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White pine (*Pinus strobus* L.) regeneration dynamics at the species' northern limit of continuous distribution

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Abstract The abundance of eastern white pine (*Pinus strobus* L.) has been significantly reduced across its distribution range over the past few centuries. The species' regeneration dynamics is well documented in the centre of its range, but is poorly understood at the northern limit of continuous distribution. To address this knowledge gap, we quantified natural white pine regeneration in unmanaged mature stands, identified the most important variables influencing it, and evaluated the impact of damaging agents, namely white pine blister rust (*Cronartium ribicola* J.C. Fisch.), white pine weevil (*Pissodes strobi* Peck), and herbivory. We also quantified the influence of remnant stands and residual trees on the spatial distribution of regeneration in logged sites. The results reveal continuous but low recruitment in mature stands. The basal area of balsam fir (*Abies balsamea* (L.) Miller) had a strong negative effect on white pine regeneration. Regeneration was more abundant than expected on moister substrates, including moss, decaying wood and organic matter. White pine regeneration was noted in recently logged areas, where distance from remnant stands had a significant effect on the abundance of white pine regeneration. The northern limit of continuous distribution holds potential for white pine restoration, for example by preserving remnant white pine stands that can provide seed sources for natural regeneration in a shelterwood cut system, or in adjacent clearcut areas. This study illustrates that different management strategies should be used near northern range limits, where effects of site conditions and disturbance agents are different than in the center of a species' range.

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Introduction

Eastern white pine (*Pinus strobus* L.) has historically been one of the most important species in North America for its ecological, economic, social, and cultural values (Wendel and Smith 1990; Steen-Adams et al. 2007). The species' abundance decreased across its natural distribution range over the last few centuries due to extensive logging and fire management practices that eliminated seed sources and seed beds (Carleton et al. 1996; Weyenberg et al. 2004). White pine restoration and management are deemed problematic because of its specific site requirements, slow initial growth rate, susceptibility to damage from white pine blister rust (*Cronartium ribicola* J.C. Fisch.) and white pine weevil (*Pissodes strobi* Peck), and heavy browsing by herbivores (Katovich and Morse 1992; Burgess et al. 2005; Steen-Adams et al. 2007; Latremouille et al. 2008). Nevertheless, there is a sustained interest in white pine restoration and management (Carleton et al. 1996; Pitt et al. 2009).

The interaction between site characteristics, light availability, and interspecies competition is considered important in determining the success or failure of natural white pine regeneration (Ahlgren 1976; Hibbs 1982; Stearns 1992). Historically, low intensity surface fires played an important role by clearing competing vegetation, opening the canopy, and preparing seed beds for seedling establishment (Heinselman 1981; Bergeron et al. 1997). White pine blister rust and white pine weevil can affect growth, thus reducing wood quality and postponing the onset of seed production (Belyea and Sullivan 1956; Wendel and Smith 1990; White et al. 2002; Major et al. 2009). In severe cases, blister rust and weevil can kill seedlings or saplings (Wendel and Smith 1990).

Site characteristics and the prevalence of natural disturbances can vary significantly throughout the species' range (Abrams 2001). Existing knowledge regarding white pine ecology and management, both scientific and practical, largely relates to the central part of the species' range (e.g., Ahlgren 1976; Dovčiak et al. 2001, 2003; Burgess et al. 2005), with few studies conducted at the northern distribution limit (e.g., Holla and Knowles 1988; Bergeron et al. 1997; Engelmark et al. 2000). There is considerable potential for white pine restoration and management between these two areas near the limit of continuous distribution. However, a better understanding of the species' regeneration dynamics in this region is needed, especially with regards to potential damage by blister rust and weevil. The present study aims to (1) quantify white pine regeneration at the species' northern limit of continuous distribution; (2) evaluate the impact of blister rust, weevil, and herbivory; and (3) determine which microhabitat characteristics are most important to white pine regeneration patterns. We tested the following hypotheses: (1) canopy cover (inversely related to light availability) is the most important variable explaining white pine regeneration; (2) competition from other species reduces white pine establishment potential; (3) remnant white pine stands or living residual trees in logged areas influence the spatial pattern of white pine regeneration; (4) damaging agents such as blister rust and weevil affect white pine regeneration; and (5) suitable germination sites are available to ensure long-term white pine presence. We wanted to determine if these hypotheses, based on previous studies conducted in the central part of the species' range, were also valid at the northern limit of continuous distribution, where the climate is cooler, the growing season is shorter, and site characteristics are different.

Methods

Study area

The study area is located in the La Vérendrye Wildlife Reserve in western Quebec (Fig. 1), and is part of the ancestral territory of the Kitcisakik Algonquin community. Average annual temperature is 1.2–3.3 °C, and average precipitation is 914–1,014 mm/year, with 22–33 % falling as snow (Val-d'Or and Mont-Laurier weather stations, Environment Canada: http://www.climate.weatheroffice.gc.ca/climate_normals). The altitude ranges from 316 to 415 m with an average of 368 m. Surface deposits are mostly glacial and fluvioglacial.

The study area corresponds to the northern limit of continuous white pine distribution. In northwestern Quebec and northeastern Ontario, the species' northern limit is reached in the Lake Duparquet and Lake Abitibi regions where scattered stands and trees are present (Bergeron et al. 1997; Engelmark et al. 2000). The study area is located in the balsam fir (*Abies balsamea* (L.) Miller)—yellow birch (*Betula alleghaniensis* Britton.) bioclimatic domain (Saucier et al. 1998). Mixed forests are dominant in the region, with balsam fir and black spruce (*Picea mariana* (Mill.) BSP.) accompanied by white spruce (*Picea glauca* (Moench) Voss), white pine, eastern white cedar (*Thuja occidentalis* L.), yellow birch, paper birch (*Betula papyrifera* Marsh.), sugar maple (*Acer saccharum* L.), red maple (*Acer rubrum* L.), and trembling aspen (*Populus tremuloides* Michx.). Red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.) are present on xeric sites. Since the 1970s, more than 60 % of the productive forest land within the study area has been harvested by timber companies (Saint-Arnaud et al. 2009). Logging has replaced fire as the main disturbance in the study area. Fire cycles of the pre-industrial and industrial periods were estimated at 257 and 2,083 years, respectively (Bergeron et al. 2006).

Site selection and data collection

Mature stands dominated or co-dominated by white pine were located on ecoforestry maps of the Québec Ministry of Natural Resources. From those, 22 stands were accessible (i.e., less than a 30 min walk from a forest road) and were selected for sampling. At each stand, we established a 20 m × 20 m quadrat ensuring that at least three white pine seed trees were included. The precise location of the quadrats was determined randomly.

Good seed production can be expected when white pine trees are at least 20–30 years old (Ahlgren 1976; Wendel and Smith 1990), corresponding to a diameter at breast height (DBH) of 10–15 cm (Holla and Knowles 1988). We used this criterion to identify white pine seed trees. Old cut stumps were present at one site, but the other 21 sites showed no indication of logging.

Within each quadrat, the DBH of every tree ($\geq$10 cm) was measured and the species was noted. Basal area was calculated for each species. For white pine, we recorded any indication of damaging agents, namely the presence of blister rust, weevil, *Ribes* spp. (an alternative host of blister rust, see Zambino 2010), herbivory, or seed predation by red squirrel (*Tamiasciurus hudsonicus* Erxl.). We also measured slope, aspect, and elevation at each plot. The type of surface deposit (e.g., clay, till) was obtained from ecoforestry maps.

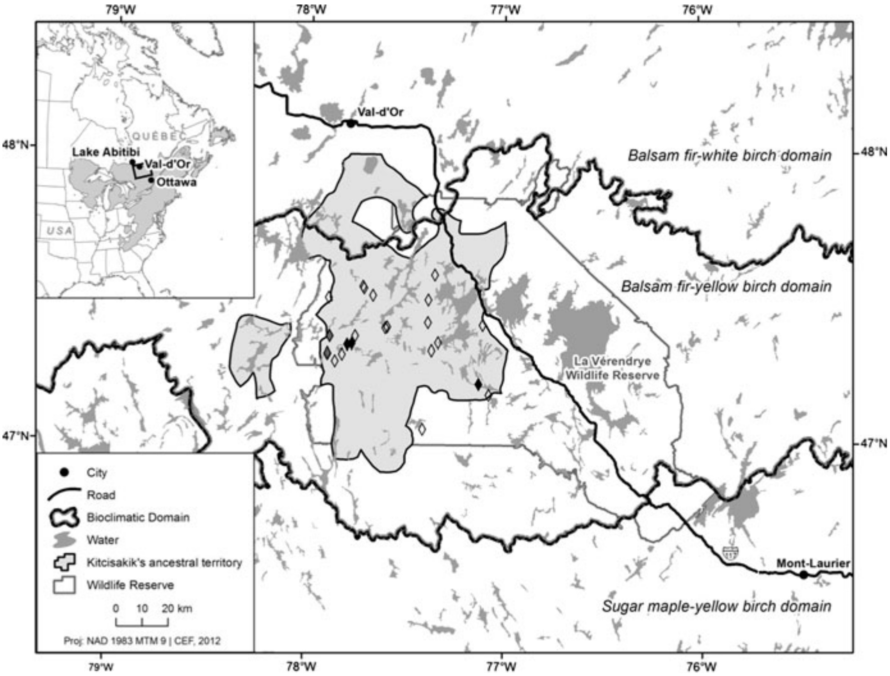


Fig. 1 Location of the study area (Kitcisakik's ancestral territory) in the balsam fir—yellow birch bioclimatic domain in western Quebec. The 22 sampled stands are indicated by *diamonds*. *Black diamonds* are stands where transects extending into logged areas were also sampled, and *grey diamonds* are sites where roadside transects were also sampled (two transects at the northernmost stand). The *shaded area* in the *inset* shows the continuous distribution of eastern white pine (*Pinus strobus* L.) in northeastern North America (after Wendel and Smith 1990)

Detailed regeneration study

To study regeneration, five 4 m × 4 m subplots were positioned in a 4 m × 20 m strip at the centre of each 400 m^2 quadrat following a north–south axis. White pine seedlings (stems <1.37 m tall) were counted and assigned to one of three height classes (0–50, 51–100 and 101–137 cm), and substrate type was recorded. Seedlings were likely <10 years old, and thus substrate type probably still reflected that on which germination occurred (Weyenberg et al. 2004). Saplings were also counted and assigned to one of two DBH classes (0.1–5.0 and 5.1–10 cm). On all subplots, percent cover was visually estimated to the nearest 5 % for substrate types, herbs, and shrubs. Ten different substrate types were identified: conifer litter; hardwood litter; mixed conifer and hardwood litter; fern litter; undecomposed dead logs; decaying wood; moss; bare rock; organic matter (decomposed litter); and mineral soil. Canopy cover was estimated in each subplot and assigned to one of three classes (0–32, 33–65 and 66–100 %). Evidence of blister rust or weevil damage was also recorded, if any. The depth of the organic soil layer was measured in the four corners of each subplot and averaged.

Regeneration according to distance from a remnant stand

We sampled three recently clearcut stands (<10 years) that were located close to undisturbed white pine remnant stands to evaluate the importance of distance from seed trees in explaining regeneration patterns. At each site, we sampled a 4 m × 96 m long transect divided into 24 subplots (4 m × 4 m), extending from the edge of the remnant stand into the cutover. White pine basal area in the three remnant stands was 10.87, 14.06, and 23.75 m^2/ha, corresponding to 3–7 white pine seed trees per stand. We counted seedlings in each subplot. Scattered residual white pine seed trees were located along the transects. For each subplot, we measured the DBH of the nearest residual tree, as well as its distance to the centre of the subplot.

Blister rust and weevil damage according to canopy cover

To determine the effect of canopy cover on blister rust and weevil occurrence, we counted white pine seedlings and saplings in three 4 m × 80 m transects, each starting from a roadside and extending into an undisturbed forest (3 different sites). These transects were divided into 20 subplots (4 m × 4 m) where we visually estimated canopy cover and assigned it to one of three classes (0–32, 33–65 and 66–100 %). We recorded presence/absence of blister rust and weevil damage on individual seedlings and saplings in each subplot.

Data analysis

Detailed regeneration study

We analyzed the data using linear mixed-effects models to account for the multiple measurements in each quadrat (i.e., 5 subplots each). Thus, we treated quadrat as a random effect. We excluded a number of variables from the analysis because of low or no variability. Specifically, all stands had glacial or fluvioglacial deposits. Elevation was also excluded from the analysis as it showed little variation. No evidence of disturbance by weevil or blister rust was noted, so these variables were not included in the analysis. Herbivory [probably by snowshoe hare (*Lepus americanus* Erxl.), moose (*Alces alces* Clin.), or white-tailed deer (*Odocoileus virginianus* Zimm.)] and seed predation by squirrels were noted (in 13 and 45 % of the stands, respectively), but were not included in the analysis as mast years were expected to counteract the effects of seed predation (Smith 1970; Gurnell 1983; Parker et al. 2013) and herbivory was not present in enough quadrats.

We used an information-theoretic approach based on Akaike's information criterion to determine the importance of different variables on white pine regeneration. We formulated 14 candidate models (Table 1) to test our hypotheses, each model corresponding to a single variable or to combinations of variables and based on the published literature. Some of our models were based on aboriginal knowledge, as we included balsam fir basal area. Indeed, an Algonquin legend mentions that white pine and balsam fir are enemies (Uprety et al. 2013). We used Pearson correlations to identify collinearity among numeric explanatory variables and we avoided entering variables with $|r| > 0.7$ in the same models.

Parameters were estimated by maximum likelihood in R with the nlme package (Pinheiro et al. 2011, R Development Core Team 2012). To meet assumptions of homoscedasticity and normality of the residuals and to linearize the relationship, we log-transformed the response variable (white pine regeneration). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to quantify the support in favor of each model (Burnham and Anderson 2004; Mazerolle 2006). We also computed Akaike weights for each model, which quantify the probability that any given model is the most parsimonious in the model set. When more than a single model had support (i.e., Akaike

Table 1 Candidate linear mixed-effects models used to explain white pine regeneration abundance

Model	Tested hypothesis	Explanatory variable(s)
mod1	Seed trees (Wendel and Smith 1990; Fredericksen and Agramont 2013)	Basal area of white pine
mod2	Microsite conditions (Ahlgren 1976; Hibbs 1982; Stearns 1992)	Slope, aspect, depth of organic matter, moss cover
mod3	Seed trees and microsite conditions (Dovčiak et al. 2003)	mod1 + mod2
mod4	Canopy cover (Major et al. 2009)	Canopy cover
mod5	Seed trees and canopy cover	mod1 + mod4
mod6	Understory cover (Abrams 2001)	Herb cover and shrub cover
mod7	Competition from overstory and understory (Smidt and Puettmann 1998; Abrams 2001; Dovčiak et al. 2003; Major et al. 2009)	mod4 + mod6
mod8	Seed trees and competition (Dovčiak et al. 2003)	mod1 + mod6
mod9	Microsite conditions and canopy cover	mod2 + mod4
mod10	Seed trees, microsite conditions and canopy cover	mod1 + mod2 + mod4
mod11	Balsam fir (Smidt and Puettmann 1998; Uprety et al. 2013)	Basal area of balsam fir
mod12	Hardwood species (Pitt et al. 2009, 2011)	Percentage of total basal area represented by hardwood species
mod13	Null model	–
mod14	Global model	All variables

Each model reflects biological hypotheses from the literature and is translated into explanatory variables to be entered in the model

weights of top model <0.90), we based our inferences on the entire model set by computing model-averaged estimates of the variables using the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2006, 2012). Multi-model inference (model averaging) produces parameter and error estimates for each explanatory variable that are not conditional on any single model but instead derived from weighted averages from all models (Symonds and Moussalli 2011). In other words, models with strong support contribute more to estimates than poor models.

We determined the suitability of the different substrate types as seedbeds for white pine by comparing their availability (%) with the proportion of the total seedlings they supported (%) using Chi square (χ^2) analysis following Simard et al. (1998) and Parent et al. (2003). Some substrates such as undecomposed dead logs and bare rock are not germination substrates and were thus excluded from the analysis. Mineral soil was not included in the analysis since it covered too little area in the sampled stands. Some substrates representing similar growth conditions were combined in order to meet the assumptions of the Chi square test. Hence, moss, decaying wood, and organic matter were combined as they all have good moisture retention capacity. Mixed hardwood and conifer litter, hardwood litter, and fern litter were also combined, but conifer litter was treated as a separate class.

Regeneration according to distance from a remnant stand

We analyzed the abundance of white pine regeneration in cutover stands according to distance from remnant stands using linear mixed-effects model and multimodel inference, as described in the previous section. This time, we considered the transect as a random effect. We tested four different hypotheses: (1) effect of distance from remnant stand (regeneration should decrease with distance: Asselin et al. 2001; Weyenberg et al. 2004); (2) effect of distance from residual trees and their DBH (regeneration clumps are expected near residual trees: Asselin et al. 2001); (3) combined effect of distance from remnant stand, distance from residual trees and their DBH; and (4) a null model (intercept only) to evaluate the effects of unmeasured variables. The response variable (abundance of white pine seedlings) was log-transformed to meet the assumption of normality. We used a variance function to homogenize variances (Pinheiro and Bates 2000).

Blister rust and weevil damage according to light availability, dryness, and white pine density

Data on weevil damage were scarce and we do not discuss them further. We analysed the effect of canopy cover on blister rust damage using logistic regressions with random effects (i.e., transect and subplot within transect as random effects) and multimodel inference, because our response variable was binary (presence or absence of blister rust damage). We tested six hypotheses: (1) canopy cover (as an inverse proxy of light availability, shaded sites being less prone to blister rust infection: White et al. 2002); (2) combined effect of canopy cover and distance from the road margin (as a more complete inverse proxy of light availability, as light not only arrives from above, but also from stand edge: Greene et al. 2002); (3) distance from the road margin (as an inverse proxy of dryness, roadsides being drier than interior forest and dry sites being less prone to blister rust infection: Katovich and Mielke 1993); (4) white pine seedling and sapling density (sites with higher white pine density are more prone to blister rust infection: Field et al. 2012); (5) combined effect of canopy cover, distance from the road margin, and density of white pine seedlings and saplings; and (6) a null model (intercept only). Parameters were estimated by maximum likelihood with lme4 package in R (Bates et al. 2012).

Results

Tree species composition of white pine stands

Apart from white pine, 11 tree species were recorded in the quadrats (Table 2). Jack pine and eastern larch (*Larix laricina* (Du Roi) K. Koch) were also present in the surrounding forest area but not recorded in the quadrats. Balsam fir, black spruce, paper birch, red maple, and red pine were the most frequent companion species.

Detailed regeneration study

Only 59 seedlings and 48 saplings were counted in the total 110 subplots. Canopy cover varied between subplots, 30 had low cover (0–32 %), 23 medium (33–65 %), and 57 high (66–100 %). A combined histogram ($N = 22$ sites) showing the abundance of all white pine individuals according to 19 DBH classes follows a negative exponential (Fig. 2). Six models had $\Delta AIC_c < 4$, meaning that they were all reasonably good at explaining white pine regeneration abundance (Table 3). The top-ranked model consisted of the basal area of balsam fir as a single predictor, and this model had 4 times more support than the second-

Table 2 Frequency of occurrence and basal area of tree species in the 22 sampled quadrats of undisturbed forest

Species	Percentage of the sites	Mean basal area (m^2/ha)	Mean relative basal area (%)	Maximum relative basal area (%)
Pinus strobus L.	100	25.78 ± 13.40	57.71	91.73
Abies balsamea (L.) Miller	90	4.89 ± 4.59	10.91	26.08
Picea mariana (Mill.) BSP	82	4.55 ± 5.01	12.74	50.63
Betula *papyrifera* Marsh.	54	2.98 ± 4.00	8.26	40.10
Acer rubrum L.	50	1.30 ± 2.28	3.25	25.28
Pinus resinosa Ait.	50	1.06 ± 2.72	2.32	17.07
Thuja occidentalis L.	18	1.00 ± 3.30	2.24	35.75
Acer saccharum L.	9	0.06 ± 0.20	0.13	2.08
Picea glauca (Moench) Voss	9	0.15 ± 0.38	0.42	5.18
Populus tremuloides Michx.	9	1.05 ± 4.50	1.90	38.38
Betula alleghaniensis Britton.	4	0.01 ± 0.08	0.04	1.00
Prunus pensylvanica L.f.	4	0.02 ± 0.08	0.07	1.60

ranked model which included only microsite condition (evidence ratio = 0.40/0.10 = 4). The abundance of white pine regeneration decreased with balsam fir basal area (model-averaged estimate: −1.12, 95 % CI −1.99, −0.25; Fig. 3). The abundance of white pine regeneration increased weakly with moss cover (model-averaged estimate: 0.0092, 95 % CI 0.0030, 0.0153) and herb cover (model-averaged estimate: 0.0074, 95 % CI 0.0002, 0.0146). White pine regeneration did not vary with any other of the variables we considered.

Substrate–seedling associations in white pine stands

The observed frequency distribution of seedlings per substrate type differed significantly from the expected distribution according to the area covered by the substrate types (Fig. 4; $\chi^2 = 113.78$; $P < 0.001$). Seedling density was higher than expected on moss, decaying wood, and organic matter, and lower than expected (in fact, 0) on conifer litter.

Regeneration according to distance from a remnant stand

Two models had support in explaining the distribution of white pine along the transects (Table 4). Both models included distance to the remnant stand as a predictor, suggesting a strong effect of the variable. Indeed, white pine abundance decreased with distance to the remnant stand (model-averaged estimate: −0.0063, 95 % CI −0.0099, −0.0028; Fig. 5). The abundance of white pine was not influenced by any other variables we considered.

Blister rust and weevil damage according to canopy cover

Only 3.6 % of the seedlings and saplings found in the roadside transects showed damage from weevil, a value deemed too low to justify inclusion in our models. Blister rust damage was common enough (28 %) to warrant analysis. Although the top-ranked model consisted of the distance from the road margin, the model was followed closely by the null model, which suggests weak evidence for an effect of distance from the road margin (Table 5). In fact, none of the explanatory variables we considered could explain the occurrence of blister rust damage.

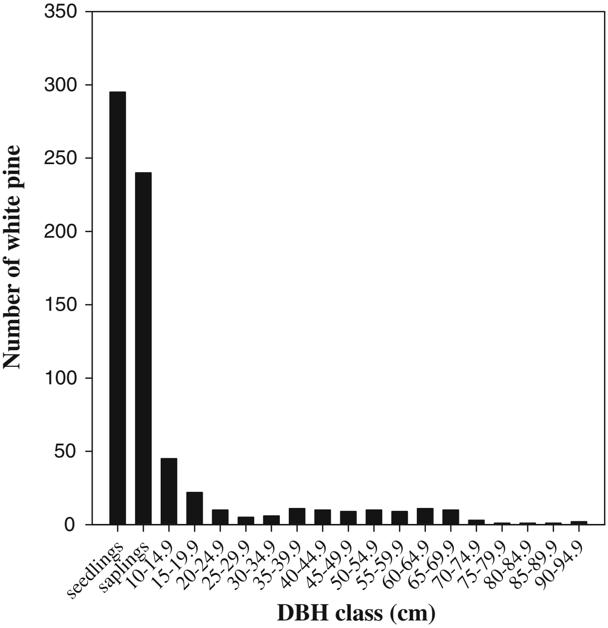


Fig. 2 White pine combined size distribution, i.e., total no. of stems in 22 quadrats, each of 400 m^2. Seedlings and saplings counts were done in 80 m^2 belt transects. Values for these two classes were multiplied by 5 to be reported as individuals per 400 m^2

Table 3 Ranking of linear mixed models predicting the abundance of white pine regeneration based on AIC_c

Model	Tested hypothesis	Log-likelihood	K^a	AIC_c	ΔAIC_c	w_i
mod11	Balsam fir	−93.40	4	195.17	0.00	0.40
mod2	Microsite conditions	−91.41	7	197.93	2.76	0.10
mod4	Canopy cover	−93.92	5	198.42	3.25	0.08
mod6	Understory cover	−93.95	5	198.49	3.31	0.08
mod13	Null model	−96.19	3	198.61	3.44	0.07
mod3	Seed trees and microsite conditions	−90.84	8	199.10	3.93	0.06
mod12	Hardwood species	−95.45	4	199.27	4.10	0.05
mod9	Microsite conditions and canopy cover	−90.08	9	199.95	4.78	0.04
mod7	Competition from overstory and understory	−92.50	7	200.11	4.94	0.03
mod8	Seed trees and competition	−93.88	6	200.58	5.41	0.03
mod5	Seed trees and canopy cover	−93.92	6	200.65	5.47	0.03
mod1	Seed trees	−96.19	4	200.76	5.59	0.02
mod10	Seed trees, microsite conditions and canopy cover	−89.64	10	201.51	6.34	0.02
mod14	Global model	−86.98	14	206.38	11.21	0.00

Note that ΔAIC_c gives the difference in AIC_c of each model compared to the top-ranked model, and Akaike weights (w_i) indicate the probability that any given model is the best among the candidate model set

[a] Parameter count, including intercept, residual variance, and variance of random effect

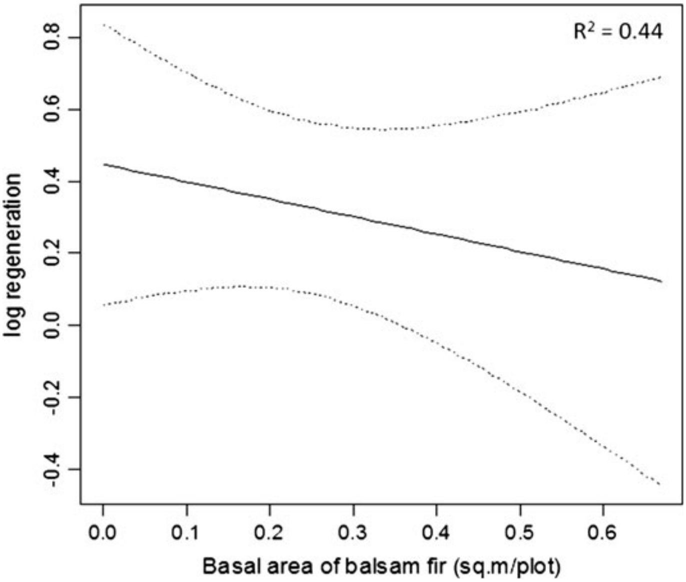
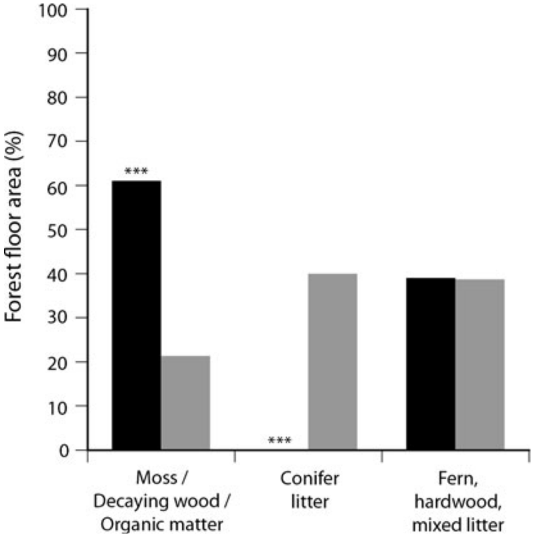


Fig. 3 Effect of balsam fir basal area (m^2/*plot*) on white pine regeneration (seedlings + saplings) abundance (log regeneration/*subplot*). Results are based on model-averaged predictions. *Dotted lines* indicate 95 % confidence intervals. R^2 is also provided

Fig. 4 Percent area of forest floor covered by each substrate type (*grey bars*) and percent seedlings found on each substrate type (*black bars*). *Asterisks* indicate that observed seedling numbers are significantly ($p < 0.001$) lower or higher than expected according to the area covered by the substrate type



Discussion

White pine was found with eleven accompanying tree species in our study area, confirming previous studies conducted at the species' northern distribution limit (Quinby 1991; Latremouille et al. 2008). The widespread occurrence of supercanopy white pine trees in our study area suggests that these scattered individuals are remnants of former more

Table 4 Ranking of linear mixed models predicting the effects of remnant stands and residual trees on the abundance of white pine regeneration in logged stands, based on AIC_c

Model	Variables	Log-likelihood	K^a	AIC_c	ΔAIC_c	w_i
mod3	Distance from the remnant stand	−52.53	6	118.35	0.00	0.80
mod1	Distance from the remnant stand + distance to the nearest residual tree + DBH of the nearest residual tree	−51.57	8	121.42	3.07	0.17
mod2	Distance to the nearest residual tree + DBH of the nearest residual tree	−54.88	7	125.51	7.16	0.02
mod4	Null model	−59.72	5	130.35	12.00	0.00

Note that ΔAIC_c gives the difference in AIC_c of each model compared to the top-ranked model, and Akaike weights (w_i) indicate the probability that any given model is the best among the candidate model set

[a] Parameter count, including intercept, residual variance, and two variance function parameters to homogenize variances

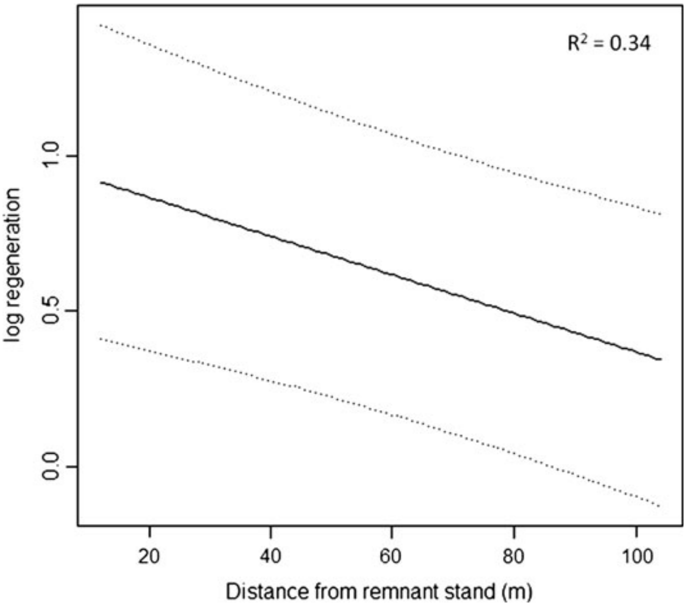


Fig. 5 Effect of distance from a remnant stand on white pine regeneration (seedlings + saplings) abundance (log regeneration/subplot). Results are based on model-averaged predictions. *Dotted lines* indicate 95 % confidence intervals. R^2 is also provided

extensive stands (Stearns 1992). White pine size-class distribution shows a typical negative exponential trend perhaps explained by constant mortality and recruitment by fire at the landscape scale (Bergeron et al. 2002). A similar pattern was found in another study of white pine at its northern distribution limit (Holla and Knowles 1988). Such a size class distribution indicates continuous recruitment, but at very low levels compared to other temperate or boreal species in comparable areas (Bergeron et al. 2002), or for white pine in the centre part of its range (Dovčiak et al. 2001). Thus, while very few seedlings become established, those that do can survive and enter the canopy with a success equivalent to that

Table 5 Ranking of logistic regressions with random effects predicting the effect of canopy cover on blister rust damage in roadside transects, based on AIC_c

Model	Variables	Log-likelihood	K^a	AIC_c	ΔAIC_c	w_i
mod3	Distance from the road margin	−104.89	4	218.03	0.00	0.42
mod6	Null model	−106.62	3	219.39	1.36	0.21
mod1	Canopy cover	−104.88	5	220.13	2.10	0.15
mod2	Canopy cover and distance from the road margin	−104.15	6	220.81	2.78	0.10
mod4	White pine seedling and sapling density	−106.61	4	221.47	3.44	0.08
mod5	Canopy cover, white pine seedling and sapling density, and distance from the road margin	−104.10	7	222.90	4.87	0.04

[a] Parameter count, including intercept, and two random effects (variance between transects, variance between plots nested in transect)

of other species. Indeed, white pine seedlings suffer high mortality the first years after initial establishment (Holla and Knowles 1988; Carleton et al. 1996), but seedlings that survive this period have a high probability of canopy recruitment (Holla and Knowles 1988). One explanation for low white pine regeneration is the lack of fire in our study area. The current stand-replacing fire cycle in the study area is considerably longer than in the pre-industrial era (Grenier et al. 2005; Bergeron et al. 2006), and surface fires have been actively suppressed since the 1970s. Fire, especially surface fire, creates good regeneration conditions for white pine by removing competing vegetation, both on the ground and in the canopy (Heinselman 1981). Engelmark et al. (2000) have indeed shown continuous recruitment for white pine in frequently burned sites at the species' northern limit. However, low but continual white pine recruitment is possible even without recent fire disturbance, provided that seed trees are present and small scale canopy gaps suitable for regeneration are available (Holla and Knowles 1988; Quinby 1991).

Recruitment is the result of several processes including seed dispersal, availability of suitable seedbeds, germination, seedling establishment, and subsequent survival (Houle 1995; Cornett et al. 1997). The abundance of seed trees did not have a significant effect on white pine regeneration abundance in our detailed regeneration study in undisturbed forest. It could be because we sampled stands that were dominated or co-dominated by white pine, and that seed availability and the number of seed trees/ha were always higher than a minimum threshold. Tree canopy cover had no effect on white pine regeneration abundance and we rejected our hypothesis that tree canopy cover was the most important variable explaining regeneration in white pine stands. Regeneration can occur in the shaded understory, and survival and slow growth can be maintained as long as light levels are at least 20 % of full sunlight (Wendel and Smith 1990). However, transition into the sapling stage requires higher light conditions (Duchesne et al. 2000; Fredericksen and Agramont 2013).

Interspecific competition is often stated as a possible mechanism limiting white pine regeneration (Ahlgren 1976; Carleton et al. 1996; Pitt et al. 2009; Parker et al. 2012). Herb cover in our study area was low (mean = 16.82 %) and had a very weak *positive* association with white pine regeneration abundance. It is possible that low herb cover provides moist conditions favouring white pine establishment, or that herbs and white pine have similar habitat requirements. Although shrub cover was higher than herb cover (38.69 %), it did not affect white pine regeneration abundance. This is contrary to Weyenberg et al.

(2004) who reported a negative effect of shrub cover on seedling and sapling densities. We also did not find an effect of hardwood species abundance on white pine regeneration. Potential effects of shrubs or hardwoods were probably masked by the very strong negative effect of balsam fir basal area, by far the most important factor explaining white pine regeneration abundance. A negative effect of coniferous species (including balsam fir) in the overstory on white pine regeneration was previously reported (Ahlgren 1976; Carleton et al. 1996; Smidt and Puettmann 1998). Our study is the first to show a disproportionate negative effect of balsam fir (but not of other coniferous species) on white pine regeneration, whereas other variables have considerably less impact. Interestingly, a negative effect of balsam fir on white pine was reported by people of the Kitcisakik Algonquin community, who claimed that, according to legend, balsam fir and white pine are enemies (Uprety et al. 2013). Our study area was located in a balsam fir-dominated bioclimatic domain, contrary to previous studies conducted in more southern regions of the white pine range. Balsam fir is an aggressive shade tolerant species, with abundant regeneration leading to development of dense, compact stands allowing very little light to penetrate to ground level (Messier et al. 1998; Duchesne et al. 2000). Furthermore, balsam fir foliar leachates have strong inhibitory properties on nitrification and oxidation of ammonium (Thibault et al. 1982) that could potentially impair white pine regeneration and establishment. This could explain our finding that white pine regeneration was absent on conifer litter, contrary to findings of Weyenberg et al. (2004), where balsam fir was not dominant and where other coniferous species were more abundant.

Regeneration was more abundant than expected on moss, decaying wood and organic matter, even though the moss variable only had a weak effect according to our analysis. Moss provides a compact, moist seedbed relatively free from competition (Ahlgren 1976), and was found to be a favorable germination substrate for white pine (Weyenberg et al. 2004) and other conifer species (Simard et al. 1998, Parent et al. 2003). None of the other microsite conditions tested had an effect on white pine regeneration abundance.

Distance from a remnant stand played a significant role in explaining white pine regeneration abundance in logged areas, as observed in previous studies on white pine (Weyenberg et al. 2004) and other conifer species (Greene and Johnson 1996; Asselin et al. 2001). Contrary to our hypothesis, residual seed trees in cutovers did not play a significant role, probably because the net effect of a single tree was too small to detect relative to the influence of the adjacent remnant stand. An alternative explanation is that residual trees were present all along transects, so their effect was continuous and difficult to isolate.

Contrary to our hypothesis, damaging agents such as blister rust and weevil were not major problems affecting white pine in mature stands in our study area. We found no evidence of damage by blister rust and weevil in closed forests, in contrast to previous findings from areas further south (Van Arsdel 1972; White et al. 2002). We also did not record any occurrence of *Ribes* spp., the alternative host of blister rust (Zambino 2010). We did note some blister rust damage in open areas along roadsides, but the percentage of affected trees was lower than reported in other studies conducted in open areas (Latremouille et al. 2008; CFS 2012). Moreover, we found no effect of canopy cover and distance from the road (into the forest) on the occurrence of blister rust damage. This could be due to blister rust incidence being already low near roadsides (28 %), and much lower in undisturbed forest understory than expected, as the climate of the northern part of white pine's distribution is supposed to be more conducive to infection by this pathogen (Van Arsdel 1972; Katovich and Mielke 1993). Cool, humid climatic conditions favorable for the spread and infection of blister rust usually prevail at the northern limit of continuous distribution of white pine (Lavallée 1986). However, Katovich and Mielke (1993) and

Fahey and Lorimer (2013) showed that even in high hazard zones, the incidence of rust was very low in some parts of the Lake States. Our roadside transects were south-east facing and thus drier than the general conditions in the study area, which could explain the low occurrence of blister rust (White et al. 2002; CFS 2012). Hence, maybe the positive effect on blister rust of accrued light at roadsides was cancelled-out by the negative effect of dryness. In contrast, we observed 100 % blister rust infection in a plantation site (visited but not sampled), comparable to high infection rates recorded in other plantations (Latremouille et al. 2008; CFS 2012). The plantation we visited (one of only a few in the study area) was on a cool lower slope, exposed to the north, surrounded by mature forest. Such conditions are highly favorable for blister rust infection (Katovich and Mielke 1993).

We observed very low incidence of weevil infestation (3.6 %) in full light conditions. White pines grown in open conditions are deemed particularly susceptible to repeated attacks (Katovich and Morse 1992). Major et al. (2009) have reported 42 % of weevil infestation in full light conditions in the centre of white pine's distribution. In another study, damage due to weevil in open canopies affected almost 100 % of the trees (Stiell and Berry 1985).

Low incidences of blister rust and weevil in our study area do not correspond with the hazard maps developed for Quebec (Vlasiu et al. 2001 for weevil and Lavallée 1986 for blister rust), maybe because sampling effort was lower at the northern limit of continuous distribution, or maybe because most of our sampling took place in the understory of mature stands. Browsing by herbivores was not important inside white pine stands, even in roadside plots, where white pine regeneration was more abundant. It could mean that herbivory of white pine is only a problem where and when deer, moose or hare populations are high, or that there was a sufficient supply of preferred food sources (Pastor 1992; Saunders and Puettmann 1999). The snowshoe hare population in the study area was in a cycle trough at the time of sampling (Paul and Trudeau 2010).

Conclusion

Natural white pine regeneration does occur at the species' northern limit of continuous distribution, but in relatively low amounts compared to more southern forests in the core of the natural range. Recruitment was more abundant on moister substrates, but was strongly influenced by competition and inhibitory effects of balsam fir. The northern limit of continuous distribution holds potential for white pine restoration, for example by preserving remnant white pine stands that can provide seed sources for natural regeneration in a shelterwood cut system, or in adjacent clearcut areas. This study illustrates that different management strategies should be used near northern range limits, where effects of site conditions and disturbance agents are different than in the center of a species' range.

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