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Survival and growth of northern white-cedar and balsam fir seedlings in riparian management zones in northern Minnesota, USA

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ABSTRACT

Northern white-cedar (*Thuja occidentalis*) and balsam fir (*Abies balsamea.*) are co-occurring species in riparian forests of the western Great Lakes region. Throughout much of the region, northern white-cedar has been experiencing population declines due to herbivory by white-tailed deer (*Odocoileus virginianus*). Preferential browse on northern white-cedar removes seedlings and saplings, allowing balsam fir, as less-preferred browse species, to recruit into larger size classes and potentially out-compete northern white-cedar. There is great interest in restoring and sustaining northern white-cedar in riparian forests, but the factors that contribute to success or failure of established seedlings are not well understood. We used a riparian harvesting experiment in northern Minnesota, USA to study factors that encourage or deter survival and growth of planted northern white-cedar seedlings in riparian areas, relative to the response of balsam fir. The factors we manipulated experimentally included amount of overstory basal area (uncut or partially harvested), establishment microsite (mound, pit, slash), and browse (protected or not).

Browse frequency was significantly higher on northern white-cedar than on balsam fir, particularly in the partially-harvested forest. Northern white cedar survival was similar to balsam fir when unprotected from browsing, but was higher when browsing was excluded. When protected, northern white-cedar survival approached 100% in both uncut and partially-cut forest on mound and slash microsites, whereas survival of balsam fir was significantly lower in uncut compared to partially-cut forest. Both species had low survival in pit microsites. Relative height growth rates were similar between the two species when protected from browsing, and both species had higher growth with partial-harvest. When unprotected from browsing, relative height growth of northern white-cedar was often negative, while height growth of balsam fir was only minimally reduced compared to the protected seedlings. The two species had similar relative diameter growth in the unprotected treatment, and growth of both species was reduced compared to growth when protected. When protected, northern white-cedar had a relative diameter growth advantage over balsam fir, particularly in the partial-harvest treatment. Our results suggest that a strategy to establish northern white-cedar in riparian forests may be to plant seedlings in uncut forest on raised microsites and protect these seedlings from browsing. After these seedlings are well-established, and perhaps balsam fir is intentionally eliminated, a partial-harvest may be used to release the northern white-cedar seedlings, while still maintaining pre-harvest browse protection.

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1. Introduction

Riparian forests are valued for the functional role they have in sustaining water quality and aquatic habitat, for their contributions to biodiversity, and for the timber and recreation resources they provide (Gregory et al., 1991; Palik et al., 1999). A challenge facing foresters is how to maintain the ecological integrity of riparian forests, while managing these forests for timber and other resources. Sustaining component tree species is part of this challenge, as individual species can play an integral role in providing riparian functions, and may they be a valuable timber resource (Palik et al., 1999). One such species is northern white-cedar (*Thuja occidentalis*), a long-lived shade tolerant boreal and sub-boreal conifer that is characteristic of riparian forests in the Great Lakes region of North America (Burns and Honkala, 1990). In particular, northern white cedar in riparian settings can be a source of large

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woody debris to streams, provide stream and bank shading, and contribute to bank stability.

Beginning in the 1940s, forest managers across the range of northern white-cedar began to see a lack of advance regeneration and recruitment into the overstory. The absence of sapling size classes in many stands demonstrated a consistent lack of height ingrowth (Rooney et al., 2002; Forester et al., 2008; White, 2012). Research in northern white-cedar stands has shown that in at least some locations, seed production and germination rates are sufficient to sustain populations (Heitzman et al., 1997; Cornett et al., 2000; Forester et al., 2008), suggesting other causes for the decline in recruitment. Herbivory from white-tailed deer (*Odocoileus virginianus*) is cited as the primary factor restricting recruitment of regeneration into the sapling and overstory layers (Heitzman et al., 1997; Forester et al., 2008; Hofmeyer et al., 2009; Boulfroy et al., 2012; White, 2012).

Herbivory on established seedlings and saplings serves as a major physical suppressor of northern white-cedar; slow growth rates and the ability to survive suppression for many years further contribute to a delay in recruitment. In combination, these factors may allow other species, e.g., with faster growth rates and/or not a preferred browse, to gain overstory dominance (Larouche et al., 2010; White, 2012). The co-occurring species that is most often cited as likely to benefit from preferential browse on northern white-cedar is balsam fir (*Abies balsamea*) (Chimner and Hart, 1996; Van Deelen et al., 1996; Cornett et al., 2000; Hofmeyer et al., 2009). Balsam fir is a shade tolerant species that is not a preferred browse for white-tailed deer and is reported to be capable of growing more successfully than northern white-cedar into the overstory under low light conditions (Johnston, 1986; Schaffer, 1996; Davis et al., 1998; Hofmeyer et al., 2009).

Previous studies have documented the importance of light and forest floor microsites in establishment of northern white-cedar regeneration (St. Hilaire and Leopold, 1995; Cornett et al., 1997; Simard et al., 2003). However, the long-term roles of light availability and microsites for growth and eventual recruitment of established seedlings into larger size classes are not well understood. Increased light availability should enhance growth of established northern white cedar seedlings, even though it is shade-tolerant, as long as the light increase does not result in competitive inhibition by more responsive species. Microsite influences may be complex and variable. Raised mounds, formed by tree-fall root wads, may provide nutrient-rich organic soils and protection from flooding (St. Hilaire and Leopold, 1995; Chimner and Hart, 1996; Simard et al., 2003), which could enhance survival and growth in riparian settings. In comparison to mounds, pits formed by tree-falls may have higher soil moisture, lower soil temperature, and a higher danger of flooding (Webb, 1988; Cornett et al., 1997; Clinton and Baker, 2000). The latter especially could be detrimental to survival and growth of seedlings. Finally, slash microsites, formed from the branches of fallen trees or from logging slash, may provide microclimate amelioration and protection from browsing (Verme and Johnston, 1986; Schaffer, 1996).

Using a riparian harvesting experiment as our setting, we studied factors that encourage or deter survival and growth of northern white-cedar regeneration in riparian areas, relative to the response of balsam fir. The harvesting experiment consisted of different levels of partial overstory removal within 45 m wide riparian management zones along streams in northern Minnesota, USA. Our objectives were to examine the influence of the amount of residual basal area (as an index of understory light levels) on northern white-cedar and balsam fir planted seedling response, as well as the role of surface microsite and herbivory on the survival and growth of seedlings. We addressed the following questions: (1) does herbivory, largely by white-tailed deer, differ between northern white-cedar and balsam fir seedlings and is browse frequency influenced by overstory basal area or microsite in riparian settings, (2) do survival and growth of northern white-cedar seedlings differ with amount of overstory basal area, planting microsite, and herbivory, and (3) is there a difference in survival and growth response of northern white-cedar and balsam fir due to these factors? Answers to these questions will help guide practices that encourage the establishment of northern white-cedar in riparian areas.

2. Methods

2.1. Study area and sites

This study was conducted in three forested riparian areas that were part of a larger study in northern Minnesota, USA that examined the influence of riparian harvesting on stream and forest characteristics (Blinn et al., 2004). The study areas were all within the Laurentian Mixed Forest Province, which is a broad ecotone between the eastern deciduous forest and boreal forest biomes. The region has a cool temperate climate with mean annual temperatures between 1 and 4 °C, and average annual precipitation between 53 and 81 cm. Long-term average maximum snow depths range from 36 to 51 cm. Soils originated from Pleistocene till and included well drained loamy sands that are shallow to bedrock in the uplands, with sandy loams in lower landscape positions in stream valleys.

The study sites were selected in 2003 to meet the following criteria: (a) riparian forests were located adjacent to perennial streams that were less than 6 m in width; (b) a minimum contiguous forested area of 6.5 ha with a minimum of 426 m of stream frontage; (c) forests were mature in both the riparian zones and adjacent uplands. Prior to harvest treatment, dominant tree species included paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam fir, black ash (*Fraxinus nigra*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American basswood (*Tilia americana*), with lesser amounts of northern red oak (*Quercus rubra*), bur oak (*Quercus macrocarpa*), green ash (*Fraxinus pennsylvanica*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), big-tooth aspen (*Populus grandidentata*), balsam poplar (*Populus balsamifera*), yellow birch (*Betula allegheniensis*), silver maple (*Acer saccharinum*), ironwood (*Ostrya virginiana*), and northern white-cedar.

2.2. Experimental design and treatments

At each of three study sites, two 3.3-ha treatment stands (block) were delineated on one side of the stream, with the two stands separated by at least 60 m of unharvested forest (Fig. 1). Within each treatment stand, a 0.8-ha riparian management zone (RMZ) was delineated along the length of the stream (183 m) that extended 45 m towards the upland. The remainder of the treatment unit (2.5 ha) was outside of the RMZ and considered to be upland forest.

In each block, the following treatments were assigned to the two experimental units: (1) RMZ uncut control (RMZC) and (2) RMZ partially harvested (RMZH). For both of these treatments, the forest outside and upland of the RMZ was clearcut. The mean (± standard error) residual basal area of the three harvested RMZs and mean percent of pre-harvest basal area remaining was 15.6 (2.6) $m^2\ ha^{-1}$ and 61 (4)%, respectively. Tree species favored for retention included, where possible, longer-lived species, conifers, and hard mast-producing species. To lessen confounding impacts of harvesting on streams, the RMZC treatment was always established upstream of the RMZH treatment. Timber harvesting in the RMZ (and adjacent upland) was conducted on frozen ground,

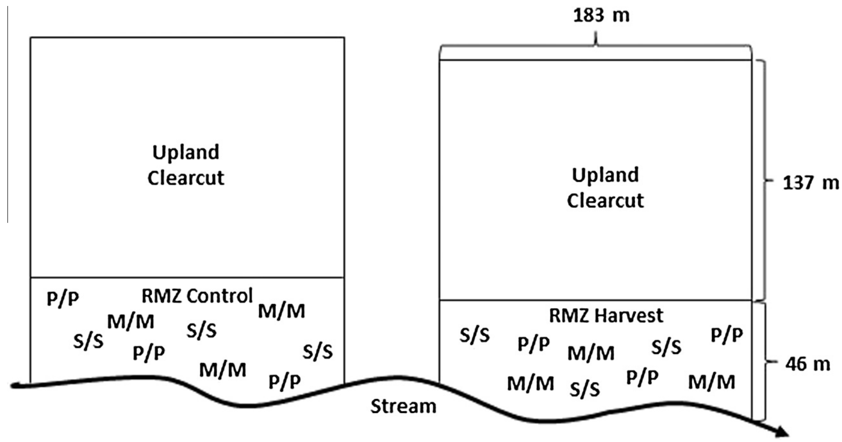

Fig. 1. Layout of experimental design. Within the Riparian Management Zones, letter pairs refer to planting microsites: M = mound, P = pit, S = slash. One microsite of each pair was fenced for deer exlosure while the other microsite was unfenced.

after sufficient snow had accumulated, during the winter of 2003–2004, using a feller-buncher and grapple skidder.

2.3. Planted seedling study

The seedling study was established in May 2004 as a randomized block experiment within the larger riparian harvesting experiment. The seedling study was a 2 × 2 × 3 × 2 factorial experiment replicated at three blocks (sites), and consisted of two species (northern white-cedar and balsam fir), two overstory treatments (control and partial-harvest), three microsite treatments (mound, pit, and slash), and two browse treatments (fenced and unfenced).

Seedlings were planted within plots associated with the three microsite types. Three pairs of each microsite were selected in each treatment stand for a total of nine pairs (18 plots) per overstory treatment stand (Fig. 1). Plot locations were selected from naturally occurring microsite features that were distributed throughout the control and harvested RMZs. Mound microsites were either decomposing tree stumps in decay class 4 (wood is mostly rotten), as described by Fraver et al. (2002), or soil slumps from tree root tip-ups. Pit microsites were distinct depressions in the forest floor formed by tree root tip-ups, abandoned stream channels, or dips in underlying rock substrate. Slash microsites were piles of coarse and fine woody debris of different dimensions, ranging from solid boles of wind thrown trees to logging debris. In general, slash microsites were selected if the feature was at least 0.25 m in height and 2 m in length.

At each microsite pair location, a fenced plot (browse exclusion) was established within, around, or adjacent to a microsite and a second unfenced plot was established in association with the other microsite. For the exclusion plots, 2.8 m tall polypropylene fencing having a grid size of 5 cm^2 was secured to steel fence posts to encompass an area of 9 m^2.

Four northern white-cedar and four balsam fir seedlings were planted in both the fenced and unfenced plots on a 0.5 m spacing. Seedlings were planted on the sides and tops of mounds, around the sides and floor of pits, and along the north side of slash to maximize shading. Seedlings of both species were three year-old nursery stock grown by Minnesota DNR Badoura State Forest Nursery. Aluminum nursery tags with individual identification codes were attached loosely around the stem of each seedling.

Baseline measurements of height (from ground just below litter to the tip of longest leader) and basal diameter (averaged from two measurements taken at right angles to each other at ground level just below the litter) were taken within four weeks after planting. Subsequent height and basal diameter measurements were collected annually in the fall after most growth was complete.

Browse data were collected biannually in spring and fall. Data were recorded as the presence or absence of seasonal browse on a seedling, starting the fall after the first growing season through the fall of the fourth growing season, for a total of seven observations. Browse damage was determined by a visual examination of each seedling and by comparing heights with previous measurements. White-tailed deer browse was recognizable by a shredded stem tip and uneven removal of foliage. Infrequent lagomorph browse was noted as a stem clipped with a clean, sharp 45° angle and was combined with deer browse in the analysis. Survival data were collected each spring and fall. Seedlings were scored as alive (green foliage and green cambial tissue were evident) or dead (all foliage removed and the seedling lacked a green cambial layer).

2.4. Data analysis

Browse frequency (percent) was calculated as *number of browse events observed/seven total observations* × 100. Only seedlings that were alive at the end of the study were included in the browse analysis. Percent survival after four years was calculated by species on each plot as *the number of surviving seedlings/four* (*original number of seedlings*) × 100.

The different growth habits of northern white-cedar and balsam fir made direct comparisons of height and diameter growth inappropriate. Instead, we used relative growth rates (RGR) to compare height and diameter growth between species. Relative growth was defined as *log final diameter or height – log initial diameter or height/four*, where *final diameter or height* was the last measured value, *initial diameter or height* was the value at planting, and *four* was the number of growing seasons. Seedlings that died were not included in the growth analysis.

General linear models were used to compare responses among treatments, with site included as a blocking factor ($n = 3$). Tukey–Kramer pairwise tests were used for means comparisons when the overall model was significant. Dependent variables included survival (%), browse frequency (%), relative height growth (RHG), and relative diameter growth (RDG). Independent variables included species (northern white-cedar and balsam fir), browsing (unfenced, fenced), overstory treatment (control and harvest), and microsite (mound, pit, and slash), and their interactions. Transformations were performed to meet assumptions of normality and homogeneity of variance. Statistical analyses were performed with SAS/STAT® software, Version 9.1.3. Results were considered significant at $p \leqslant 0.05$.

Table 1
General linear model ANOVA for browse frequency. Data were arcsine square-root transformed for analysis.

Source	DF	Type III SS	Mean square error	*F*-stat	*P*-value
Block	2	0.0955	0.0478	na	na
Species (S)	1	0.8456	0.8456	47.90	<0.0001
Microsite (M)	2	0.1677	0.0839	4.75	0.0212
Overstory treatment (O)	1	0.1348	0.1348	7.64	0.0124
S × M	2	0.0579	0.0290	1.64	0.2201
S × O	1	0.0193	0.0193	1.09	0.3087
M × O	2	0.0034	0.0019	0.10	0.9094
S × M × O	2	0.0439	0.0220	1.24	0.3106
Model	13	1.4090	0.1084	6.14	0.0002
Error	19	0.3354	0.0177		
Corrected total	32	1.7444			

Table 2
General linear model ANOVA for percent survival. Data were arcsine square-root transformed for analysis.

Source	DF	Type III SS	Mean square error	*F*-stat	*P*-value
Block	2	5.1887	2.5944	na	na
Species (S)	1	0.8133	0.8133	9.58	0.003
Fence treatment (F)	1	0.9110	0.9110	10.73	0.002
Overstory treatment (O)	1	0.4341	0.4341	5.11	0.029
Microsite (M)	2	3.9508	1.9754	23.26	<0.0001
S × F	1	0.1311	0.1311	1.54	0.220
S × O	1	0.5070	0.5070	5.97	0.019
S × M	2	0.0614	0.03107	0.36	0.699
F × O	1	0.0420	0.0420	0.49	0.485
F × M	2	0.3478	0.1739	2.05	0.141
O × M	2	0.0391	0.0196	0.23	0.795
S × F × O	1	0.0071	0.0071	0.08	0.774
S × F × M	2	0.0030	0.0015	0.02	0.983
S × O × M	2	0.0393	0.0196	0.23	0.795
F × O × M	2	0.0835	0.0418	0.49	0.615
S × F × O × M	2	0.0243	0.0122	0.14	0.867
Model	25	12.5836	0.5033	5.93	<0.0001
Error	46	3.9072	0.0849		
Corrected total	71	16.4908			

3. Results

3.1. Browsing on unfenced seedlings

Browse frequency of surviving seedlings outside of the fencing differed significantly between species ($p < 0.0001$) and overstory treatments ($p = 0.015$), and among microsites ($p = 0.014$). No interactions were significant (Table 1). Pooled across overstory treatment and microsite, browse frequency was 37% for northern white-cedar seedlings and 13% for balsam fir seedlings (Fig. 2). Pooled across species and microsite, browse frequency was 30% in the harvest treatment and 20% in the control treatment (Fig. 2). Pooled across species and overstory treatments, browse frequency in mounds was 33%, which was significantly higher than pits (16%) ($p = 0.018$), but not slash (24%) ($p = 0.165$), while the latter two did not differ significantly ($p = 0.403$) (Fig. 2).

3.2. Survival

Seedling survival after four years differed significantly between species ($p = 0.003$), fencing treatment ($p = 0.002$), overstory treatment ($p = 0.029$), and among microsites ($p < 0.0001$) (Table 2, Fig. 3). Only the interaction of species and overstory treatment was significant ($p = 0.019$). Pooled across fencing treatment and microsite: (i) northern white-cedar survival was significantly higher than balsam fir in the overstory control (74% vs. 48%; $p = 0.002$); (ii) survival did not differ between northern white-cedar and balsam fir in the harvest treatment (75% vs. 73%; $p = 0.935$); (iii) survival of balsam fir in the harvest treatment was significantly higher than in the control treatment (73% vs. 48%; $p = 0.009$); and (iv) survival of northern white-cedar did not differ between the control and harvest treatments (74% vs. 75%; $p = 0.999$). Pooled across species, overstory treatment, and microsite, seedling survival was significantly higher inside than outside of fencing (75% vs. 60%; $p = 0.002$). Pooled across species, overstory treatment, and fencing treatment, survival of both species was lower in pits (46%) than in mounds (79%) or slash (77%) ($p < 0.0001$), while the latter two microsites did not differ significantly ($p = 0.964$).

3.3. Growth

Relative height growth (RHG) differed significantly between species ($p = 0.004$), fencing treatment ($p = 0.001$), overstory treatment ($p = 0.002$), but not among microsites ($p = 0.370$) (Table 3 and Fig. 4). The interaction between species and fencing treatment

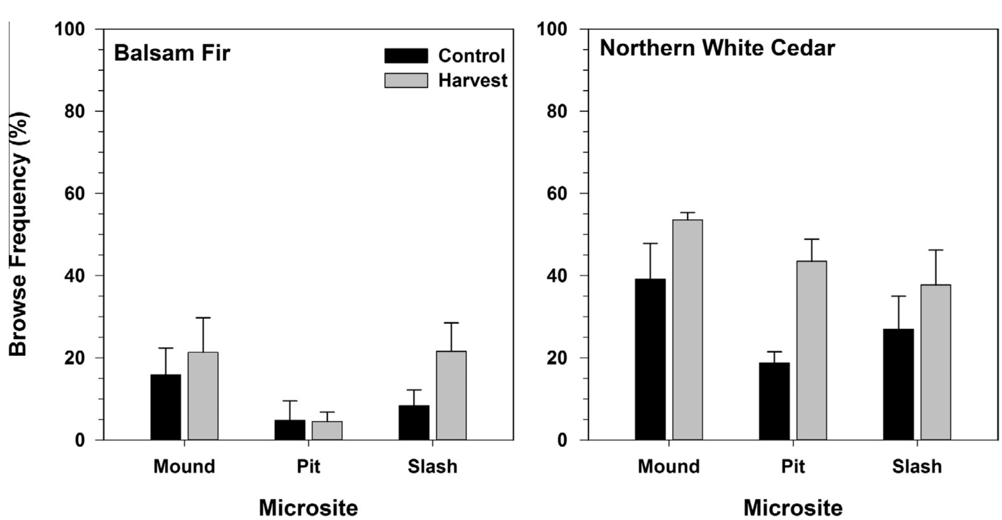

Fig. 2. Browse frequency on planted balsam fir and northern white-cedar seedlings outside of fencing. Frequency was calculated as the percentage of times (of seven observations over a four year period) that a seedling was browsed. Values are means (±se) of three replicates.

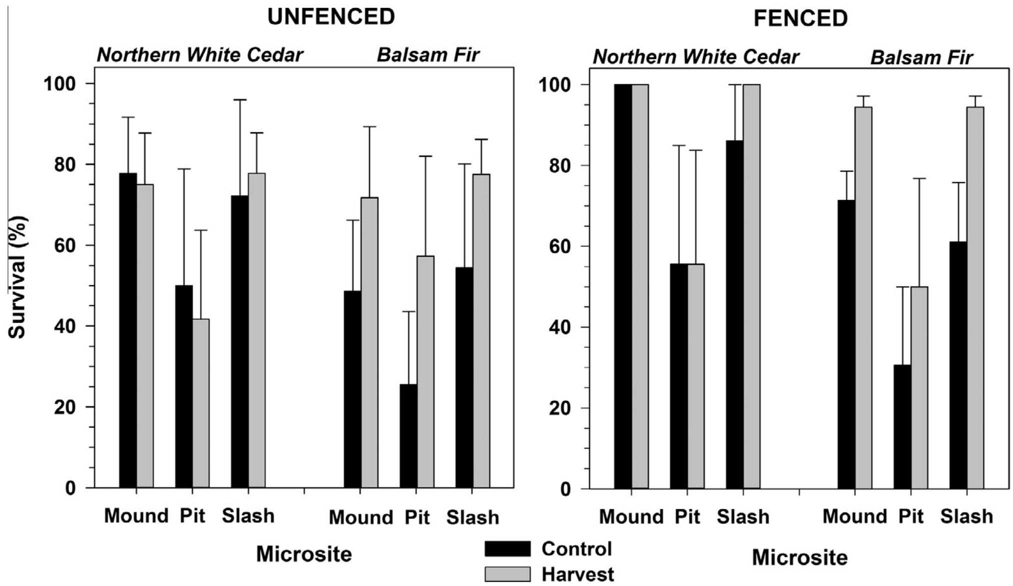

Fig. 3. Survival of planted balsam fir and northern white-cedar seedlings. Survival was calculated as the percentage of seedlings surviving after four years. Values are means (±se) of three replicates.

Table 3
General linear model ANOVA for relative height growth. Data were arcsine square-root transformed for analysis.

Source	DF	Type III SS	Mean square error	*F*-stat	*P*-value
Block	2	0.1563	0.0782	na	na
Species (S)	1	0.0529	0.0529	9.21	0.0043
Fence treatment (F)	1	0.0710	0.0710	12.37	0.0011
Overstory treatment (O)	1	0.0616	0.0616	10.72	0.0022
Microsite (M)	2	0.0117	0.0059	1.02	0.3700
S × F	1	0.0885	0.0885	15.41	0.0003
S × O	1	0.0221	0.0221	3.86	0.0567
S × M	2	0.0034	0.0017	0.29	0.7482
F × O	1	0.0261	0.0261	4.54	0.0394
F × M	2	0.0043	0.0022	0.38	0.6876
O × M	2	0.0054	0.0027	0.47	0.6261
S × F × O	1	0.0034	0.0034	0.59	0.4455
S × F × M	2	0.0308	0.0154	2.68	0.0813
S × O × M	2	0.0177	0.0088	1.54	0.2274
F × O × M	2	0.0079	0.0039	0.69	0.5097
S × F × O × M	2	0.0023	0.0012	0.21	0.8147
Model	25	0.5725	0.0229	3.99	<0.0001
Error	39	0.2240	0.0057		
Corrected Total	64	0.7965			

($p = 0.0003$), species and overstory treatments ($p = 0.05$), and overstory and fencing treatments ($p = 0.039$) were all significant. Pooled across overstory treatments and microsites, RHG of northern white-cedar and balsam fir was not significantly different within fencing (0.20 vs. 0.19; $p = 0.924$), but was significantly different outside of the fencing (−0.005 vs. 0.11; $p < 0.0001$). Pooled across fencing treatments and microsites, RHG of balsam fir was greater in the harvest treatment than in the control (0.18 vs. 0.11; $p = 0.003$), while RHG of northern white-cedar was not different between overstory control and harvest treatments (0.09 vs. 0.11; $p = 0.795$). Finally, pooled across species and microsites, RHG in the overstory harvests was greater than the controls within the fencing (0.24 vs. 0.16; p = 0.003), but not outside of them (0.06 vs. 0.04; $p = 0.847$).

Relative diameter growth (RDG) differed between species ($p = 0.001$), fencing treatment ($p < 0.0001$), overstory treatment ($p < 0.0001$), but not among microsites ($p = 0.474$) (Table 4 and Fig. 5). Interactions between species and fencing ($p = 0.013$) and fencing and overstory treatment ($p = 0.034$) were significant. Pooled across overstory treatments and microsites: (i) RDG of northern white-cedar was significantly greater than balsam fir inside the fencing (0.20 vs. 0.13; $p = 0.001$), but RDG did not differ outside of fencing (0.13 vs. 0.12; $p = 0.934$) and (ii) RDG was higher for northern white-cedar inside than outside fencing (0.20 vs. 0.13; $p < 0.0001$), but RDG of balsam fir did not differ inside and outside fencing (0.13 vs. 0.12; $p = 0.468$). Pooled across microsites and species, RDG in the harvest treatment was significantly higher than the control inside the fencing (0.22 vs. 0.14; $p < 0.0001$), but not outside (0.14 vs. 0.11; $p = 0.247$).

4. Discussion

4.1. Factors influencing browse frequency

Preferential browsing by white-tailed deer on northern white-cedar is widely reported in the literature (Alverson et al., 1988; Heitzman et al., 1997; Forester et al., 2008; Hofmeyer et al., 2009) and is supported by the results of our study. Browse frequency across overstory treatments and microsites was significantly higher on northern white-cedar than on balsam fir. For both species, frequency of browsing was also generally higher in the partially harvested overstory treatment compared to the control. Because deer habitually feed where shrub and grass forage is most available (Smith et al., 2007; Forester et al., 2008; White, 2012), planting in harvested areas where higher light promotes such growth may put seedlings at the greatest risk of herbivory. This suggests the potential for greater northern white-cedar seedling success when planted in unharvested riparian areas.

Browse frequency on northern white-cedar and balsam fir was significantly greater on mounds than in pits or, for cedar, adjacent to slash. The exposed nature of mounds may have left seedlings particularly vulnerable to browse. Pits especially appeared to offer some protection perhaps due to deer avoidance of wet depressions, although we could find no reference to this in the literature. Alternatively, it may be that low survival of seedlings in pits (see below) eliminated the evidence of browsing in this microsite.

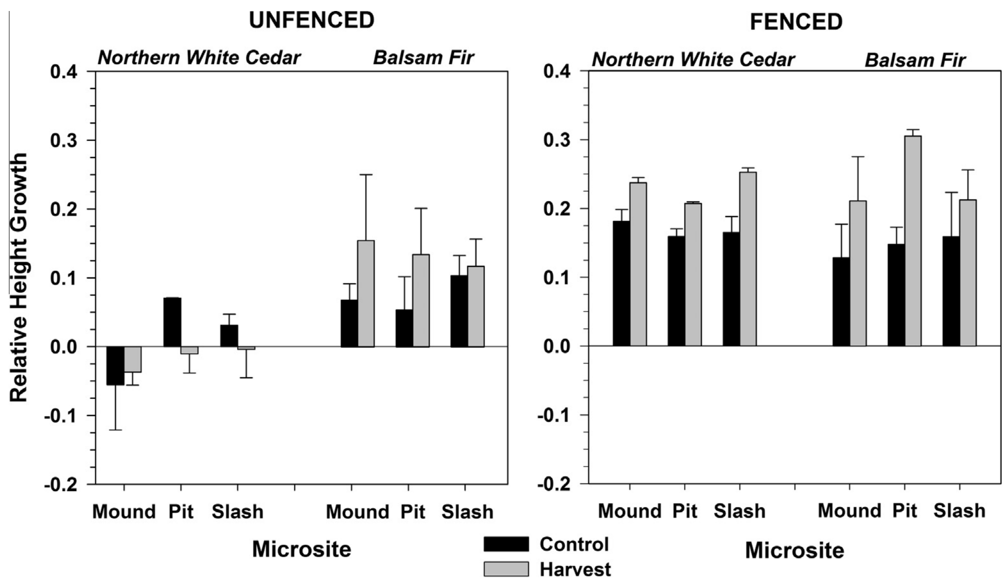

Fig. 4. Relative height growth (RHG) of planted balsam fir and northern white-cedar seedlings. RHG was calculated as the relativized difference between final height after four years and initial height. Values are means (±se) of three replicates.

Table 4
General linear model ANOVA for relative diameter growth. Data were untransformed for analysis.

Source	DF	Type III SS	Mean square error	*F*-stat	*P*-value
Block	2	0.0290	0.0145	na	na
Species (S)	1	0.0253	0.0253	11.80	0.0014
Fence treatment (F)	1	0.0466	0.0466	21.70	<0.0001
Overstory treatment (O)	1	0.0506	0.0506	23.59	<0.0001
Microsite (M)	2	0.0033	0.0016	0.76	0.4739
S × F	1	0.0146	0.0146	6.78	0.0130
S × O	1	0.0030	0.0030	1.40	0.2443
S × M	2	0.0028	0.0014	0.65	0.5264
F × O	1	0.0104	0.0104	4.85	0.0337
F × M	2	0.0028	0.0014	0.66	0.5229
O × M	2	0.0030	0.0015	0.69	0.5073
S × F × O	1	0.0004	0.00004	0.02	0.8896
S × F × M	2	0.0064	0.0032	1.50	0.2357
S × O × M	2	0.0002	0.0001	0.05	0.9469
F × O × M	2	0.0035	0.0018	0.82	0.4468
S × F × O × M	2	0.0007	0.0004	0.17	0.8417
Model	25	0.2066	0.0083	3.85	<0.0001
Error	39	0.0837	0.0021		
Corrected total	64	0.2903			

4.2. Northern white-cedar survival and growth

Survival of northern white-cedar was significantly reduced by browsing outside of fencing. However, better survival inside fencing was overridden by poor survival in pit microsites. As others have shown, seasonal flooding in pits resulted in increased mortality. For example, Cornett (1996) found nearly complete mortality of planted northern white-cedar seedlings in pits that experienced periodic inundation, and Chimner and Hart (1996) reported very low northern white-cedar establishment in microsites with seasonally pooled water.

The partial harvest treatment had no effect on northern white-cedar survival. This result differs from Cornett et al. (2000) in which planted northern white-cedar seedlings, subject to browse, were more likely to die with higher canopy cover compared to those with lower cover.

While 60% of unfenced northern white-cedar seedlings remained alive after four years, their true physical condition was not captured by our survival metric. After four years, most unfenced northern white-cedar seedlings were in poor condition from recurrent browsing (personal observation). Continued decline in survival in unfenced seedlings over the coming years might be expected as herbivory will further impacts these seedlings. For instance, in a browse study in northern Wisconsin, Davis et al. (1998) reported elimination of advance regeneration of northern white-cedar in ten years when subjected to herbivory.

Relative height and diameter growth of unfenced northern white-cedar were significantly lower than growth within fencing, reflecting the negative impact of browsing on seedlings. Relative height growth of unfenced northern white-cedar seedlings was often negative. For protected seedlings, diameter growth was greater in the partial-harvest treatment than in the uncut forest, presumably reflecting increased light availability. This benefit was negated in the face of browsing, which became the equalizing factor that overcame the positive effect of partial overstory removal. Cornett (2000) found similar results, reporting that browse influences on planted northern white-cedar seedlings was stronger than canopy influences. No microsite influences on relative growth were found, suggesting that microsite benefits important to seedling establishment and short-term survival are not as essential to the recruitment of seedlings into larger size classes.

4.3. Comparing northern white-cedar and balsam fir

Balsam fir is a near ubiquitous species in mature forests of the study region, it occurs across a wide range of sites conditions, and when coupled with lower palatability to white-tailed deer, is viewed as a strong competitor with northern white-cedar in riparian settings (Johnston, 1986; Schaffer, 1996; Davis et al., 1998; Hofmeyer et al., 2009). Based on results from our experiment, a survival and growth advantage of balsam fir over northern white-cedar is only realized in the face of browsing and then it is only marginal and largely restricted to greater height growth in the (presumably) higher resource environment of the partially harvested forest. It is important to note that these results were based on only four years of observation. It is likely that continued browsing of unprotected northern white-cedar will result in further

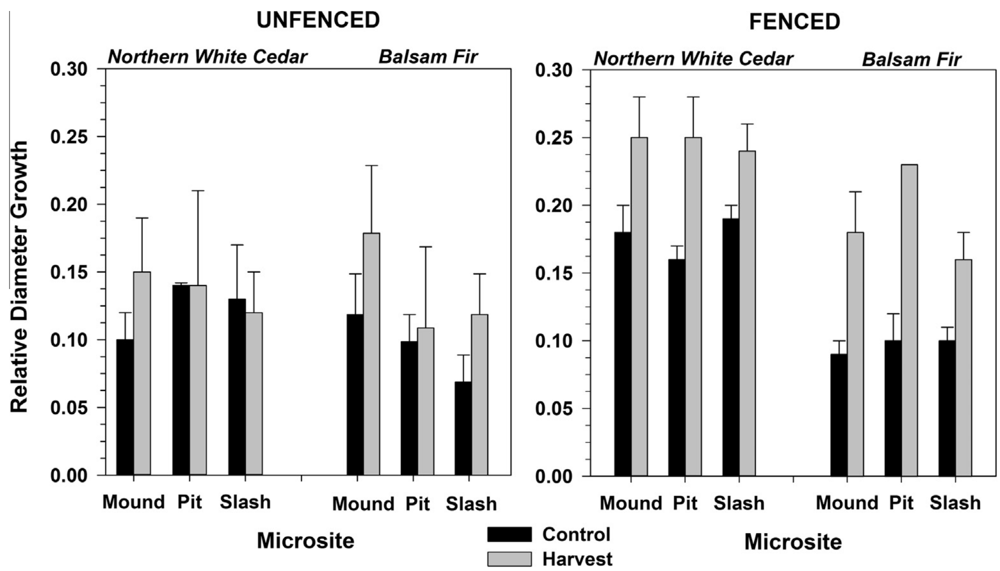

Fig. 5. Relative diameter growth (RDG) of planted balsam fir and northern white-cedar seedlings. RDG was calculated as the relativized difference between final diameter after four years and initial diameter. Values are means (±se) of three replicates.

height growth reductions and greater mortality (Boulfroy et al., 2012), giving balsam fir an advantage over longer time periods.

Northern white-cedar did have significantly higher survival than balsam fir when protected from browsing, particularly in the unharvested forest. Reduced survival of balsam fir compared to northern white-cedar in the uncut forest is at odds with the description of the former as a shade-tolerant seedling (Logan, 1969; Frank, 1990). It is possible that our planted seedlings, which were grown for three years in an open light environment of a nursery, may not have had the morphological and physiological characteristics that could adapt effectively to lower light levels when first transplanted, at least over the time period of the study.

We did find that relative diameter growth of unfenced northern white-cedar and balsam fir were similar, despite reduced relative height growth of the former species. This demonstrated that even under browse pressure, northern white-cedar seedlings continued to allocate resources to diameter growth, which in turn reflects the difference in growth strategy between species. The indeterminate growth of northern white-cedar, compared to determinate growth for balsam fir, allowed foliage lost during spring browse events to be replaced during the growing season, generating resources for diameter growth. In this manner total height growth was negative, but total diameter growth was positive.

5. Management application

In the riparian settings we examined in this study, most unprotected northern white-cedar seedlings may die due to high browse frequency and continued loss of leaf area and terminal leader growth, while more balsam fir seedlings may likely survive due to low browse frequency and pressure. Moreover, balsam fir has a height growth advantage compared to northern white-cedar when both are unprotected from browsing, which eventually will result in more seedlings recruiting into larger sizes. However, if herbivory is prevented, then northern white-cedar is competitive with balsam fir in terms of survival and growth and may be at an advantage in an uncut riparian forest due to higher survival in that setting. The results suggest that competition from balsam fir can be minimized by establishing northern white-cedar seedlings in an uncut forest, while protecting these seedlings from browsing until regeneration is well established and balsam fir regeneration, if present, has been reduced. At that point, the overstory may be partially-harvested to release the northern white-cedar advance regeneration.

Another strategy for successful regeneration of northern white-cedar is to reduce deer densities. Some studies suggest that a population of eight deer/km^2 is a standard land base carrying capacity (Alverson et al., 1988), but others indicate that a level of one to four deer/km^2 is the maximum level that will avoid a detrimental impact to browse-sensitive species (Alverson et al., 1988). During the period of our study (2004–2007), pre-fawn deer densities in region of the study sites were estimated at four to eight/km^2 for the Nemadji State Forest, four to nine/km^2 at Shotley Brook, and one to six/km^2 at East Branch Beaver River (MN DNR, 2007). Given the high browse frequency on northern white-cedar that we and others document, and the generally detrimental effects of browsing on growth, population levels lower than eight deer/km^2 appear to be necessary to avoid impact of herbivory. In the face of high deer densities, deer exclosures may be effective, but they may be cost prohibitive, when assessed over the time period needed to grow seedling above browse height.

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