5-1-2009

Seedlings' Substrate Preferences in a Minnesota Old Growth Thuja-Betula Forest

Stephen C. Rossiter
Connecticut College, srossite@conncoll.edu

Recommended Citation
Rossiter, Stephen C., "Seedlings' Substrate Preferences in a Minnesota Old Growth Thuja-Betula Forest" (2009). *Environmental Studies Honors Papers.* Paper 2.
http://digitalcommons.conncoll.edu/envirohp/2

Seedlings' Substrate Preferences in a Minnesota Old Growth *Thuja-Betula* Forest

Stephen Rossiter

May 1, 2009

Abstract: Northeastern Minnesota's logging history has altered the forests enough to cause concern about the reproduction of *Thuja occidentalis* and *Betula alleghaniensis*. I studied a rare old growth example of an already rare mesic *Thuja-Betula* forest and asked how well those species were regenerating in that mostly unaltered ecosystem. In managed forests, a lack of suitable substrate is thought to be limiting their seedling establishment so I asked which substrates the seedlings preferred in the old forest. To answer both questions, I measured the seedling densities of all canopy tree species across height classes and substrate types within twenty $100m^2$ plots. *T. occidentalis*, *B. alleghaniensis*, and the uncommon *Picea glauca* were found exclusively on coarse woody debris (CWD) rather than leaf litter. I used a generalized linear mixed effects model to rank the influence of each type of CWD on seedling density while comparing their influence to that of site level variables. *T. occidentalis* regeneration is failing, with no seedlings >10cm tall, due to either herbivory or a lack of light. Its seedlings did show significant preferences for CWD that was, in decreasing order of importance: moss covered, highly decayed, conifer wood. Site level variables did not influence *T. occidentalis* seedling density. *B. alleghaniensis* may be replacing itself in the canopy but only just, and is also limited by the availability of canopy gaps. Its seedlings preferred CWD that was, in decreasing order: moss covered, highly decayed, moderately decayed, *Thuja* wood, a stump (rather than a log). For *B. alleghaniensis* seedlings, CWD traits were almost twice as influential as site level variables. High decay class CWD was the most important factor for seedlings of the uncommon canopy species *P. glauca*, *Abies balsamea*, and *Acer saccharum*. Although CWD covered 5% of the ground in this old forest, it is much less abundant in rotation harvested forests. Adequate quantity and quality of CWD is a vital factor for natural regeneration of *T. occidentalis*, *B. alleghaniensis*, and *P. glauca* in *Thuja-Betula* forests.

Key words: coarse woody debris, nurse logs, *Betula*, *Thuja*, tree seedlings, mixed hardwood-conifer forest, herbivory, logs, woody debris, dead wood, leaf litter, decay, moss, stump, regeneration, canopy gap, mixed effects model

Introduction

Forests around the world are being changed by human actions. Many forests are being cleared and converted to agriculture while timber and pulp production affects almost all of the forest ecosystems that remain. Only a tiny fraction of original forests remain unaltered. In intensively managed forests, community compositions are dramatically simplified compared to the natural ecosystem because of changes made to the canopy species, disturbance regime, and physical structure. Even forests protected from harvests are influenced by landscape level changes in climate, fragmentation, and populations of other species that have swung out of balance. In severe cases, these combined changes can threaten the reproduction of native species.

The hardwood-conifer forests of the Great Lakes region serve as an example. In northeastern Minnesota, these forests have been logged for over 100 years. As much as 60-70% of the pre-European forest landscape was old growth but the arrival of colonists saw the land cleared and burned by slash fires. Continuing management since then has led to numerous changes in these forests. The majority of the landscape is kept in the form of young, mostly deciduous, short rotation forests. Less than 5% of the northern hardwood-conifer forests are now older than 150 years (Mark White, pers. comm.). Coniferous species, which are more profitable, have been harvested so aggressively that there are now significantly fewer conifers throughout the landscape (Mark White pers. comm.). The structural diversity of the managed forests has decreased as snags and logs decay away and are not replaced before the forests are harvested again (Hura and Crow, 2004). Uncoordinated timber harvesting, along with housing developments, are increasing fragmentation of mature forest patches (White and Host, 2008). Herbivory levels are currently high due to white-tailed deer (*Odocoileus virginianus* Zimmermann) populations which have increased since Europeans arrived (Dave Ingebrigtsen, pers. comm.). And of course, climate change is gradually altering the plant and animal species compositions of these forests (Susan Galatowitsch, pers. comm.). With all the changes that are occurring in these forests, it is not surprising that The Nature Conservancy, for whom this work was conducted, is concerned about negative impacts on biodiversity and is working to protect and restore forest habitat.

Reproduction is necessary for the persistence of all ecosystems, both natural and managed, and the seedling stage of regeneration is most vulnerable to those changes mentioned above. The dispersal of seeds and their differential establishment determine the extent of an ecosystem's next generation (Grubb, 1977). If conditions prevent seedlings from establishing for too long, a species may become extirpated from the area. For tree seedlings, a lack of suitable substrate for growth is of particular concern.

All young plants have requirements for the proper amounts of light, heat, nutrients, and water they need to survive. However, seeds can land on several different substrate types which vary in all these factors. Bare mineral soil, soil mounds or pits created by uprooted trees, stumps or logs (hereafter coarse woody debris or CWD), leaf litter, a crack on a cliff, or a moss or lichen mat are all possibilities, though they are not all equally abundant. The amount of each favorable substrate type can partly determine the abundance of seedlings.

In many forests, the germination, survival, and/or growth of seedlings of some tree species is higher on fallen logs or other CWD. This characteristic has been known since at least the turn of the last century (Knechtel, 1903), but research showing the requirement for CWD took off in the early 1980s with work on the seedlings of several conifer species in the Pacific Northwest (Franklin and Dyrness, 1973; Christy and Mack, 1984; Harmon and Franklin, 1989) and with white cedar (*Thuja occidentalis* L.; hereafter referred to as cedar) in Michigan (Scott and Murphy, 1987). The work continued with yellow birch (*Betula alleghaniensis* Britton; hereafter referred to as birch) in the Adirondacks (McGee and Birmingham, 1997). In the Great Lakes region, cedar (Cornett et al., 2000b; Cornett et al., 2001), white spruce (*Picea glauca* (Moench) Voss; hereafter referred to as spruce) (Simard et al., 2003), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and birch (Marx and Walters, 2008) can all prefer CWD over leaf litter.

Furthermore, the type of CWD can influence the establishment of seedlings. Cedar seedlings were found to grow better on cedar rather than birch CWD (Cornett et al. 2001), while birch seedlings grew better on *Tsuga* rather than *Betula* or *Acer* CWD (Marx and Walters, 2008). Seedling densities of other species have been linked to a log's stage of decay (Zielonka, 2006) and moss covering (Caspersen and Saprunoff, 2005). These factors may be related to each other. However, no studies have examined all of these characteristics at the same time and it is not clear which characteristics of CWD are most important for seedling growth and survival.

In typical even-aged rotation forests, cut stumps account for most of the CWD. The surface area of CWD there is thus a tiny fraction of what it would be in unmanaged forests and species that need CWD to regenerate may be limited. Recent forest inventories by the Minnesota Department of Natural Resources (DNR) observed surprisingly low birch sapling densities in managed cedar-birch forests (Minnesota DNR, 2009). Studying densities in old forests with natural amounts and varieties of CWD can help us determine if a lack of CWD is a limiting factor. For birch in a Quebec mixed forest, it was the most limiting factor (Caspersen and Saprunoff, 2005). Because of cedar's preference for CWD, the same issue may be limiting its regeneration in managed forests.

Other factors besides substrate that can determine seedling establishment and growth include seed dispersal, herbivory, light levels, and site-to-site variation. Seed dispersal is rarely limiting in forests where the species in question is a canopy dominant. However, this can easily be limiting in managed forests where many or all of the mature seed producing individuals have been removed.

Herbivory, if it is severe enough, can eliminate entire cohorts of seedlings and over time can change the species composition of forests (Brandner et al., 1990). Many plants throughout the Great Lakes region are threatened by over browsing by white-tailed deer (Rooney et al., 2002) or moose (*Alces alces* L.). Woodland caribou (*Rangifer tarandus caribou* L.), not deer, lived in these forests before 1900 but were extirpated by the hunting and forest clearing of European settlers (Dave Ingebrigtsen, pers. comm.). White-tailed deer were then able to survive in the region. They could find plentiful food in the many recently cut areas and could migrate down to the milder conditions along the lake shore to survive the winters.

Any leaves within reach of deer are vulnerable, which means that the entirety of a seedling is vulnerable. Several deer exclusion studies are in progress in forests near the shore of Lake Superior, measuring the vegetation changes that the deer population has caused. Initial results are forecasting a dire situation for cedar regeneration (Cornett et al., 2000*a*).

Light availability is very important for the continuing health of seedlings. For example, brighter conditions have been shown to help seedlings survive browsing events (Cornett et al., 2000*a*). Light availability varies by canopy composition. Cedar seeds that dispersed away from the dense, continuous canopy of a cedar forest grew better under the sparser canopy of a nearby birch dominated forest (Cornett et al., 2001). While some seedlings have adapted to survive low light levels for long time periods (Forcier et al., 1975), eventually, all species require more light than typically reaches the forest floor. Several species depend on the large increase in light under canopy gaps to propel their seedlings into the canopy (Burns and Honkala, 1990). Gaps cover an estimated 9.5% of mature mesic forests in the eastern US at any given time (Runkle, 1982) because of continually occurring disturbances like wind storms, ice storms, or pathogens.

Finally, there is spatial variation in seedling success. For usually unquantified reasons such as geomorphology, microclimate, competition, and other unexplained causes, spatial variation is an important influence in structuring ecosystems (Legendre and Fortin, 1989). Other works have used location as a "synthetic variable" to account for such factors (Borcard et al., 1992; Boone and Krohn, 2000) but no work related to seedlings has compared the spatial component of variation to the importance of variation in the characteristics of pieces of CWD.

My Work

The forest I studied is one of the last remaining unharvested stands of an ecosystem that was uncommon even before European settlement. That plant community, found only on mesic sites, is co-dominated by white cedar (*Thuja occidentalis*) and yellow birch (*Betula alleghaniensis*). The forest's age, with some trees a few hundred years old, makes it particularly uncommon because of the intense logging history in the region. I studied this forest for three reasons.

First, while other studies have examined seedling establishment in hardwood-conifer forests, none have taken a thorough look at this rare type. This forest is part of the western edge of the band of northern hardwood-conifer forests that stretch to the Atlantic coast, but east of here, including the Michigan forest studied by Marx and Walters (2008), cedar is replaced by eastern hemlock (*Tsuga canadensis*). The work by Cornett et al. (2001) was conducted in forests nearby, but unlike mine, those forests were fire-adapted and had a cedar canopy mixed with paper birch (*Betula papyrifera* Marsh), aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill; hereafter referred to as balsam), and spruce.

Second, as I mentioned above, there are concerns about the regeneration of cedar and birch. Regionally, the abundance of both species has declined significantly from pre-European settlement levels (White, 2001). Although my study forest is now protected from logging within a state park, conservationists would like to protect this rare ecosystem from any other potential threats. Studying this forest will allow me to assess its health, to see whether cedar and birch are successfully regenerating.

Third, by studying an old growth forest, I can recommend management strategies for restoring ecological integrity to working forests. This is valuable because despite their limited distribution, most of the other stands of this forest type are in areas managed for timber production. In order to protect the biodiversity of this region, groups like The Nature Conservancy want to increase the habitat value of managed forests, especially for species threatened by the decline of old growth and conifers. This can be done by extending rotations so that forests spend more time in mature growth stages, by using gap and single tree selection cuts rather than clear cuts, and by mimicking structural characteristics of old growth forests in managed forests. If the old growth stands I study are healthy enough, they can serve as a reference for what “natural” old growth conditions are when developing guidelines for the latter strategy. It would help managers to know what quantity and quality of CWD is necessary for natural regeneration.

In line with the objectives above, I will first examine the following question: Is this forest regenerating itself? I will then focus on coarse woody debris as a key requirement for regeneration: Which tree seedlings in this forest establish better on coarse woody debris than on leaf litter? I will simultaneously compare multiple types of CWD to examine: Which characteristics of CWD have the greatest influence on seedling density? Finally, I will ask: How much variation in seedling density is accounted for by the characteristics of the CWD compared to larger scale factors?

Methods

Study Site

The stands I studied are located near the town of Finland in Lake County in northeast Minnesota, around 47°28’19N and 91°6’11W. They are within George H. Crosby Manitou State Park, and are 4 to 5km inland from Lake Superior, just over the ridge that runs along the western shore of the lake (Fig. 1). My sites were located between 1300ft and 1400ft elevation, 700-800ft above the lake.

Fig. 1. Copyrighted map removed. See: http://maps.google.com/maps?f=d&source=s_d&saddr=47.475703,-91.103611&daddr=&geocode=&view=map&hl=en&mra=mi&mrsp=0&sz=13&sll=47.472953,-91.094599&sspn=0.059757,0.10231&ie=UTF8&ll=47.471735,-91.106873&spn=0.239031,0.670166&t=h&z=11.

I studied stands classified by the Minnesota DNR as the cedar-birch subtype of the Northern Mesic Hardwood-Cedar Forest (MHn45b in the Minnesota DNR Native Plant Community Guide, 2008). This rare forest type is distinguished from others in the region by dominance of cedar and birch in the canopy (Figs. 2 and 3). The characteristic herbs of this forest type, including rose twistedstalk (*Streptopus roseus* Michx.), blue-bead lily (*Clintonia borealis* (Aiton) Raf.), wild sarsaparilla (*Aralia nudicaulis* L.), Canada mayfower (*Maianthemum canadense* Desf.), starfower (*Trientalis borealis* Raf.), long beech fern (*Phegopteris connectilis* (Michx.) Watt), and Canada yew (*Taxus canadensis* Marsh.) were common in the understory of my stands. None of the plants at the site were invasive. The soils at my sites were silty-to-sandy clay loams, between zero and a few meters thick over glacial scoured bedrock.

Fig. 2. A typical view of a cedar-birch stand at my site.

Fig. 3. A typical view of a cedar-birch stand at my site.

This area has averaged 800mm of precipitation annually from 1971 to 2000, most of it falling in the summer (Minnesota Climatology Working Group, 2009). Wind and temperature data is from the Two Harbors airport (KTWM). That station is 68km away but it is just over the ridge that runs along the lakeshore, just like my site, and the weather is often very different between the shore and the hilltop. Prevailing winds at KTWM are from the west and northeast throughout the year. From 1970 to today, the average highest and lowest winter temperatures were 25° to 0°F, the average highest and lowest summer temperatures were 76° to 55°F (Weather Underground, 2009).

The regional landscape is a matrix of mesic birch-aspen-fir-spruce forests with lowland conifers in the wetter places and the northern hardwood-conifer forests on higher ridges. In the state park, the cedar-birch stands are found only on north facing slopes. They are mostly surrounded by sugar maple (*Acer saccharum* Marsh; hereafter referred to as maple) dominated forest (MHn45c) which is common and secure and was found on south facing slopes and hilltops (Figs. 4 and 5). Unlike most of the forest types in the landscape, these hardwood forests are not considered fire dependent. Stand replacing fires and other disturbances are estimated to occur only once every 1000-3000 years, possibly due to the topographic position (Minnesota DNR, 2008). The park's forests have never been cleared but a selection cut removed some scattered high quality cedar and white pines (*Pinus strobus* L.), and maybe a few birch trees in the early 20th century. Waist high cedar stumps with flat tops are still visible scattered sparsely throughout the area.

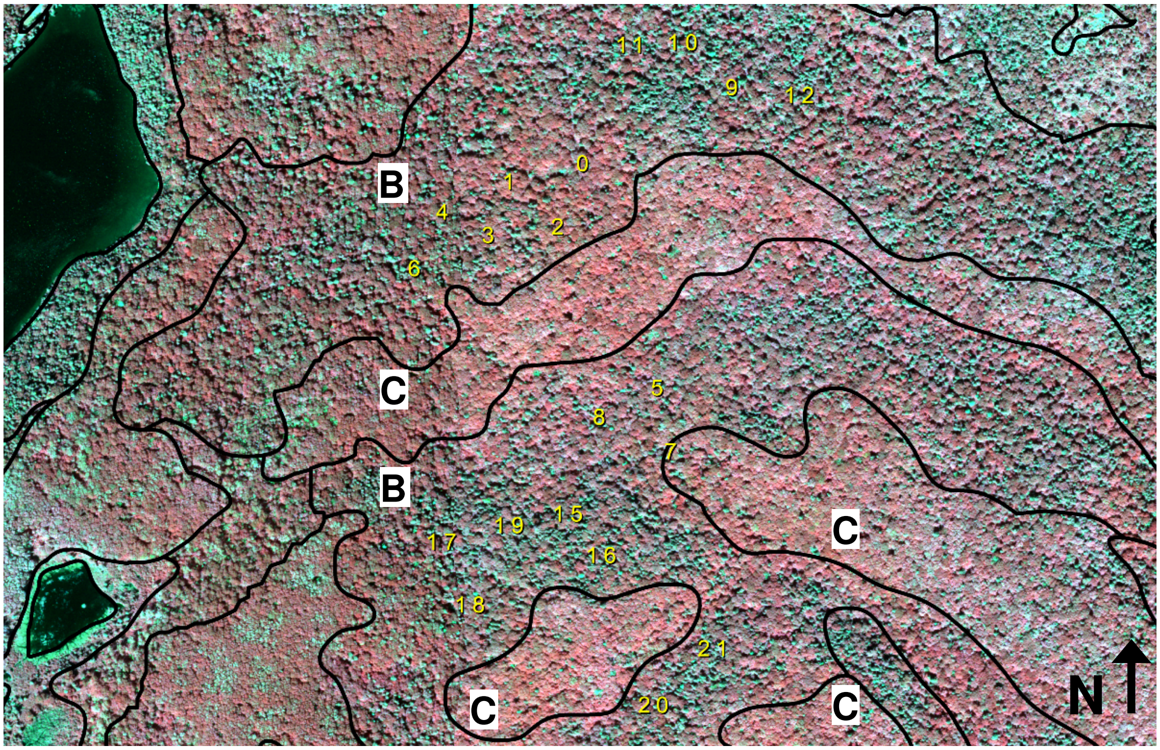

Figure 4. Stitched Landsat image of the study area taken in 2006 with bands 2, 3, and 4. Cedar trees are bright blue, maples are bright pink, and paper and yellow birch trees are the greyer pinks that appear in both forest types. Black lines demarcate the boundaries of plant community types based on the DNR's satellite image classification. The letter B marks MHn45b, cedar-birch forest, and the letter C marks MHn45c, maple forest. Yellow numbers identify the locations of each of the twenty points. The lake in the top left is Benson Lake. 1 inch = 220 meters.

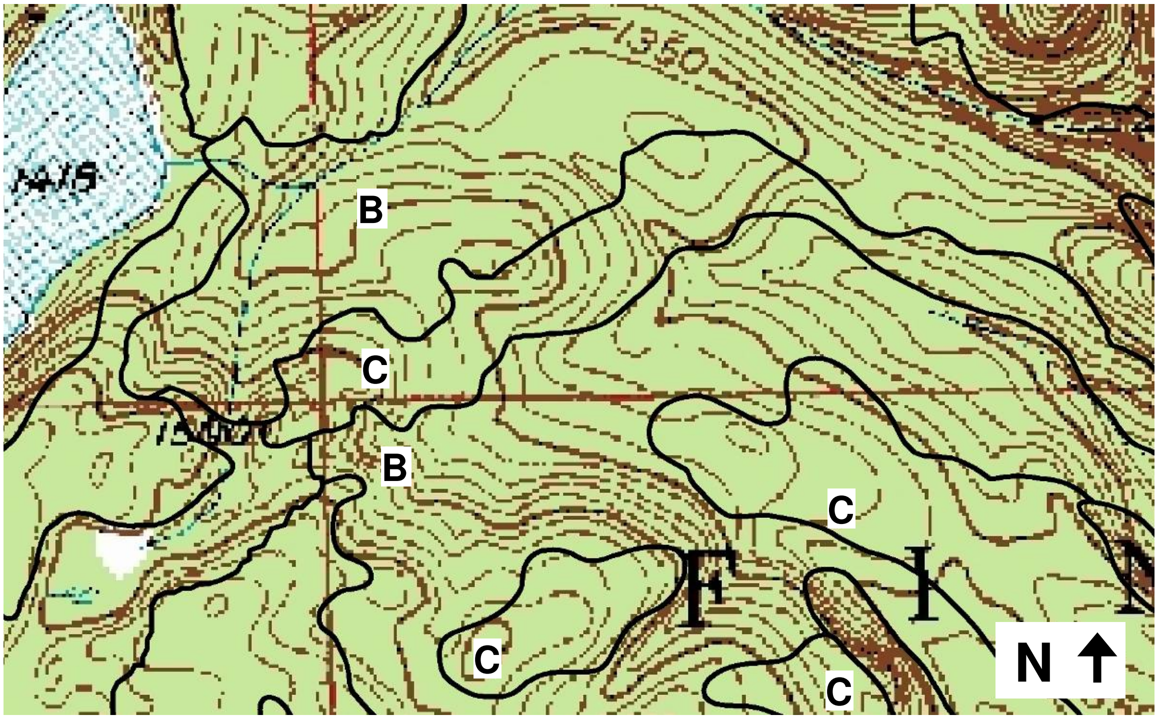

Fig. 5. USGS topographic map. Black lines demarcate the boundaries of plant community types. The letter B marks MHn45b, cedar-birch forest, and the letter C marks MHn45c, maple forest. 1 inch = 220 meters

Data collection

I located 20 points in the cedar-birch forest during June and July of 2008. Points were placed within the areas where the canopy was dominated by cedar and birch but could also contain spruce, maple, balsam, and some paper birch (Table 1). Points were separated from each other and from the border of another forest type by at least 50m. Lowland White Cedar Forests (WFn53a) were also present near the stands but were avoided. Points were clustered in groups of three to six depending on the size of the patch of forest.

Table 1. Canopy tree composition over all points by basal area density.

	Yellow Birch	Paper Birch	Cedar	Spruce	Balsam	Maple	Total
basal m^2 / ha	10.56	0.92	20.89	1.61	0.80	2.53	37.3

I recorded the following at each point: GPS coordinates, slope, aspect, and position of the point on the hillside. Canopy composition was measured with a 10 factor prism that defined a variable radius plot (Husch et al., 1982) in which stems >10cm dbh were identified to species, and counted as living or dead. To survey CWD and stem densities, a 2x50m belt transect was laid in a random compass bearing with the point as its center. All stems surveyed were grouped into the following height classes: <1 year old (cotyledons present), one year old (cotyledons not present or a terminal bud scar present) to 10cm tall, 10-50cm, 50-100cm, 100cm tall to 2.5cm dbh, 2.5-10cm dbh, and canopy trees (>10cm dbh). Leaf litter depth, the depth of decomposed organic matter (duff), and soil type were measured at three places spaced out along the 2x50m transect. The number of canopy gaps directly above the length of the transect was recorded at 17 of the points.

The survey design was adapted from previous TNC surveys. All sampling was non-destructive. This thesis is focused on the cedar-birch forest but data from this survey protocol is available for two other old growth forest types in the state park, the maple forest (MHn45c) and a fire dependent white pine forest (Fdn43a).

For each piece of CWD that intersected the 2x50m transect I measured the length of that piece *within* the belt transect, horizontal for logs and vertical for stumps, and three diameters evenly spaced along that length. The middle diameter had to be >10cm to be considered coarse woody debris. Seedlings on that piece, *within* the transect, were counted by species and height class. To determine whether species preferred CWD, I placed a circular plot on leaf litter as close as possible to each piece of CWD. Each plot had the same area as the corresponding CWD piece. I counted all tree seedlings within the paired plot by species and height class.

A 2x20m plot was placed in the center of the 2x50m belt transect to measure stems not growing on visible CWD. In it, stems 2.5 to 10cm dbh were counted by species and their heights recorded. The half of the 2x20 plot north of the transect's center line was used as a 1x20m plot to measure tree seedlings not growing on wood or on wood pieces too small or too decayed to be considered CWD (wood fibers were often apparent in the soil below seedlings). In it, tree stems <2.5cm dbh were counted by species and height class.

Regeneration Profile

I measured the current height structure of tree populations by combining stem density measurements taken on CWD and the forest floor. Densities was calculated for each point and then averaged. Densities for each of the five shortest height classes were calculated from plots described above with the formula:

$$\text{stems / m}^2 \text{ of forest} = ((\text{\# on CWD in 2x50} + 5*(\text{\# on floor in 1x20})) / 100 \text{ m}^2)$$

Density for the 2.5 to 10cm dbh height class was measured directly the 2x20 plot. Canopy density was calculated from the prism data. Because a 10 factor prism was used, each tree counted represents 10 ft^2 basal area/acre. The canopy density formula for each species was:

$$\text{trees / m}^2 \text{ of forest} = (\Sigma_{\text{all trees}} (1 / (Y^2 * 0.00545415) * 10 / 4047)) / 20$$

where Y is the diameter of each tree in inches, from Husch et al. (1982).

Stems in gaps

To supplement the transect based densities, I surveyed 2 canopy gaps near each point in the cedar-birch forest. This method was designed with speed as the primary consideration. Each gap was ranked qualitatively by size (based on the estimated number of trees that fell or died) and age. The stems in the gap were counted by species in height classes 1-4m or 4-10m, which are roughly equivalent to the height classes 1m tall to 2.5cm dbh and 2.5 to 10cm dbh. Stems were considered “in the gap” if they received a noticeable increase in light, so this would include some stems underneath the edge of the canopy. Any birch individuals with their crowns above the other vegetation in the gap were noted. Because gap area was not measured in the field, to calculate stem density in gaps I estimated each gap’s area based on its size rank. The estimate of total gap area surveyed ranged from 780m^2 to 2780m^2 to 5500m^2.

Measurement of CWD characteristics

I determined the species of each CWD piece by examination of its large scale characteristics such as bark, branching structure, and diameter, and if necessary the wood grain structure. I determined the decay class of each piece using the characteristics listed in table 2 (based on Newton, 2007). The percentage of the piece covered by moss and whether the piece was a log or a stump was also recorded. Only characteristics of the log within the 2x50m transect were considered.

Table 2. Decision rules for determining decay class.

Assigned decay class	*Characteristics*
1	Most of bark present Branches retain twigs Solid wood Original color
2	Some bark may be present Twigs absent Decay beginning but still solid
3	Bark absent (except for cedar) Log supports own weight Extensive decay but structurally sound Fungal bodies may be present
4	Kicked log will cleave into pieces or can be crushed Can be partly solid or with remaining (sometimes large) solid chunks Bark absent Small soft blocky pieces Brach stubs rotted down, removable by hand Invading roots (when present) throughout
5	Soft and powdery when dry Log can't support own weight Not original shape, flattened or spread out over ground

Statistical Analysis

For the following analyses I investigated only seedlings that no longer had their cotyledons but were still less than 50cm tall (hereafter "established seedlings"). I used these seedlings to exclude year to year variability in seed production but still retain a large sample size. If seedlings had only non-seed leaves, they must have survived at least one winter and are therefore able to grow in that location. This categorization of seedlings allows close comparison to the Marx and Walters (2008) study which measured seedlings from 1 year old to 30cm tall.

To identify species that prefer CWD, I compared abundances of established seedlings between CWD pieces and their equal area litter plot with a two-tailed paired t-test.

To calculate seedling densities on CWD, surface area for each log was calculated by adding the areas of two trapezoids. Area = length/2 * ((diameter1 + diameter2)/2) + length/2 * ((diameter2 + diameter3)/2). This gives approximately 1/3rd the surface area of a conic section. This is equivalent to the area on the top of a log that is not too steep to seedlings to anchor on. For stumps, area was calculated to be = π(base diameter/2)^2.

I used a generalized linear mixed effects (GLME) model (Dunteman and Ho 2006) to measure the influence of CWD traits on the density of seedlings. I performed this analysis with the "lme4" package in R 2.7.2 (Bates et al., 2008; R Development Core Team, 2008). The response variable was the number of established seedlings on a CWD piece. A Poisson (log link) function was used to constrain the model to non-negative integer values and the piece's surface area was included as the offset term. A generalized model was used because of the unequal variance in seedling densities. Mixed effects were used because different pieces in the same transect cannot be considered as independent as pieces in different transects due to their close proximity (Luke, 2004).

The model included four fixed effects: categorical variables for the piece's species, its decay class, and whether it was a log or a stump, and a continuous variable for the piece's moss cover. The random effect term used was either the point or the stand (a grouping of nearby points, which was useful for species with smaller samples). The best model was selected by starting with all the variables included and then excluding those whose removal decreased the residual deviance, although using Akaike's information criterion produced the same result (Dunteman and Ho, 2006). Lumping decay classes 1 and 2, and 4 and 5 together improved the model, as did lumping all non-cedar conifer wood and all deciduous wood.

I compared the relative importance of CWD piece level characteristics (the fixed effects) with site level variation that was not directly measured (the random effect) by how much each reduced the model's deviance. From the null deviance (no model fitted), I compared the reduction in deviance between the model with only the fixed effects, and the model with only the random effect. This is similar to the method Boone and Krohn (2000) used to compare the explained and unexplained variation in their data. They used an R^2 value to show the amount of variance explained but because of the unequal variance of my data, I used deviance, the generalized model's replacement for R^2. The model output included the magnitude of the random effect for each point or stand. I checked for correlations between these values and the values for slope, transect bearing, total CWD area, canopy composition, and canopy gaps at each point.

For birch and cedar I evaluated each significant variable independently. I compared average densities of established seedlings among species of CWD, decay class, and form of CWD using t-tests or ANOVA with Tukeys post hoc test. Because moss cover could not be analyzed like the other variables, I examined seedling densities and presence/absence ratios as a function of moss cover.

In addition to ANOVA, I used electivity (Jacobs, 1974) to examine seedling preferences for species of wood but only birch seedlings had a large enough sample size to analyze this way. This index allowed me to quantify the presence/absence of seedlings between substrate types while correcting for the different abundances of those types. It was calculated by the formula:

$$\text{electivity score} = \ln (x * (1 - y) / y * (1 - x))$$

where x is the proportion of a certain species of CWD that has established birch seedlings and y is the proportion of all the CWD that is that certain species.

Results

Regeneration Profiles

All species showed decreasing density as height class increases but the decline was extreme for cedar (Fig. 6). No cedar stems >10cm tall were found and the density of seedlings <10cm was already as low as the density of cedar trees in the canopy. Maple was by far the most common species in the forest in each height class except the canopy. Birch seedlings were the second most abundant and were more common than any conifer species. However, spruce stems between 100cm and 2.5cm dbh were ten times denser than their canopy trees. Birch and balsam stems in that height class were only twice as dense as their canopy trees.

Only sugar maple and mountain maple (*Acer spicatum*) were found in the 2.5 to 10cm dbh class. Mountain maple density in that class was $0.052/m^2$ but it was never in the canopy. A total of twenty five black ash (*Fraxinus nigra* Marsh) seedlings were found but ash was never recorded in the canopy. Paper birch (*Betula papyrifera*) was present in the canopy but at the lowest density ($0.0005/m^2$) and none of its seedlings were found.

Birch between 1m tall and 10cm dbh were denser in gaps than along my random transects (Fig. 6a) but even so, in those gaps birch was much less dense than the shrubs *Acer spicatum* and *Corylus cornuta* (Fig. 7). Of the 39 gaps, 20 had birch saplings and in 7 of those, one or two birch plants had their crowns above the other competing saplings. I observed no cedars taller than 10 cm in gaps.

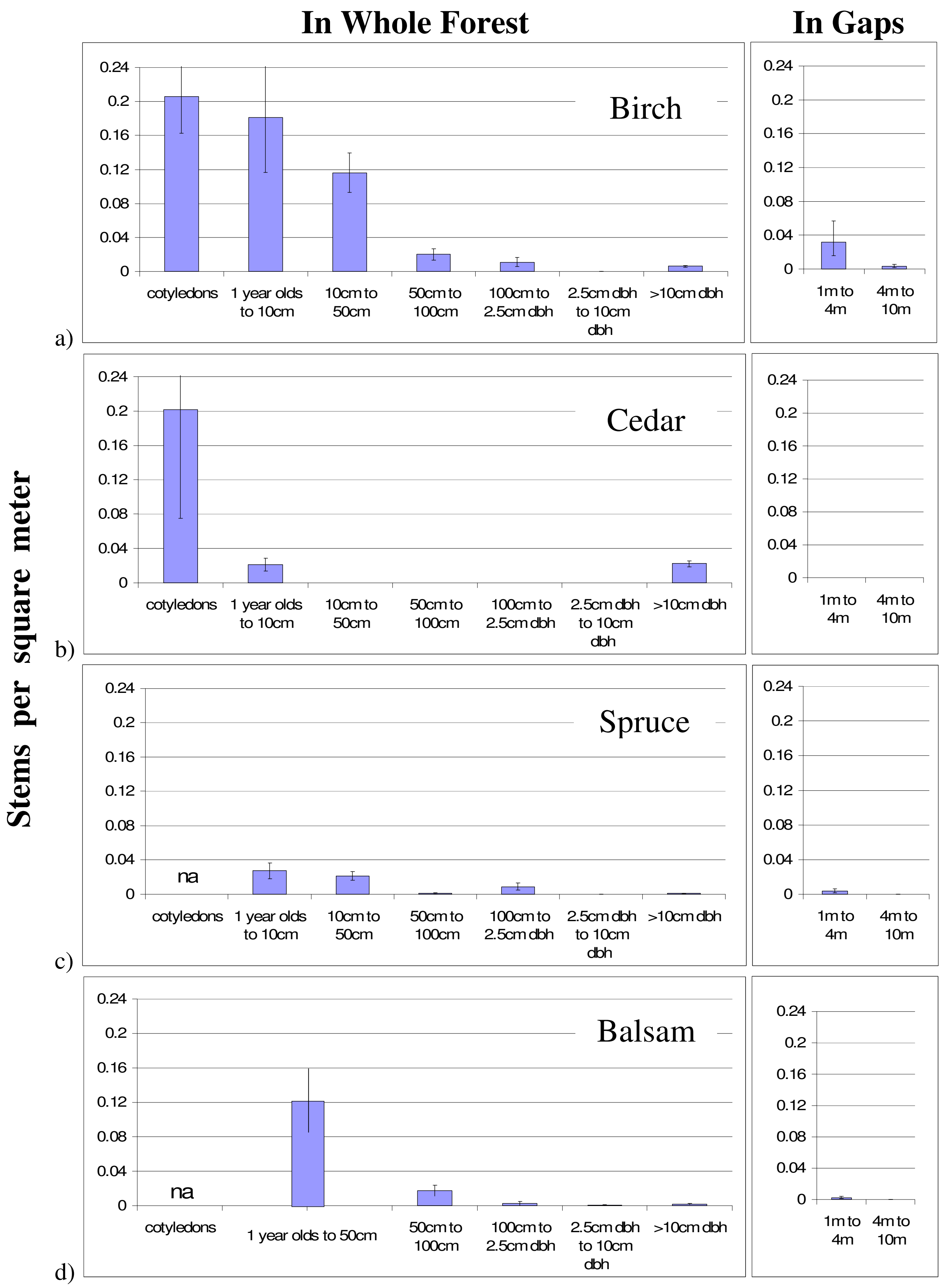

Fig. 6 continued on next page.

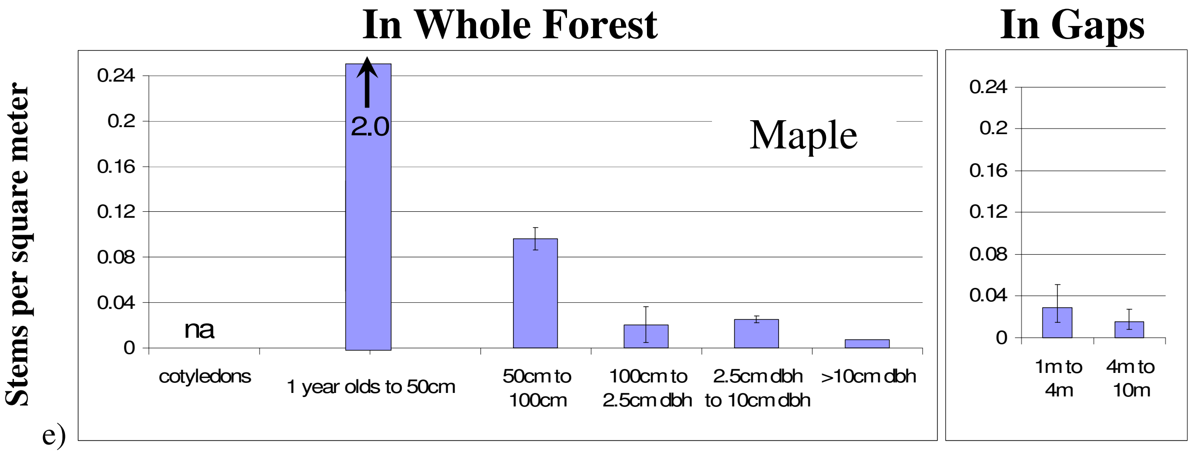

Fig. 6. Average densities of canopy components a) birch, b) cedar, c) spruce, d) balsam, and e) maple observed over all substrates by height class. Bars represent one standard error. For spruce, balsam, and maple, new germinants were not counted and for balsam and maple, 1 year old to 50cm tall seedlings were counted together. Densities from gap measurements are shown in the graphs on the right side. Bars for those graphs are based the high and low estimates of the total area of gaps surveyed.

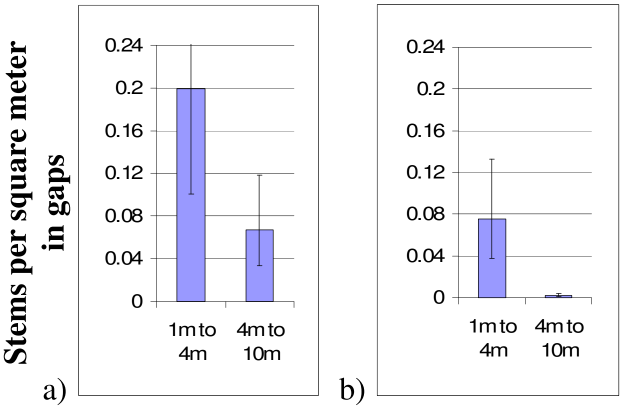

Fig. 7. a) *Acer spicatum* and b) *Corylus cornuta* densities in gaps. Y axes are the same height as those in figure 6. Bars are based the high and low estimates of the total area of gaps surveyed.

Density on CWD vs Leaf Litter

Birch, cedar, and spruce were found solely on CWD (Fig. 8). Balsam also preferred CWD but could be found on litter. The *Acer* species were found on both substrates but sugar maple preferred litter by a wide margin.

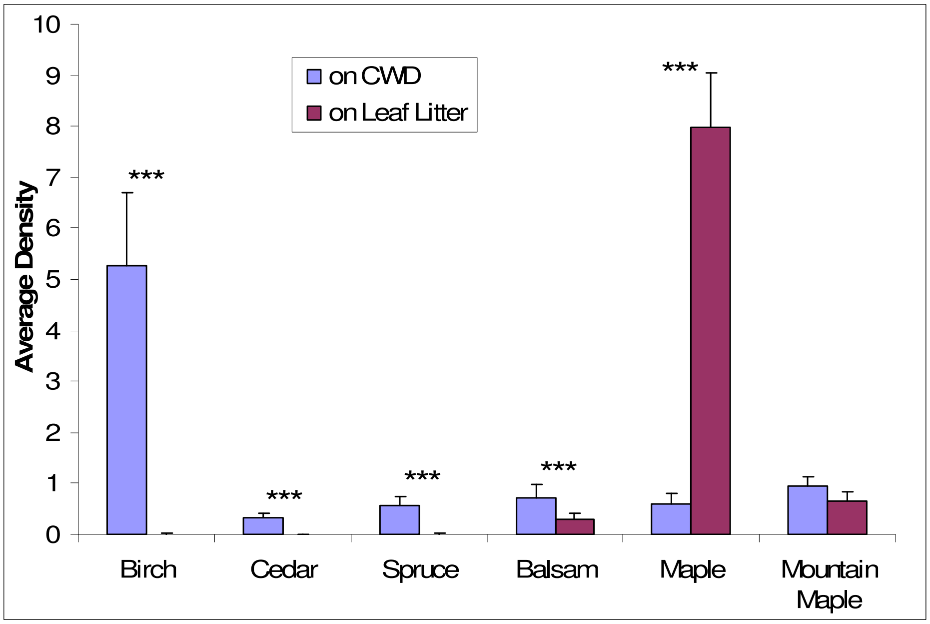

Fig. 8. Number of established seedlings per m^2 of CWD or leaf litter. Bars represent one standard error. *** indicates $p < 0.001$.

There was an average of $489m^2$ of CWD per hectare (±35 SE). The majority of this was cedar wood and pieces in intermediate decays classes (Fig. 9). Very little deciduous wood was present in high decay classes. There was no relation between transect bearing and the amount of CWD contained. The rest of the forest floor was covered with an average of 23mm (±1.5 SE) of mostly birch and some maple and cedar leaf litter on top of an average of 70mm (±9.1 SE) of decomposed organic matter. I almost never encountered exposed mineral soil.

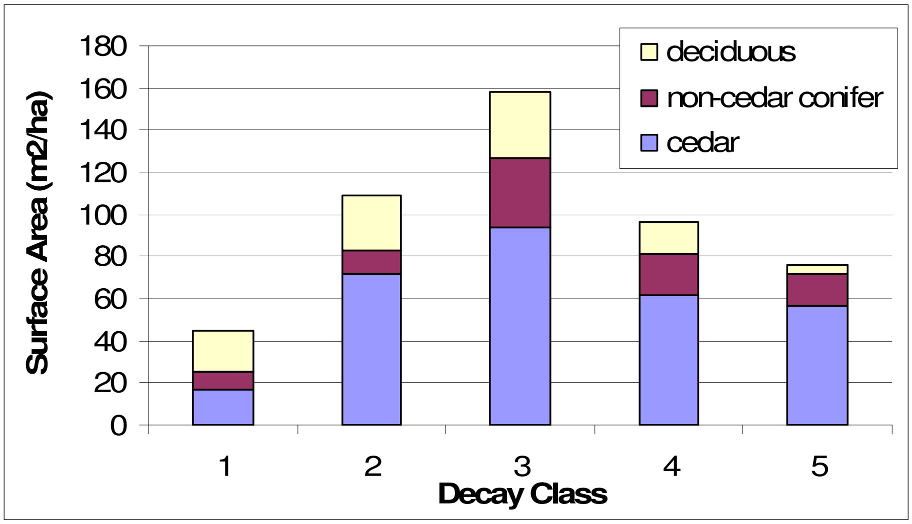

Fig. 9. CWD surface area per hectare by decay class and species. 489m^2/ha total.

CWD Type Preferences

Birch seedlings occurred on the most pieces and had several seedlings per piece while cedar and maple were the most uncommon species (Table 3). Thus the GLME model for birch was based on the most information.

Seedlings of every species strongly preferred to grow on pieces in an advanced stage of decay (Table 4). Moss cover positively influenced birch and cedar seedling densities but negatively influenced maple. The species of CWD only affected the densities of birch and cedar. Birch, balsam, and possibly spruce showed preferences for stumps over logs. There were no strong correlations between any of the variables.

Birch was the only species for which random effects accounted for a notable part of the variation and it was also the only species for which the model's residual deviance was less than half the null deviance.

Table 3. Abundances of all occupied pieces and of all established seedlings in the 20 points surveyed.

	Birch	Cedar	Spruce	Balsam	Maple	Mountain Maple
Pieces with established seedlings (284 possible)	78	21	33	46	23	54
Number of established seedlings	514	31	85	71	58	94

Table 4. GLME model coefficients for all tree species. n=266 CWD pieces because 18 pieces were excluded due to missing decay, wood species, or moss cover values. + indicates borderline significance $p<0.05$, * denotes a $p<0.01$, the minimum required to be considered significant after Bonferroni correction, ** for $p<0.001$, *** for $p<0.0001$.

	Birch	Cedar	Spruce	Balsam	Maple	Mountain Maple
Intercept	-12.7 ***	-16.7 ***	-12.6***	-12.4***	-13.4***	-11.0***
Stump	0.851***	na	0.907 +	1.28***	-1.44	na
Non-cedar conifer	0.416	2.50 +	-0.096	0.936	1.34	-0.039
Cedar	0.971***	1.96	0.596	0.784	1.00	-0.158
Decay class 3	2.21***	1.78	1.33	1.12	2.11 +	0.982
Decay class 4/5	2.46***	2.94*	2.48**	2.45***	3.374***	2.43***
Moss cover %	0.0289***	0.0308***	0.0079	0.0035	-0.0105 +	0.0043
Random Effect SD	1.06	0.91	0.96	0.68	1.44	0.39
Null Deviance	1916	169	243	318	266	284
Residual Deviance	789	113	168	215	164	213
% explained by fixed effects	40%	27%	19%	27%	22%	23%
% explained by random effects †	p 18%	s -2%	s -1%	s 3%	p 7%	s -10%

† The spatial level used for the random effect term was either individual points (p) or grouped points in the same stand (s).

Birch Preferences

Densities of established birch seedlings on individual CWD pieces were extremely non-normally distributed (Fig. 10). Of the 284 pieces, 69% had no birch seedlings while 3 pieces had more than 100 seedlings per m^2. High densities were not usually the result of 1 or 2 seedlings on a very small wood piece. For pieces with seedlings, the average abundance was 4.9 per piece (±6.5 SD), as well as one outlier with 134 established seedlings. The outlier was verified and therefore included in all analyses.

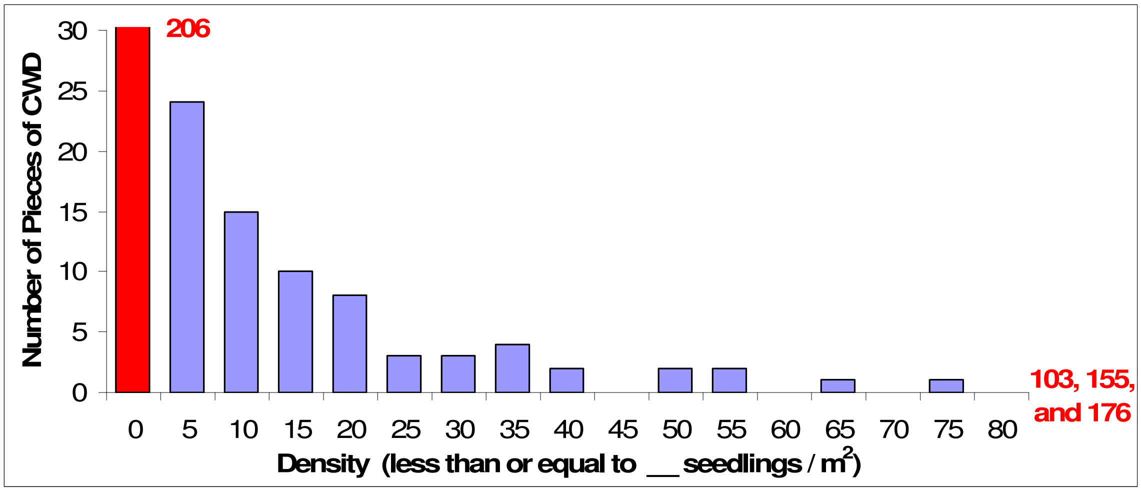

Fig. 10. Established birch density frequencies. There were 206 pieces that had no seedlings and there were pieces with 103, 155, and 176 stems/m^2.

From the GLME model coefficients, birch significantly preferred CWD that was, in order of decreasing influence: mostly covered by mosses, in decay class 4 or 5, in decay class 3, cedar wood, and a stump (Table 4). Because the moss coefficient relates to a continuous variable and can be multiplied by up to 100, it was the most influential factor. However, variation was large enough so that even CWD with ideal characteristics often had no seedlings. Of the 12 pieces with all the preferred characteristics, 3 still did not have seedlings. Log diameter was initially included in the GLME model but showed no relationship to birch density.

Transect level factors were only half as important as the traits of the individual CWD pieces (Table 4). The random effect for each point showed no relation to the slope, transect bearing, the canopy density of birch (Fig. 11) or any other species, or total CWD area. Transects 1-4 were physically close to each other and all had negative random effects while transects 15-19 were also grouped together and all had positive random effects. There was a nearly significant relationship (*T* = 1.75, *p* = 0.09) between the random effect and whether the transect had 1 or more canopy gap (Fig. 12). While this is only a qualitative measure, it begins to explain the variation between transects.

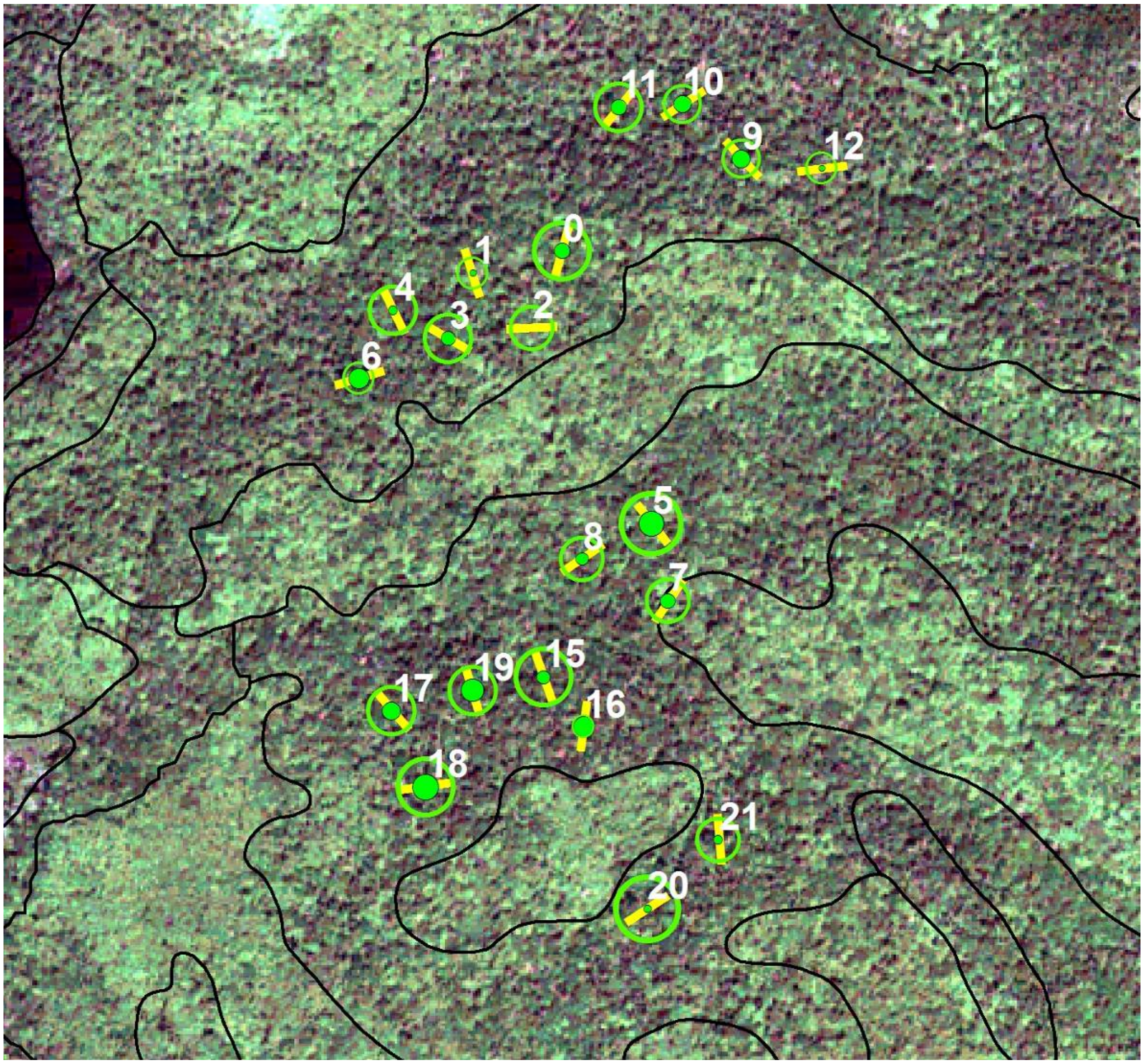

Fig. 11. Comparison of densities of established birch seedlings (inner dot) and birch in the canopy (outer circle). Larger size denotes a higher density. Yellow lines show the length of the 2x50m transects. The background is a true color Quickbird satellite image.

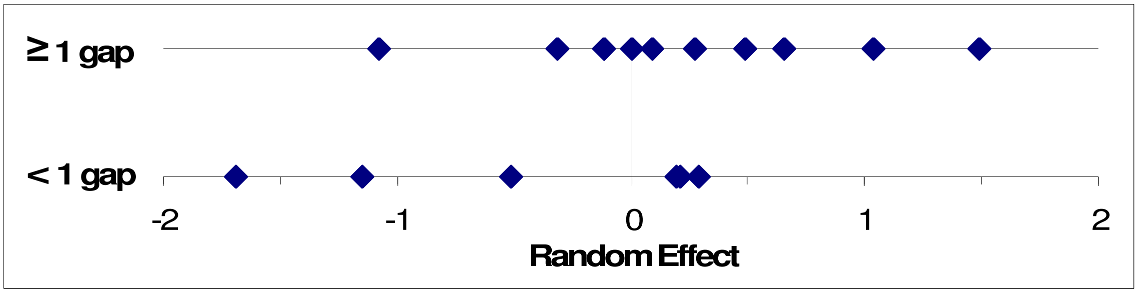

Fig. 12. Distribution of random effects on birch density at points with and without gaps. n = 17 points.

Pieces in higher decay classes had more established seedlings. Because of high variability, the ANOVA showed no significant differences between densities ($F = 1.40$, $p = 0.23$) but there was a clear trend (Fig. 13) that is supported by the model result (Table 4). Class 1 pieces had no established seedlings but both the average densities and the model coefficients for decay classes 3 through 5 were much higher. Seedling presence increased with decay. Only 16% of class 2 pieces were occupied compared to 27% of class 3 pieces and 38% of class 4 and 5 pieces. Because decay class 1 effectively ruled out the presence of seedlings, those pieces were excluded from subsequent seedling density analyses.

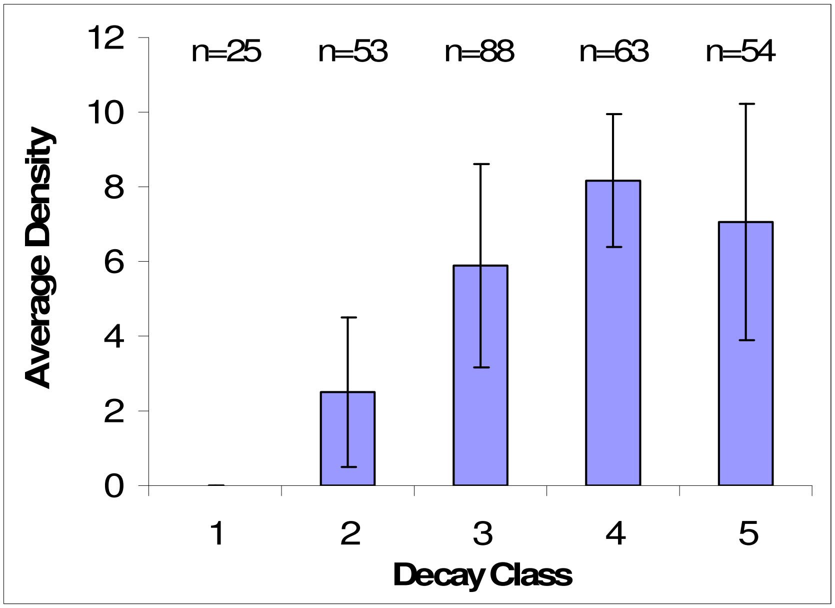

Fig. 13. Average density of established birch seedlings on CWD by decay class. Bars represent one standard error.

Moss had a strong correlation to birch density (Table 4, Fig. 14). Although there was large variation in seedling density on pieces with high moss cover, pieces with <30% moss cover always had low density. Pieces with high moss cover were more likely to have seedlings and have them at a high density. There was no correlation between decay classes 2-5 and moss cover, with pieces in each class having an average close to 46% cover, but class 1 pieces had only an average 13% moss cover.

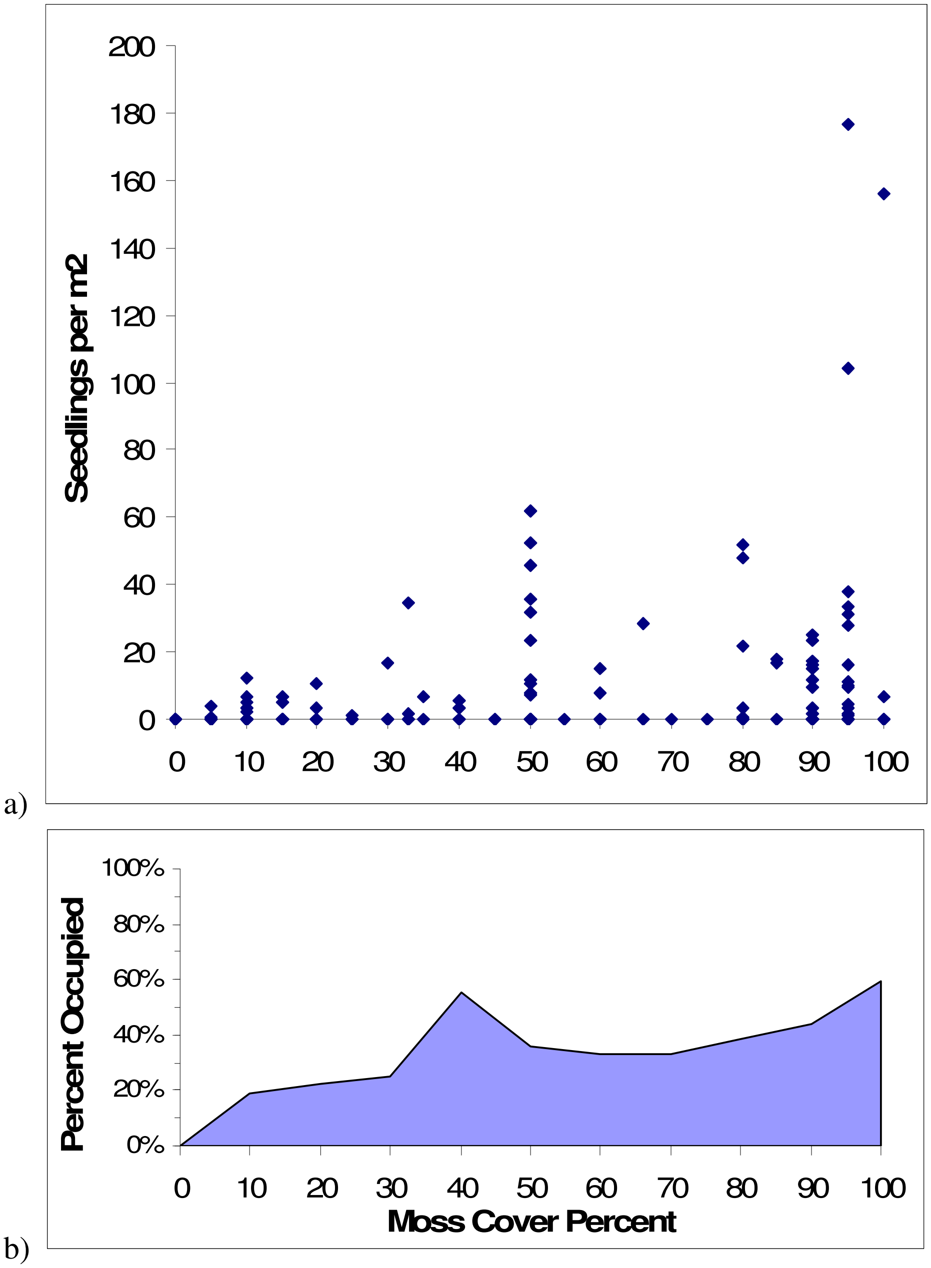

Fig. 14. a) Plot of established birch density on CWD by moss cover. b) Percent of pieces with 1 or more established seedlings. Both graphs exclude decay class 1 pieces. n = 246 pieces.

Densities of established birch seedlings were greatest on cedar wood and least on deciduous wood (Fig. 15). The differences among species were marginally significant ($F = 2.53$, $p = 0.08$), however the GLME model identified a significant difference between cedar and deciduous wood (Table 4). Electivity analysis, which compares seedling presence/absence and substrate availability, gave the same result of a preference for cedar over all other species of wood (Fig. 16). It showed different preferences between species of wood that had been lumped by the GLME model, with balsam wood being particularly avoided by seedlings.

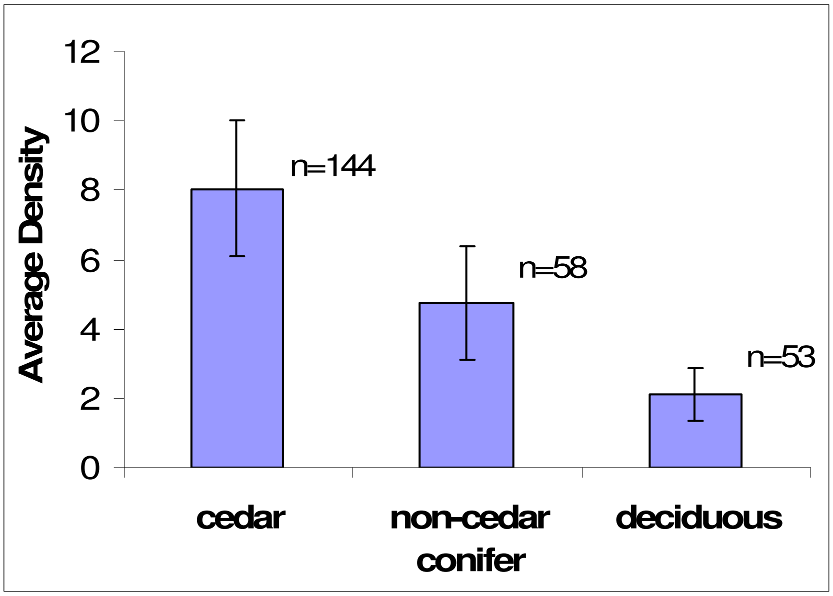

Fig. 15. Average density of established birch seedlings by species of CWD, excluding decay class 1 pieces. Bars represent one standard error.

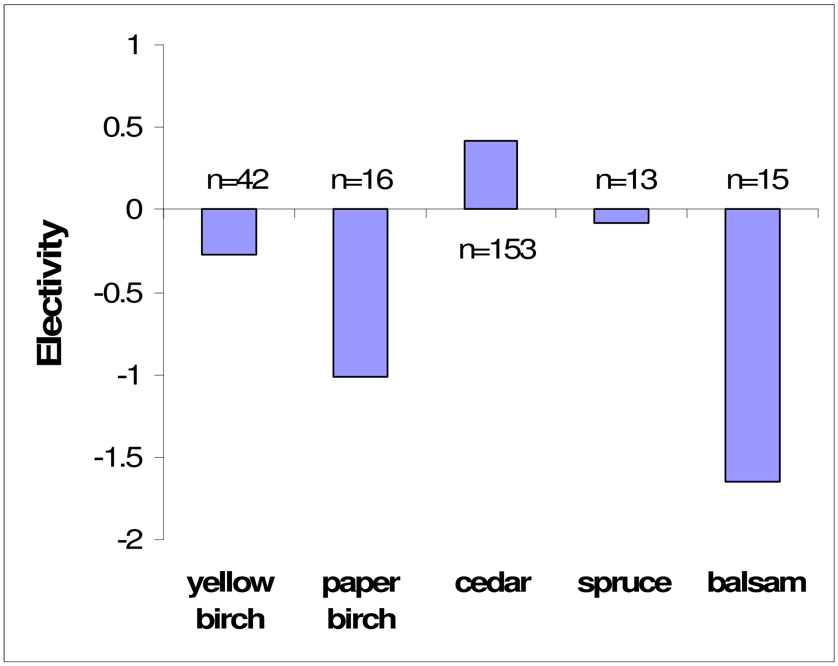

Fig. 16. Electivity by species of CWD. Positive values indicate birch preferred that species, negative values indicate avoidance. CWD pieces not identified to species were excluded.

Stumps and logs were equally likely to have seedlings present (30% had seedlings) but stumps have marginally significantly higher densities ($T = 1.68$, $p = 0.096$; Fig. 17).

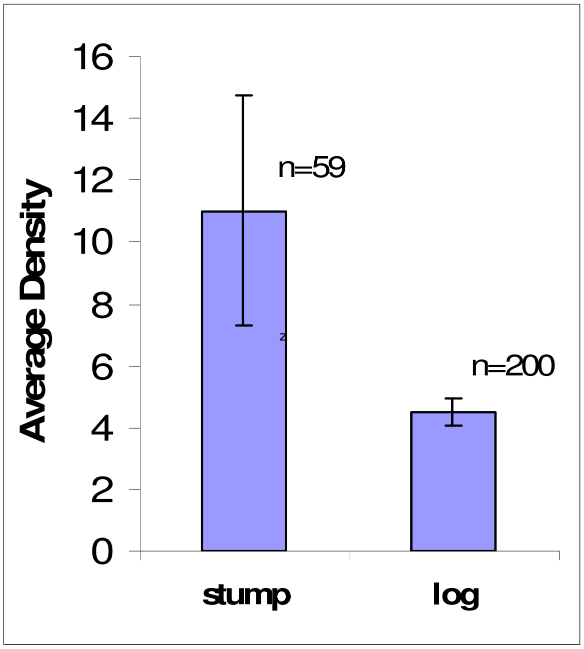

Fig. 17. Average densities of established birch seedlings on stumps and logs, excluding decay class 1 pieces. Bars represent one standard error.

Cedar Preferences

Cedar seedlings were rare with only 31 seedlings on 21 pieces. Despite the small sample, cedar seedlings significantly preferred pieces with high moss cover and advanced decay (Table 4). Of the 19 pieces with cedars for which moss cover was recorded, only 3 had <50% cover (Fig. 18). Density is highest on decay class 5 wood (Fig. 19), but the difference among decay classes was only marginally significant, (F = 2.40, p = 0.11). Only 2 of the 21 pieces with seedlings were deciduous wood and densities on conifer wood were much higher. The GLME model showed a marginally significant, but large coefficient for non-cedar conifer wood (Table 4) but because of high variability the ANOVA of wood species was not significant (F = 3.03, p = 0.33; Fig. 20).

There was some spatial variation in cedar densities even though the random effects did not reduce deviance in the GLME model (Table 4). The density at points 9 through 12 was much higher densities than in any of the other areas. However, there was no correlation between a stand's random effect and any point variable I recorded.

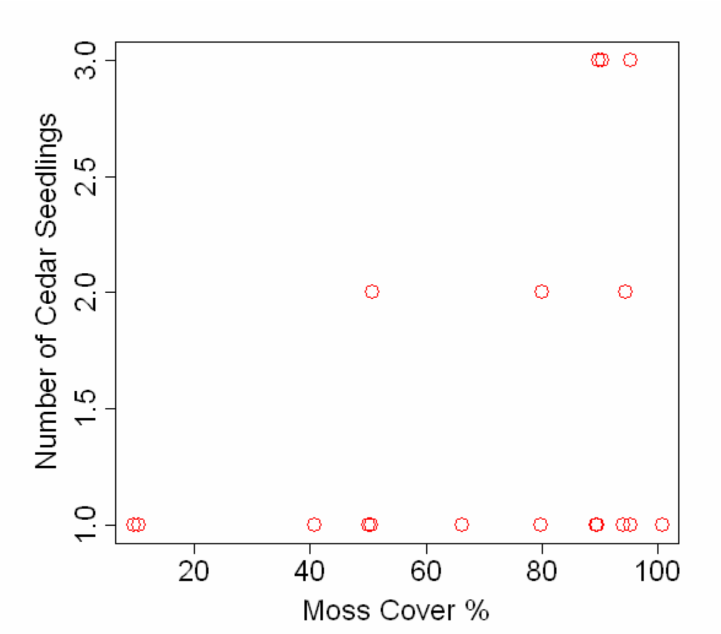

Fig. 18. Cedar abundances by moss cover. n = 19.

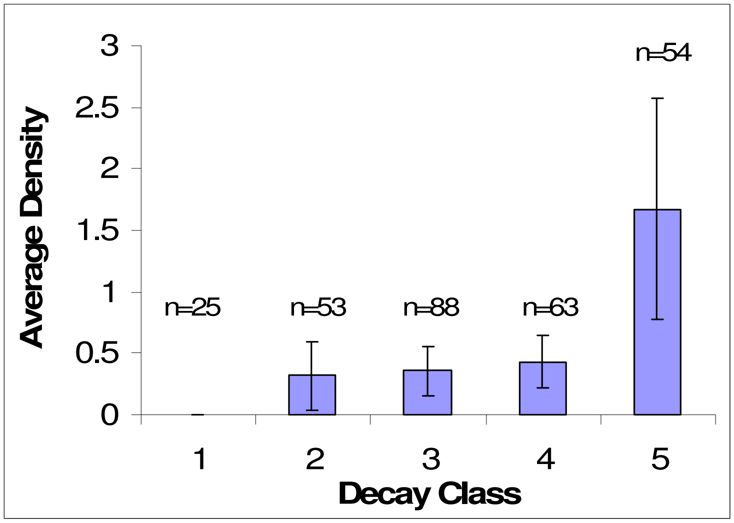

Fig. 19. Average cedar density by decay class. Bars represent one standard error.

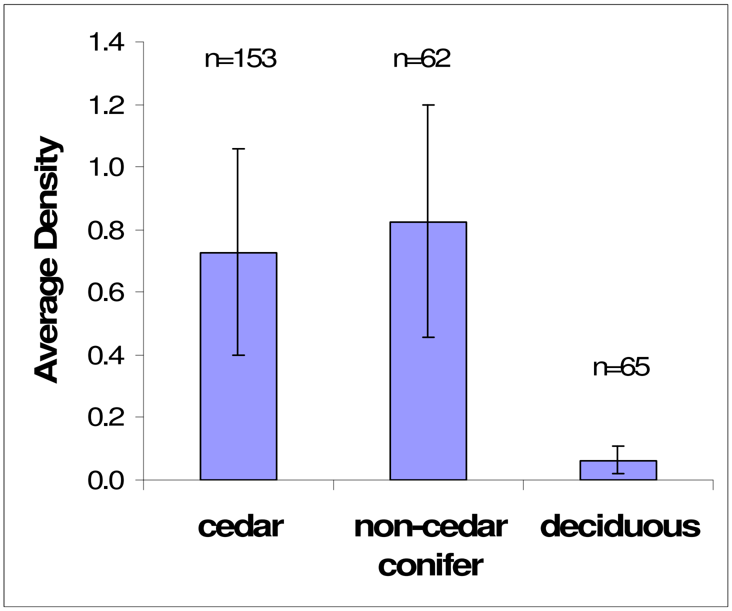

Fig. 20. Average cedar density by species of wood. Bars represent one standard error.

Discussion

Regeneration

Yellow birch appears to have enough seedlings to maintain a place in the canopy but those seedlings require canopy gaps to finally propel them into the canopy. White cedar has a very limited number of seedlings and it will not regenerate in this forest unless conditions change.

The birch population shows the decreasing densities typical of even healthy populations, however the curve bottoms out in the sapling stages (Figure 6a). The plots along the randomly located transects did not find any birch saplings greater than 2m tall. This could indicate a regeneration bottleneck or that my 2x20m sapling plots were too small.

The density of established seedlings that I observed, $0.297/m^2$ of forest floor, was five times higher than the corresponding density at a Michigan *Tsuga-Betula* forest where Marx and Walters (2008) reported there was no severe restriction on young seedlings. In that study, 23% of birch germinants survived to be a year old or more and assuming that seedlings remain in the 1 year old to 10cm height class about 4 years, the corresponding ratio from my study would be close to that percentage. Both comparisons suggest that the density of established birch seedlings in this forest was not abnormally low.

In the DNR's description of this ecosystem, birch is considered a gap strategist whose seedlings must already be established in order to sprint for the canopy when a gap opens up above them (Minnesota DNR, 2009). My surveys in gaps showed that birch >2m tall were present, almost common in the gaps. The gaps themselves though were uncommon enough that they were not adequately sampled by the random 2x20m plots.

However, the presence of birch saplings in gaps does not guarantee that they will make it to the canopy. Competition from both *Acer* species, and from *Corylus cornuta* below 4m, meant that a birch was the tallest, healthiest sapling in only 20% of those gaps. I was concerned that the birch seedlings I surveyed, which were all <2m tall, might be too short to compete successfully and reach the canopy if a gap opened up above them, but in northern Wisconsin, birch plants that captured gaps ranged from 1 to 3m tall, and were 6 to 14 years old at the time the gap formed (Webster and Lorimer, 2005). That study also showed that birch grew fastest in gaps $\geq 200m^2$ but that growth rate, and thus competitive ability, declined with decreasing gap size. Seventy percent of the gaps in my forest were only roughly $50m^2$ so that may be hampering birch recruitment. Even if birch does capture about 20% of the gaps, it is not clear if that is enough to maintain its canopy density.

In sum, it appears that birch regeneration is proceeding slowly in this forest, limited by lack of light. Gap forming disturbances, such as wind, lightning, ice, and disease, are vital processes that allow birch to persist in this forest. .

Cedar is certainly not regenerating itself. Newly germinated seedlings were reasonably common on CWD but seedlings 1 year old or older were uncommon. None of the surveys found any seedlings taller than 10cm (Fig. 21). Outside the plots, I walked several kilometers through the park and the tallest cedar seedling I ever saw was 30cm. The one exception was a 2m tall plant on an inaccessible cliff face. The next taller cedar I found in the park was already in the canopy.

Fig. 21. A cedar seedling about 6cm tall on a common moss species. Few, if any, other seedlings were taller.

Poor cedar regeneration has been reported throughout the Great Lakes region. Only 1% of cedars growing on CWD in a Michigan forest survived to reach over 25cm tall (Scott and Murphy, 1987). In upland, fire dependent cedar forests in this region, Cornett et al. (1997) also found no seedlings more than 25cm tall. However, for cedar seedlings ≥1 year old they found average densities between 5 and 25/m^2 of CWD (Cornet et al., 2001), much higher than my observed 0.32/m^2 of CWD. Scott and Murphy (1987) did find >25cm tall cedars to be more common in gaps but none of the cedars at my site reached that height.

White spruce and Balsam fir both have low seedling densities but they also have very low density in the canopy. Neither species shows a sharp drop in density in the higher height classes which is consistent with enough regeneration to maintain those low canopy abundances.

Possible Limiting Factors

Possible factors that could be limiting the regeneration of cedar, and to a lesser extent birch, include herbivory by deer, a change in the dominant forest type, a lack of light or disturbance, a lack of substrate, or any combination of these.

White-tailed deer have increased in abundance due to mild winters over the last decade. Although they must still concentrate by the shore of Lake Superior to survive the winters, on warmer winter days they may travel up onto the ridge, near the area of my sites (Dave Ingebrigtsen, pers. comm.). Even tiny cedar seedlings are vulnerable to hungry deer. The young plants are usually quickly covered under snow. However, according to Dave Ingebrigsten, a wildlife biologist in the DNR, just one winter with below normal snow fall or an early snow melt will see even the short cedars consumed because they are one of the few green things at that time of year. Another indication of winter browsing at my site was the typical sight of balsam skeletons less than a meter tall, missing all their needles except for those on the very lowest branches. Although not common, spruce saplings were present throughout the forest. Spruce is the only evergreen plant the deer here won't eat in the winter (Sauvé and Côté, 2007).

In some places near the lake shore, wire cages or repellant sprays are the only way to grow cedars tall enough to escape death by deer. Both Cornett et al. (2000*a*) and Rooney et al. (2002) warn that if action is not taken to control deer in the forests near Lake Superior, cedars will cease to be part of the canopy there.

Deer will eat birch when the leaves are out in the summer (Dave Ingebrigtsen, pers. comm.) but at that time the deer density near the shore drops as most deer spread out inland. There was a patch of lowland cedar forest adjacent to my sites, it was much moister than my sites and also had a much higher density of birch seedlings. This suggests that deer are not abundant enough in the park in the summers to limit birch. If they were, densities would likely be evenly low throughout the park. In the same lowland cedar forest, I didn't notice cedars any taller than those at my sites, which would be consistent with high herbivory throughout the park during the winter.

A different branch of the DNR disagrees with the idea that herbivory is the main cause of cedar mortality. The forestry division suggests that cedar seedlings die in their first few years, well before they are tall enough to be noticed by deer (but if they did grow much higher then they would certainly be browsed by deer.) They note that cedar seedlings only grow well in full sun, which restricts their survival and recruitment to large gaps (Minnesota DNR, 2009). If suitably large gaps were always as uncommon as they are now, it is possible that the successional trajectory of this forest type would not naturally have cedar and birch regenerating at this stage. A succession model proposed by John Almendinger, a forester in the DNR, based on pre-harvest public land survey records, suggests that in forests over 110 years old, like mine, cedar and birch have decreasing reproductive success and spruce, which is tolerant of long periods of shade, gradually becomes dominant in the canopy (Minnesota DNR, 2009). This idea is supported by the fact that the ratio of saplings to current canopy trees for spruce was much higher than that of birch or cedar. A contrasting idea is that because cedars can live to be 400 years old in these stands (Frelich and Reich, 2003), even a very small number of recruits to the canopy each year will permanently maintain their density in the canopy.

Another possibility is that the boundary between the cedar-birch forest and the neighboring maple dominated forest (MHn45c) is shifting. Maple seems to be poised for expansion at the expense of cedar and birch. It has much higher seedling densities under the canopy so it is in a better position to take advantage of gap formation. Maple is tolerant enough to recruit via gaps that would be too small for cedar or birch to succeed in (Minnesota DNR, 2009). Indeed, in the typically small gaps in this forest, maple and birch densities were equal for 1-4m stems but for stems taller than that, maple was four times more abundant than birch. If this change is occurring, it would be similar to the successional pathway that was found in a birch-maple-*Fagus* forest in the Adirondacks, with the more shade tolerant maple seedlings recruiting to replace birch (Forcier et al., 1975). However, this expansion hypothesis cannot give a satisfying explanation of why is there such a clear demarcation of canopy composition associated with the topography. The fact that cedar-birch forest is restricted to north facing slopes while maple dominates the forests on the south slopes and hilltops suggests that a large scale environmental factor such as temperature is more important for determining their distributions. Or, as maple is predicted to expand dramatically over the next 150 years (Ravenscroft et al., in press), it is possible that it has only recently begun its expansion as an early effect of climate change.

It has been suggested that regeneration is limited by the thick leaf litter that covers the mineral soil (Mark White, pers. comm.), a substrate on which both cedar and birch can grow well (Burns and Honkala, 1990). In a Quebec forest, cedars on mineral soil had germination and survival rates equal to those on CWD (Simard et al., 2003). Exposed mineral soil was very rare in my cedar-birch forest. Bare soil is usually found in forests where trees have tipped over but most of the dead trees in this forest had broken off along their trunk, not leaving a soil pit/mound. While this forest is not classified as a fire-dependent, it is possible that cool burning ground fires could have periodically exposed large extents of mineral soil, potentially over 90% of the forest floor, and thus spurred regeneration. However, any soil exposed by a surface fire would be covered by fallen leaves in just one or two autumns. Other evidence of surface fires also disappears quickly and so we have no information concerning ground fires in this forest prior to the last few decades, in which there have been no fires.

A potential mechanism to create permanently exposed soil is invasion by exotic earthworms. European earthworms are a well known problem in these forests that cause the litter and decomposed organic layers to decrease significantly or even disappear in places (Hale et al., 2005*a*; Holdsworth et al., 2007). From litter depth surveys conducted throughout the park, it appears that earthworms are expanding in the park, presumably after being introduced at campsites along the Manitou River. In the future this could actually increase the extent of bare mineral soil at my sites. However, earthworms also increase the soil's bulk density (Hale et al., 2005*b*) causing a decrease in water holding capacity, which may decrease the suitability of bare soil for seedlings (Mark White, pers. comm.).

The final limiting factor to consider is the availability of suitable CWD substrate. CWD is currently abundant in this forest, and is probably not too different from its abundance in pre-European times. But, if any of the processes listed above limit or prevent cedar from replacing itself in the canopy, total CWD abundance might not change, but cedar CWD would eventually decline or disappear. Any tree that prefers to establish on well decayed cedar wood, i.e. birch, would also face a major decline.

The preference for CWD and CWD types

I found that seedlings of four of the five canopy species preferred to establish on CWD. Only three of the four had been previously reported to do this. In contradiction to Simard et al.'s (2003) findings, balsam seedlings significantly preferred CWD over leaf litter at this site. Young birch had their highest densities on CWD in Ontario (Caspersen and Saprunoff, 2005) and specifically on *Tsuga canadensis* wood in a Michigan hardwood-conifer forest (Marx and Walters, 2008). Cedars preferred CWD over litter in a southern boreal forest in Quebec (Simard et al., 2003) and in upland fire-dependent cedar forests in the region they preferred their own wood over birch wood and other soil or litter substrates (Cornett et al., 2001). Spruce seedlings grew better on their own CWD than any other non-CWD substrate after a disease disturbance in Alaska (Boggs et al., 2008) and in a mature Quebec forest (Simard et al., 2003).

Reasons for seedling's preferences for CWD may include the size of seeds, the leaf litter shedding properties of CWD, the difference in height between CWD and the forest floor, and the nutrient and water availability conditions of CWD, none of which are mutually exclusive.

For several tropical trees, their seed size relates to whether their seedlings will establish on CWD or leaf litter (Lusk, 1995). That study suggested that small seeds do not have enough energy to send their root down through the leaf litter to the soil. The same should apply due to the thick litter layer at my site. Cedar (1.3 mg/seed) and birch (10 mg) have much smaller seeds than maple (65mg; Burns and Honkala, 1990). Thus the results from this study are consistent with the idea that smaller seeded species are more likely to be restricted to CWD.

Burial under fallen dead leaves is another notable cause of mortality for cedar seedlings (Simard et al., 2003). It has been suggested that the height, and thus exposure to wind, and the sloping edges of CWD prevent the accumulation of leaf litter (Harmon et al., 2004). In the summer, the leaf litter becomes dry, hot, and deadly to small seedlings (Burns and Honkala, 1990) leading Koroleff (1954) to consider CWD a "refuge from leaf litter."

Seedlings starting on CWD have a height advantage to help them compete against what could sometimes be a continuous carpet of other plants on the forest floor (Fig. 22). In some cases the CWD's surface was more than a half meter high, taller than most maple seedlings. Seedlings faced little competition from other herbs growing on CWD. The few herbs I did observe on CWD were on extremely decayed pieces, class 5 or beyond. The height of CWD may also help it warm faster in the spring giving seedlings a slightly longer growing season (Harmon et al., 2004).

Harmon et al. (2004) mentioned that the height could also be a disadvantage. As the CWD decays it can fragment and dislodge seedlings. They suggested that despite a preference for CWD, seedlings had a better chance of reaching maturity on the forest floor. However, Harmon et al. (2004) were working with big logs, close to 1m diameter, in the Pacific Northwest. The average height of the logs in this forest was less than 23cm meaning they are more supported by the ground and thus more likely to slowly subside rather than fragment.

Fig. 22. Birch and spruce seedlings getting started on CWD in a gap, above a tangle of tall ferns.

The fact that every species had significantly higher densities on highly decayed logs suggests that the process of decay provides basic conditions necessary for seedling survival (Fig. 23). The trend of increasing seedling density does slightly level out once a piece reaches class 3. Before class 3, leaching and rot have not weakened the wood enough to allow roots to push themselves through, and so seedlings can find few places to anchor themselves securely.

Available nitrogen levels also increase with decay. Concentrations of nitrogen, the limiting nutrient, are actually lower in CWD than in the mineral soil and the duff (made from fallen N rich twigs and leaves) but both of those are inaccessible to seedlings because they are covered with thick leaf litter. However, several experiments in different ecosystems and with different species of CWD have shown that there is a net increase in available nitrogen, ranging from 40 to 300%, from tree death until the piece completely decays (Harmon et al. 2004). Asymbiotic nitrogen fixing bacteria living in CWD contribute influential amounts of useable nitrogen (Hicks et al., 2003). Newly discovered associations between ectomycorrhizal fungi and nitrogen fixing bacteria, which are both present in the later stages of decay, lead Tedersoo et al. (2008) to call CWD a "long term, slow release nutrient source" for seedlings. The presence of additional nitrogen in the advanced decay classes may be particularly important for seedling survival under conditions of limited light (Walters and Reich, 2000).

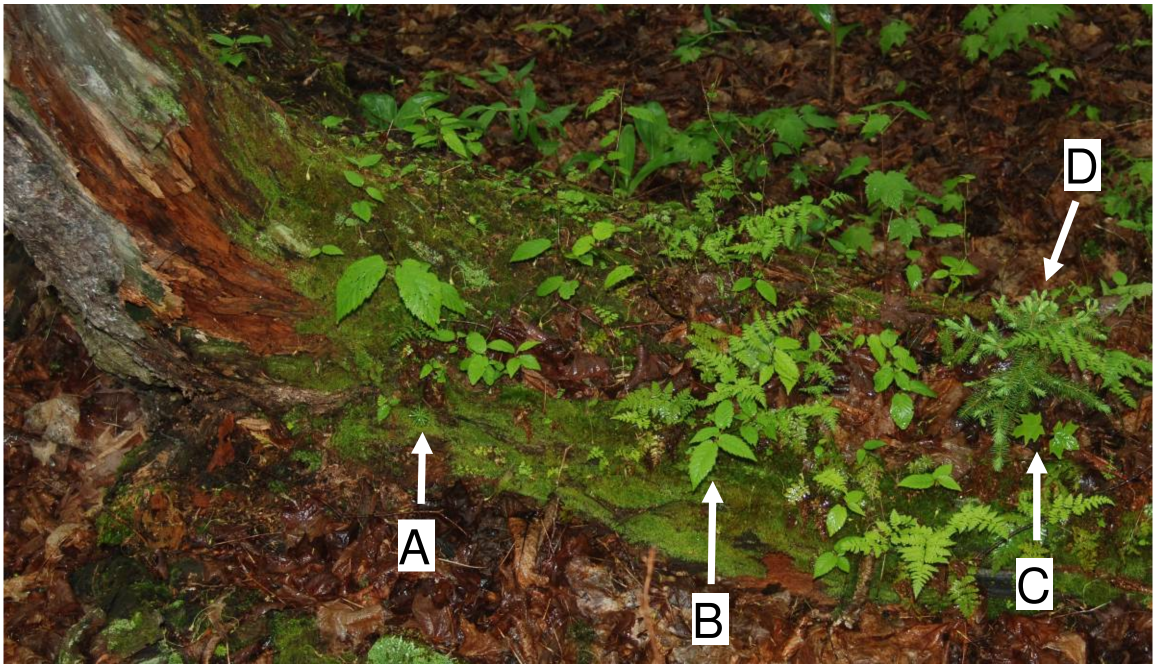

Fig. 23. A moss covered, decay class 4 cedar log with balsam (a), birch (b), maple (c), and spruce (d) seedlings.

The water holding capacity of CWD also increases with decay. All seedlings need access to adequate water. As pieces become more sponge like, they can hold moisture longer than other substrates (Harmon et al., 2004), even duff (Place, 1950; Harvey et al., 1976), thus providing a less stressful water environment for seedlings.

Cedar seedlings are especially susceptible to death by drying out (Burns and Honkala, 1990) but it has been shown in a greenhouse experiment that the ability of CWD to retain water during times of scarcity has a positive influence on their survival (Cornett et al., 2000*b*). The importance of water availability for birch is illustrated by the result that, among the four sites in Michigan studied by Marx and Walters (2008), the highest overall seedling abundances were found at their wettest site.

It is very likely that moss correlates to water availability. This may be the reason why moss coverage was the trait that had the greatest influence on both cedar and birch seedling densities. The fine structure of moss helps it and the CWD below it remain wetter for longer and thus may help seedlings resist drying even more than CWD by itself. In Quebec, birch seedlings preferred moss covered logs to plain logs but plain logs over moss by itself (Caspersen and Saprunoff, 2005). It has been shown that by cooling below the dew point at night, the tips of moss shoots can collect not only water from the surrounding air, but they can also intercept water that had just evaporated from the material below them, a process called "nocturnal distillation" (Carleton and Dunham, 2003). Furthermore, this process functions best in the later, hotter part of the summer.

Moss had been reported to compete with tree seedlings (Harmon and Franklin, 1989) but that finding was from forests in Washington State. The mosses there are much taller than those at my site. The mosses on CWD here, including some in the genus *Heterophyllium*, were usually shorter than 3cm. The tangled structure of the mosses of any height may also retain the seeds better than the bare surface of CWD (Harmon and Franklin, 1989). However, for the 24 pieces with birch seedlings >50cm tall, moss cover ranged evenly from 0% to 100% suggesting that moss and the water it provides may be most important to seedlings only in their first few years.

The fact that both cedar and birch preferred coniferous CWD reaffirms the similar results of Cornett et al. (2001) and Marx and Walters (2008) respectively, but the reason behind this preference is still unclear in the literature.

Nutrient availability is variable between species. In a Michigan study, birch seedlings were healthier on *Tsuga canadensis* wood than on birch wood because of insufficient phosphorus (Marx and Walters, 2006). The microbial community of the *Tsuga* wood was also making nitrogen available by mineralization six times faster that in birch CWD. Another variable is pH. *Tsuga* and birch logs maintained a pH close to 4 in all conditions, whereas the pH of maple logs was almost 7, which makes seedling uptake of N, P, K, Mg, and Zn much less efficient (Marx and Walters, 2006).

The water transport structures of angiosperm wood are generally wider and more interconnected than those of gymnosperms. This is known to help decay microbes and roots to colonize angiosperm CWD faster (Harmon et al., 2004) but it may also have some effect on water retention. A greenhouse experiment found no difference in cedar germination between birch and cedar wood when water availability was high (Cornett et al., 2000*b*) but because cedar is known to prefer coniferous CWD in the field, this supports the idea that water retention varies between species. However, in a greenhouse simulation of drought, birch wood was preferred to cedar (Cornett et al., 2000*b*).

CWD contains chemicals that are unique to each species or genus. For example, *Thuja* species have polyphenolic molecules that have anti-fungal properties as well as a molecule that gives the characteristic cedar scent. Chemicals in other species of CWD may have various allelopathic or anti-microbial properties (Harmon et al., 2004) with variable effects on seedlings.

Conifer wood is rich in lignin (Harmon et al., 2004), a hard to decompose component of plant cell walls, and partly because of this, the wood of coniferous trees decays more slowly than deciduous wood, particularly in decay classes 4 and 5. It may be that, despite the low correlations between the decay and species variables in the GLME model (all < 0.05), part of the preference for coniferous CWD was due to the fact that 82% of decay class 4 and 5 pieces were coniferous. The wood of *Picea* species and balsam was shown to spend an average of 10 to 17 years in each decay class (Zielonka, 2006; Campbell and Laroque, 2007) and *Thuja* wood is used commercially for its exceptional decay resistance. By comparison, maple wood spent an average of 6 years or less in each decay class (Hale and Pastor, 1998). With such a slow decay rate, coniferous CWD can last for decades as a suitable substrate that resists the accumulation of leaf litter, has available nitrogen, and is usually moist.

Surprisingly, birch, spruce, and balsam all showed significant preferences for stumps over logs. I did not expect to find a difference and I don't think my calculations underestimated the surface area of the stumps. It's possible that more seeds are trapped on the very uneven vertical shreds of wood on a stump, rather than being more likely to fall off the side of a log. It's possible that the surface of each stump is more hospitable to seedlings because of its vertical grain and because most of the surface is the heartwood. Those factors may enable seedlings to establish their roots sooner and deeper than on the harder outer grain of horizontal logs. However, it may be that water drains out of stumps faster than logs. Stumps would also be more unstable and more likely to cast off seedlings as they decay and fragment, rather than small diameter logs which would be more likely to gently subside into the earth.

Birch, but not cedar, was abundant enough in the neighboring maple dominated forest to show the same general pattern of preferences, albeit less significantly due to the confounding effects of lower seed supply (data not shown).

Other factors influencing seedling density

Seedling densities were low for some species and highly variable for all species. For example, for birch, 25% of the pieces with all the most favorable traits still had no seedlings, but there were also the "super-density" pieces. As I walked through either the cedar-birch or the adjacent maple forest, occasionally I would see a log with almost completely covered by birch seedlings. In the transects I observed 3 pieces with between 10 and 134 seedlings on them for calculated densities of >100 seedlings/m^2 of CWD. All three were cedar wood with >95% moss cover but there must have been something else about these pieces, or their location, that made them unusually hospitable.

CWD type explains some of the variation but other factors that I did not measure directly, including seed dispersal, microclimate, herbivory, and light availability, may also have considerable influence. The addition of the random effect term to the model was meant to account for these.

With a species like spruce, which consistently had so few canopy trees, it is reasonable that its low seedling density was caused by a lack of seeds. However, seed dispersal also varies with time, due to mast years, and space, due to chance. Both cedar and birch produce mast seed crops every 2 to 5 and 2 to 3 years respectively (Burns and Honkala, 1990). Densities of seedlings, particularly the youngest, <10cm tall, fluctuate with this cycle but without knowing when the last mast crop was, I can't say if the numbers I observed were higher or lower than average. Either way, this would not affect seedlings' preferences. There certainly is randomness that prevents an even distribution of seeds across the ground. Air currents, microtopography, and snow drifts can easily deposit more or fewer seeds than average on random CWD pieces or patches of ground. Small scale variability in seed distribution would be the simplest explanation for the few super-density logs and yet is consistent with the overall lack of correlation between birch seedling and canopy densities.

Like seed dispersal, seed predation by rodents (Simard et al., 2003) and microclimate are both factors that affect densities and can vary within the same transect, or even for each piece. However, because of their small scales, the random effect underestimates their influence. It is only able to incorporate the average trend from each transect and can not detect more specific influences.

Alternately, factors may operate on a scale too large to be captured by the random effects. Herbivory can certainly change seedling densities but it may to operate on a scale larger than individual transects or stands. If a factor has a constant effect over the whole study area, the random effect would not notice it and thus not incorporate its influence on seedling densities.

Light availability varies drastically between closed canopy and gaps. Increased light has a significant effect on cedar, or any seedling's survival and growth (Cornett et al., 2001). In fact, it may be important enough to account for most of the unexplained variation in the seedlings densities I observed. For birch, there was a correlation between random effect and canopy gaps, but because gaps covered only part of a transect, the influence of light may have been underestimated. If pieces had also been grouped by "in" or "out" of gaps at each transect, the pattern would have been clearer.

Problems with scale of influence meant the random effect captured only some of the spatial variation. This likely explains why the random effects accounted for unreasonably small proportions of the variability.

Management Recommendations

Globally, humans are realizing that forests should now be sustainably managed to preserve biodiversity, water quality, and to regulate atmospheric carbon dioxide. Truly sustainable forest management is possible, but our current efforts need improvement. For example, soil scarification, or raking away the litter and duff, is used as a simple way to promote establishment of tree species like birch that can use mineral soil as well as CWD, but this procedure can have very disruptive effects on the rest of the ecosystem (McGee and Birmingham, 1997). As a step towards improving the management of rotation forests of the same type as the one I studied, this study defines what conditions support tree regeneration in a natural setting and points out potential threats to that regeneration. It can be used as a reference to address what should be done about problems of substrate limitation in managed forests.

Results from this study suggest that increasing CWD in managed forests, where it has become very uncommon, may help to increase the regeneration of birch and long lived conifers such as cedar and spruce. Recovery of those conifers will in turn help protect the biodiversity of the entire landscape. Therefore the establishment and retention of long-lived conifers in the region is a primary goal of The Nature Conservancy (Mark White, pers. comm.).

The Minnesota DNR has guidelines for managing mixed mesic cedar-birch and maple forests (MHn45) to allow natural regeneration. They recommend that 2-5 logs, >12in diameter with the bark still on them, be left on the ground per acre as future nurse logs (Minnesota DNR, 2003). That is roughly equivalent to 10-25m^2/acre, a very small fraction of the 200m^2 of CWD/acre that I observed. My results suggest that the state's management recommendations are outdated for both the quantity and quality of CWD they specify and should be changed in both respects.

CWD Quantity – More CWD is needed to support adequate levels of regeneration. As amount of CWD increases, there will be more seedlings from uncommon tree species and pieces with high densities will become more frequent. The presence of more CWD will mimic the structure of old growth structure and should enhance biodiversity of trees and other organisms. It may even enhance tree growth due to nitrogen fixing in the CWD (Harmon et al., 2004). Leaving timber unharvested and letting it die may seem inefficient, but CWD performs such important functions that including it in management plans actually improves long term productivity (Hura and Crow, 2004). Maintaining the roughly 40 logs/acre (or CWD covering 4-5% of the ground) that I observed would be a good target for cedar-birch forests.

CWD Quality – Birch seedlings grow best on cedar CWD and cedar seedlings prefer any coniferous CWD so those species should make up the largest proportion of left logs and seed tree retention, not just the least profitable pieces (i.e. maple). Fresh CWD is also of little use to seedlings. Twenty to thirty years, or more, before a planned harvest, wood of a suitable type should be present on the ground so it can decay and seedlings can establish on it before the canopy is harvested. When harvesting, standing trees of varying ages should be left to provide a supply of some CWD for the future.

Even with sufficient CWD, cedar regeneration may be limited. For small, high value areas, protecting cedar seedlings with deer exclusion cages might be the only way for cedar to survive long enough to reach the canopy. Changing hunting regulations should be considered to keep the deer population in check long enough for some seedlings to grow above browsing height. Gap selection harvests rather than larger cuts should also be considered. Gaps of 200-600m^2 gaps may favor cedar and birch regeneration after a harvest, but work on this idea is ongoing (Tony DeMatto, pers. comm.). While there are other management questions to consider, such as whether enough seed trees remain in a managed forest, if natural regeneration of this cedar-birch forest is desired, CWD is required.

Acknowledgements:

I thank the Connecticut College CELS program for funding my fieldwork, the Minnesota chapter of The Nature Conservancy for giving my this project to work on, Mark White and Professor Chad Jones for advising and guiding me, Gabriel Chandler for helping me better analyze the data, and Richard and Lynn Rossiter for reading and commenting on my drafts. Finally, thank you to whoever is reading this.

Feel free to contact me with questions or to obtain a copy of the raw data.
srossiter1@gmail.com

References:

Bates, D., Maechler, M., and Dai, B. 2008. lme4: Linear mixed-effects models using S4 classes. Version 0.999375-28. http://cran.r-project.org.

Boggs, K., Sturdy, M., Rinella, D.J., and Rinella, M.J. 2008. White spruce regeneration following a major spruce beetle outbreak in forests on the Kenai Peninsula, Alaska. For. Ecol. Manage. **255:** 3571-3579.

Boone, R.B., and Krohn, W.B. 2000. Partitioning sources of variation in vertebrate species richness. J. Biogeogr. **27:** 457-470.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology **73:** 1045-1055.

Brandner, T.A., Peterson, R.O., and Risenhoover, K.L. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology **71:** 155-164.

Burns, R.M., and Honkala, B.H. technical coordinators. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC.

Campbell, L.J., and Laroque, C.P. 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. For. Ecol. Manage. **238:** 293-301.

Carleton, T.J., and Dunham, K.M.M. 2003. Distillation in a boreal mossy forest floor. Canadian Journal of Forest Research **33:** 663-671.

Caspersen, J.P., and Saprunoff, M. 2005. Seedling recruitment in a northern temperate forest: The relative importance of supply and establishment limitation. Canadian Journal of Forest Research **35:** 978-989.

Christy, E.J., and Mack, R.N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. J. Ecol. **72:** 75-91.

Cornett, M.W., Reich, P.B., and Puettmann, K.J. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. Ecoscience **4:** 353-364.

Cornett, M.W., Puettmann, K.J., Frelich, L.E., and Reich, P.B. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of Northeastern Minnesota. Restor. Ecol. **9:** 386-396.

Cornett, M.W., Frelich, L.E., Puettmann, K.J., and Reich, P.B. 2000*a*. Conservation implications of browsing by Odocoileus virginianus in remnant upland *Thuja occidentalis* forests. Biol. Conserv. **93:** 359-369.

Cornett, M.W., Reich, P.B., Puettmann, K.J., and Frelich, L.E. 2000*b*. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. Am. J. Bot. **87:** 1807-1814.

Dunteman, G.H. and Ho, M.R. 2006. Introduction to Generalized Linear Models. Sage Publications, Thousand Oaks, CA.

Forcier, L.K. 1975. Reproductive strategies and the co-occurrence of climax tree species. Science **189:** 808-810.

Franklin, J. F. and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-GTR-008.: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, OR.

Fraver, S., Wagner, R.G., and Day, M. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. Canadian Journal of Forest Research **32:** 2094-2105.

Frelich, L.E., and Reich, P.B. 2003. Perspectives on development of definitions and values related to old-growth forests. Env. Rev. **11:** S9-S22.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65:** 325-346.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. **52:** 107-145.

Hale, C.M., and Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A. Canadian Journal of Forest Research **28:** 1276-1285.

Hale, C.M., Frelich, L.E., and Reich, P.B. 2005*a*. Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA. Ecol. Appl. **15:** 848-860.

Hale, C.M., Frelich, L.E., Reich, P.B., and Pastor, J. 2005*b*. Effects of European earthworm invasion on soil characteristics in Northern Hardwood Forests of Minnesota, USA. Ecosystems **8:** 911-927.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology **70:** 48-59.

Harmon, M.E., and Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., and Cummins, K.W. 2004. Ecology of Coarse Woody Debris in Temperate Ecosystems. Advances in Ecological Research **34:** 59-234.

Harvey, A.E., Jurgensen, M.F. and Lanen, M.J., 1976. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. **24:** 203–208.

Hicks, W.T., Harmon, M.E., and Myrold, D.D. 2003. Substrate controls on nitrogen fixation and respiration in woody debris from the Pacific Northwest, USA. For. Ecol. Manage. **176:** 25-35.

Holdsworth, A.R., Frelich, L.E., and Reich, P.B. 2007. Regional extent of an ecosystem engineer: Earthworm invasion in northern hardwood forests. Ecol. Appl. **17:** 1666-1677.

Hura, C.E., and Crow, T.R. 2004. Woody Debris as a Component of Ecological Diversity in Thinned and Unthinned Northern Hardwood Forests. Nat. Areas J. **24:** 57-64.

Husch, B., Miller, C.L., and Beers, T.E. 1982. Forest mensuration. J. Willey & Sons. New York, NY.

Jacobs, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia **14:** 413-417.

Knechtel, A. 1093. Natural reproduction in the Adirondack Forests. Forest Quarterly **1:** 50-55.

Koroleff, A. 1954. Leaf litter as a killer. J. For. **52:** 178–182.

Legendre, P., and Fortin, M.J. 1989. Spatial pattern and ecological analysis. Vegetatio **80:** 107-138.

Luke, D.A. 2004. Multilevel Modeling. Sage Publications, Thousand Oaks, CA.

Lusk, C.H. 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. Journal of Vegetation Science **6:** 249-256.

Marx, L., and Walters, M.B. 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock-hardwood forests. J. Ecol. **96:** 505-513.

Marx, L.M., and Walters, M.B. 2006. Effects of nitrogen supply and wood species on *Tsuga canadensis* and *Betula alleghaniensis* seedling growth on decaying wood. Canadian Journal of Forest Research **36:** 2873-2884.

McGee, G.G., and Birmingham, J.P. 1997. Decaying logs as germination sites in northern hardwood forests. Northern Journal of Applied Forestry **14:** 178-182.

Minnesota DNR. 2009. Silviculture Interpretation. http://files.dnr.state.mn.us/forestry/ecssilviculture/plantcommunities/MHn45.pdf, accessed 4/28/2009.

Minnesota DNR. 2008. Native Plant Communities Guide. http://files.dnr.state.mn.us/natural_resources/npc/mesic_hardwood/mhn45.pdf, accessed 6/1/2008.

Minnesota DNR. 2003. Voluntary Site Level Forest Management Guidelines for Landowners, Loggers, and Resource Managers. Minnesota Forest Resources Council, St. Paul, MN.

Minnesota Climatology Working Group. 2009. Minnesota DNR and the University of Minnesota. http://climate.umn.edu/doc/historical/temp_norm_adj.htm, accessed 3/12/2009.

Newton, A.C. 2007. Forest ecology and conservation: a handbook of techniques. Oxford University Press.

Place, I.C.M. 1955. The influence of seedbed conditions on the regeneration of spruce and balsam fir. For. Branch Bull. 117, Dep. North. Aff. and Nad. Resour., Ottawa, Ontario.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ravenscroft, C., Scheller, R.M., Mladenoff, D.J., and White, M.A. in press. Simulating forest restoration in a mixed ownership landscape under climate change. Ecol. Appl.

Rooney, T.P., Solheim, S.L., and Waller, D.M. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. For. Ecol. Manage. **163:** 119-130.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63:** 1533-1546.

Sauvé, D.G., and Cotě, S.D. 2007. Winter forage selection in white-tailed deer at high density: Balsam fir is the best of a bad choice. J. Wildl. Manage. **71:** 911-914.

Scott, M.L., and Murphy, P.G. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. Am. Midl. Nat. **117:** 10-16.

Simard, M.-., Bergeron, Y., and Sirois, L. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Canadian Journal of Forest Research **33:** 672-681.

Tedersoo, L., Suvi, T., Jairus, T., and Kõljalg, U. 2008. Forest microsite effects on community composition of ectomycorrhizal fungi on seedlings of *Picea abies* and *Betula pendula*. Environ. Microbiol. **10:** 1189-1201.

Walters, M.B., and Reich, P.B. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology **81:** 1887-1901.

Weather Underground. 2009. http://www.wunderground.com/US/MN/Two_Harbors/KTWM.html#History, accessed 3/12/2009.

Webster, C.R., and Lorimer, C.G. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. Ecol. Appl. **15:** 1245-1262.

White, M.A., and Host, G.E. 2008. Forest disturbance frequency and patch structure from pre-European settlement to present in the Mixed Forest Province of Minnesota, USA. Canadian Journal of Forest Research **38:** 2212-2226.

White, M.A. 2001. Growth Stage Summaries for Mesic white pine-red pine and Mesic aspen-birch-spruce-fir. Natural Resources Research Institute, University of Minnesota, Duluth, MN.

Zielonka, T. 2006. When does dead wood turn into a substrate for spruce replacement? Journal of Vegetation Science **17:** 739-746.