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Microsite requirements for successful regeneration in lowland northern white-cedar (*Thuja occidentalis* L.) forests

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ABSTRACT

Throughout much of its range, northern white-cedar (*Thuja occidentalis* L., hereafter cedar) has experienced a bottleneck in recruitment: cedar seedlings are often abundant in these stands, particularly in lowland settings, yet cedar sapling densities are quite low, leading to concerns that cedar canopy trees are not being replaced. Several barriers to cedar recruitment have been suggested; however, findings from previous studies have been inconsistent with regard to limiting factors. Our objective was to characterize the microsite conditions associated with the establishment of cedar seedlings and saplings. We achieved this objective by mapping the location of seedlings, saplings, and overstory trees in 15 lowland cedar stands at five sites in Maine, USA, and examining the fine-scale site conditions (microtopographic features, canopy openness) in which cedar seedlings and saplings occurred. In particular, we recorded the occurrence of seedlings and saplings on microtopographic mounds, pits (small depressions), and flats (transitional features between mounds and pits). Substrate moisture content in these features decreased in the order pits > flats > mounds. Contingency-table results demonstrated that live cedar seedlings, and to a slightly lesser extent saplings, were found more often than expected by chance on mounds, and less often on flats and pits. Logistic regressions using status (live vs. dead) as the response variable generally supported these findings: dead seedlings were strongly associated with pits; however, the occurrence of live seedlings and saplings did not differ between flats and mounds. A companion planted-seedling experiment strongly supported these results, showing that after two growing seasons, survival was significantly lower in pits (12%) when compared to flats and mounds, which had similarly high levels of survival (62 and 80% respectively). Logistic regressions also showed live seedlings and saplings to be prevalent under more open canopy conditions (mean 19%, range 6 to 42% openness); though results from a planted-seedling experiment suggested that greater canopy openness (mean 32%, range 13 to 57%) was detrimental to survival. Regressions also showed that browsed seedlings were more likely to be found dead. These findings point to management prescriptions that maintain microtopographic diversity, create moderately open canopy conditions, and protect stands from browsing to promote viable cedar populations in these ecologically and economically important forests.

1. Introduction

Recent studies have identified regeneration failures across a range of forest types, leading to changes in canopy species composition (Bradshaw and Waller 2016, Miller and McGill 2019). Such failures can occur even where regeneration is abundant if regenerated stems fail to advance to larger size classes due to high rates of mortality or prolonged suppression. This may result from, or be exacerbated by, a changing climate, invasive species, changes in browsing pressure, and other alterations to site conditions (Dey et al. 2019). Regeneration failure presents challenges for management and threatens the long-term persistence of certain tree species and forest types.

Northern white-cedar (*Thuja occidentalis*, hereafter cedar) stands represent one such forest type. Barriers to regeneration of this species have been noted for decades (Curtis 1946, Nelson 1950) and across its geographic range (Heitzman et al. 1997, Saucier et al. 2018). While cedar seedlings are often plentiful in cedar stands, these seedlings may exhibit mortality rates greater than co-occurring species (Curtis 1946, Larouche et al. 2011). High mortality leads to decreased cedar densities as aging cedar canopies are replaced by other tree species (Heitzman

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et al. 1999). Proposed causes for this regeneration barrier include increased competition, deer browsing, and unfavorable harvesting practices; however, the conditions associated with successful establishment and recruitment of cedar regeneration remain poorly understood (Heitzman et al. 1997, Larouche et al. 2010). This knowledge gap hinders the development of appropriate management strategies for this forest type.

Due to the ecological and economic value of northern white-cedar, focused research initiatives into this species are essential (Boulfroy et al. 2012). Its lightweight, rot-resistant wood supplies a specialty timber market for shingles, fence posts, and other decorative outdoor products. Cedar has long been significant to indigenous peoples for ceremonial and practical purposes (Geniusz 2015). Additionally, cedar stands provide habitat for rare plants and lichens and act as winter shelter for white-tailed deer (*Odocoileus virginianus*) (Gawler and Cutko 2010, Boulfroy et al. 2012).

Microtopography – the fine-scale variability of forest floor elevation consisting of elevated mounds, depressed pits, and the intervening flat areas– is associated with within- and between-site variability in cedar regeneration density, especially in poorly drained sites (Curtis 1946, Chimner and Hart 1996). This suggests that various microtopographic positions confer advantages or disadvantages for cedar germination and/or survival. Microtopographic heterogeneity is also thought to control fine-scale variability in moisture conditions (Cornett et al. 1997, Palik et al. 2015), and allow for variable soil chemistry that can support a diverse plant community (Diamond et al. 2020).

Cedar regeneration and recruitment also benefit from the increased light conditions afforded by canopy gaps. By analyzing tree-ring series from old-growth cedar stands, Fraver et al. (2020) found that 77% of cedar canopy trees showed at least one growth release following periods of suppressed growth, suggesting that canopy gaps in the past allowed them to advance beyond subcanopy status. Similarly, Ruel et al. (2014) documented substantial increases in cedar growth following canopy openings resulting from natural disturbances and partial harvests. Nevertheless, Larouche (2009) found that excessively large gaps (resulting from group selection harvests) were detrimental to cedar seedling establishment. A greater understanding of the role played by canopy openness and microtopography in cedar seedling and sapling survival may shed light on barriers to regeneration of this species.

Our objective in this study was to characterize the microsite conditions associated with the occurrence of live, naturally regenerated cedar seedlings and saplings, making use of a range of lowland cedar stands. Fifteen stands at five sites throughout Maine, USA, were selected for study, which included detailed mapping and measuring of seedlings, saplings, and trees. In addition, we used a planted-seedling experiment for analyzing seedling survival and associated microsite characteristics. Findings from this study may benefit recent concerted efforts to identify appropriate management for this understudied forest type (Boulfroy et al. 2012).

2. Materials and methods

2.1. Study sites

This work was conducted at five forested sites currently under conservation status or otherwise set aside from harvesting. These sites were located throughout Maine, USA, and were known to include substantial cedar populations (Fig. 1). At each of the five sites, we selected three lowland cedar stands that (1) had > 65% cedar relative basal area of overstory trees, (2) were large enough to accommodate a 35 × 35 m research plot, given that cedar stands in this region often occur as 'micro-stands' (*sensu* Boulfroy et al. 2012), and (3) had no recent history of harvest (cut stumps, if present, were in advanced stages of decay, suggesting harvests occurring decades prior). A total of 44 potential stands were visited and evaluated before selecting the 15 (three at each of five sites) used in this study. Many stands were rejected because they

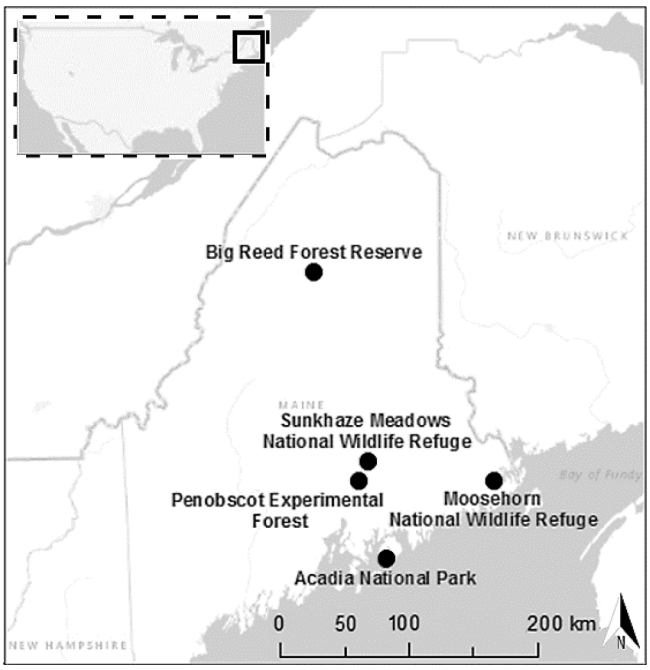

Fig. 1. Plot locations. Five northern white-cedar study sites in Maine, USA.

contained only small or narrow linear areas of cedar dominance. The sites selected for this study represent the diversity of stand structures and apparent natural disturbance histories typical of the region's lowland cedar communities: these include Acadia National Park (ANP), Big Reed Forest Reserve (BR), Moosehorn National Wildlife Refuge (MH), Penobscot Experimental Forest (PEF), and Sunkhaze Meadows National Wildlife Refuge (SM). The Big Reed Forest Reserve represents old-growth (never harvested) conditions (Fraver et al. 2009); the remaining sites had been previously harvested.

Annual precipitation ranges from 1073 to 1352 mm across sites and mean annual temperature ranges from 3.5 to 7.5 °C (PRISM, 2020, 30-year normals) (Table 1). Soils are deep, poorly drained mucky peats with lower horizons composed of loam or muck (Web Soil Survey,

Table 1
Site locations and characteristics. Climate data based on 30-year normals from 1981 to 2010, sourced from PRISM Climate Group, Oregon State University. NWR, National Wildlife Refuge; EF, Experimental Forest.

Site	Site Abbrev.	Lat., Long.	Elevation (m)	Annual Precip. (mm)	Mean Annual Temp. (°C)
Acadia National Park	ANP	44°17′ N, 68°22′ W	36	1352	7.5
Big Reed Forest Reserve	BR	46°21′ N, 69°03′ W	372	1082	3.5
Moosehorn NWR	MH	44°51′ N, 67°14′ W	37	1267	6.2
Penobscot EF	PEF	44°50′ N, 68°37′ W	41	1073	6.4
Sunkhaze Meadows NWR	SM	44°59′ N, 68°31′ W	40	1098	6.4

2020). As is typical of this forest type, these sites have well-developed pit-and-mound (or hummock-and-hollow) microtopography (Gawler and Cutko 2010). Seasonal flooding in this forest type is common (Thompson and Sorenson 2005). Our study stands typically had standing water in the spring and dried down over the summer; however, varying levels of flooding were seen during summer field work, generally following a rain event.

The forests in this study align with the Evergreen Seepage Forests and Northern White-Cedar Swamps natural communities as described by Gawler and Cutko (2010). Cedar dominated the overstory of all stands, with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) also common. Shrub communities consisted of patchy populations of several shrubs, mostly small and deciduous, with sheep laurel (*Kalmia angustifolia*), speckled alder (*Alnus incana*), and fly honeysuckle (*Lonicera canadensis*) the most common. Herbaceous understories were generally sparse and presumed largely inconsequential with regard to tree regeneration. Nevertheless, substantial graminoid (Cyperaceae species) and fern (*Osmunda cinnamomea*, *Onoclea sensibilis*, *Thelypteris palustris*) communities existed at four stands. Ground cover largely consisted of bryophyte mats, most commonly *Sphagnum* species, *Hylocomium splendens*, and *Bazzania trilobata*. Additional details on plant species composition can be found in Allogio (2020).

2.2. Plot establishment

Within each of the 15 stands, we established one 35 × 35 m plot. Plots were generally placed in the geographic center of the stands, oriented such that plot borders followed cardinal directions. Estimated stand areas ranged from 1.0 to 7.8 ha (mean 3.6 ha), providing ample space for the 0.12-ha plots. However, when stand shape, property boundary, or other constraints precluded such placement, plots were shifted or oriented differently to avoid these obstacles. In all cases, plots were positioned entirely within the cedar-dominant overstory while avoiding patches of other vegetation types as well as transition zones between the cedar community and adjacent communities. In the center of each of these full plots, we established a 15 × 15 m interior plot for more detailed inventory of seedlings, saplings, and microtopography. All plot sampling was conducted between May and August of 2019.

2.3. Substrate moisture

To assess variation in substrate moisture among microtopographic features, volumetric water content was recorded on 25 mounds, 25 flats, and 25 pits within each interior plot, using a Fieldscout TDR 150 (Spectrum Technologies, Inc.) fitted with 7.5 cm tines. Features were selected subjectively to ensure that a representative sample of each feature was obtained across the interior plot. This survey was never conducted during rain or within 24 h after a rain event, and all measurements in a plot were made within 30 min of each other. These measurements were intended to reflect relative substrate moisture of the three features at that point in time for a given plot.

2.4. Occurrence of microtopographic feature

To examine the relationship between microtopography and cedar regeneration abundance, we quantified the proportions of each plot occupied by the three microtopographic features. Microtopographic features were defined as follows: mounds are raised areas on the forest floor from which water is expected to drain, pits are depressions where water would pool, and flats are level expanses or transitions between mounds and pits. Although coarse woody debris may have underlain microtopographic features classified as mounds and flats, we did not attempt to ascertain its presence, as doing so would have required extensive excavation. We used a line-point intercept survey along seven equally spaced, 15-m-long transects running north–south through the interior plot to obtain percent occurrence of each feature. Where the transect crossed the bole of a standing tree or bare rock, the survey point was moved ~ 10 cm perpendicular to the transect, as these obstructions were considered unavailable for seedling establishment. Microtopographic feature was recorded every 0.5 m along each transect (N = 217 points per plot).

2.5. Plot inventory and canopy openness

All trees with diameter at breast height (DBH) ≥ 10 cm in the full plot were inventoried, recording DBH, species, and status (live or dead). Stem centers at tree bases were mapped to the nearest decimeter as X and Y coordinates. The plot borders were used as axes wherein the southwest corner was (0, 0 m) and the northeast corner was (35, 35 m). We did not record microtopographic location for trees, as we did with seedlings and saplings (described below), because over extended time periods trees create their own apparent mounds as litter and sloughing bark are deposited at stem bases (Harrington, 2012), thereby confounding any determination of the substrate present at tree establishment.

All cedar saplings (live and dead stems taller than 1.4 m and DBH < 10 cm) in the full plot were mapped in the same manner as trees, recording DBH, status (live or dead), presence of browse, and microtopographic feature on which the sapling was rooted. Browse (observed or not) was recorded, as well as apparent browser (ungulate or hare). Hare (*Lepus americanus*) browse was identified as clean, 45° shears, and ungulate browse was identified as jagged tears, as described by Pierson and DeCalesta (2015) (Figure S1, Appendix). Only live branches within reach of deer (up to 2 m height) were examined for browse determinations (Pierson and DeCalesta 2015). Because cedar regeneration can persist in a suppressed low-vigor state in the understory for decades (Ruel et al. 2014, Larouche and Ruel 2015, Fraver et al. 2020), the presence of presumably older, non-vigorous sapling-sized stems – recognizable by their poor form with many dead branches and low live crown ratio – in our sapling inventory could potentially confound analyses of current microsite effects on regeneration. We therefore classified each sapling as either 'vigorous' or 'low-vigor', with the latter suggesting recruitment long ago and thus possibly under different stand conditions. Sapling data were analyzed with and without the non-vigorous saplings included, for comparison.

Cedar seedlings (live and dead) were mapped (X, Y coordinates, nearest cm) and measured (height, nearest cm) in the 15 × 15 m interior plot. Seedlings were defined as individual stems no taller than 140 cm in height. In order to exclude the ephemeral seedling bank, we inventoried only those individuals that had developed three branches with scale-like (mature) foliage, indicative of successful establishment (adapted from Curtis 1946). Status (live or dead), browse, and microtopography were recorded as for saplings. Cedar regeneration occurs both by seed and by layering (Curtis 1946, Nelson 1950). However, because we were unable to distinguish between these modes of regeneration without damaging the seedlings, we recorded all individual stems as seedlings in this study.

To characterize canopy openness experienced by seedlings, we used hemispherical photos taken on a regular grid throughout the interior plot. Thus, 25 canopy photos were taken from a height of 140 cm along parallel transects separated by 2.5 m. Additional canopy photos were taken above all dead cedar saplings and a subset of live cedar saplings. Photos were either taken above individual saplings, or where saplings of similar height were growing in close proximity (≤ca. 3 m spacing), a single photo was taken above the center of the sapling group. The subset of live saplings included all those in the interior plot plus additional saplings from the full plot as needed to obtain photos above at least 20 saplings total where available. Photos were taken using a fish-eye camera set in a Regent Instruments (Ste-Foy, Quebec, Canada) Mini-OMount gimbal system; for saplings, this gimbal system was mounted on a telescoping pole.

Hemispherical photos were processed using Gap Light Analyzer software (Frazer et al. 1999) to obtain canopy openness, excluding outer

rings beyond a 60° zenith angle. Canopy openness values for cedar saplings were derived directly from the hemispherical photos taken above individual saplings or sapling groups. Seedling canopy openness was interpolated by applying kriging to the 25 grid photos taken in each interior plot. Kriged surfaces were created using ordinary kriging based on spherical (or best fit) models using the 'gstat' R package (Gräler et al. 2016). Kriging produced a grid of 1 m^2 cells, the values of which were extracted and applied to all seedlings located in that cell.

2.6. Planted-seedling experiment

Because our observational study could not capture cedar that died and were no longer present, we conducted a separate experimental study to assess seedling survival in mounds, flats, and pits. In May 2019, we planted 160 two-year-old bare-root cedar seedlings in a range of environmental conditions resulting from the recent partial harvest of a cedar stand adjacent to our PEF1 stand. Seedlings were individually mapped, tagged and planted along a 250-m belt transect (ca. 5 m wide) purposely positioned to pass through a gradient of canopy openness, ranging from harvest gaps, thinned forest, and intact (unharvested) forest. Seedlings were alternately planted in mounds, flats, and pits, in roughly equal proportions. Seedlings ranged from 7 to 29 cm in height once planted, and each was protected from browsing by a mesh protector tube. Hemispherical photographs were taken every 5 m along the transect and were processed as above. Canopy openness experienced by each seedling was calculated as the mean of the two nearest photographs, inversely weighted by the distance to each. Some pits were flooded at the time of planting, as is typical of these lowland forests, though this effect may have been greater due to above average precipitation in central Maine during spring and summer 2019 (Annual Climate Report 2019 & 2020). We inventoried seedlings in August 2020 (after two growing seasons) to assess survival. Precipitation in 2020 was below average overall, with average or slightly below average precipitation during the 2020 growing season.

3. Analyses

3.1. Substrate moisture

We tested the relationship between relative substrate moisture and microtopographic feature to explore how variations in observed substrate moisture among the features might influence occurrence and densities of seedlings and saplings. We developed a linear mixed-effects model to test if volumetric water content varied by microtopographic feature, treating features as fixed variables. Plots-within-sites was included as a random variable to account for variation among plots. The 'nlme' R package (Pinheiro et al. 2020) was used to develop the model. Tukey's tests were then used as *post-hoc* analyses of the model results to assess pairwise moisture differences among microtopographic features at a significance level of $\alpha = 0.05$.

3.2. Occurrence by microtopographic feature

To determine if living cedar seedlings or saplings were more likely to be found on particular microtopographic features (mounds, flats, pits), we used chi-squared goodness-of-fit tests. Frequencies of seedlings or saplings and frequencies of features were averaged across sites. *P*-values were calculated for the residuals resulting from the chi-squared test to determine if there were more or fewer seedlings or saplings than expected on a given feature, based on the frequency of features. The PEF site was excluded from the sapling analysis due to an insufficient number ($N < 20$) of saplings.

3.3. Modeling regeneration status

To explore potential relationships between microsite conditions and the occurrence of live cedar regeneration, we created and evaluated two sets of generalized logistic mixed-effects regression models – one for saplings and one for seedlings – in which status (live or dead) served as the response variable. Site was treated as a random effect, and microsite conditions were treated as fixed effects. These fixed effects included canopy openness (expressed as the natural log transformation of percent open canopy) and microtopographic feature on which the stem was rooted (expressed categorically as mound, flat, or pit). Additionally, browse (observed or not) was included in the seedling models, and DBH (expressed in centimeters) was included in the sapling models. Seedling height was not used because a portion of dead seedlings were browsed or otherwise broken preventing a reliable determination of height at the time of death. Browse was not included in the sapling models because many larger saplings had no live branches within reach of browsers, which would have introduced bias. In specifying the models, we used various combinations of all available predictors; thus, the full model for seedlings was specified as: Status = *f*(microtopographic feature + canopy openness + (feature × openness) + browse + site), and the sapling model was: Status = *f*(microtopographic feature + canopy openness + (feature × openness) + DBH + site), where status refers to living vs dead.

In both analyses, null models were created including only site as a random effect, and for saplings, DBH as a fixed effect. Additional models were then created with every possible combination of individual microsite variables and the one interaction, with the exception of DBH which was included in all sapling status models given the well-documented association between size and growth/survival (Coomes and Allen 2007). Because we had too few observations at the plot level (total saplings at certain plots and individuals of both size classes on certain microtopographic features), plots within site were pooled for analysis. The PEF and SM sites were excluded from the sapling status analysis due to small numbers of dead saplings. Of the saplings at the remaining three sites, we included only those for which we derived canopy openness values from hemispherical photographs ($N = 354$). These analyses were conducted with the 'lme4' R package (Bates et al. 2015). All possible combinations of predictor variables in the seedling and sapling status (live or dead) logistic regressions yielded sets of ten and five models, respectively. All candidate models within the two analyses were ranked by the Akaike information criterion (AIC) and evaluated using conditional and marginal R^2.

3.4. Planted-seedling experiment

To assess the influence of microsite conditions on planted seedling survival, we employed a logistic regression in which status (live or dead) served as the response variable and microtopographic position, canopy openness, microtopography × openness interaction, initial seedling height, and distance along transect (to assess autocorrelation) served as predictors. Initial screening revealed that seedling height and distance were not statistically significant predictors of survival and were thus dropped from further analysis. The analysis was conducted with the 'aod' package in R (Lesnoff and Lancelot 2012).

4. Results

4.1. Stand structure and composition

Cedar clearly dominated the overstory, with relative basal areas ranging from 67 to 94% among plots (Table 2). Notably, cedar was the most abundant species in the seedling layer (plots pooled, Table S1, Appendix); however, the sapling layer (plots pooled) was dominated by balsam fir (average 2,189 balsam fir saplings/ha vs. 622 cedar saplings/ha), with cedar saplings being clearly dominant in only three plots and co-dominant with balsam fir, black ash, or tamarack on three others (Table S2, Appendix). At all but one site (Big Reed) cedar trees outnumbered cedar saplings (Table 2). Across all tree and shrub species

Table 2
Site summary metrics. Means (and ranges, N = 3 plots) are shown. Cedar seedling and sapling densities derived from interior (15 × 15 m) plots. Rel. BA, relative basal area; NWR, National Wildlife Refuge; EF, Experimental Forest.

	Basal Area (m^2/ha)	Cedar Rel. BA (%)	Cedar (stems/ha)		
			Seedlings	Saplings	Trees
Acadia National Park	41	84	54,617	267	1,165
	(31–50)	(79–89)	(11,288–74,125)	(0–622)	(727–1,486)
Big Reed Forest Reserve	57	89	31,597	1,155	765
	(49–63)	(81–94)	(12,843–44,574)	(933–1,733)	(686–857)
Moosehorn NWR	50	83	14,221	711	1,018
	(42–61)	(69–92)	(6,310–19,554)	(0–1,289)	(971–1,078)
Penobscot EF	51	76	2,533	44	1,665
	(38–63)	(67–93)	(1,244–3,422)	(0–133)	(1,404–1,951)
Sunkhaze Meadows NWR	49	82	16,798	400	1,118
	(40–63)	(78–85)	(7,644–24,131)	(0–667)	(873–1,306)

included, a total of 12,257 seedlings and 2,971 saplings were mapped and measured. The ratio of cedar seedling:sapling densities (stems/ha) ranged from 11:1 to more than 126:1 across the 15 plots. Tables S1, S2, and S3 (Appendix) present abundance of all tree and shrub species in the seedling size class, sapling size class, and overstory, respectively.

When the relevant stem- and stand-level analyses (occurrence by microtopographic feature and modeling regeneration success) were conducted with all saplings and again with only saplings judged to be 'vigorous', the results for the two groups were sufficiently similar as to yield identical interpretations. For this reason, we chose to include both the 'vigorous' and 'low-vigor' saplings, for a total of 1,906 cedar saplings. A total of 8,331 cedar seedlings were used in the seedling analyses.

4.2. Substrate moisture

Our mixed-effects model results indicated that microtopographic feature was a strong predictor of relative substrate moisture as measured at our study sites during the summer (F-value = 925, $P < 0.01$), with mean moisture decreasing in the order pits > flats > mounds. The Tukey's *post-hoc* test demonstrated that the pair-wise differences between mean moisture for the three features were significant ($P < 0.01$) (Fig. 2).

4.3. Occurrence by microtopographic feature

Flats were the most abundant microtopographic feature at all sites, accounting for ca. 54–64% of the interior plot area averaged across sites; pits were the least abundant at all sites except PEF, which had a smaller proportion of mounds. The chi-squared goodness-of-fit tests (α at 0.05) showed the observed numbers of seedlings on mounds to be significantly greater than expected based on mound prevalence, and significantly fewer seedlings than expected were found on flats and pits (Fig. 3). The same general trend was observed among saplings; however, while seedlings showed a stronger negative association with flats, saplings showed a stronger negative association with pits (Fig. 3).

4.4. Modeling regeneration status

A ΔAIC threshold of 10 was chosen to distinguish high-ranking models in the regeneration status model analyses based on a natural break observed in the results (Burnham and Anderson 2003). Three models in each set were thus classified as high-ranking (Table 3). All predictor variables in each model set appeared in at least one high-ranking model.

All three high-ranking seedling status models included browse and microtopography (Table 3a). The low marginal R^2 values compared to the larger conditional R^2 values suggest that a relatively small portion of the variability in these models lies with the fixed effect. The interpretation of various forms of R^2 when used in logistic regression has been subject of much debate (Menard 2000, Tjur, 2009); however, we note

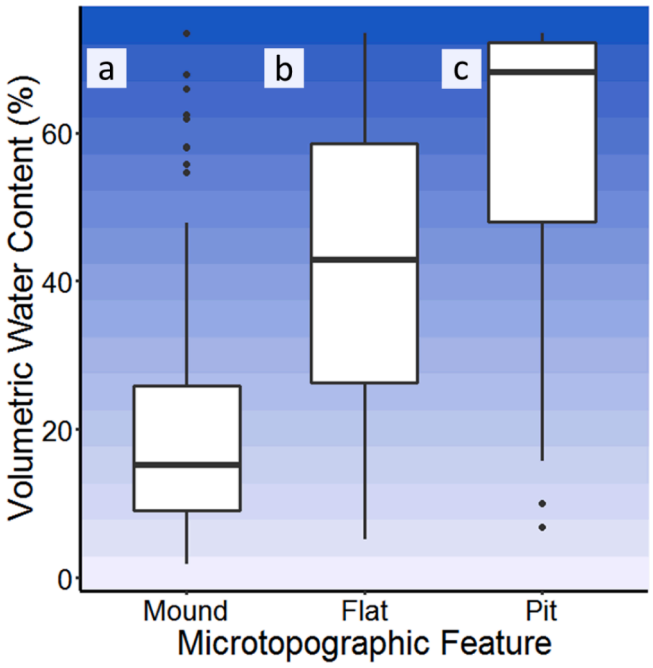

Fig. 2. Soil moisture by microtopographic feature. Boxplot shows the distribution of volumetric water content values recorded during summer on mounds, flats, and pits (N = 375 for each feature), with the box representing the range from the first to the third quartile and the horizontal line representing the median. Letters indicate results of Tukey's *post-hoc* test, where different letters indicate statistically different means ($P < 0.01$).

our use of R^2 was not to evaluate relative model performance, but rather to assess marginal (fixed-effects only) and conditional (entire model) contributions to variability, as is done with standard generalized linear mixed models (Nakagawa and Schielzeth 2013). Browse and pits were generally associated with dead seedlings, while mounds, flats, and absence of browse were generally associated with live seedlings. Canopy openness appeared in two top models and was positively associated with status (live seedlings were more likely to occur under greater canopy openness). While the interaction term (microtopography × openness) was not significant on its own, it appeared in one top model showing a better fit than other, more parsimonious models. Fig. 4 shows the location of living seedlings in relation to a gradient of canopy openness (mean 19%, range 6 – 42% open) in the interior plots. On some plots, seedlings occur in relatively open conditions; on other plots this was not evident. This figure also suggests spatial clustering of seedlings, which was borne out by point pattern analyses (for both seedlings and saplings) (Allogio 2020). Figure S2 (Appendix) provides mapped locations of all trees on the full plots, depicting a range of densities and opening sizes.

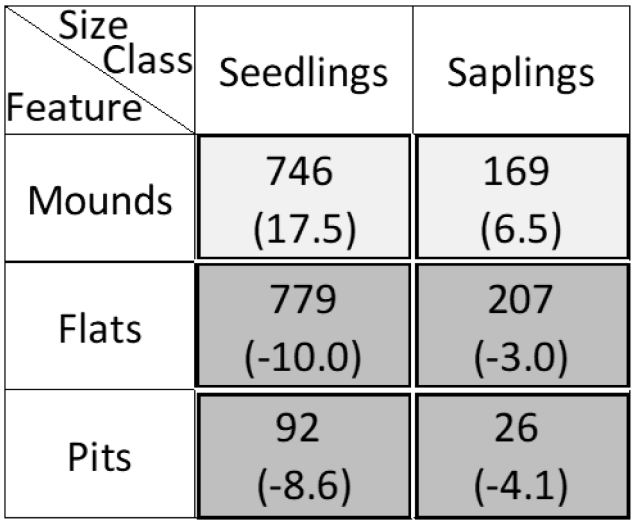

Fig. 3. Cedar regeneration occurrence by microtopographic feature. Chi-squared goodness-of-fit tests were used to compare numbers of cedar seedlings and saplings with the proportions of three microtopographic features (frequencies averaged across sites). Average-across-site numbers of stems present are displayed first in each cell followed by the residual of the chi-squared test in parentheses. Light gray shading indicates more stems than expected; darker gray shading indicates fewer stems than expected ($P \leq 0.05$).

All sapling models included the obligatory predictor DBH; however, the effect was not significant. Canopy openness (mean 20%, range 4 to 41%) appeared as a significant predictor in all three high-ranking models, with greater openness associated with live saplings. Microtopography (mounds and flats only, as there were too few dead saplings found in pits for analysis) appeared in two models where flats were more associated with live saplings than were mounds. The interaction term (microtopography × openness) appeared in one top model but its insignificant *P*-value indicates this is not likely an influential variable. Compared to seedlings, the sapling status models yielded both greater marginal and conditional R^2 values. Furthermore, the considerably larger marginal R^2 values suggest that the explanatory power of the fixed effects was greater in the sapling models than in the seedling models.

4.5. Plot-level trends

Although our analyses were intended to focus on individual stems (as above), we conducted analyses at the plot level to assess general trends. First, we found significant negative correlations between tree density (a proxy for canopy openness that can be used for all plots) and both seedling and sapling abundance ($R^2 = 0.26, 0.47$, respectively, *P* values ≤ 0.05). Second, we found a significant positive correlation between CWD volume and sapling abundance ($R^2 = 0.35$, *P* value = 0.02).

4.6. Planted-seedling experiment

Analysis of planted seedling survival revealed that microtopographic position ($P < 0.001$) and canopy openness ($P = 0.02$) were significant predictors of survival after two years, but their interaction was not highly significant ($P > 0.15$). Wald tests (α at 0.05) indicated that survival did not differ significantly between mounds and flats (80% and 62% survival, respectively); however, both had greater survival than did pits (12%). Survival decreased slightly with increasing canopy openness, which ranged between 13 and 57% openness. However, we note that mean openness in this planting experiment (32%) was significantly higher than that of the plot inventory (19%) ($t = -6.27$, $P < 0.0001$, after log transformation), and the distributions of openness values also differed (Kolmogorov-Smirnov $D = 0.25$, $P < 0.05$; Figure S3, Appendix).

5. Discussion

The species composition and stand structure of our sites correspond well with the community descriptions provided by Curtis (1946) and Gawler and Cutko (2010) (Northern White-Cedar Swamp and Evergreen Seepage Forest types). Cedar clearly dominated the overstory and seedling layers; however, it was much less abundant in the sapling layer. In fact, at all but one site (Big Reed) cedar trees outnumbered cedar saplings (Table 2). Although ages were not determined for seedlings or saplings, the shift from high abundance of cedar seedlings to low abundance of cedar saplings corroborates the recruitment bottleneck observed early on by many authors including Curtis (1946) and Scott and Murphy (1987) and confirmed in more recent studies (Larouche and Ruel 2015, Reuling et al. 2019). Although our results do not provide a definitive solution to the bottleneck, they do identify microsite conditions under which seedlings and sapling were found to be successful.

Our results show strong and consistent differences in growing-season

Table 3
Mixed-effects logistic regression model summaries. Seedling (a) and sapling (b) status (live vs dead) used as response variables. High-ranking models are shown along with null models containing only site (seedling and sapling analyses) and DBH (saplings only). Fixed predictor variables represent stem-level environmental characteristics with site included as a random effect. Models with ΔAIC > 10 were considered low-ranking are not shown. Model estimates are presented, with positive results representing an association with live status and negative results representing an association with dead status. Brws., browse; Y, browse observed; N, no browse observed; CO, natural log of canopy openness; Micro., microtopographic feature; M, mounds; F, flats; P, pits; DBH, natural log of stem diameter; k, number of model parameters; AIC, Akaike information criterion; *, $P < 0.05$.

a. Seedling Status

	Browse			Microtopography			CO • Microtopography					R2	
Model (Live/Dead =)	Y	N	CO	M	F	P	CO•M	CO•F	CO•P	k	ΔAIC	Conditional	Marginal
Brws. + CO + Micro.	–	1.75*	0.83*	–	0.14	−0.76*				6	0.0	0.23	0.08
Brws. + Micro.	–	1.76*		–	0.14	−0.75*				5	3.7	0.23	0.06
Brws. + CO + Micro. + (CO • Micro.)	–	1.76*	0.80	–	0.07	−1.10	–	0.02	0.12	8	4.0	0.23	0.08
Null model										2	109.3	0.19	0.00

b. Sapling Status

		Microtopography		CO • Microtopography				R^2	
Model (Live/Dead = DBH +)	CO	M	F	CO•M	CO•F	k	ΔAIC	Conditional	Marginal
CO + Micro.	2.94*	–	0.47			5	0.0	0.43	0.28
CO	2.99*					4	0.2	0.44	0.28
CO + Micro. + (CO • Micro.)	3.13-	–	1.71	–	−0.47	6	1.7	0.43	0.28
Null Model						3	32.8	0.03	0.01

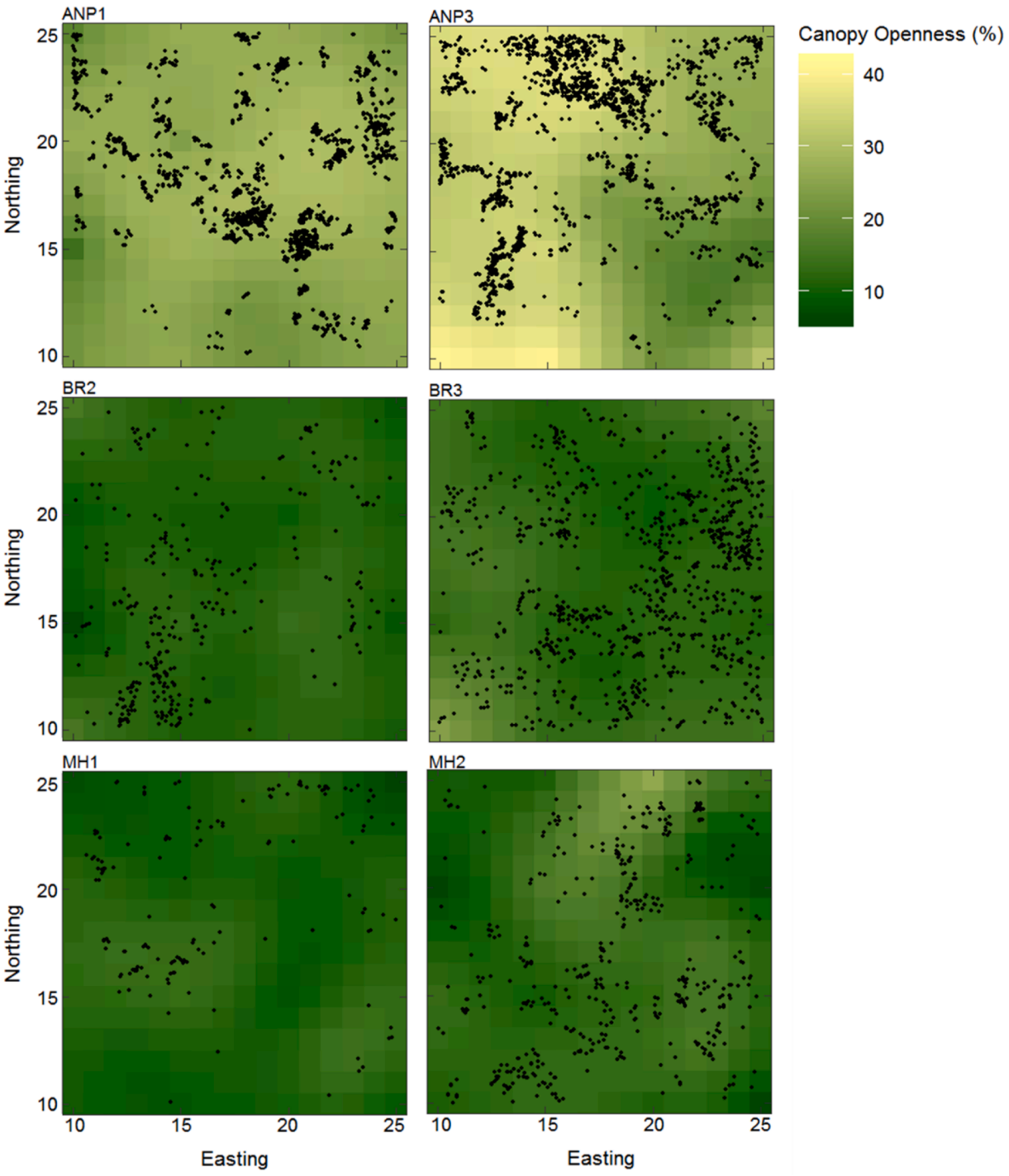

Fig. 4. Seedling locations with respect to canopy openness. Location of living cedar seedlings (dots) relative to canopy openness in the interior plots. Six (of 15) plots shown here to illustrate the range of conditions. These maps demonstrate that seedlings are clustered, but not necessarily clustered under canopy gaps.

substrate moisture among microtopographic positions – pits significantly wetter than flats and flats significantly wetter than mounds – which no doubt drive many of our subsequent findings. These findings corroborate those of Ehrenfeld (1995) who monitored moisture along a fine-scale elevational gradient from pits to mounds in a forested wetland. Similarly, previously reported differences in nutrient status, species composition, and stem abundance among microtopographic features are likely driven by soil moisture (Beatty 1984, Chimner and Hart 1996, Diamond et al. 2020). We acknowledge that growing-season substrate moisture conditions on such sites vary according to rain events and generally experience a dry-down during late summer (Nelson 1950). Yet when our moisture data are arranged by increasing sampling day-of-year (first through last plot sampled), no temporal pattern is evident in relative moisture among the three microtopographic features (data not shown). Nevertheless, inclusion of plots-within-sites as a random effect in our regression model analysis accounts for variation among plots arising from location as well as possible seasonal differences or weather conditions at the time of sampling.

Live cedar seedlings were found more often than expected by chance on mounds, and less often on flats and pits. Point pattern analyses for all plots indicated clustering of seedlings (Allogio 2020), and our field observations indicated that these clusters were often associated with

mounds; however, without high resolution digital elevation models for these plots, we cannot confirm this phenomenon. The prevalence of seedlings on mounds has been noted throughout the species' range (St. Hilaire and Leopold 1995, Chimner and Hart 1996, Forester et al. 2008, Saucier et al. 2018, Reuling et al. 2019). This trend was evident, yet less pronounced, for saplings. Indeed, chi-squared analyses of individual sites (not presented here) reveal saplings at two of the four sites analyzed were found on flats no more or less frequently than would be expected by chance. Sapling results at one site, Sunkhaze Meadows, differed from the others, showing no deviation from expectations on any of the three features. We speculate that competition on mounds may contribute to this difference: plots at this site had unusually high densities of balsam fir regeneration, which has been shown to strongly favor mounds (Cornett et al. 1997). Further research is needed to determine the influence of inter-species competition on cedar microsite associations.

Results of our regression analyses support the conclusions above, particularly regarding pits, where dead seedlings were strongly associated with this feature. The planted-seedling experiment yielded identical results; seedling survival was significantly lower in pits when compared to flats or mounds. Similarly, Chimner and Hart (1996) rarely found cedar growing in pits, instead finding an abundance of cedar on mounds presumably because these raised features provide sufficient areas of unsaturated substrate. Although to the best of our knowledge, no studies of flooding tolerance exist for cedar seedlings, our results suggest that moisture in pits – leading to anaerobic conditions – is excessive for this species in typical years. Poor establishment or survival in pits could be further exacerbated by localized cold air drainage, leading to freezing early in the growing season (Marquis et al. 2021), which is known to cause mortality of cedar seedlings (Nelson 1950). In contrast, Cornett et al. (1997) point out that during droughts, cedar regeneration in pits may be abundant, as pits could offer a moist refuge.

Although seedlings were found less often than expected on flats in the previously discussed analysis, established seedlings (those with three or more branches with mature foliage) growing on flats were as likely to be alive as those on mounds. Similarly, Kangas et al. (2016) found relatively high seedling survival on flats. This was particularly evident at drier sites where flats are rarely inundated, highlighting the importance of microtopography in the context of site-specific hydrologic regimes. Microtopography also influenced sapling status (live vs. dead), suggesting that live saplings were more common on flats than mounds; however, microtopography appeared in fewer of the top sapling regression models than in the corresponding seedling analysis. This suggests that microtopography was less influential to sapling status than to seedling status, while canopy openness was more influential for saplings (as discussed below). Future research may focus on among-site variations in microtopography paired with water table data, as we might expect to see greater survival and recruitment of cedar regeneration at sites with heterogeneous microtopography as well as sites with greater proportions of mounds.

The importance of maintaining adequate substrate moisture for the establishment and survival of cedar seedlings and saplings was suggested long ago (Nelson 1950, Caulkins 1967), and has been confirmed by more recent studies (Chimner and Hart 1996). The seasonal flooding typical in this forest type results in a shallow rooting zone for cedar (Curtis 1946, Pregitzer 1990), which poses risks of desiccation as the water table drops (Curtis 1946). The ability of both the seedling and sapling size classes at our sites to survive on flats suggests that, after establishment (having excluded the most immature seedlings), these microsites – with substrate moisture conditions intermediate between those of mounds and pits – may serve as adequate refugia from desiccation during dry years. We propose that both flats and mounds are beneficial to seedling and sapling survival, with flats being more beneficial in drier periods (or drier sites), and mounds in wetter periods (or wetter sites). Further research involving monitoring of the depth to water table to account for hydrological differences among sites would clarify this relationship.

As expected, browse was also a strong predictor of seedling biotic status (i.e., browsed seedlings were more likely to be found dead). Cedar stands provide needed shelter for white-tailed deer, particularly in winter, and cedar is reported to be highly palatable to deer (Bradshaw and Waller 2016). The capacity of deer browsing to impede or prevent cedar recruitment has been documented in a number of controlled studies (e.g., Cornett et al. 2000, Larouche and Ruel 2015, Palik et al. 2015); however, attempts to link stand- and region-scale deer populations to regeneration density and survival have occasionally proven inconclusive (Villemaire-Côté et al. 2017, Reuling et al. 2019).

We pooled all browse identified as being caused by either ungulate or hare in these analyses due to a desire to characterize the total effect of browsing; however, we found deer or moose (*Alces alces*) (combined as ungulate browse) to be the dominant browsers overall, followed by hare. We note that as in previous studies of seedling browse, we were unable to tally seedlings that had been browsed to the ground, as no part of the seedling would have been visible. Although the number of such seedlings is unknown, their presence would have strengthened these results and may have revealed a more pronounced negative effect of browse on seedling success.

While microtopography and browse were the most influential predictors of seedling status, canopy openness was also significant, with a majority of the top regression models showing live seedlings to be more prevalent under open conditions. These results are similar to those of two previous studies that found slight positive associations between canopy gaps and cedar seedling densities (Rooney et al. 2002, Forester et al. 2008). Yet size of canopy openings may be important. In our planted-seedling experiment, we found that survival decreased slightly with increasing canopy openness. As noted above, seedlings in the planting experiment experienced greater canopy openness (mean 32%, range 13 to 57%) than those in the inventory plots (mean 19%, range 6 to 42%), and the distributions of openness values differed significantly. We suggest that the greater openness in the planting study includes light levels sufficiently high to be detrimental to seedling survival. This suggestion is consistent with findings that group-selection harvests – which created canopy openings similar in size (ca. 625 m^2) to those of our planting area – had lower cedar seedling survival when compared to harvests resulting in smaller canopy openings (Larouche 2009). Sapling status was also strongly influenced by canopy openness, as a strong positive association was seen between increasing canopy openness (mean 20%, range 4 to 41%) and live biotic status of saplings. More specific information on the size of gaps most beneficial to cedar regeneration may be an area for future research.

Our interpretation of results requires the mention of two caveats. First, all small cedar stems were recorded as seedlings, implying establishment from seed, yet many of them were undoubtedly established vegetatively. Previous studies have documented high rates of vegetative reproduction for this species (Curtis 1946, Nelson 1950, Caulkins 1967). In all but a few cases, vegetative origin on our sites could not have been determined definitively without destructive sampling. By combining the two modes of regeneration, we were unable to evaluate any differences between the two regarding the important predictors identified above. For example, cedar regenerating from seed is known to be less shade tolerant than that arising vegetatively (Boulfroy et al. 2012); perhaps meaningful differences likewise exist regarding flooding tolerance and substrate requirements.

Second, our results may have been affected by presumably older, suppressed, sapling-sized stems in our sapling inventory. We noted such individuals during the field inventory (see 'low-vigor' saplings in Methods). Roughly 15% of cedars in the sapling size class were judged to have these characteristics. Future research on this species should similarly consider potential differences in site associations and ecology for these individuals.

Finally, although our analyses focused on individual stems, we note several findings at the plot level. The significant negative correlations

between tree density and both seedling and sapling abundance (as above) corroborate our finding regarding plot-level canopy openness; that is, regeneration is more abundant on plots with moderately open canopies. The significant positive correlation between CWD volume and sapling abundance supports our findings regarding the importance of mounds (CWD formed a portion of the mounds) and/or canopy openness (CWD presence suggests past canopy-tree mortality). One aspect likely influencing plot-to-plot variability is the local hydroperiod, particularly considering that wetter sites typically have more pronounced microtopographic variation (Diamond et al. 2019). Unfortunately, we did not collect hydroperiod data, which would have required water-table monitoring wells at each plot.

6. Management implications

The findings presented here suggest the establishment and recruitment of cedar regeneration can be fostered using management strategies that aim to (1) maintain diverse microtopography and typical site hydrology, (2) allow for or create moderate sized canopy openings that promote both establishment and recruitment of cedar regeneration, and (3) reduce browsing impact.

First, our findings support management practices that protect the natural microtopography of cedar stands, as mounds were strongly associated with occurrence of live seedlings and saplings, while flats may also contribute to sapling recruitment. This finding mirrors recommendations by previous authors who noted the negative effect of harvest-related ground disturbance on cedar regeneration and microtopography (Chimner and Hart 1996, Cornett et al. 1997). We recommend that management activities are conducted in ways that minimize the impact of machinery on the forest floor, which may homogenize microtopographic variability. This can be achieved by minimizing harvesting trails, and conducting harvesting activities in winter when the ground is frozen and protected by snow. This recommendation is specific to lowland stands typified by pit-and-mound microtopography and seasonal flooding; we recognize that cedar regeneration in drier, less topographically-variable sites may not benefit from these same strategies. For instance, leveling of microtopography resulting from machinery may not inhibit cedar regeneration on drier sites where flooding is not a frequent concern. While our study did not address coarse woody debris as a substrate, nurse logs create mounds that are thought to provide excellent microsites for cedar seedling establishment (Caulkins 1967). Managers may, therefore, consider retaining and protecting coarse woody debris on site when possible. Although specific recommendations do not exist for this forest type, the Minnesota Department of Natural Resources recommends a minimum of 5 to 12 logs, 30 cm diameter or greater, per ha be retained as future nurse logs in *Thuja-Betula* communities (Minnesota DNR 2003).

Although the present study does not evaluate the role of gap size on cedar regeneration, our results showed that greater canopy openness (within the 4 to 42% range observed in inventory plots) was associated with greater likelihood of live seedlings and saplings. As noted in previous studies, the formation of gaps through particular silvicultural systems may create moderate-light microsites advantageous to regeneration success (Boulfroy et al. 2012). Our results suggest that after being recruited to the sapling size class, most saplings were associated with gaps or sparser canopies. Therefore, we suggest that managers consider multi-aged forest structures with a light canopy thinning such as that achieved through single-tree selection during seedling establishment to allow for increased light while mitigating the risk of growth of competing species. Previous work has suggested gaps smaller than one tree height in width (i.e., gaps $<$ ca. 200 m^2) to foster cedar germination (Boulfroy et al. 2012). When possible, after seedling cohort establishment, a gradual opening of the canopy using group selection, irregular shelterwood, or similar treatments may encourage growth and recruitment into larger size classes, as suggested by previous studies (Larouche et al. 2011, Ruel et al. 2014, Palik et al. 2015).

These silvicultural prescriptions would also maintain site hydrology. Given that complete canopy removal is known to significantly raise the water table in similar lowland forested sites (Slesak et al. 2014), the partial canopy removals mentioned above would likely maintain water tables at a level favorable to cedar establishment and recruitment. Other activities such as road building can also cause flooding in lowland forests (Chimner et al. 2017). While more research is needed to shed light on the impacts that such activities and the associated changes to the water table have on cedar stands, we recommend that care is taken to plan silvicultural treatments and construct roads to reduce hydrologic alterations.

Finally, because our results show that dead seedlings are associated with browsing, we recommend that managers consider excluding deer from stands managed for high production if large deer numbers are anticipated. Deer may be excluded or otherwise controlled after harvesting while new seedlings are establishing and when advance regeneration is released and growing into larger size classes (Verme and Johnston 1986, Palik et al. 2015). Leaving logging slash and other woody debris on site at time of harvest represents a simple means of partial deer exclusion, as the slash tends to limit deer access to seedlings (Verme and Johnston 1986). When possible, protection from deer should continue until sufficient regeneration has grown beyond the reach of deer (ca. 2 m, Allogio 2020), allowing the stems to advance to larger size classes and eventually replace aging overstory cedar trees.

CRediT authorship contribution statement

Jeanette A. Allogio: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft. **Shawn Fraver:** Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **Laura S. Kenefic:** Resources, Writing – review & editing. **Jay W. Wason:** Formal analysis, Writing – review & editing. **John-Pascal Berrill:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119639.

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