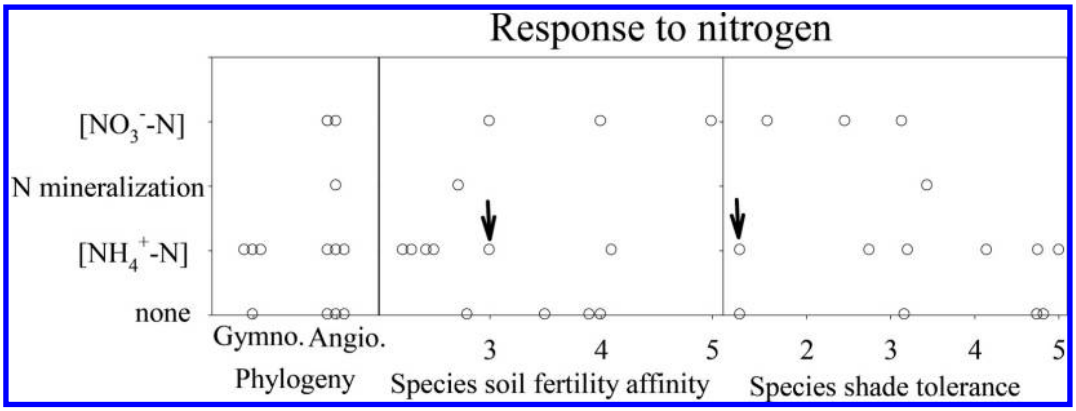
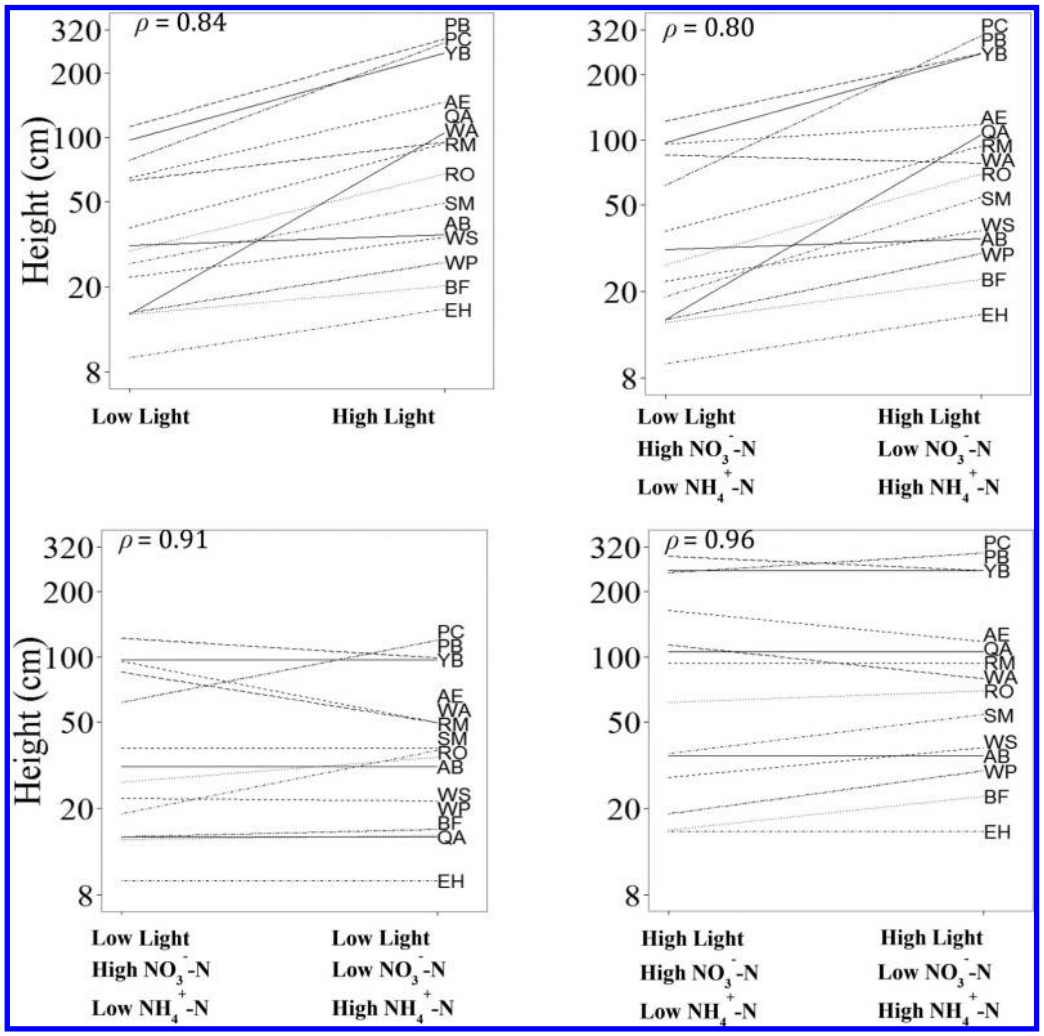


Fig. 6. Height predicted from contrasting levels of light, or light and soil mineral N forms. Values of resources used for these simulations are in Materials and methods. Values of ρ are Spearman's rank correlation coefficients between the levels of resource(s) contrasted. Smaller values indicate greater changes in ranks. Species are indicated by their common name acronyms (Table 1).



measurement dates in 2007, plot N concentrations were correlated between dates (Table 2). Furthermore, 2010 and mean 2007 [NO_3^--N] values were correlated (r = 0.67, P < 0.0001) and species height responses to 2010 N characteristics (data not shown) were similar, though generally weaker, than those for 2007 values (Table 2). Second, tree seedling subplots were kept weeded and adjacent soil resource measurement subplots were not. This could create differences in N dynamics between plot types and result in bias. However, for the 2007 resource measurements, which we primarily relied upon, seedling and resource measurement sub-

plots were similarly free of naturally established vegetation and seedling subplots were not weeded. Thus we conclude that our in situ measurements of natural variation in soil N provide a relatively accurate index of seedling soil N environments over the duration of the treatments (2007–2010). Lastly, growth or uptake responses to N form, or nitrate reductase activity, have been reported for some of our study species and these patterns are generally consistent with the pattern that we documented (Truax et al. 1994; Rothstein et al. 1996; Bauer and Berntson 2001; Miller and Hawkins 2007; Yanai et al. 2009; Scott and Rothstein 2011; Tang et al. 2012; but for white ash, see Scott and Rothstein 2011). Thus, we conclude that our statistical modeling of growth responses to natural variation in soil N forms provided an accurate assessment of species N-form specificity.

Shade tolerance predicts height-growth responses to light

Although growth responses to light and their relationships to shade tolerance is a well-worn topic, the vast majority of these studies focus on mass growth and traits related to mass and (or) carbon capture (see reviews by Veneklaas and Poorter (1998), Walters and Reich (1999), and Vallardes and Niinemets (2008)). Much less common are multispecies comparisons that explicitly consider height growth as an important feature of shade intolerance (e.g., Janse-ten Klooster et al. 2007, 10 species; Kunstler et al. 2009, six species,). Interest in mass growth is justified given its conceptual and functional relationship with carbon balance physiology and allocation, but it is just one factor of at least four that determine height, i.e., height is a function of mass, mass allocation to stem, stem tissue density, and stem morphology. We argue that the strong negative height growth vs. shade-tolerance relationship that we observed across a broad range of light levels (Fig. 3), including lower light levels in which intolerant species mortality can be high (Kobe et al. 1995), reflects a clear "reach for the sky or die" strategy for intolerant species. This strategy is likely a consequence of light predictably increasing with height in forests (Hutchison et al. 1986; Schwinning and Weiner 1998) plus the necessity of maximizing light availability given the high respiration demands that accompany the high growth capacity of shade-intolerant species (Walters and Reich 1999; Baltzer and Thomas 2007). The general trend that we found of intolerant species outgrowing tolerant species in both higher and lower light is consistent with that of Kitajima (1994), who advanced the notion that variation in shade tolerance is characterized by a high light growth vs. low light survival trade-off and not a high light growth vs. low light growth trade-off. However, despite this general trend, our model predictions provide modest evidence of growth rank changes between high and low light (Fig. 6). In 8% light vs. 30% light, the most shade-intolerant species, quaking aspen and pin cherry, showed the greatest decline in height rank among species, and the tolerant American beech showed the greatest increase in height rank. A light level lower than 8% might have elicited an even larger change in size rankings. Thus, our results suggest that both high light growth vs. low light growth (Sack and Grubb 2001) and high light growth vs. low light survival trade-off mechanisms (Kitajima 1994) contribute to variation in shade tolerance.

Shade tolerance, nutrient affinity, and phylogeny predict height-growth responses to soil [NH_4^+-N] and [NO_3^--N]

Given the caveat of a small sample size of nine species, our results suggest that variation in species responses to [NH_4^+-N] vs. [NO_3^--N] can largely be explained by the combination of differences in shade tolerance, soil fertility affinity, and phylogeny. The trend of shade-tolerant species responding to [NH_4^+-N] is consistent with the notion that lower energetic costs favor NH_4^+-N uptake by shade-adapted species (Fredeen and Field 1992) and is also consistent with the lower [NO_3^--N] generally found in their undisturbed forest (Jerabkova et al. 2011) and small gap regeneration niches (Fig. 2; Canham 1988). Conversely, shade-intolerant species tended to respond to NO_3^--N, which is consistent with the higher light energy and elevated [NO_3^--N] of their open, early successional regeneration niches. A striking anomaly to the pattern is the pin cherry, which is among the most shade-intolerant species in mesic northern forest communities and yet it responded to [NH_4^+-N]. Pin cherry's response, however, is consistent with the reported lack of NO_3^- reductase in its leaves (Truax et al. 1994).

Patterns in species mineral N-form responses to the nutrient affinity index are generally consistent with the availability of N forms in the soil fertility gradients over which our species are distributed in the upper Great Lakes region (Zak et al. 1989; Walters and Reich 1997; Baribault et al. 2010; Walters and Gerlach 2013). Of the species that responded to [NO_3^--N], American elm and white ash are restricted to the most fertile glacial moraine soils. Here, nitrification and [NO_3^--N] can be many fold higher than in other upland soils (e.g., Zak et al. 1989). Paper birch, although distributed broadly relative to elm and ash (Burger and Kotar 2003), is early successional and [NO_3^--N] ephemerally increases following disturbance, even on low-fertility sandy outwash soils (Rothstein and Spaulding 2010). The species with the highest nutrient affinity index that responded to [NH_4^+-N] was sugar maple, which is also among the most shade-tolerant species that we examined. Much greater uptake rates of [NH_4^+-N] than [NO_3^--N] have been reported for sugar maple despite its association with high [NO_3^--N] soils (Templer and Dawson 2004). Gymnosperm conifers responded solely to NH_4^+-N, which is consistent with the notion that conifers are NH_4^+-N specialists (Kronzucker et al. 1997), the negative impacts that their acidic litter has on nitrification rates, and the greater [NH_4^+-N] vs. [NO_3^--N] generally found in mature conifer vs. broadleaved deciduous forests (Jerabkova et al. 2011). However, an important qualifier is that the gymnosperms in this study generally had lower soil fertility index values and higher shade-tolerance values than the angiosperm species. Thus, phylogeny is partially confounded with shade tolerance and the soil fertility affinity index, making it difficult to draw clear conclusions about their independent contributions to species N-form responses.

Community-scale multiple-resource variation results in modest species growth rank changes

Despite species-specific growth responses to substantial and largely orthogonal variation in resource availability, modelled changes in species size rankings to near extremes in [NH_4^+-N], [NO_3^--N], and light were modest. Although positive N × light interactions for three of the species indicate an expected increase in N effects as light increases (Walters and Reich 2000), N had a greater effect on species rankings in low light than in high light. This occurs because differences in the magnitude of light effects among species at high light are much larger than for N effects, so differences in light effects dominate. Furthermore, the only model in which rank changes in height growth were greater for high vs. low light alone (i.e., low light – high[NO_3^--N] – low[NH_4^+-N] vs. high light – low[NO_3^--N] – high[NH_4^+-N]) is also one of the least likely contrasts to occur naturally at the community scale given that [NO_3^--N] increases with light (via recent disturbance) more strongly than [NH_4^+-N] (Jerabkova et al. 2011; this study). Although modest overall, growth rank changes that occurred were consistent with species distributions. For example, low light growth responses of elm, ash, and oak to [NO_3^--N] and [NH_4^+-N] were large enough to drive changes in species rankings consistent with their soil fertility affinities.

Conclusions

High spatiotemporal variation in mineral N-form availability, species specialization on mineral N forms, and strong associations of N-form specialization with species' ecologies and phylogenies suggest that specialization on [NO_3^--N] vs. [NH_4^+-N] could be an important and relatively unexplored functional mechanism influ-

encing ecological processes (Ashton et al. 2010; Boudsocq et al. 2012). At the community scale of our harvest gap experiment, species differences in height-growth responses to natural variation in light and soil [NO_3^--N] and [NH_4^+-N] could contribute modestly to the maintenance of tree species diversity. This mechanism may be more important at coarser landscape scales where the range of soil [NO_3^--N] and [NH_4^+-N] regimes and consequent growth responses are likely greater. It is also possible that performance metrics that included growth and survival responses to light and N form or that included within species variance in performance responses to resources (Clark 2010) would reveal more detail about potential niche partitioning to light and N form than growth responses alone.

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Appendix A

In Fig. A1, results are shown for analyses of actual seedling height vs. harvest gap light availability (2008 nonlinear fit, no data shown; 2010 nonlinear fit, data shown), vs. height predicted by light from nonlinear regression model, and vs. height predicted by light and the soil nitrogen characteristics that resulted in both the greatest decrease in AIC and decreased AIC > 2.0 when added to the model already including light. See Table 1 of main text for other N characteristics decreasing AIC scores > 2.0. For species with no panel in column C of Fig. A1, no added soil N characteristic decreases AIC > 2.0. For some species, adding light × soil resource interactions did not improve model fit (indicated as light and [NH_4^+-N]), whereas interactions improved model fit for others (indicated as light × [NH_4^+-N]). Data used for relationships in columns 2 and 3 of Fig. A1 are restricted to those gaps and (or) understory plots with values for both light and the soil N characteristics. Thus, due to missing soil N data for $n = 3$ gaps at the May measurement time, there are three fewer data sets for relationships in columns 2 and 3 than in column 1 for white ash (May [NO_3^--N]) and American elm (May N nitrification). Pseudo-adjusted R^2 values are shown in Fig. 3 of the main text for column 1 and in Fig. A1 for columns 2 and 3.

[Figure A1 appears over the next three pages.]

Fig. A1. (Column 1) Actual seedling height vs. harvest gap light availability (2008 nonlinear fit, no data shown; 2010 nonlinear fit, data shown). (Column 2) Actual seedling height vs. height predicted by light from nonlinear regression model. (Column 3) Actual seedling height vs. height predicted by light and the soil nitrogen characteristics that resulted in both the greatest decrease in Akaike's information criterion (AIC) and decreased AIC > 2.0 when added to the model already including light (column 2). [Figure A1 continues on the next two pages.]

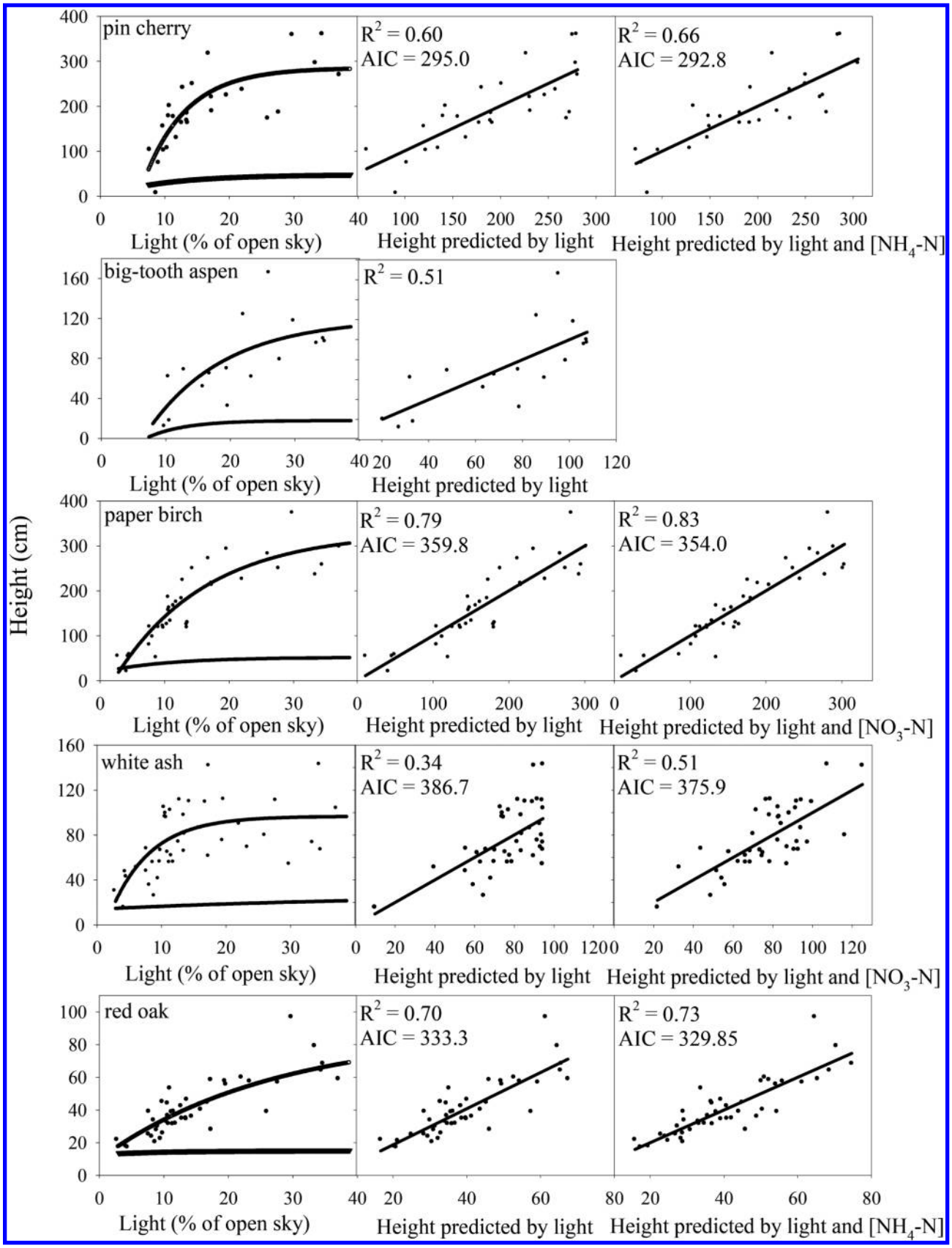

Fig. A1 (*continued*).

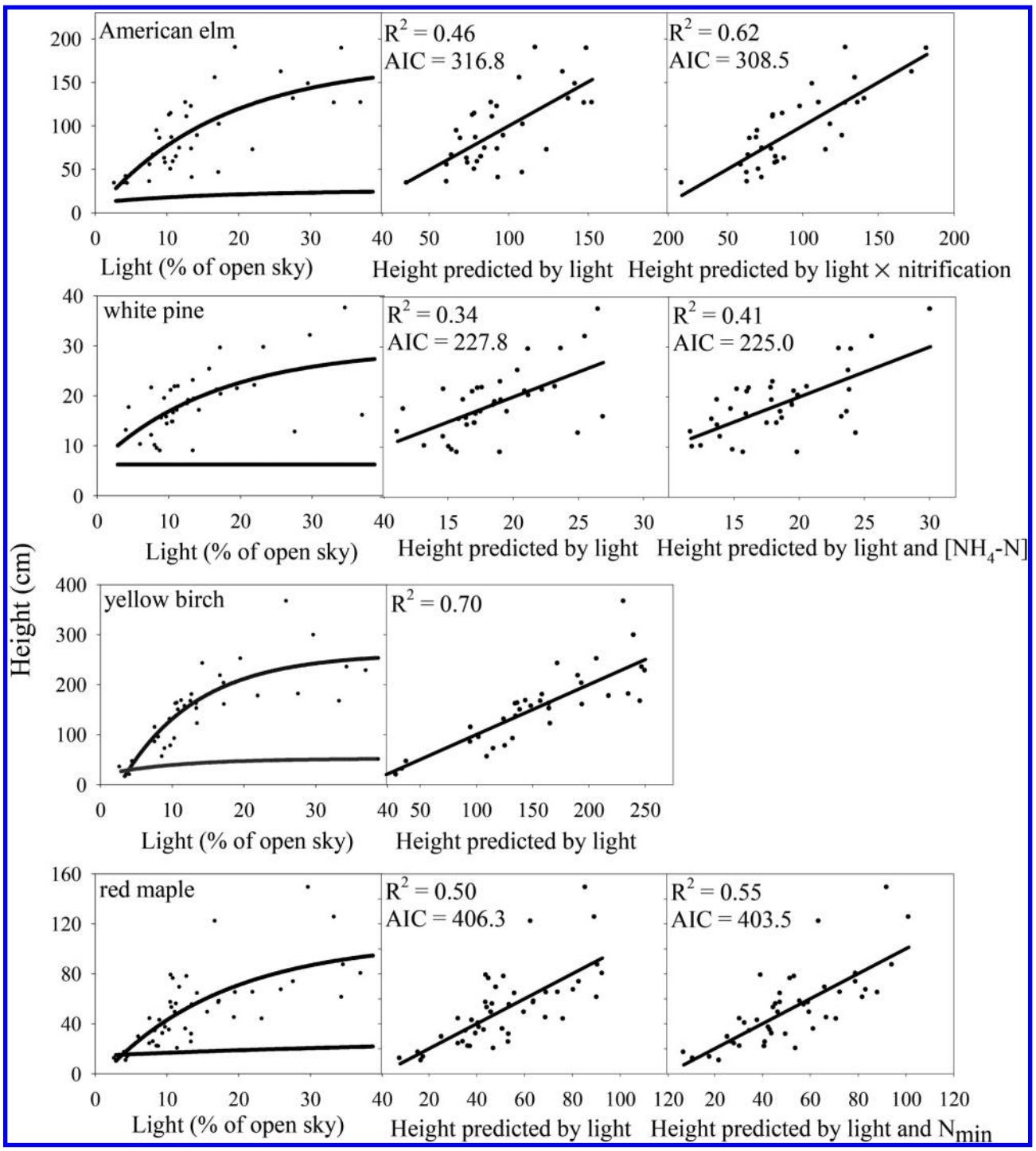
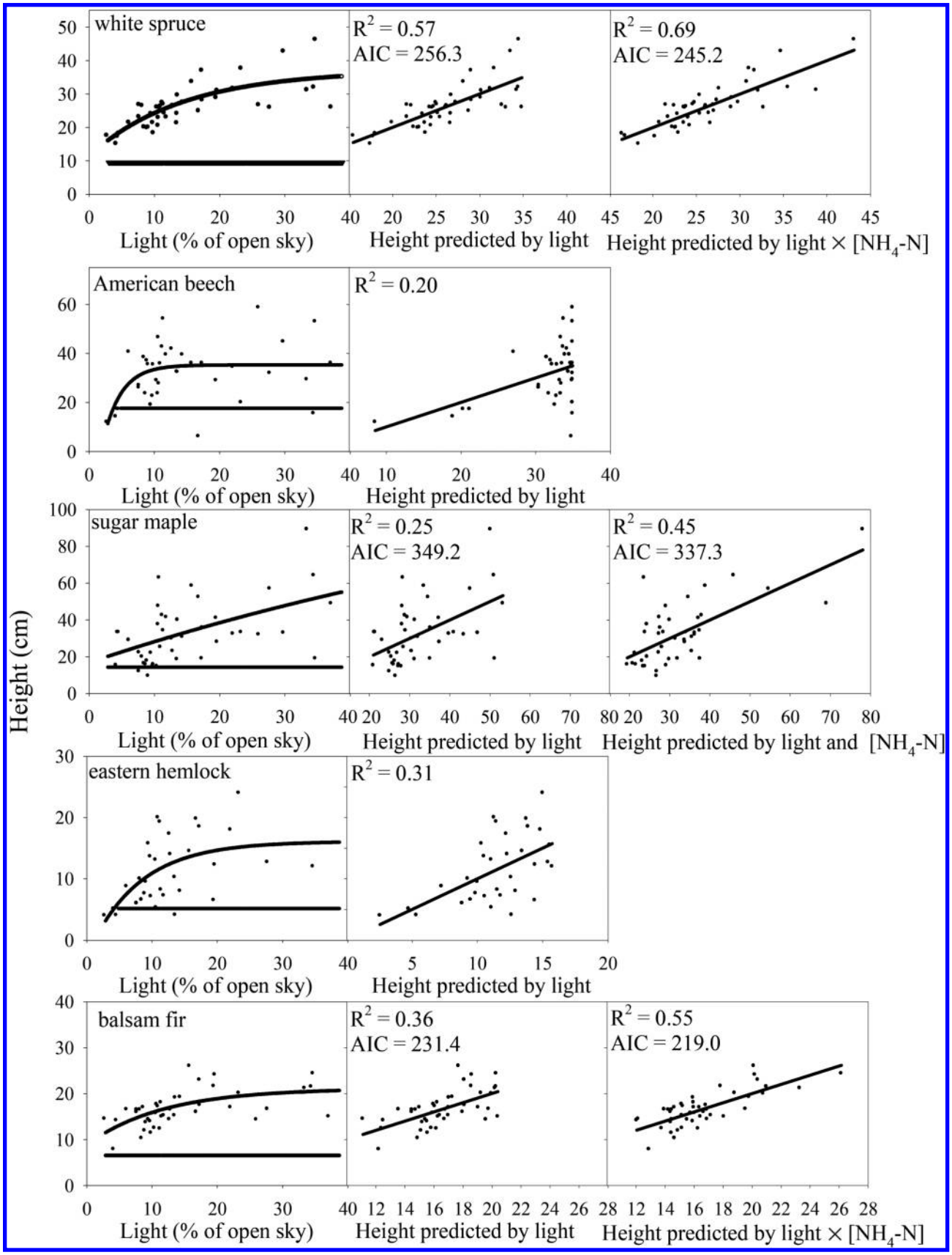
Fig. A1 (*concluded*).