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Managing for diversity: harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings

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Abstract. Many managed northern hardwood forests are characterized by low-diversity tree regeneration. Small harvest gaps, competition from shrub–herb vegetation, and browsing by white-tailed deer (*Odocoileus virginianus*) contribute to this pattern, but we know little about how these factors interact. With a stand-scale experiment, we examined the effects of gap size (0–3234 m^2), vegetation (weeded:unweeded), and deer (fenced:unfenced) on seedling growth and survival for 18 tree species. With increasing gap size and light, shrub–herb vegetation density increased, while deer browsing on seedlings in unweeded plots decreased. Fenced:weeded seedlings of all species increased in height up to 35–45% light, with optimal growth in large-group selection and patch cut harvest gaps. Height growth rank order among tree species changed between gap sizes, but growth varied little in small, low-light gaps. Instead, a low-light survival (i.e., shade tolerance) vs. high-light growth tradeoff we observed is likely more important for species sorting of gap sizes. Shrub–herb vegetation decreased seedling survival and growth, especially in larger harvest gaps, shifting gap size optima to smaller gaps, but had little effect on growth/survival rank order among species. In contrast, deer had strong impacts on growth rank order, especially in larger gaps where species differences in growth potential were trumped by differences in deer browsing pressure responses. However, contrary to their consistently negative main effects, vegetation and deer had two positive interacting effects: dense shrub–herb vegetation in large gaps protected seedlings of faster-growing species from browsing and deer browsing of shrub–herb vegetation modestly increased light and growth of short, suppressed, browsing-avoided species. In summary, harvest gap size-mediated light availability, shrub–herb vegetation, and deer herbivory had strong interacting effects on tree seedling interspecific performance ranks and intraspecific optimal gap sizes. For management, a broad range of harvest gap sizes and rapid establishment of tree regeneration (naturally or planted) to minimize shrub–herb competition should increase tree diversity in forests with few deer. However, with deer browsing pressure, a more limited set of lesser-browsed species are likely to recruit successfully regardless of gap size, except in large patch cut gaps, where recruitment of faster-growing, shade-intolerant species is possible.

Key words: deer browsing; deer herbivory; gap partitioning; harvest gaps; northern hardwood forest; plant competition; shade tolerance; tree diversity; tree seedling growth; tree seedling survival; uneven-aged management; white-tailed deer.

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Introduction

Extending from Minnesota east through the Great Lakes region to New England and Nova Scotia, northern hardwood (NH) forests cover millions of hectares of North America. Although capable of supporting over 20 native tree species, NH forests are currently dominated by sugar maple (*Acer saccharum* Marsh.) (Schulte et al. 2007). Large extents of NH forests are managed by uneven-aged selection silvicultural systems to perpetuate sugar maple dominance because of its valuable wood products. Selection silviculture has been used for over 60 yr in this region and is typically implemented as partial stand harvests at 8- to 20-yr intervals, with approximately 20–40% of stand volume removed at each harvest as dispersed individual and small groups of trees. This harvest pattern creates mostly small harvest gaps (e.g., median gap size 155 m^2; Matonis et al. 2011), which produce favorable regeneration conditions for a new cohort of sugar maple and other shade-tolerant tree species (Crow et al. 2002, Angers et al. 2005, Poznanovic et al. 2013). Consistent recruitment of canopy trees from naturally regenerated seedlings to replace those harvested essentially defines long-term sustainability of the uneven-aged selection system. Ideally, tree regeneration in NH forests would include sugar maple among a mix of tree species because, depending on species composition, increased tree diversity can increase structural complexity and food sources for wildlife, as well as provide ecological and economic resilience to environmental and economic variation. This variation may include changing forest product markets as well as severe disturbances like climate change and invasive pest and pathogen epidemics (Niese and Strong 1992, Schulte et al. 2007, Sturrock et al. 2011, Anderson-Teixeira et al. 2013, Duveneck et al. 2014). Unfortunately, diverse regeneration is uncommon in selection-managed NH forests. Instead, harvest gaps are either dominated by seedlings and sprouts of sugar maple (Neuendorff et al. 2007), other shade-tolerant, but less commercially valuable species (e.g., *Ostrya virginiana* (Mill.) K. Koch, *Fagus grandifolia* Ehrh.), or worse yet, by nothing at all (Nyland et al. 2006, Matonis et al. 2011).

The selection system likely contributes to low species diversity in NH forests, as the single-tree and small-group selection canopy gaps commonly used by forest managers narrow the potential regeneration pool to a relatively small set of more shade-tolerant species (Niese and Strong 1992, McClure et al. 2000, Webster and Lorimer 2005, Kneeshaw and Prèvost 2007). Recognizing this problem, managers and scientists, informed by gap partitioning theory (Ricklefs 1977, Denslow 1980) and species' silvics (Burns and Honkala 1990), have tried varying harvest gap size to promote more species-diverse tree regeneration, collectively characterized by a broader range of shade tolerances. However, the outcomes of these efforts have often fallen short of expectations (Shields et al. 2007, Falk et al. 2010, Gasser et al. 2010, Bolton and D'Amato 2011, Kern et al. 2012, 2013, Fahey and Lorimer 2013, Poznanovic et al. 2013, 2015). In addition, reliance on small harvest gaps does little to explain why sugar maple seedling/sapling density is often low in stands where it dominates the overstory (Matonis et al. 2011). Thus, factors in addition to harvest gap size are affecting tree regeneration patterns in NH forests. Among others, these factors include herbivory by abundant white-tailed deer (*Odocoileus virginianus* Z.) (Witt and Webster 2010, Kain et al. 2011, Matonis et al. 2011, Nuttle et al. 2014), competition from shrub–herb layer vegetation (Royo and Carson 2006), seed availability (Caspersen and Saprunoff 2005), and seedling establishment substrates (Caspersen and Saprunoff 2005, Marx and Walters 2008, Bolton and D'Amato 2011, Willis et al. 2015). In this report, we focused on the impacts of gap size, deer herbivory, and shrub–herb vegetation.

The effects that white-tailed deer are having on NH forests of Eastern North America are well documented. These include declines in tree seedling and sapling densities (Stoeckeler et al. 1957, Matonis et al. 2011) as well as reduced species diversity via elimination of tree species sensitive to deer browsing pressure (Rooney et al. 2000, 2002, Côté et al. 2004, Long et al. 2007, Matonis et al. 2011, Randall and Walters 2011). Some older studies comparing discrete harvest treatment pairs suggest that deer herbivory impacts can be greater in smaller than in larger harvest gaps (Curtis and Rushmore 1958, Ripley and

Campbell 1960, Harlow and Downing 1969). In contrast, Kern et al. (2013) report that deer likely limited tree regeneration regardless of gap size but their maximum harvest gap size was only 1660 m^2 and they were unable to tease apart shrub competition vs. deer effects on regeneration. Collectively, these findings suggest that larger harvest gaps might increase tree regeneration density and diversity in deer-impacted areas. Testing this idea will require quantification of deer herbivory–gap size impacts on tree regeneration for a wide range of harvest gap sizes and the co-consideration of other factors (e.g., competing shrub–herb vegetation) impacts on these relationships.

Competition from shrub–herb vegetation can pose a formidable impediment to tree regeneration (Royo and Carson 2006). In NH forests, canopy disturbance elicits the rapid establishment of shrub–herb vegetation in the 0–2 m tall stratum (Shields and Webster 2007). Often dominated by tall-statured shrubs and also containing herbs, grasses, and sedges, this stratum may inhibit regeneration by many mechanisms, but predominantly by shading of subordinate tree seedlings (Royo and Carson 2006, Bèland and Chicoine 2013, Kern et al. 2013). Although the effects of shading seem obvious, the nuanced details of shrub–herb–tree seedling interactions are unknown and could have large implications for regeneration dynamics. For example, increasing light by increasing harvest gap size should increase the growth of shrub–herb vegetation and its competitive impacts on tree seedlings, but should also increase tree seedling growth, with responses varying among species (Walters et al. 2014). Nonparallel responses of shrub–herb vegetation and tree seedling growth to harvest gap size could lead to species-specific ranges of gap sizes/light availability where tree seedlings could outcompete shrub–herb vegetation. Furthermore, given their higher low-light survival, shade-tolerant tree species ought to be less impacted by shrub–herb vegetation than shade-intolerant species (Bellefleur and Petillion 1983, Gasser et al. 2010). However, the greater height growth potentials of shade-intolerant species (Walters et al. 2014) may allow them to maintain their canopies above the growing shrub–herb canopy following overstory harvest, perhaps lessening the impacts of shrub–herb competition compared to slower-growing, shade-tolerant species. The degree to which the outcome of competition with shrub–herb vegetation is a product of growth potential vs. shade tolerance is little explored.

Here, we report the results of a manipulative, stand-scale harvest gap experiment that examines how harvest gap size mediates the interacting effects of light, shrub–herb vegetation, and deer herbivory on the growth and survival of seedlings of 18 temperate tree species that represent broad ranges of juvenile growth rates, shade tolerance, and deer browsing preferences/tolerances. Fifteen of the species represent a significant proportion of the potential tree diversity in NH forests. The other three have ranges that are more southerly and disjunct from NH forests and represent potential NH migrant species in response to climate change. We interpret the results as they apply to both fundamental theories of vegetation dynamics (e.g., gap partitioning theory; Ricklefs 1977, Denslow 1980) and the development of silvicultural practices aimed at managing NH and similar forests globally for greater sustainability and diversity.

Methods

Study site

We used two experimental closed-canopy NH forest stands within larger NH forests in the northern Lower Peninsula, Emmet County, Michigan, USA: one 31.7-ha stand near the town of Good Hart (N45.574624–W85.074373) and an 18-ha stand near the town of Levering (N45.614486–W84.895990). Input these coordinates at http://www.latlong.net for Google Earth imagery of the study sites. Most of the data in this report come from Good Hart, as only for this site did we examine interactions of gap size, shrub–herb vegetation, and deer herbivory on seedling survival and growth. At Levering, we measured gap size/light and deer impacts on seedling height for seven yr compared to only four at Good Hart. These made the Levering data useful for evaluating the longer-term impacts of deer on seedling height, some of which were suggested, but not conclusive for the shorter-term Good Hart data.

Both sites are characterized by postglacial moraine topography, dominance by mesic-rich to very rich habitat types (*Acer–Fagus–Osmorhiza,*

AFO; *Acer–Fagus–Osmorhiza–Caulophyllum*, AFOCa; Burger and Kotar 2003), and forest overstories dominated by sugar maple, with white ash (*Fraxinus americana* L.) and American beech (*Fagus grandifolia* Ehrh.) well represented. There were also relatively high admixtures of paper birch (*Betula papyrifera* Marsh.) and black cherry (*Prunus serotina* Ehrh.) at Good Hart, and basswood (*Tilia americana* L.) at Levering. Deer populations based on the estimates of a sex–age–kill deer population model (Mattson and Moritz 2008) using check station data from 2010 to 2012 and calculated at the resolution of Emmet County were 10.4 deer/km^2 (Brent Rudolf, Wildlife Division, Michigan Department of Natural Resources). Deer fecal pellet count data collected in April 2014 revealed very low deer density at both sites from the end of October (leaf fall) to the end of April (< 1/km^2; Hill 2001). This was likely due to deep winter snowpacks that occur most years at both sites (E. Farinosi, *personal observation*), which force deer to locally migrate. Based on our unstructured observations, most deer browsing of tree seedlings at our study sites occurred in early autumn.

We established plot locations at the center of 40 harvest gaps at Good Hart, 41 at Levering, and in four unharvested areas at each site. At least 30 m of unharvested forest separated harvest gap edges and unharvested plot perimeters from one another. At privately owned Levering, we marked trees for harvest gaps in autumn 2006 and administered a harvest by hand-felling and horse skidding in winter 2006–2007. At publically owned Good Hart, Michigan Department of Natural Resources personnel marked trees' harvest gaps in autumn 2009 and administered a mechanized harvest in winter 2009–2010. As part of the logging operations, slash was cleaned from the interior of each gap and left along gap borders at both sites.

Plot design

Plots were laid out as a square checkerboard of 16 2 × 2 m subplots at both sites. Buffers surrounded all subplots at a width of 0.5 m at Levering and 1 m at Good Hart. Plots were either fenced with 8 ft tall plastic mesh fencing (DeerBusters, Waynesboro, Pennsylvania, USA) to exclude deer (29 at Good Hart, 31 at Levering) or left unfenced (15 at Good Hart, 14 at Levering). Fenced and unfenced plots were distributed randomly within gap size strata. Tree seedlings were planted in randomly assigned subplots with other subplots left unplanted. Hereafter, these are referred to as fenced:unfenced treatments.

We used seedlings of 16 species from Good Hart and 13 from Levering for this report. With considerable species overlap between sites, we present data for 18 total species. They are referred to by their common names in this report (see Table 1 for Latin binomials). Fifteen of our species are components of NH forests in Northern Lower Michigan. The other three species have distributions disjunct from most of Michigan's NH forests, with black walnut and bitternut hickory associated with central hardwood biomes and chestnut blight (*Cryphonectria parasitica* (Murrill) Barr)-decimated American chestnut formerly distributed throughout the Appalachian ecoregion. We included these regionally exotic species in our experiment because, given climate change projections (http://nca2014.globalchange.gov/report), they may now or soon be climatically adapted to NH forests. Thus, via natural or assisted migration, they could contribute to tree diversity in future NH forests (Duveneck and Scheller 2015).

We raised tree seedlings at the Michigan State University Tree Research Center. Seeds were collected, donated, or purchased from commercial sources and were all from our study sites' Hardiness Zone (5). We cold-stratified seeds during the winter and germinated them the following spring in sand-filled trays or directly in commercial seedling containers in a temperature-controlled glasshouse. Those in trays were transferred to containers soon after germination. Containerized seedlings were allowed to establish in the glasshouse for 2–3 months before being transferred to a 50% shade outdoor lath house. For Levering, seedlings germinated in spring 2007 were planted autumn 2007. For Good Hart, seedlings germinated spring 2010 were planted spring 2011. At each site, seedlings were planted in a single day by a contract planting crew. At Good Hart, in spring 2012, a small number of seedlings (484 of the 8832 total) left over from the previous year were planted in spaces where seedlings had died and tagged to distinguish them from seedlings planted in 2011. In this report, seedlings planted in 2012 contribute to survival estimates but not

Table 1. Species of tree seedlings used in this report and some of their basic features.

Common name	Latin name	Maximum height	Shade tolerance	Mortality <5% light
Paper birch	*Betula papyrifera* L.	331	1.54	33.3
Yellow birch	*Betula alleghaniensis* Britton.	258	3.17	20.1
American chestnut	*Castanea dentata* (Marsh.) Borkh.	255	3.06	18.0
Quaking aspen	*Populus tremuloides* Michx.	233	1.21	49.3
American elm	*Ulmus americana* L.	221	3.14	39.1
Black walnut	*Juglans nigra* L.	207	1.93	19.2
Red maple	*Acer rubrum* L.	174	3.44	39.3
White ash	*Fraxinus americana* L.	152	2.46	17.7
Red oak	*Quercus rubra* L.	129	2.75	28.9
Sugar maple	*Acer saccharum* Marsh.	107	4.76	15.2
White spruce	*Picea glauca* (Moench) Voss	80	4.15	3.0
White pine	*Pinus strobus* L.	69	3.21	22.2
Balsam fir	*Abies balsamea* (L.) Mill.	43	5.01	9.7
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	41	4.83	11.0
Bitternut hickory	*Carya cordiformis* (Wangeh.) K. Koch	34	2.07	18.0
Northern white cedar	*Thuja occidentalis* L.	24	3.45	13.7
Pin cherry†	*Prunus pensylvanica* L.	–	–	–
American beech†	*Fagus grandifolia* Ehrh.	–	4.75	–

Notes: Maximum height is an index of height growth potential and is estimated as the maxima of height vs. light regressions for fenced:weeded seedlings (Fig. 2). Shade tolerance score is from Niinemets and Valladares (2006) with 1 indicating most intolerant and 5 indicating most tolerant; Mortality is the percentage of seedlings alive at the end of the 3rd year in treatments that died by the end of the 4th year in treatments for plots receiving < 5% light.

† Only grown at Levering site and only shown in Fig. 4.

height values or browsing estimates. Although glasshouse-grown seedlings were used for most species, seedlings that had naturally established on site and were of the same age as planted seedlings were used for white ash and pin cherry at Levering, and white ash and sugar maple at Good Hart.

Prior to planting at Good Hart, the generally sparse shrub–herb vegetation (mostly *Rubus* spp. and *Sambucus racemosa* L. shrubs, with lesser density of herbs, grasses/sedges) and most naturally established tree seedlings (except those to be tagged and included in the experiment; see further in Methods) and saplings were cut to ground height. The protocol for vegetation control at Levering was the same as at Good Hart except, as part of a different experiment at Levering, tree seedlings and saplings were removed from most plots and left intact in the rest. Differences in vegetation control between sites had no bearing upon the particular analyses and comparisons made between Levering and Good Hart seedlings in this report and thus are not discussed further.

After tree seedlings were planted, some cut seedlings and saplings resprouted and shrub–herb vegetation grew quickly such that in weeded treatment subplots (six in each gap), these vegetation groups were recut to near-ground height later in the initial planting year and several times a growing season each year thereafter. Cut vegetation was left in the plots. In the unweeded subplots, which were only at Good Hart (two in each gap), shrub–herb vegetation was cut the first couple months following planting to ensure establishment, and then left unclipped thereafter. This treatment will hereafter be referred to as weeded:unweeded.

As the planted tree seedlings grew larger over the years, we had to remove some by cutting aboveground portions to prevent crowding and competition among seedlings. Seedlings prioritized for removal were those (1) considered to compete for light with other individuals, (2) without size bias relative to other seedlings of same species in the same subplot/plot, and (3) of the most abundant species among individuals considered competing.

Gap size and light measurements

Gap sizes, reported for Good Hart, were estimated by mapping a polygon from polar coordinates based upon distances and bearings measured with a laser range finder (LaserAce

1000; Trimble Navigation, Sunnyvale, California, USA) from gap center to the bole of each gap boundary tree and then composing and computing the polygon area with a CAD program (Solidworks; Dassault Systemes, Velizy, France). Light availability was estimated as percentage of open sky total transmission from analyses of hemispherical photographs taken in July of 2007, 2009, and 2010 at the Levering site and 2011 and 2014 at the Good Hart site. We used the averages of these values for analysis. Hemispherical photographs were taken with a digital Canon EOS 5D fitted with a Sigma 8 mm f/4.0 EX fisheye lens (Sigma Corporation, Kawasaki, Japan) above the shrub–herb layer (~2 m height) at the center of each 2 × 2 m subplot. For later dates (e.g., 2014 at Good Hart), some planted trees in the larger harvest gaps had grown taller than 2 m, necessitating that we bend them down so they would not interfere with photographs. Black–white pixel threshold values were computed using SideLook software (Nobis and Hunziker 2005) and manually altered if automatic threshold values appeared unrealistic before analysis with the Gap Light Analyzer v 2.0 program (Frazer et al. 1999) parameterized with a custom lens distortion correction supplied by Sigma Corporation (contact corresponding author for values). The values estimated from canopy photographs are intended to depict light as modified only by the midstory and overstory trees at gap edge and beyond (i.e., vegetation above the shrub–herb layer). These estimates of light availability will hereafter be called gap light.

In addition to gap light, we measured diffuse noninterceptance (DIFN) values at Good Hart with an LAI-2000 (LI-COR, Lincoln, Nebraska, USA) in mid-summer 2013. In each 2 × 2 m unweeded subplot, we took four measurements at a height of 20 cm (at the center of each 1 × 1 m sub-subplot) and, for subplots with planted seedlings, one at the top of the canopy of each planted seedling. These values were referenced to subplot values measured seconds before directly above the shrub–herb layer (i.e., at the height canopy photographs were taken). Resulting DIFN values are interpreted as the proportion of diffuse light transmitted through the shrub–herb layer canopy (DIFN) to individual seedling canopies or to a height of 20 cm. We interpreted these measurements as being inversely proportional to the competitive strength of vegetation in the shrub–herb layer for light at a standardized height of 20 cm (i.e., low proportional light transmission = dense shrub–herb canopy = strong competitor for light). The 20 cm height values we report are for unplanted subplots so that planted seedlings would not influence results. Values taken at the top of individual seedling canopies are interpreted as an index of the competitive impact of shrub–herb vegetation on light availability to that seedling. We also estimated the combined effect of the residual overstory tree canopy and the shrub–herb layer canopy on light at a height of 20 cm and to individual seedlings as the product of gap light (from photographs) and DIFN values. To supplement DIFN values we further characterized shrub–herb vegetation for each subplot by ocular estimation of percentage of canopy cover to the nearest 5% interval by species and measured mean canopy height with a calibrated height pole to the nearest cm using nine predetermined locations in a grid pattern within each subplot.

Tree seedling measurements

All seedlings alive in spring 2008 from the fall 2007 planting at Levering and those alive in autumn 2011 from the spring 2011 planting at Good Hart were fitted with uniquely numbered metal tags. Seedling height was measured on tagged seedlings every autumn from 2008 or 2011 through 2014 after annual height growth had ceased. Thus, we measured height at the end of seedlings' 2nd–5th growing seasons (1st–4th in treatments) at Good Hart and 2nd–8th growing seasons (1st–7th in treatments) at Levering. We also took stem base diameter measurements with calipers when we measured height, but we do not present diameter data for three related reasons: (1) brevity, (2) diameter is less responsive to light availability than height for most species (Walters et al. 2014), and (3) height, not diameter, defines size-dependent escape of growing trees from deer browsing and shrub–herb competition because these factors have minimal impacts on trees > 2.0 m tall (M. B. Walters et al., *unpublished manuscript*). At Good Hart, seedlings used for height measurements were also used to census survival.

Time zero for the census was autumn 2011 when seedlings were tagged. Thus, seedlings were likely beyond proximal transplant shock effects on growth and survival and responding primarily to the experimental treatments.

Seedlings were examined for tissue loss from herbivores at the same time height was measured. Herbivore agents we observed damage from were deer (identified by characteristic tearing pattern) and porcupines. Several seedlings browsed by porcupines (nearly all yellow birch) were removed from the experiment as was the perpetrator. We did not see damage from small mammals (e.g., voles, *Microtus*). All seedlings browsed by deer were in unfenced plots. Thus, we are confident that height responses to fencing treatments were due to deer vs. no deer rather than some other agent.

Analysis

Plots (gap centered and nongap) were considered the experimental unit for analyses. Therefore, seedling height, deer browsing damage, survival, and light measurements were summarized at the plot level. All analyses were performed with JMP statistical software (JMP 9.0; SAS Institute, Cary, North Carolina, USA).

We used least squares models to examine relationships of gap size and light characteristics and relationships of seedling height and light availability with gap light, fencing, and weeding treatments. Preliminary analyses indicated species-specific and often nonlinear seedling light and height responses to gap light. Therefore, we analyzed tree seedling responses by species and considered both linear and knotted splines to fit the main effects of light. Our protocol was to start with a linear fit, then add three knots, four knots, etc., retaining the added knots if they were supported by Bayesian information criterion (BIC) scores (i.e., decreased BIC scores by two units). For seedling height and light availability models where gap light main effects and/or interactions with fencing and/or weeding treatments were significant ($P < 0.05$), we fit regressions for fencing and/or weeding treatments separately using the same linear/nonlinear fitting criteria as for whole models. We followed the same protocol to fit gap size and light relationships. For regression models of height vs. gap light from Levering, we estimated height at 18.7% light using the "factor profiler" within the "fit model" platform of JMP. This light value was chosen to facilitate comparisons of Levering and Good Hart data, as 18.7% is the mean light level for small-group selection gaps (see further for definition) at Good Hart. For seedling light availability models, our focus was on the effects of shrub–herb vegetation, so we used only data from unweeded subplots and examined the effects of gap light and fencing. In cases where gap light effects were significant, we fit data with regressions as described previously. In cases where the fencing effect was significant and gap light was not, we generated least squares means (adjusted for light), for fencing treatments.

We used parametric survival analysis to examine the effects of gap light, fencing, and weeding main effects and interactions on mortality over 3 yr for each species. Seedlings used for survival analysis (8552 total) ranged from 98 for black walnut to 944 for white ash. Differences in seedlings numbers were due to a combination of the numbers available for planting (or naturally established) and survival during the first growing season. For this analysis, seedlings removed during the experiment (mostly all via thinning) and seedlings surviving at the end of the experiment (i.e., autumn 2014) were right censored for the analysis, which allowed them to contribute to estimates of mortality. We compared Weibull vs. log-logistic hazard distributions for our models. Both are two parameter models commonly used for parametric survival analysis. The Weibull models a constant hazard rate (i.e., exponential) or hazard rates monotonically increasing or decreasing with time. The log-logistic allows for nonmonotonic increasing followed by decreasing hazard rates and for decreasing hazard rates with time. The distribution we chose for each species was the one with the lowest BIC score. Based on the often nonlinear effects of light on survival we found in preliminary analyses, we also tested models with knotted splines fit to the main effects of light, and chose final models based on criteria previously described for evaluating knotted models.

Our nominal variable for deer browsing (browsed = yes, unbrowsed = no) considers whether or not individual seedlings alive through at least the third growing season (2013) showed any evidence of deer browsing in the 2013 census, the 2014 census, or both. These browsing data from Good Hart were analyzed

with a generalized linear model with a binomial distribution and a logit link function. First iteration analyses revealed that fences were completely successful in preventing deer browsing and that due to the near perfect fit for fenced data, a Hessian matrix suggested quasicomplete separation of the data that could result in fits and results for unfenced data of questionable value. Thus, to improve model fits for unfenced data we excluded fenced data and reran models for unfenced data only.

Although gap light and gap size are highly related (Walters et al. 2014), we report seedling responses to both because they emphasize different information. Light availability is functionally related to seedling growth and survival as well as shrub–herb canopy development. As such, light is more generalizable to seedling responses to a broad range of overstory disturbance intensities and spatial arrangements and compositions of the residual overstory canopy than are values specific to the centers of roughly circular harvest gaps. On the other hand, seedling responses to harvest gap size categories provide forest resource managers with information that is readily translatable to well-defined silvicultural methods. Our experiment was designed to examine the effects of continuous variation in gap size and light and not discrete, replicated gap sizes; thus, we restrict our main statistical analyses to the former. As such, data shown by gap size category are primarily for qualitative comparison and evaluating relative differences in seedling performance among gap sizes and treatments (see next paragraph). We grouped plots into gap size categories defined by regional silvicultural practices (State of Wisconsin Silviculture Handbook, http://dnr.wi.gov/topic/ForestManagement/documents/24315/24315.pdf). These were unharvested (no gap), single-tree selection (i.e., gaps created by removal of a single tree), small-group selection (< 1012 m^2 in size, i.e., < 0.25 acre), large-group selection (1012–2023 m^2, 0.25–0.5 acre), and patch cuts (2023–8094 m^2, 0.5–2 acres).

We developed two approaches for examining the effects of gap size categories and fencing × weeding treatment combinations on relative tree seedling performance; optimal gap size, an index of performance based mostly on height that emphasizes a species' performance relative to other gap size categories and rank order differences among species in height growth and survival.

We prioritize height over survival for our optimal gap size index for two reasons; the critical importance of juvenile height growth for escaping the height-dependent hazards of deer browsing and shrub–herb competition (M. B. Walters et al., *unpublished manuscript*) and the weaker responses of survival than height to light/gap size in our data. Optimal gap size is defined as the set of harvest gap size categories where mean seedling height is > 75% of the maximum gap size category for a particular treatment combination (e.g., fenced:weeded). Gap size categories passing the height criterion are then subject to modification by eliminating those where survival or height were < 33% of the maximum value observed for that species among all gap size categories and treatment combinations. This modification discriminates against misapplication of optimal gap size status to gap size–treatment combinations, where height or survival are so severely impacted by deer browsing and/or shrub–herb vegetation that eventual canopy recruitment is highly unlikely. We acknowledge that the specific criteria of our index have an arbitrary component and that values are informative for qualitative comparative purposes only.

Changes in rank order among species in height growth, survival, or growth vs. survival over gap size gradients would provide evidence consistent with gap partitioning theory. For most of our analyses of rank order changes, we contrast large-group selection gaps and single-tree selection gaps, as this comparison represents large differences in gap size that are also realistic management options for NH forests. Although fenced:weeded conditions are unlikely in either managed or unmanaged forests, this treatment combination represents benchmark reference conditions where tree seedlings are responding primarily to gap light environments and are unconstrained by the impacts of deer herbivory and shrub–herb competition. For these interspecific comparisons, we chose to use mean annual height growth over the interval autumn 2011–autumn 2014, as it does not incorporate pretreatment (i.e., 2010) seedling height differences among species and it corresponds to the same interval used to determine survival. We evaluated rank order changes between treatment combinations with Spearman's rank correlations.

Correlation coefficients are interpreted as a relative scale of rank order changes where ρ ranges from 1, indicating no change in ranks, to −1, indicating complete reversal of ranks (i.e., the larger the difference from 1, the greater the rank order changes in performance between treatments) (Walters et al. 2014).

Results

Gap size, shrub–herb vegetation, and light availability

At Good Hart, gap size ranged from 107 to 3234 m^2 and scaled closely with light in gap centers; from 3.1% beneath undisturbed forest canopy, to 70% in the largest patch cuts (Fig. 1A). At Levering, gap size ranged from 127 to 955 m^2 and light from 4.1% to 36% (data not shown). Given their high degree of scaling, hereafter we often use the terms gap size and gap light interchangeably. The largest harvest gap created by single-tree selection was a 459 m^2 gap at Good Hart created by removal of a 70 cm diameter (at 1.4 m height) American beech tree. At Good Hart, the number of gaps in each management-based category and their mean light levels were as follows: no harvest gap (4, 4.3%), single-tree (7, 7.0%), small-group (13, 18.7%), large-group (12, 39%), and patch cut (8, 61.7%). At Levering, these values were as follows: no harvest gap (4, 4.6%), single-tree (12, 7.2%), and small-group (29, 15.1%). Unless otherwise indicated results that follow are for Good Hart.

Shrub–herb vegetation responded strongly to harvest gap creation (Fig. 1B). As gap size increased, shrub–herb canopy height in gap centers increased up to approximately 1.8 m tall in 1500 m^2 gaps (35% light) and then declined slightly thereafter. Peak height at 35% light coincided with *Sambucus* peak abundance, which has taller canopies than *Rubus* (the most

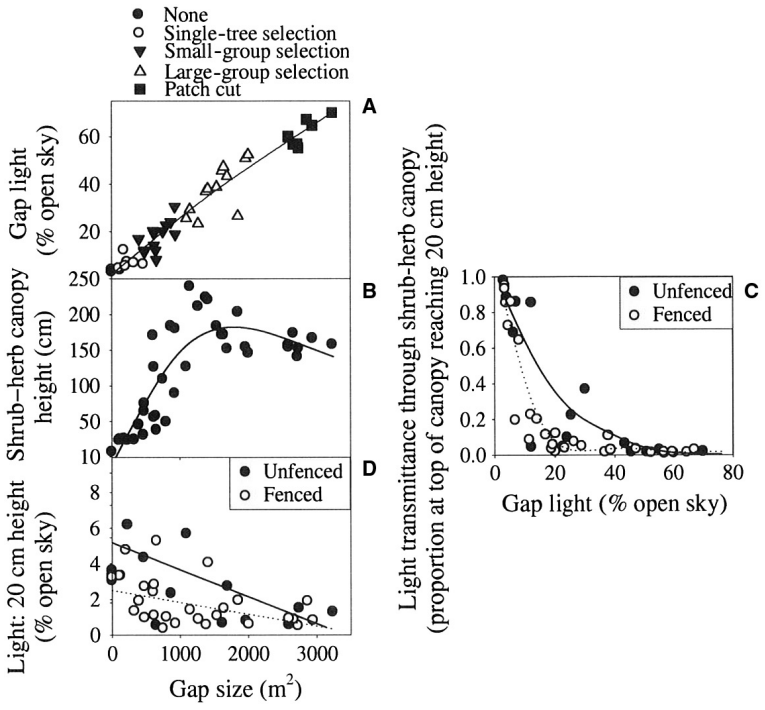

Fig. 1. Effect of overstory canopy gap size on (A) light reaching the top of understory vegetation strata (2 m height, gap light) at gap center, and (B) understory shrub–herb vegetation development (height). Effect of (C) gap light on proportional light transmission through shrub–herb canopy, and the (D) combined impacts of gap size and the shrub–herb canopy on light availability at 20 cm height. Fenced plots exclude deer herbivory, while unfenced do not exclude deer.

Table 2. Levels of significance (partial $P > |t|$) for the effects of fencing (deer excluded, not excluded), weeding (shrub–herb vegetation intact or removed), harvest gap light (continuous), and their interactions on seedling height from least squares models.

Species	Fencing	Weeding	F × W	Light	F × L	W × L	F × W × L
Paper birch	****	ns	*	****	**	ns	*
Yellow birch	****	ns	*	****	**	ns	**
American chestnut	****	ns	*	****	ns	ns	*
Quaking aspen	****	*	ns	****	ns	**	***
American elm	****	ns	ns	****	***	ns	ns
Black walnut	**	ns	ns	***	ns	ns	ns
Red maple	****	ns	*	****	**	ns	**
White ash	***	ns	ns	****	ns	ns	ns
Red oak	****	ns	*	****	**	*	**
Sugar maple	****	ns	ns	***	**	ns	ns
White spruce	ns	**	ns	****	ns	***	ns
White pine	****	ns	ns	****	ns	ns	ns
Balsam fir	ns	**	**	****	ns	**	ns
Eastern hemlock	ns	*	ns	**	ns	**	*
Bitternut hickory	ns	ns	ns	****	ns	ns	ns
Northern white cedar	ns	ns	ns	ns	ns	ns	ns

Notes: Fitting the main effects of light with a 3-knot spline was supported by Bayesian information criterion (BIC) scores (> 2 BIC scores lower) over linear fits for all species except sugar maple and northern white cedar. See Appendix S1 for a more complete summary of these models. ns $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

abundant shrub–herb species group). Unlike *Rubus, Sambucus* abundance diminished greatly in gaps > 1500 m^2 (data not shown). The proportion of light transmitted through shrub–herb canopies decreased as gap size increased, such that only ~2% of light incident on the top of the shrub–herb canopy reached the 20 cm reference height in the largest patch cut gaps (Fig. 1C). Decreasing shrub–herb light transmission (i.e., increasing canopy density) with increasing gap light resulted in shrub–herb vegetation negating the effects of gap size on light availability at 20 cm height; beneath shrub–herb canopies light was < 5% of open sky regardless of gap size (Fig. 1D). There was higher proportional light transmittance through the shrub–herb canopy in unfenced than fenced plots, presumably due to deer herbivory (Fig. 1C). This resulted in higher light at the 20 cm reference height in unfenced than fenced plots, with greater differences between smaller harvest gaps than larger harvest gaps (Fig. 1D).

Height responses to light, deer, and shrub–herb vegetation

For seedling height, the main effects of light were significant ($P < 0.05$) for 15 of 16 species. Fencing main effects were significant for 11 of 16 species, with shorter, slower-growing species less affected than taller, faster-growing species. In contrast, weeding main effects on height were significant for four species, with three of those being shorter, slower-growing conifers (Table 2, Appendix S1). Numerous significant interactions among light, fencing, and weeding effects, plus differences in the light distributions of plots among species and fencing × weeding treatment combinations (due to differences in mortality over 4 yr among them) necessitated that we compare height among species treatment combinations as functions of light (Fig. 2), qualitatively by gap size categories (Fig. 3), and, between Good Hart and Levering, at common light values (Fig. 4).

Among the four fencing × weeding treatment combinations, fenced:weeded seedlings, unconstrained by the negative impacts of deer herbivory and shrub–herb vegetation, were generally the tallest, and responded most strongly to gap light. Height increased with light up to approximately 35–45% of gap light for most species and then plateaued or decreased with further increases in light. Hereafter, we use the maxima of height vs. light regressions in the fenced:weeded treatments as a relative index of species growth

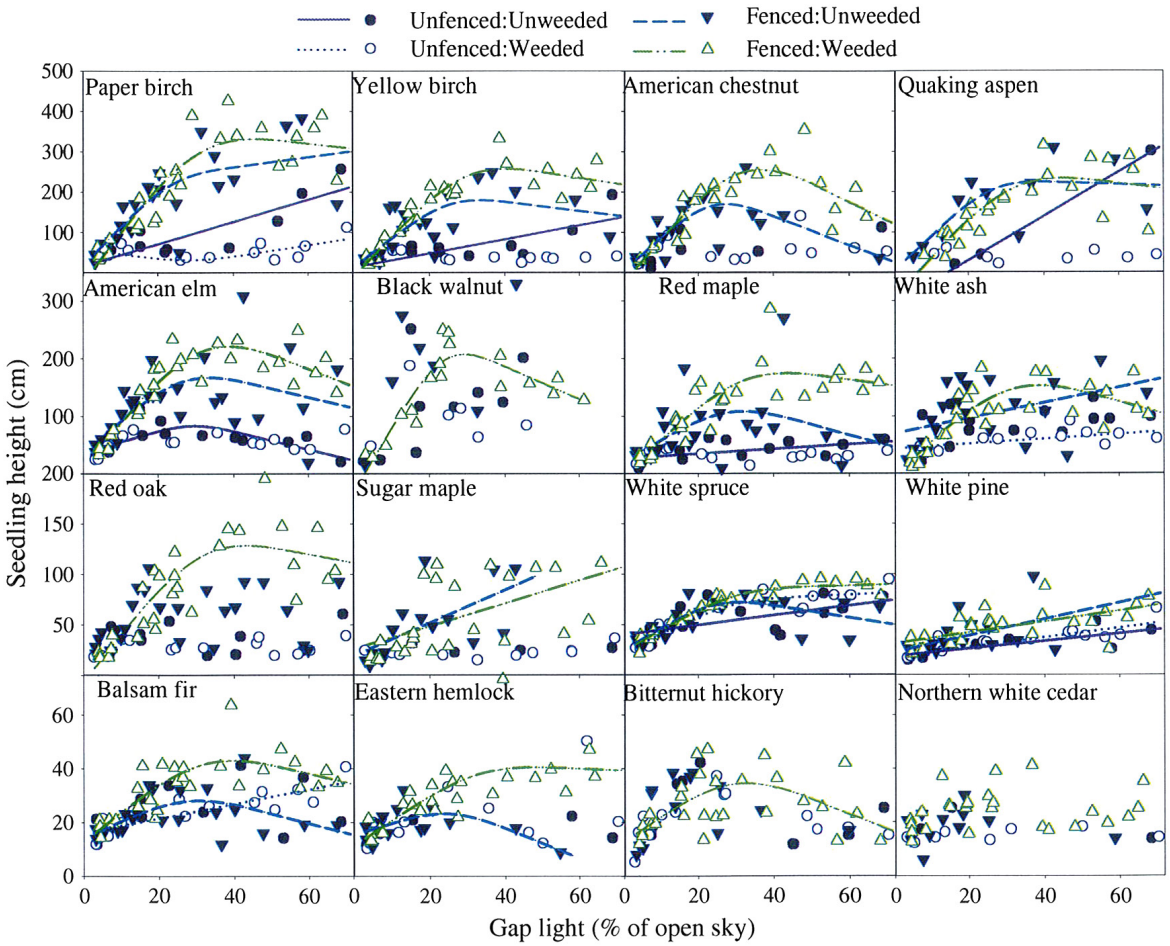

Fig. 2. Seedling height responses to harvest gap light. Data are plot means. For each species and fencing × weeding treatment combination, regression fits are shown if $P < 0.05$. Fits are either linear or modified with a 3-knot spline depending on Bayesian information criterion scores (see *Methods*). Species are arranged from top left to bottom right in descending order of species predicted height maxima in the fenced:weeded treatment (see Table 1). The scale of the *y*-axis is different for each row of panels.

potential (i.e., faster-growing vs. slower-growing) (Table 1).

In fenced plots (i.e., no deer impacts), shrub–herb vegetation negatively affected height, and more so at higher than lower light for nine of 16 species (i.e., light × weeding or light × weeding × fencing interactions were significant; Table 2, Figs. 2 and 3). This pattern parallels increases in shrub–herb density with increasing light (Fig. 1C). In unfenced plots, deer browsing negatively impacted height for most species, with decreases generally greater for faster-growing species (Table 2, Figs. 2 and 3). For unfenced:weeded seedlings, deer browsing negated the effects of light on height for all species except balsam fir, white pine, and white spruce.

Deer browsing impacts at Levering mostly confirm and extend the results from Good Hart (i.e., seven vs. four growing seasons, respectively). For seven of 11 species common to both sites, height was negatively impacted at both sites (Fig. 4). Of the other four species common to both sites, deer browsing impacted sugar maple and white pine at Good Hart but not Levering. This suggests that deer browsing pressure might be somewhat lower at Levering than Good Hart, which is consistent with our casual observations. The other two, balsam fir and eastern hemlock,

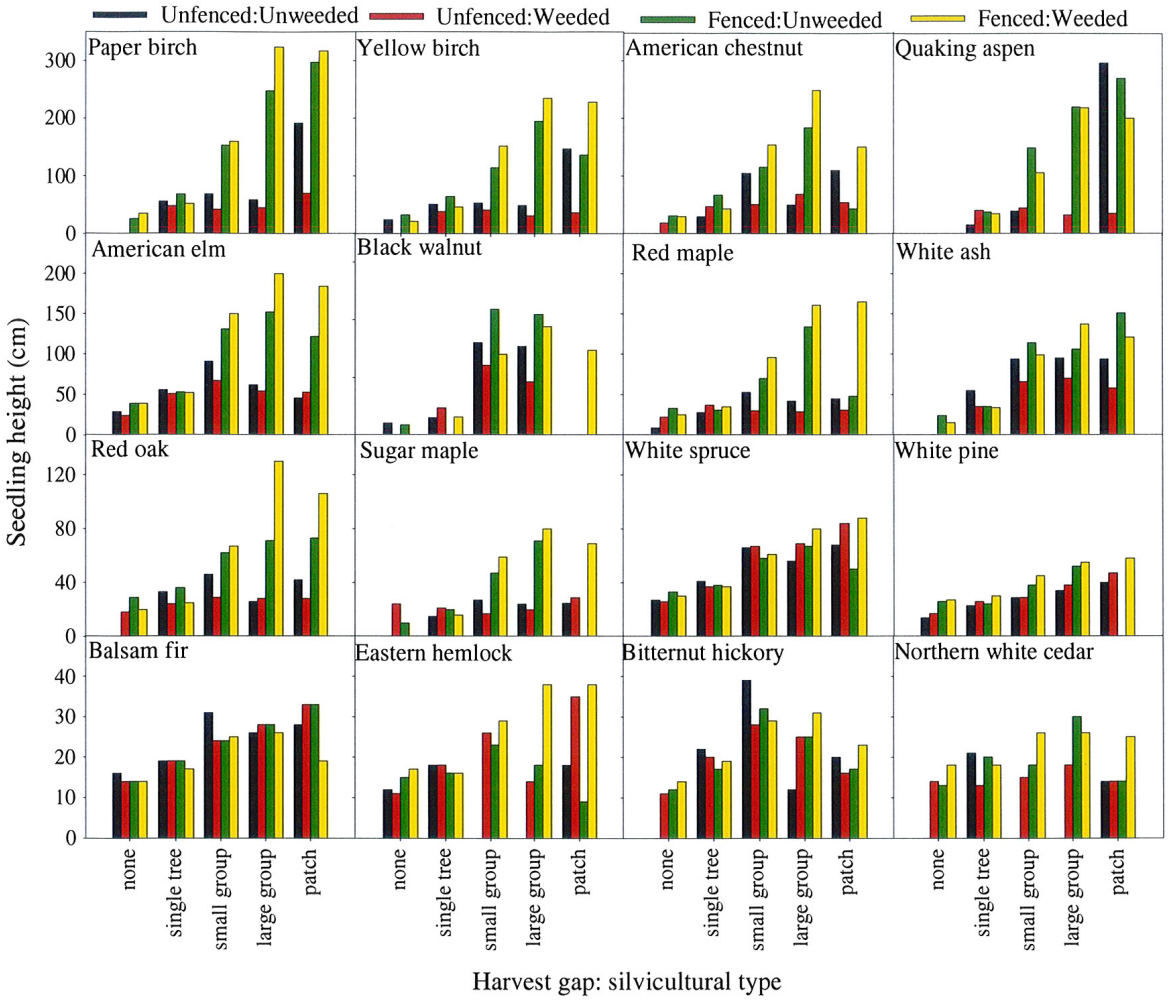

Fig. 3. Mean seedling height in the 4th growing season by harvest gap category. The scale of the *y*-axis is different for each row of panels.

were impacted at Levering but not Good Hart, but height for these slower-growing species was not diminished by deer at Levering until their 6th and 7th growing seasons, respectively. Between the two sites, there were four other species that showed no height reductions from deer: browsing-avoided American beech (only Levering) and white spruce (both sites), and slower-growing bitternut hickory and northern white cedar, which are only at Good Hart and perhaps not yet affected by browsing.

Levering data also indicate that some species strongly negatively impacted by deer still maintained positive height growth over the last 7 yr, albeit more slowly than for fenced seedlings, while others did not. Those maintaining positive height growth include American elm and white ash, whereas those with little change in height over the years include red maple, red oak, and yellow birch (Fig. 4).

Contrary to the uniformly negative impacts of deer and shrub–herb vegetation, the interaction of these factors (i.e., unfenced:unweeded) increased seedling height relative to deer only effects (unfenced:weeded) for faster-growing paper birch, yellow birch, and aspen, with this pattern driven by height differences only in the largest, highest-light patch cut gaps (Figs. 2 and 3). Several other species also showed a trend (supported in some cases by significant fencing × weeding

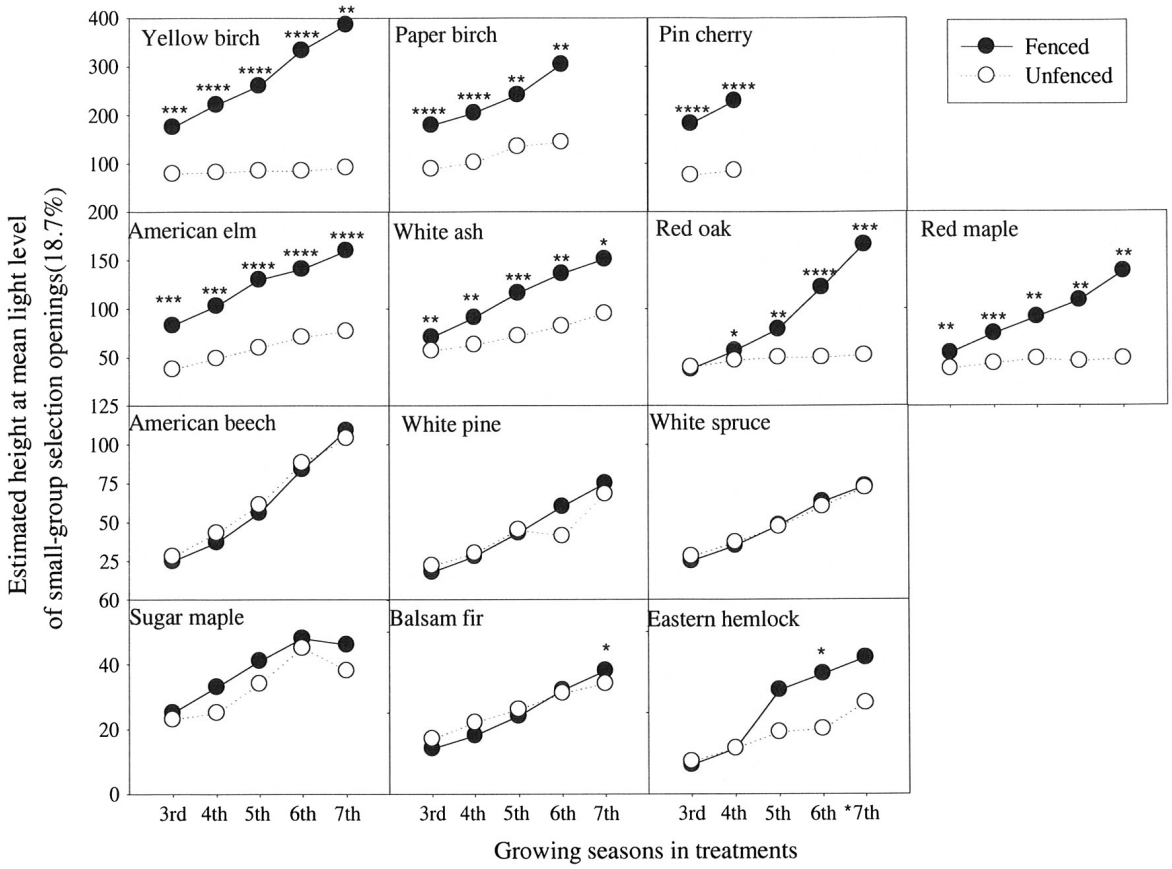

Fig. 4. Seedling height at Levering estimated from height vs. light regressions at 18.7% of open sky light (see *Methods* for rationale). Asterisks indicate significant fencing main treatment effects in models that also included light and light × fencing interactions: ****$P < 0.0001$; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; no symbol $P > 0.05$. The scale of the *y*-axis is different for each row of panels.

interactions; Table 2) for greater seedling heights in unfenced:unweeded than unfenced:weeded plots, but differences were modest and did not show the same dependence on gap size/light that faster-growing species exhibited (e.g., American chestnut, red maple; Fig. 3). For a few species and gap sizes, mean heights of unfenced:unweeded seedlings exceeded those of seedlings impacted by shrub–herb vegetation alone (fenced:unweeded) (e.g., balsam fir, white spruce, and bitternut hickory in small-group selection gaps; Fig. 3), but again, differences were modest and untested statistically (see *Methods*).

Survival responses to light, deer, and shrub–herb vegetation

Compared to height, the main effects of light and fencing on survival were weaker and significant for fewer species (eight for light, seven for fencing), whereas the main effects of weeding were stronger and significant for more species (10) (Table 3, Appendix S2). Like height, there were several significant interactions among effects and most were for light × weeding interactions (eight species). Unlike height data, survival data have similar gap/light distributions among species and fencing × weeding treatment combinations due to our planting criteria. This allows us to compare weeding and fencing effects on survival both with (Figs. 5 and 6) and without (Table 4) having to consider the inconsistent effects of light/gap size (Table 3) on these relations.

Among the four treatment combinations, survival for all species was greatest, or nearly so, in the fenced:weeded treatment (Table 4).

Table 3. Levels of significance (partial $P > \chi^2$ vales) for the effects of fencing, weeding, harvest gap light, and their interactions on seedling survival from parametric survival models.

Species	Fencing	Weeding	F × W	Light	F × L	W × L	F × W × L
Paper birch	ns	*	ns	ns	ns	*	ns
Yellow birch	ns	ns	ns	**	ns	*	ns
American chestnut	**	**	ns	ns	ns	ns	ns
Quaking aspen	**	**	ns	ns	ns	ns	ns
American elm	ns	ns	ns	**	ns	**	ns
Black walnut	—	—	—	****	—	—	ns
Red maple	****	ns	*	**	ns	**	**
White ash	ns	ns	ns	***	ns	***	ns
Red oak	**	*	ns	ns	ns	**	ns
Sugar maple	ns	*	ns	**	ns	ns	ns
White spruce	ns	**	ns	ns	ns	*	ns
White pine	ns	****	ns	ns	*	**	ns
Balsam fir	****	**	ns	ns	ns	ns	ns
Eastern hemlock	****	*	ns	****	*	ns	ns
Bitternut hickory	ns	ns	ns	ns	ns	ns	ns
Northern white cedar	****	*	ns	***	ns	ns	ns

Notes: See Appendix S2 for a more complete summary of these models. ns $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

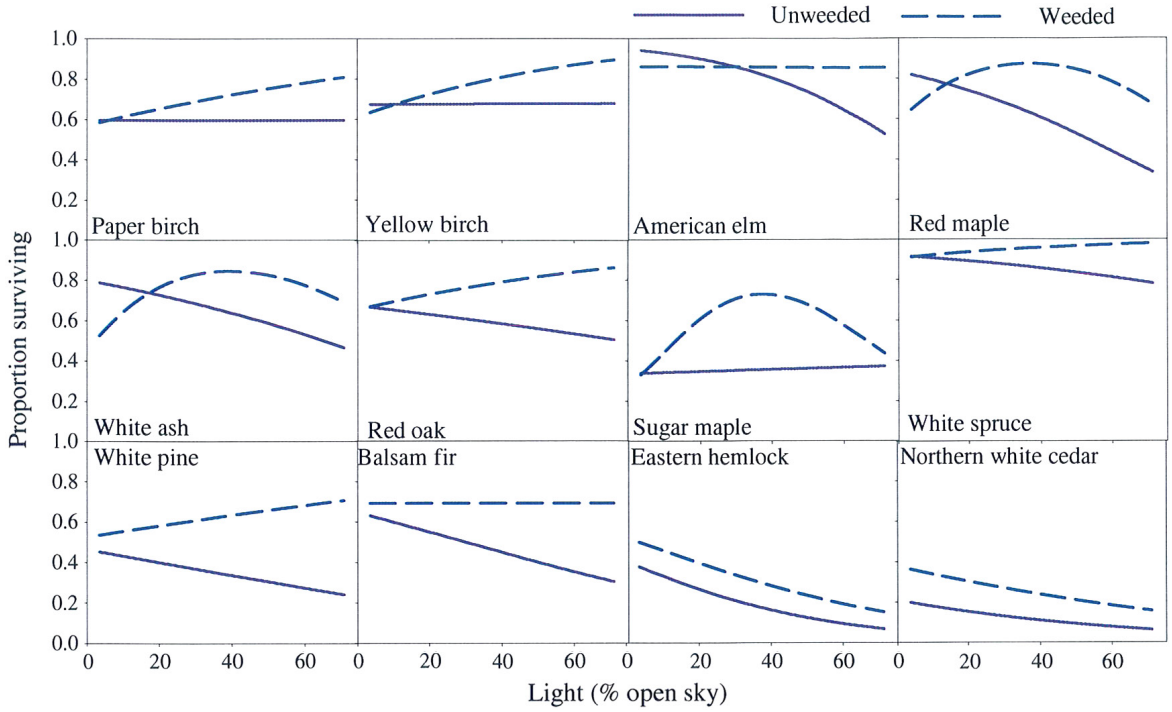

Fig. 5. Seedling survival (end of 1st–end of 4th year in treatments) vs. gap light availability by weeding treatments (fencing treatments pooled). Only those species where light and/or light × weeding effects on survival were significant ($P < 0.05$) are shown (Table 3, Appendix S2).

Three-year survival for fenced:weeded seedlings varied appreciably among species, from 40% for northern white cedar to 96% for white spruce. Deer decreased survival the most for hemlock (64%) and cedar (83%) with reductions not exceeding 36% (balsam fir) for other species. Given that hemlock and cedar heights were unaffected by fencing (Table 2, Fig. 2), our survival

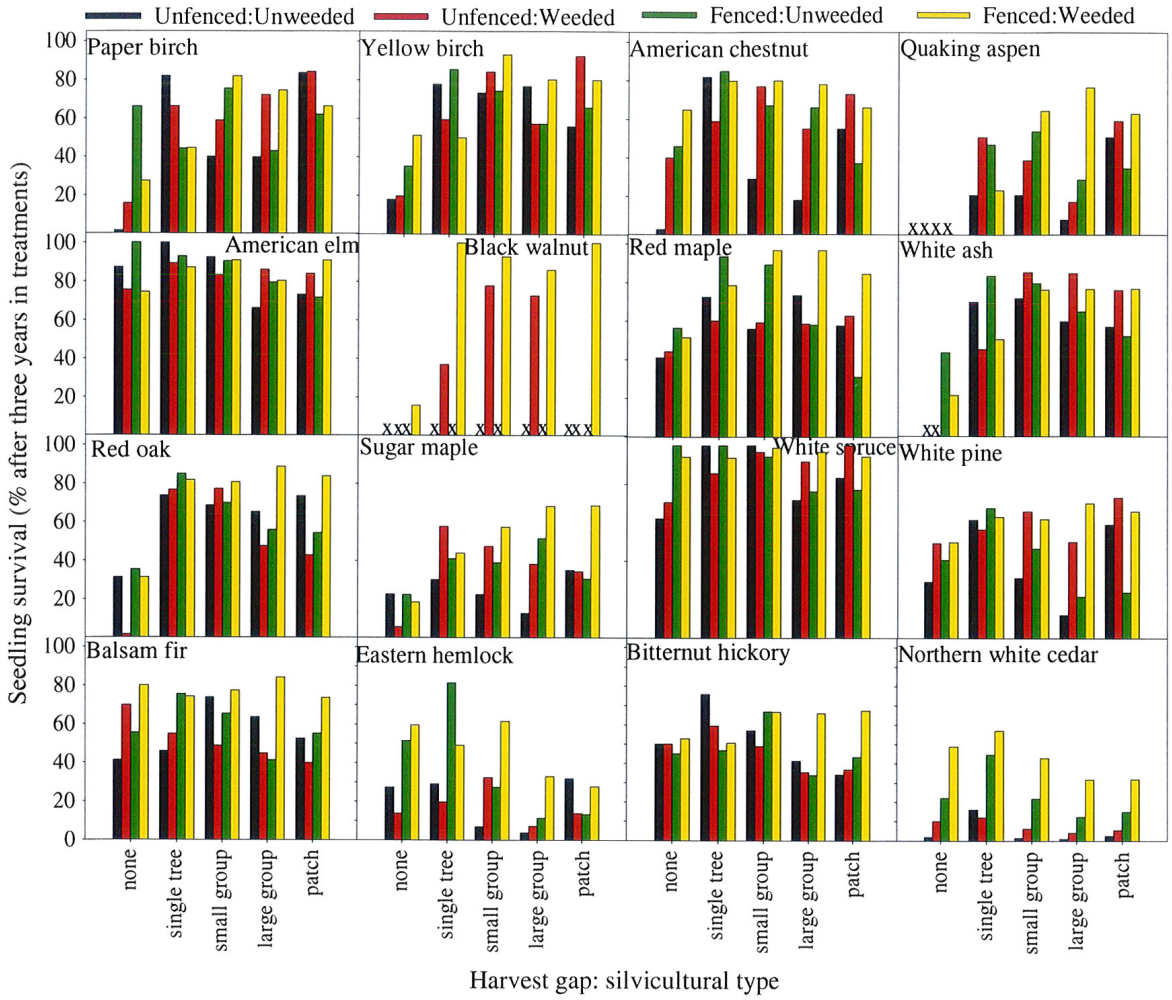

Fig. 6. Mean seedling survival (end of 1st–end of 4th growing season) by harvest gap category. "*x*" indicates that there were no or few seedlings for these treatment combinations to distinguish them from "0" values.

data indicate that seedlings of these species do not survive browsing damage. In contrast, faster-growing paper birch, yellow birch, and American elm had high survival despite seedlings being browsed so heavily that unfenced:unweeded seedling heights were 10–20% of fenced:weeded seedling heights (Table 4 vs. Fig. 2). On the other end of the spectrum, fencing affected neither survival nor height for slower-growing spruce and hickory. The greatest reductions in survival from shrub–herb vegetation (i.e., fenced:unweeded vs. fenced:weeded) were for slower-growing northern white cedar (50%), white pine (41%), and eastern hemlock (38%), despite cedar and hemlock being considered the most shade-tolerant species in our study (Tables 1 and 4). In contrast to height, for which shrub–herb vegetation partially ameliorated negative deer impacts, survival among the four treatment combinations was lowest for unfenced:unweeded seedlings for nearly all species (i.e., fencing and weeding had additive, not interacting effects on survival).

For seedlings responding primarily to light availability and not deer and/or shrub–herb vegetation (i.e., fenced:weeded seedlings), patterns of survival varied among species and in a manner roughly consistent with variation in their shade tolerance scores (Table 1, Figs. 5 and 6). Survival increased with gap light, plateauing in small- to

Table 4. Parametric survival model estimates of the proportion of seedlings that lived from the end of the 1st to the end of the 4th growing season by fencing × weeding treatment combinations and the significance level of fencing and weeding main effects and interactions for models used to develop estimates.

Species	Treatment combination†				Significance		
	UF:UW	UF:W	F:UW	F:W	Fencing	Weeding	Interaction
Paper birch	0.59	0.67	0.59	0.68		*	
Yellow birch	0.68	0.64	0.66	0.79			
American chestnut	0.40	0.64	0.63	0.76	**	**	
Quaking aspen	0.24	0.45	0.41	0.65	**	**	
American elm	0.84	0.84	0.85	0.86			
Black walnut	0.91	0.66	0.74	0.88			
Red maple	0.62	0.58	0.70	0.87	****		*
White ash	0.64	0.77	0.70	0.71			
Red oak	0.57	0.65	0.64	0.79	**	*	
Sugar maple	0.28	0.43	0.40	0.54		*	
White spruce	0.83	0.90	0.88	0.96		*	
White pine	0.38	0.55	0.37	0.63		*	
Balsam fir	0.41	0.50	0.58	0.79	****	***	
Eastern hemlock	0.16	0.17	0.29	0.47	****	*	
Bitternut hickory	0.51	0.46	0.50	0.63			
Northern white cedar	0.05	0.07	0.20	0.40	****	*	

Notes: The effects of light were not included in the generation of model estimates. See Table 3 and Fig. 5 for models including light. *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$; ****$P < 0.0001$.

† Treatment combinations are unfenced:unweeded (UF:UW), unfenced:weeded (UF:W), fenced:unweeded (F:UW), and fenced:weeded (F:W).

large-group selection gaps for some lesser-tolerant species (e.g., the birches, red oak, white pine), whereas survival decreased with increasing light/gap size for shade-tolerant eastern hemlock and northern white cedar. Shrub–herb vegetation modified survival responses to gap light for 12 species with significant light × weeding interactions for eight of the species (Table 3), consistently indicating increasingly negative impacts of shrub–herb vegetation in higher light (Fig. 5) and in larger harvest gaps (Fig. 6). For example, at 5% light, white pine survival was ~60% for both weeded and unweeded seedlings, but as light increased to 70% in patch cuts, survival increased to ~70% for weeded seedlings and decreased to ~6% for unweeded seedlings. Compared to strong light × weeding interactions on survival (Table 3) and strong light × fencing interactions on height for some species (Table 2), light × fencing interactions on survival were universally weak (Table 3) and only significant for eastern hemlock and white pine. In these two cases, however, light × fencing interactions did not impact the general pattern of light × weeding interactions (e.g., survival for eastern hemlock decreased with increasing light for weeded and unweeded seedlings [Fig. 5] regardless of whether seedlings were fenced or not [data not shown]).

What explains the positive interactions of shrub–herb vegetation and deer herbivory on tree seedling performance?

The positive impacts shrub–herb vegetation had on paper birch, yellow birch, and aspen height in unfenced, high-light patch cut plots can be partly explained by how gap size/light and shrub–herb vegetation affect the likelihood of becoming browsed (Fig. 7). For most species, as gap size/light increases, browsing probability decreases in unweeded plots and increases in weeded plots. For example, faster-growing yellow birch seedlings have an approximately 75% chance of being browsed in 5% light in weeded and unweeded plots. However, as light increases to 70% (middle of patch cut gaps), browsing probability declines to 25% for unweeded seedlings and increases to 100% for weeded seedlings. Thus, shrub–herb vegetation appears to provide some protection to seedlings from browsing deer, especially in higher-light environments where shrub–herb density is greater (Fig. 1).

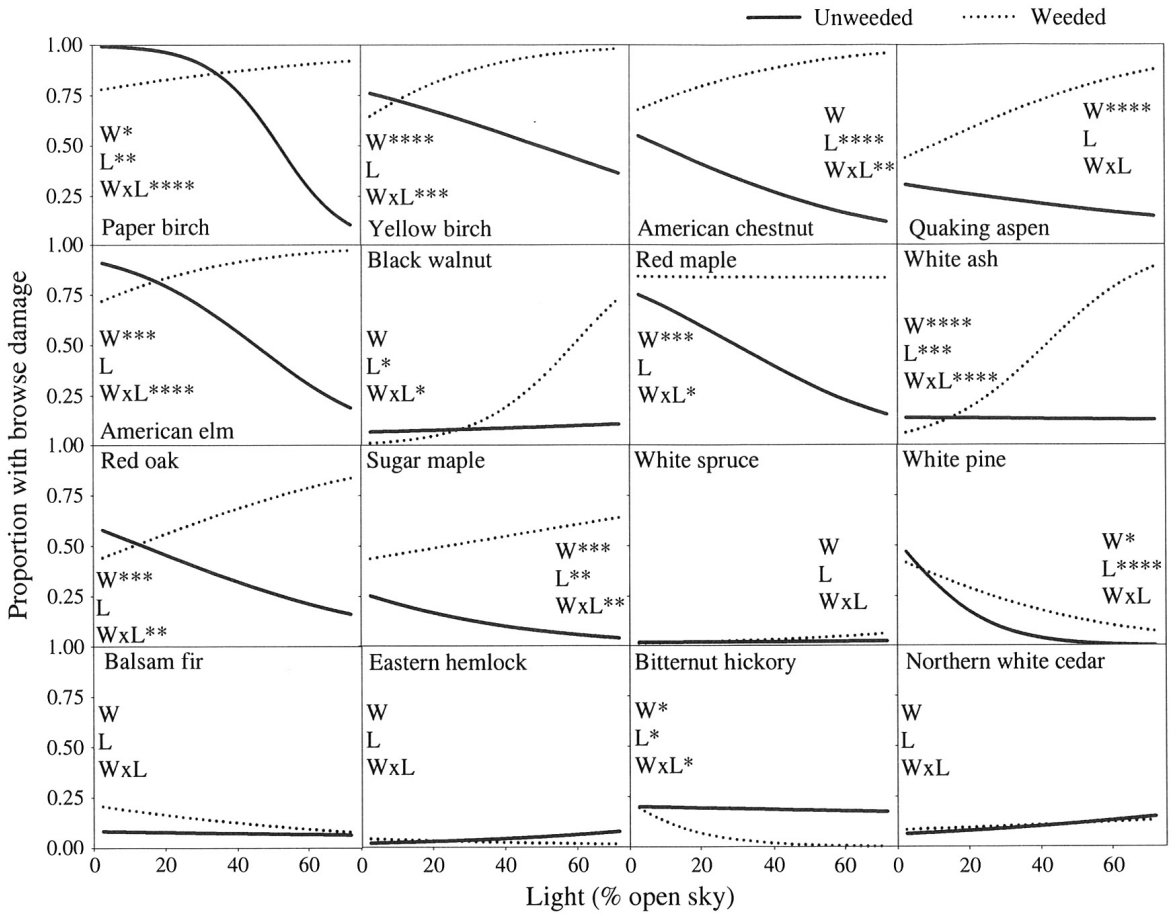

Fig. 7. Browsing probability vs. light for unfenced plots. Regressions are generalized linear model fits (see Methods). The level of significance from general linear models of browsing probability predicted by weeding (W) and light (L) effects, and their interactions (W × L) are indicated; ****$P < 0.0001$; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; no symbol $P > 0.05$.

We also found that herbivory by deer can either increase or decrease light to tree seedlings depending on the balance between increased light transmission through browsed canopies vs. decreased light to shorter, browsed seedlings. In fenced plots, light environments for faster-growing species were little affected by shrub–herb vegetation, as seedlings were able to maintain their canopies at or above the shrub–herb canopy (Fig. 8, Appendix S3), whereas seedlings of slower-growing species were beneath shrub–herb canopies and experienced low light levels. In unfenced plots, deer decreased light most for faster-growing, heavily browsed species, like elm, by decreasing seedling height to such an extent that their canopy positions were shifted from dominant to subordinate relative to shrub–herb vegetation (Fig. 8). In contrast, deer herbivory of shrub–herb vegetation increased light availability to seedlings of those slower-growing species that had little to no height reduction from browsing (i.e., white spruce, white pine, balsam fir, and bitternut hickory [Table 2, Fig. 2]). The increases in light from deer were modest (Fig. 8), but within the range where seedling growth rates responded strongly to light (Fig. 2). Deer appear to boost light levels the most around 15–30% gap light, which is consistent with the weak trend of greater height for unfenced than fenced white spruce, balsam fir, and bitternut hickory (but not white pine) in single-tree and/or small-group selection gaps (Fig. 3).

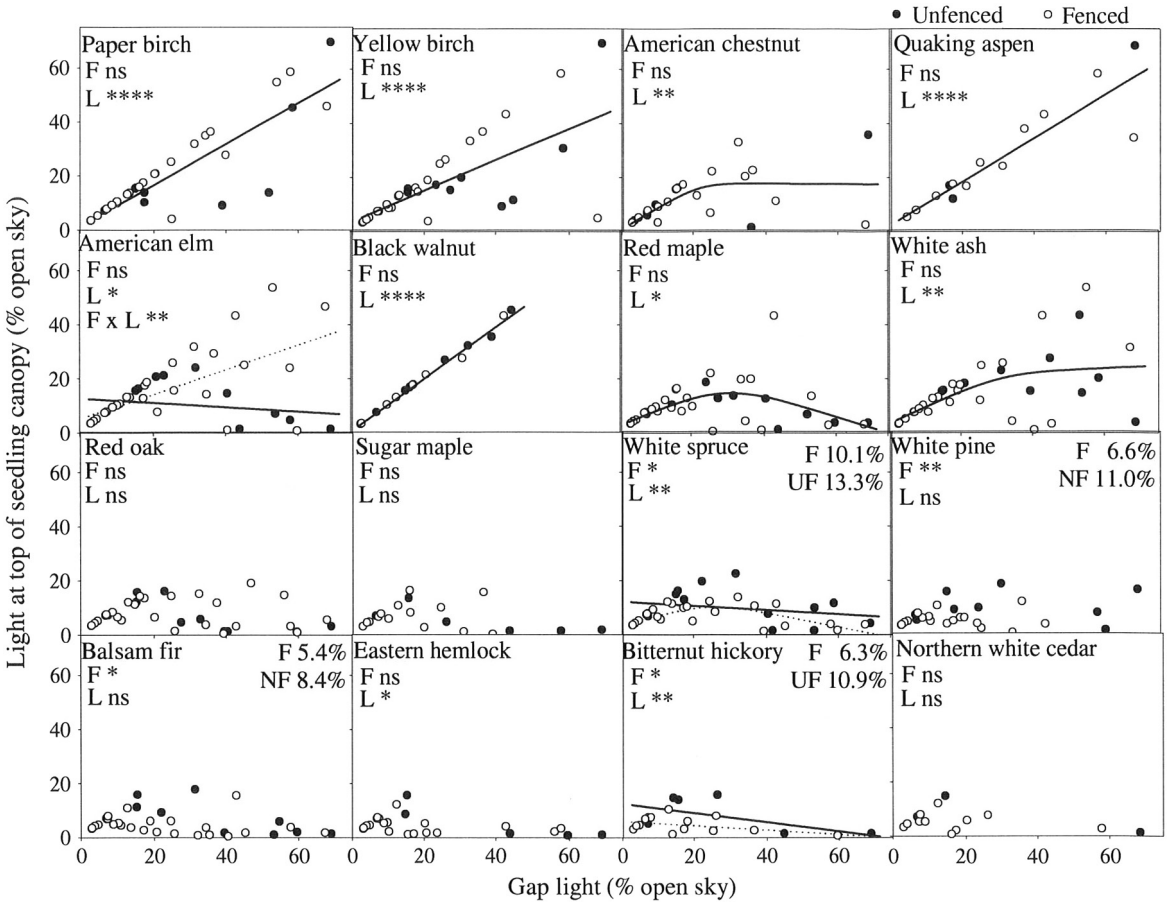

Fig. 8. Seedling light availability vs. gap light availability in fenced:unweeded and unfenced:unweeded plots. Level of significance for main effects of fencing (F), light (L) and their interactions (F × L, only when significant) are shown; ****$P < 0.0001$; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns $P > 0.05$. Straight lines or 3-knot splines are fitted to unfenced (solid line) and fenced (hatched line) treatments when light and fencing main effects or interactions were significant, a single solid line is fitted when only light effects were significant, and least squares means, adjusted for light, are presented for fenced (F) and unfenced (UF) treatments when only fencing effects were significant. See Appendix S3 for a more complete summary of these models.

Species gap size optima and performance ranks

Fenced:weeded seedlings generally had a broad range of optimal gap sizes; from large-group selection gaps and patch cuts for faster-growing species and small-group to patch cuts for slower-growing species (Table 5). Strong shrub–herb impacts in high light shifted optimal gap size to a smaller range and size of gaps for nearly all species (e.g., Figs. 3 and 6, Table 5). Shifts in optima were particularly dramatic for eastern hemlock and northern white cedar because of the high seedling mortality shrub–herb vegetation elicited in larger gap size categories (Fig. 6). Adding the effects of deer herbivory to shrub–herb effects (i.e., unfenced:unweeded) shifted optimal gap size for several species, and especially the faster-growing, more shade-intolerant species to patch cuts, where browsing was less likely to occur. For red maple, sugar maple, and northern white cedar, height and/or survival were impacted so severely that no optimal gap size could be assigned (Figs. 3 and 6, Table 5).

Evidence for gap size (large-group vs. single-tree) and fencing × weeding treatment

Table 5. Optimal gap size for tree seedlings for three fencing × weeding treatment combinations.

Species	Optimal gap size category		
	Fenced:Weeded	Fenced:Unweeded	Unfenced:Unweeded
Paper birch	LG-P	LG-P	P
Yellow birch	LG-P	LG	P
American chestnut	LG	LG	P
Quaking aspen	LG-P	LG	P
American elm	LG-P	SG-LG	SG
Red maple	LG-P	LG	—
White ash	LG-P	P	SG-P
Red oak	LG-P	SG-LG	SG
Sugar maple	LG-P	LG	—
White spruce	SG-P	SG-LG	SG-P
White pine	SG-P	SG	P
Eastern hemlock	SG-P	ST	UN-ST
Balsam fir	SG-P	SG-P	SG-P
Bitternut hickory	SG-LG	SG-LG	SG
Northern white cedar	SG-P	ST	—

Notes: Optimal gap size is the range of harvest gap sizes where mean seedling height is > 75% of the maximum height gap category for the treatment combination considered and seedling height and survival is > 33% of the maximum value among all gap size and treatment combinations. Gap size categories are unharvested (UN), single-tree (ST), small-group (SG), large-group (LG), patch (P), and no applicable optimal gap size (—).

combination contrasts eliciting rank order changes in growth, survival, or growth vs. survival among species were mixed. There was no evidence for rank order reversals (i.e., a negative Spearman ρ) for any comparison of 3-yr height growth and/or survival in large-group vs. single-tree selection gaps. Instead, results ranged from appreciable changes in rank order (Spearman's ρ nearer to 0) to little change in rank order (Spearman's ρ nearer to 1) (Figs. 9 and 10, and data not shown).

For height growth, shrub–herb vegetation had minimal impacts on species rank order in large-group selection gaps, whereas deer + vegetation had strong effects (i.e., shrub–herb vegetation, fenced:weeded vs. fenced:unweeded, Spearman's $\rho = 0.94$, $P < 0.001$, whereas deer + vegetation, fenced:weeded vs. unfenced:unweeded, $\rho = 0.27$, $P = 0.360$). In contrast, deer impacts on height growth rank order were not as dramatic in single-tree selection gaps, where rank order changes were similar for shrub–herb vegetation and deer + vegetation ($\rho = 0.63$, $P = 0.012$ and $\rho = 0.58$, $P = 0.018$, respectively) (Fig. 9). However, the rank of particular species differed between the contrasts (e.g., American chestnut ranked 1st in growth in the fenced:unweeded treatment while white ash ranked 1st in unfenced:unweeded).

There were substantial height growth rank order differences between gap sizes, with the greatest difference for the fenced:weeded pair ($\rho = 0.144$, $P = 0.593$), where growth differences between gap sizes were largest (−0.8 to 7.7 cm/yr in single-tree selection gaps vs. 5–92 cm/yr in large-group selection gaps) and least between unfenced:unweeded pairs ($\rho = 0.590$, $P = 0.0353$) (Fig. 9). Among all 15 possible treatment combination pairs, the largest height growth rank order differences were between the treatment combinations that were among the most environmentally different (i.e., single-tree selection unfenced:unweeded vs. large-group selection fenced:weeded [$\rho = 0.053$, $P = 0.846$]).

Changes in species survival rank order between treatment combination pairs were generally more modest than for height growth (Fig. 10 vs. Fig. 9). In large-group selection gaps, shrub–herb vegetation impacted rank order (fenced:weeded vs. fenced:unweeded, $\rho = 0.73$, $P = 0.002$) more than deer + vegetation (fenced:weeded vs. unfenced:unweeded, $\rho = 0.83$, $P = 0.001$), whereas deer + vegetation elicited greater changes in rank order ($\rho = 0.55$, $P = 0.035$) than vegetation alone ($\rho = 0.76$, $P = 0.002$) in single-tree selection gaps. Survival rank order changes between harvest gap size categories were similar for all three treatment

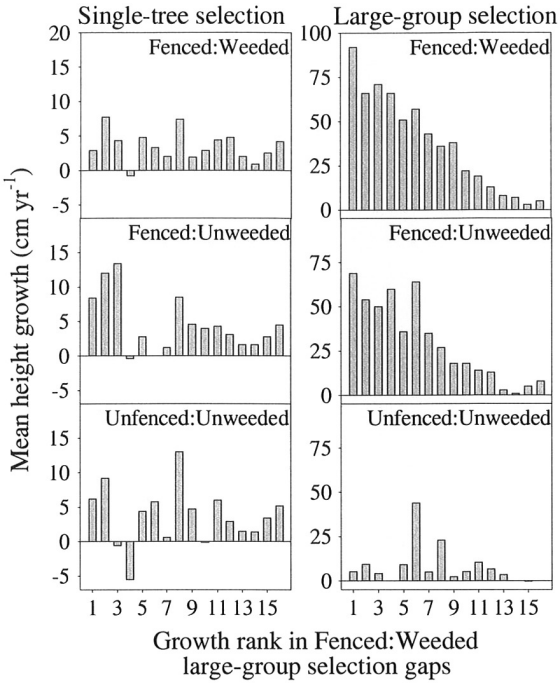

Fig. 9. Species mean annual growth rate (end of 1st–end of 4th year) for weeding × fencing treatment combinations for single-tree selection and large-group selection harvest gaps. The left to right order of species corresponds to species ranks of mean annual growth rate for fenced:weeded seedlings in large-group selection gaps (i.e., upper right panel). See Appendix S4 for species correspondence to *x*-axis order. "*x*" indicates that there were no or few seedlings for these treatment combinations to distinguish these from "0" values.

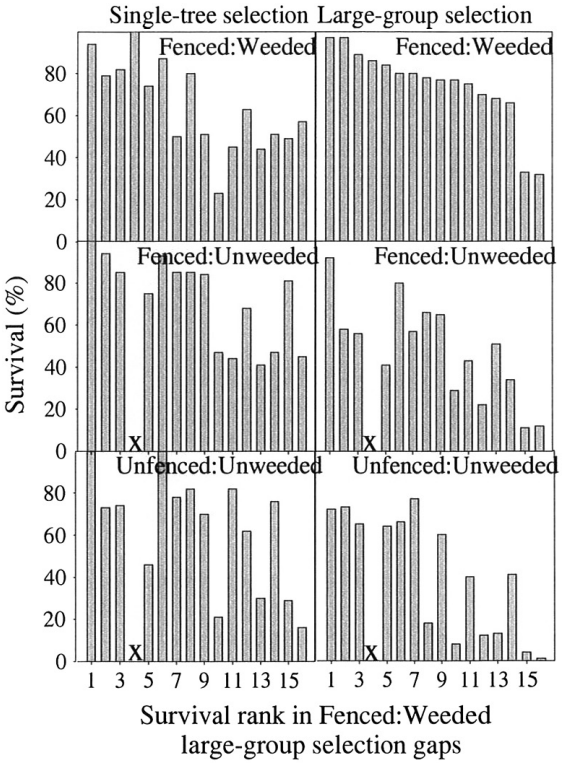

Fig. 10. Estimated survival (end of 1st–end of 4th year) by weeding × fencing treatment combinations for single-tree selection and large-group selection harvest gaps. Species rankings from left to right are for fenced:weeded seedlings in large-group selection gaps (upper right panel). See Fig. 9 legend for other details.

pairs (range in ρ = 0.67–0.70). Similar to height comparisons, the greatest change in survival rank order was for pairs that were among the most environmentally different; fenced:weeded seedlings in single-tree selection gaps vs. unfenced:unweeded seedlings in large-group selection gaps (ρ = 0.51, $P = 0.051$).

Among the 36 possible growth vs. survival treatment combination pairs, rank order correlations ranged from ρ = 0.00, $P = 0.996$ for survival in fenced:weeded, single-tree selection gaps vs. growth in fenced:unweeded, large-group selection gaps to ρ = 0.501, $P = 0.058$ for survival in fenced:unweeded, large-group selection gaps vs. growth in fenced:weeded, large-group selection gaps. Thus, growth and survival rank order was most positively associated (albeit weakly) in large-group selection gaps without deer, and were most different when contrasting rank order of survival in low light and growth in large gaps under ideal conditions (fenced:weeded). Although there was no evidence of inverse rank order for growth vs. survival between the particular treatment combinations contrasted, there was for contrast based on survival restricted to the last annual interval (3rd–4th year) and the lowest-light plots (i.e., harvest gap and unharvested plots < 5% light; Table 1) vs. height growth rate of fenced:weeded seedlings in high-light, large-group selection gaps (Fig. 11). This suggests that the negative impacts of low light levels on the survival of trees seedlings that grow rapidly in high light are just beginning to occur after four growing seasons in experimental treatments.

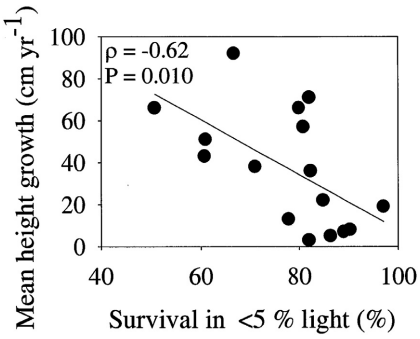

Fig. 11. Mean annual growth rate for fenced: weeded seedlings in large-group selection gaps vs. mortality for seedlings in harvest gap and unharvested plots receiving < 5% light. Survival is the percentage of seedlings alive at the end of the 3rd year in treatments that were alive at the end of the 4th year.

Discussion

Harvest gap size mediates gap light, shrub–herb vegetation, and deer herbivory impacts on regenerating tree seedlings

In mesic NH forests, harvest gap size has multiple impacts on regenerating tree seedling environments. In addition to obvious effects on light transmission to the understory, harvest gap size also affects the density of potentially competing shrub–herb vegetation and the probability of seedlings being browsed by deer. These factors had complex interacting effects on tree seedling growth and survival, with species-specific responses associated with variation in height growth potential, shade tolerance, and responses to browsing pressure.

Before harvest gap creation, shrub–herb vegetation cover is sparse and short-statured in the low (2–6%) light beneath the undisturbed, closed-canopy forest. Following harvesting, shrub–herb stature and density increase; slowly the first growing season following harvest and more rapidly thereafter (M. B. Walters, *unpublished manuscript*). Regardless of gap size, shrub–herb responses to gap harvesting result in light levels beneath their canopies that are comparable to those beneath closed-canopy forest. Thus, harvest gap increases in light to the forest floor stratum, where tree seedlings germinate and establish, are ephemeral. This dynamic suggests that faster-growing and earlier-establishing seedlings are in a better position, via height advantages, to avoid light competition with developing shrub–herb vegetation compared to later-establishing and slower-growing seedlings. The greater ability of shade-tolerant species to survive in low light could partially offset the disadvantage of slower growth in coping with shrub–herb competition. However, data from our study indicate that seedling height growth potential (maximum height in fenced:weeded plots) was more important than shade tolerance (i.e., seedling survival at < 5% light) in alleviating mortality from shrub–herb vegetation, but both factors contributed (Fig. 12).

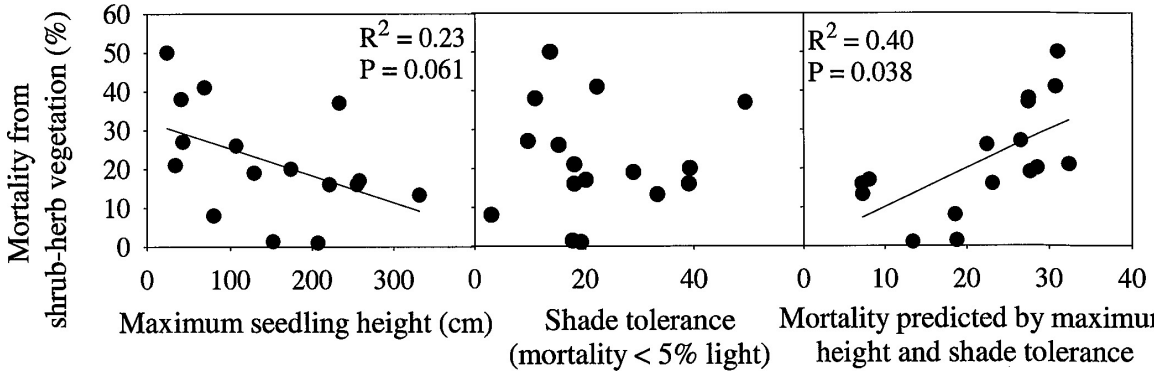

Fig. 12. Mortality from shrub–herb vegetation (from Table 4, where mortality (%) = 1 − (survival fenced:unweeded/survival fenced:weeded)) vs. maximum seedling height and shade tolerance score from Table 1. For mortality predicted by the combination of maximum height and shade tolerance in multiple regression (right panel), partial *P* values were 0.0122 for height and 0.0810 for shade tolerance.

Given these patterns, an important caveat to our conclusions regarding shrub–herb effects is that our results are influenced by the particular tree seedlings, treatments, and sites we used. Our seedlings were 1 yr old when planted at the beginning of the second growing season following harvest gap creation, and we weeded (i.e., clipped) shrub–herb vegetation in unweeded plots the first couple of months following transplanting. Patterns in seedling responses to experimental treatments within and among species could have differed somewhat from what we found had seedlings established naturally and/or at a different time (e.g., first or third year following harvest or already established prior to harvest [i.e., advance regeneration]). Furthermore, our sites are classified as the most resource-rich habitat type regionally (Burger and Kotar 2003), which supports an especially well developed and competitive shrub–herb layer following disturbance (J. Willis, *unpublished manuscript*). Thus, shrub–herb impacts on tree seedlings could be weaker on less fertile sites than the one we used.

In stands characterized by deer populations of ~10.4/km^2, deer impacts on tree seedlings were nearly universal, with 15 of 18 species across the two sites affected. However, the magnitude of impacts on survival and/or height varied appreciably among species. To help make sense of this variation, we characterize tree species responses to deer as falling into one of four categories: heavily browsed with high mortality, *sensitive/preferred* (eastern hemlock, northern white cedar, pin cherry), heavily browsed but survive, *tolerant/preferred* (paper birch, yellow birch, American chestnut, quaking aspen, American elm, red maple, sugar maple, red oak), moderately browsed and capable of maintaining positive growth despite deer, *tolerant/somewhat avoided* (black walnut, white ash, white pine, balsam fir), and *avoided* (white spruce, bitternut hickory, American beech). Of the three species not found in the region of our study sites, black walnut was somewhat avoided and bitternut hickory was avoided by browsing deer. However, these species have been found to be heavily browsed in other studies conducted within their native ranges (Benfeldt et al. 2001, Forrester et al. 2014). Perhaps learned behavior contributes to browsing preferences and deer at our study site are unfamiliar with hickory and walnut seedlings. Species native to our Upper Great Lakes study region that are in the tolerant/somewhat avoided and avoided categories are among the region's most abundant species in the tree regeneration layer (i.e., American beech, white ash, white spruce, white pine [Kain et al. 2011, Matonis et al. 2011, Hidding et al. 2013; M. B. Walters, *personal observation*]). Conversely, species most impacted in this study are among those known to be declining regionally, with deer browsing implicated as a contributing cause (i.e., hemlock, yellow birch, cedar, and red oak [Rooney et al. 2000, Hofmeyer et al. 2009, Salk et al. 2011, Thomas-Van Gundy et al. 2014]). In summary, our results indicate that in single-tree to large-group selection gaps, most NH tree species are either killed by deer browsing (i.e., hemlock, cedar) or are maintained by browsing at a stature (i.e., < 2 m tall; M. B. Walters et al., *unpublished manuscript*) where they are at continual risk of competition with shrub–herb vegetation and rebrowsing by deer. Given these associations and that deer densities in our study area (~10.4/km^2) are average compared to the larger region (e.g., Shi et al. 2006), it is clear that deer are exerting a strong filter on tree regeneration composition and density in selection-managed forests over large extents of the Upper Great Lakes region.

Deer and vegetation have unexpected interacting effects on tree seedlings

Interactions between deer, shrub–herb vegetation, and gap size had two unexpected positive effects on tree seedling environments; deer herbivory can increase light to tree seedlings beneath shrub–herb canopies and shrub–herb vegetation can protect tree seedlings from deer.

The degree that deer browsing pressure increases light penetration through shrub–herb canopies likely depends on the composition of the shrub–herb canopy. We witnessed deer browsing on the developing shoots of the dominant *Rubus* spp. shrubs, but circumstances suggest that browsing of *Sambucus* shrubs was mostly responsible for elevated light levels. Gaps with elevated light levels in unweeded plots were mostly in the middle of our light gradient (20–40% light). At these light levels *Sambucus* density was greatest in fenced plots, while being heavily browsed or absent in unfenced plots. However, the degree that increased light

penetration benefits a tree seedling's light environment depends on the degree that deer browse the tree seedlings too. All else equal, diminished tree seedling stature via browsing should decrease light availability and the competitive status of tree seedlings relative to proximal competing vegetation (Schwinning and Weiner 1998). In our study, those species benefitting most from deer herbivory of shrub–herb vegetation are slower-growing, browsing-avoided species, with the best example being white spruce. One implication of this pattern is that canopy recruitment of lesser-browsed species can be accelerated by deer herbivory not only because their height growth is less impacted than other trees they are competing with, but also because their growth environments are improved.

The second unexpected interaction we found was that shrub–herb vegetation decreased the probability of deer browsing on tree seedlings and with greater effects as harvest gap size increased. This effect resulted in the faster-growing, browsing-tolerant/-preferred species being able to escape browsing in the largest patch cut gaps. Unlike unweeded seedlings, weeded seedlings were heavily browsed in patch cuts, suggesting that deer do not have a behavioral aversion to browsing in large harvest gaps. Instead, as gap size increases, the increasingly thick shrub–herb layer could locally overwhelm the supply of browse relative to the demand of browsing deer, physically deter deer movement, and/or make tree seedlings more difficult for deer to detect. We do not have the data to assess the relative importance of these alternative mechanisms.

Shrub–herb vegetation and deer affect gap size optima and gap partitioning

Without the impacts of shrub–herb vegetation and deer (i.e., fenced:weeded), all species grew best in larger gaps. High densities of competing shrub–herb vegetation in larger gaps shifted species gap size optima to smaller gaps, and these shifts were greatest for the smallest-statured, most shade-tolerant species. Perhaps reflecting the multifactor impacts of gaps on tree seedlings, patterns among species in gap size optima more clearly reflected field-observation-based shade tolerance classifications (i.e., Baker 1949, Niinemets and Valladares 2006) when seedlings were grown with competing shrub–herb vegetation than without. Layered upon the impacts of shrub–herb vegetation, deer herbivory had strong and overriding impacts on gap size optima, either generally pushing species optima to higher light levels where deer herbivory was less likely to occur, or impacting growth or survival so strongly that canopy recruitment was unlikely in any gap size category (i.e., no optima assigned).

While gap size optima reveal gap size ranges where a species grows/survives best and how deer herbivory and shrub–herb vegetation impact these patterns, they provide no information about how these factors impact rank order in performance among species. The premise underlying the gap partitioning hypothesis is that species partitioning results from rank order changes in the performance (growth and/or survival) of young trees over gap size gradients (Denslow 1980, Gray and Spies 1996, Busing and White 1997, Schnitzer and Carson 2001, Walters et al. 2014). At its least complex, gradients of gap size might only produce gradients of gap light (i.e., fenced:weeded treatment) and gap partitioning based on a tradeoff between survival in small low-light gaps and growth in large, high-light gaps (Kobe et al. 1995). After 4 yr in treatments, we found some evidence for this mechanism, but only when we considered growth in high-light, large-group selection gaps vs. survival for the latest interval (3rd–4th year) in plots receiving <5% light. There was no such tradeoff with 1st–4th year survival in single-tree selection gaps, where survival was generally high for all species. This indicates either that growth vs. survival tradeoffs do not occur between light levels found in single-tree selection gaps vs. large-group selection gaps or that species differences in shade-induced mortality have not yet developed in single-tree selection gaps.

Low-light survival vs. high-light growth is not the only possible performance contrast underlying changes in species competitive hierarchies over gap light gradients; differences in growth, survival, and growth vs. survival ranks could all be important. However, while we found that species height growth rank order changed between gap sizes, the low variation in height growth in single-tree selection gaps suggests that those differences are unimportant for performance

differences in low-light environments. Instead, high-light growth vs. low-light survival is likely more important.

As recognized by Grubb (1977), many other factors in addition to gap light, both related and unrelated to gap size, may affect species performance rank order. Among these are biophysical factors other than light (e.g., temperature), soil resource availability (Walters et al. 2014), competing vegetation (this study), and deer herbivory (this study). In large-group selection gaps where there is large variation in species growth potential, dense shrub–herb vegetation had strong effects on growth, but had little effect on rank order, whereas deer herbivory strongly modified growth and growth rank order. Deer and shrub–herb impacts on height rank order were more modest in single-tree selection gaps; however, height rank order for seedlings subject to deer impacts was similar in small and large gaps. Collectively, these patterns indicate that deer can override the performance hierarchies established by harvest gap size, and as such, may be more influential in structuring forest communities and successional trajectories than overstory harvest designs in NH forests with high deer populations in the Upper Great Lakes region.

Although survival rank order changes between treatment combinations were neither as large as for height nor easily interpretable, the modest changes in rank order that occurred could still be important ecologically. Furthermore, like incipient reversal in rank order between low-light survival and high-light growth after 4 yr, long-term patterns in rank order changes in survival between treatment comparisons may just be beginning to occur and their relationships to species traits may become more clear in the future (e.g., some species, such as American elm and paper birch, have been browsed heavily by deer, but with little effect on mortality yet).

In summary, the shade tolerance-related differences in gap size optima and inverse rank order between low-light survival (albeit incipient) and high-light growth we found among species suggest that tree diversity in NH stands can be promoted by varying gap size. While some studies of natural seedling dynamics support this notion, others do not. The easiest explanation for these differences is that like shrub–herb vegetation and deer browsing in our study, there are many spatiotemporally varying factors that can affect tree seedling distributions in addition to gap light gradients. Other studies have found vegetation and/or deer impacts on gap sorting. Kern et al. (2013) showed minimal effects of gap size on regeneration composition and indicated that shrub–herb competition and deer herbivory were likely responsible. Nuttle et al. (2013) showed that browsing deer are capable of negating gap size effects on tree seedling composition and limit regeneration to a few browsing-avoided/-tolerant species. Other factors affecting the composition and density of seedling populations in NH forests include a scarcity of decaying wood and mineral soil substrates required by small seeded species (e.g., paper birch, yellow birch, hemlock) (D'Amato et al. 2015, Willis et al. 2015) and a lack of local seed sources (Caspersen and Saprunoff 2005). Considering the large number of factors affecting tree seedling populations, it is unsurprising that associations between gap size/light and tree seedling compositional changes are often weak. Despite these complexities, increases in the proportion of seedlings of shade-intolerant species in larger gaps have been observed in some studies. Typically, increases are modest, with regeneration overwhelmingly dominated by shade-tolerant species in all gap sizes (Bolton and D'Amato 2011, Matonis et al. 2011, Poznanovic et al. 2013, D'Amato et al. 2015). However, in larger gaps, the superior height growth rates of intolerant species (Beaudet and Messier 1998, Walters et al. 2014, this study) likely give them a greater per capita chance of obtaining a canopy position than slower-growing, shade-tolerant species. Although large growth rate advantages for shade-intolerant species may be restricted to seedlings and smaller saplings (Forrester et al. 2014), obtaining height advantage early in life may have long-term consequences for competitive hierarchies given asymmetric competition for light (Schwinning and Weiner 1998).

How do we modify management of northern hardwood forests to increase tree regeneration diversity?

Large extents of NH forests are managed by selection silviculture systems (Pond et al. 2014), and significant proportions are subject to heavy deer browsing pressure. Regeneration targets of abundant and desirable and/or diverse species

are often not met, with regeneration often poorly stocked and/or dominated by a few shade-tolerant species that are tolerant of, or avoided by, browsing deer (Bolton and D'Amato 2011, Matonis et al. 2011, Kern et al. 2012, 2013, Poznanovic et al. 2013). Importantly, none of the cited studies used harvest gaps as large as patch cuts and they are not prescribed by forest managers. Collectively, these patterns suggest that larger patch cuts and alternatives to selection silviculture should be evaluated in areas of high deer populations. Limited trials demonstrate that even-aged shelterwood systems can be used to manage NH stands (e.g., Godman and Tubbs 1973). Shelterwood systems might be particularly promising, as they have at least three advantages over other even-aged and uneven-aged systems for overcoming the particular regeneration shortcomings that deer-impacted NH stands face. First, because a residual overstory is maintained for seedling establishment, the system is better designed to increase stand-level seed availability of diverse and desirable tree species than clearcut/patch cut systems. Second, the residual overstory seed sources can be held for nearly as long as necessary (one to two decades) to increase the likelihood of establishing desirable tree regeneration via mast seed years, temporary downturns in deer density, and other factors. Third, the density of the overstory can be adjusted to promote understory environmental conditions conducive to the development of protective shrub–herb vegetation.

Given that shrub–herb vegetation confers some protection to tree seedlings, we do not recommend controlling it with herbicides or other means in areas with high deer populations. However, shrub–herb vegetation competition can also decrease regeneration diversity and density and result in regeneration delays. Thus controlling shrub–herb vegetation in areas of low deer populations could be beneficial in some cases. Controlling shrub–herb vegetation is probably unnecessary for regenerating shade-tolerant trees in smaller gaps or intolerant species in larger gaps, because shrub–herb vegetation impacts in small gaps are small, and faster-growing intolerant species are able to cope with competing shrub–herb vegetation in large gaps if they establish early. However, vegetation control could help promote the regeneration of slower-growing, less-shade-tolerant species (e.g., red oak, white pine, red maple), which are particularly sensitive to shrub–herb vegetation and need larger, higher-light gaps to successfully regenerate.

For areas with lower deer populations and the typical management scenario of no shrub–herb vegetation control, our optimal gap size values for fenced:unweeded treatments provide guidance on best gap sizes for promoting particular species. Most shade-intolerant and mid-tolerant species grew best in large-group selection gaps. Other species, mostly mid-tolerant, did equally well in small-group and large-group selection gaps. Slower-growing mid-tolerant and tolerant conifers grew best in single-tree and/or small-group selection gaps. These results generally follow classic shade tolerance expectations and indicate that the stand-scale application of silvicultural systems that vary gap size from single-tree to large-group selection could succeed in regenerating the maximum number of species if the local species pool of established seedlings is not limiting. However, at just regionally average deer populations (Shi et al. 2006, this study) this practice would likely be unsuccessful, with regeneration dominated by avoided and somewhat avoided species (beech, ash, spruce [this study], ironwood [Matonis et al. 2011]) regardless of gap size, and shade-intolerant species requiring larger harvest gaps than group selection gaps to successfully regenerate.

An important addendum to our silvicultural system recommendations is that they will not work if seedlings of target species are not present. For example, potential seedling populations of target species may be limited by insufficient local seed sources (Caspersen and Saprunoff 2005). In these situations, artificial regeneration could be used to supplement natural regeneration. If artificial regeneration is needed or desired, we recommend planting as soon after harvest as possible to maximize the potential for escaping shrub–herb vegetation competition, and that attention be paid to gap size, vegetation competition, and deer impacts on regeneration derived from this study and others to inform species selection. In addition, our silvicultural suggestions, based upon our results and limited trials (e.g., Godman and Tubbs 1973), may not necessarily be

applicable over the entirety of the broad range of site qualities and deer densities that characterize NH forests. For example, shrub–herb vegetation density is lower on lower quality sites than on the site used for this study (Burger and Kotar 2003; J. Willis, *unpublished manuscript*); thus, it could have weaker protective effects and weaker competitive effects on tree seedlings than we observed. The broader geographic applicability of our silvicultural recommendations needs to be evaluated.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1397/supinfo