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Seedbed proportions in and outside skid trails: Temporal variation following selection cutting in northern hardwood forests

Marilou Beaudet [a,b,*], Virginie-Arielle Angers [b], Christian Messier [b,c]

[a] Direction de la recherche forestière (DRF), Ministère des Ressources naturelles (MRN), Gouvernement du Québec, 2700, rue Einstein, Québec, Québec G1P 3W8, Canada
[b] Centre d'études sur la forêt (CEF), Département des sciences biologiques, Université du Québec à Montréal (UQAM), C.P. 8888, Succursale Centre-ville, Montréal, Québec H3C 3P8, Canada
[c] Institut des sciences de la forêt tempérée (ISFORT), Département des sciences naturelles, Université du Québec en Outaouais (UQO), C.P. 1250, Succursale Hull, Gatineau, Québec J8X 3X7, Canada

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A B S T R A C T

Partial harvesting during the snow-free season disturbs the forest floor and modifies seedbed characteristics. Quantitative information is lacking about the distribution of changes in seedbed proportions between areas located in and outside skid trails, and about how long these changes persist after harvest. These effects could interact with species' seedbed requirements and seed input and influence spatio-temporal patterns of seedling establishment in forests, which would have important implications for regeneration dynamics. The objectives of this study were to determine how selection cutting affects seedbed proportions in and outside skid trails in northern hardwood stands, how these seedbed proportions vary over time following harvest, and how seedbed proportions in selection cuts compare with unharvested stand conditions. We sampled 12 sugar maple-dominated stands in southeastern Quebec, Canada. Two had not been harvested in the recent decades, while 10 had been harvested through selection cutting, 1–3 years earlier. A total of 3600 quadrats were sampled to determine the proportions of 8 seedbed types and whether or not a quadrat was located in a skid trail. This was the case for 24.1% of the quadrats in selection cuts. Outside skid trails, seedbed proportions in selection cuts did not vary from those in unharvested stands ($P \geqslant 0.097$). In these stands, leaf litter was the most abundant substrate, covering 87.3% of the forest floor, followed by rotten wood (4.9%) and fresh wood (3.0%). Humus, rocks and live tree bases occupied 1–2% the forest floor, while mineral soil and moss covered less than 1%. In selection cuts, proportions of rotten wood and live tree bases were lower in skid trails than outside, and this difference persisted 13 years after harvest. In 1- and 2-year-old cuts, the proportion of litter was lower in skid trails than outside, but not later on. The proportions of mineral soil and disturbed humus increased sharply in the skid trails after harvest (17.1-fold and 2.7-fold increases, respectively), but these effects lasted only 3 years for mineral soil and 1 year for humus. Power functions were used to model variation in litter, mineral soil and disturbed humus proportions as a function of time since harvest. We discuss the implications for regeneration dynamics of the marked, but short term increase in mineral soil and disturbed humus availability. Spatially explicit models that can simulate the mid- to long-term availability of substrates in both time and space would be useful for assessing the long-term implications of harvesting on seedbed proportions and regeneration patterns.

1. Introduction

A wide range of biotic and abiotic factors affect the regeneration of tree species in forest communities and influence variation in species relative abundance (Nakashizuka, 2001; Shibata et al., 2010). Tree seedling establishment can be limited by both the supply of seeds and the availability of substrates suitable for germination (Caspersen and Saprunoff, 2005). Seed supply limitation is hypothesized to play a determinant role in defining patterns of tree species regeneration in species diverse forests (e.g., tropical forests, Vargas and Stevenson, 2013). Recruitment also tends to be limited by the supply of seeds for large-seeded gravity- or animal-dispersed tree species (Caspersen and Saprunoff, 2005). On the

* Corresponding author at: Direction de la recherche forestière (DRF), Ministère des Ressources naturelles (MRN), Gouvernement du Québec, 2700, rue Einstein, Québec, Québec G1P 3W8, Canada. Tel.: +1 418 643 7994x6554.
E-mail addresses: marilou.beaudet@mrn.gouv.qc.ca, marilou.beaudet@videotron.ca (M. Beaudet).

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other hand, substrate limitation was identified as being one of the main factor limiting seedling establishment in several temperate and boreal forests, and has been shown to be especially influential for small-seeded species (Gray and Spies, 1997; Barras and Kellman, 1998; Clark et al., 1998; Wright et al., 1998; LePage et al., 2000; Mori et al., 2004; Caspersen and Saprunoff, 2005).

Substrate properties are a strong determinant of establishment success for small-seeded species because their radicles are generally unable to penetrate thick layers of leaf litter (Houle, 1992). They therefore benefit from a direct contact with a low-porosity substrate (Greene and Johnson, 1998). Exposed mineral soil and well-decomposed deadwood are recognized as being favorable substrates for small-seeded species, and this has been observed in a diversity of forest ecosystems (e.g., Harmon and Franklin, 1989; Dalling and Hubbell, 2002; Christie and Armesto, 2003; Valkonen and Maguire, 2005; Sanchez et al., 2009). In North American hardwood forests, example of species favored by one or the other of these substrates include yellow birch (*Betula alleghaniensis* Britton), hemlock (*Tsuga canadensis* [L.] Carrière), and red spruce (*Picea rubens* Sarg.) (McGee and Birmingham, 1997).

In unmanaged northern hardwood stands, mineral soil is exposed by forest floor disturbances originating from animal digging, or from the creation of pits and tip-up mounds associated with tree uprooting (Beatty and Stone, 1986; Ruel et al., 1988; Peterson and Pickett, 1990). In managed forests, partial harvesting, especially when performed during the snow-free season, can considerably disturb the forest floor because of skidding machinery traffic (Shields et al., 2007; Lambert, 2013). In partially harvested stands, such as those managed using single- or multiple-tree selection cutting, one can expect forest floor disturbances to be spatially concentrated in the skid trails. The situation can differ when other silvicultural treatments are used, such as group selection with scarification performed in gaps (Lorenzetti et al., 2008).

Silvicultural systems such as single-tree selection cutting have been used extensively in northern hardwood forests, and in Quebec (Canada) this was especially the case during the last two decades (Guillemette et al., 2013). The selection silvicultural system aims at providing consistent yield at regular intervals, reducing residual tree mortality by harvesting trees that are at high risk of dying, and ensuring an adequate regeneration and a long-term stability in stand conditions (Nyland, 1998). These objectives are addressed by harvesting trees individually, or in small groups, to a specified residual diameter distribution (e.g., reverse-J distribution), and at intervals ranging from less than 10 to 25–30 years, depending on the residual basal area and maximum diameter (Nyland, 1998).

Since the residual basal area is generally relatively high after selection cutting (e.g., >16 m^2 ha^{-1} in Quebec northern hardwoods, Guillemette et al., 2013), one can expect the litter input from residual trees to rapidly cover patches of disturbed forest floor and exposed mineral soil (Greene and Johnson, 1998). Species that require such microsites for their establishment will therefore only have a short window of opportunity to become established.

To our knowledge, no study has yet quantified the temporal variation in the availability of different seedbed types following selection cutting in northern hardwood stands, taking into account the spatial variation in seedbed proportions between areas located in and outside skid trails. The objectives of this study are therefore to determine how harvesting, using the selection cutting system, affects the proportions of seedbed types in and outside skid trails, and to determine how these proportions vary during the post-harvest years. Results obtained in selection cuts are also compared to values recorded in unharvested stands.

2. Material and methods

2.1. Study sites

This study was undertaken in the Eastern Townships region, in southeastern Quebec (Canada). Sampling was performed on forest lands owned by Domtar Inc., between latitudes 45°05′ and 45°44′N, and longitudes 71°15′ and 72°29′W. The study sites are in the sugar maple – basswood bioclimatic domain, in the ecological sub-regions 2cT (landscape unit #8) and 3dM (landscape unit #31) defined by Robitaille and Saucier (1998). In the study area, the mean annual temperature is 5 °C, and the growing season lasts from 180 to 190 days. Mean annual precipitations range from 1000 to 1100 mm, of which 25–30% falls as snow (Robitaille and Saucier, 1998). Study sites are located at altitudes ranging from 340 to 565 m above sea level.

Twelve uneven-aged stands were sampled between the end of June and the end of August 2003. They were dominated by sugar maple (*Acer saccharum* Marsh.), with yellow birch and American beech (*Fagus grandifolia* Ehrh.) as the main companion species. The stands were located on mesic sites with good to moderate drainage and slopes ranging from 10% to 30%. Humus type was moder, while soils were mostly Dystric Brunisols (occasionally Podzols) derived from glacial till rich in mica schist and sandstone.

All of the study stands have probably been subjected to some high grading (partial harvest removing the most valuable trees without regard for residual stand condition) prior to the 1960s, but precise records of harvesting are not available. Of the twelve study stands, two had not been cut in recent decades and were sampled to characterize seedbed proportions in undisturbed stands. The remaining ten stands had been subjected to single- and multiple-tree selection cutting 1–13 years prior to sampling (two stands were sampled during each of the 1st, 2nd and 3rd post-harvest growing seasons, and one during each of the 4th, 8th, 10th and 13th growing seasons). Basal area was approximately 25–26 m^2 ha^{-1} in uncut stands and typically ranged between 16 and 21 m^2 ha^{-1} in harvested stands. We only sampled stands harvested during summer or fall, before the soil froze. Trees had been cut using a chainsaw or feller-buncher, and a wheeled cable- or grapple-skidder had been used for tree-length skidding. Field observations indicate that effects of the different types of equipment were generally comparable (R. Vanier, pers. comm.).

2.2. Field sampling

In each stand, four 150-m-long transects were established. In uncut stands, the starting point and the azimuth of the transects were randomly determined. In selection cuts, since one of our aims was to assess the proportion of forest floor affected by skid trails, only the transects origins were randomly located; their azimuth was selected so that each transect would be more or less perpendicular to the main skid trails. Stands, defined as contiguous forest areas with a homogeneous forest type and submitted to the same harvest, typically ranged in size from 10 to 50 ha. The minimum distance between transects was of approximately 30 m.

Seedbed proportions were assessed in 20 cm × 20 cm quadrats spaced every 2 m along each transect, for a total of 75 quadrats $transect^{-1}$, 300 quadrats $stand^{-1}$, and 3600 quadrats sampled in all. The percent cover of the following 8 substrate categories was recorded in each quadrat:

1. Litter: Undisturbed organic material composed of intact or partly decomposed leaves.

2. Mineral soil: Exposed mineral soil present as a result of logging activity or other causes of soil disturbances (e.g., windthrow, animal burrow).
3. Humus: Exposed humus, mixed or not with some mineral material, and present as a result of logging activity or other causes of soil disturbances.
4. Moss: Moss growing directly on the ground, on dead wood or rock.
5. Fresh wood: Solid wood associated with logs, stumps or branches with a minimum diameter of 1 cm. Branches had to be in contact with the forest floor to be recorded as a substrate, otherwise the underlying substrate was recorded.
6. Rotten wood: Wood sufficiently decomposed that it was qualitatively judged to be a potential germination substrate. The tip of a pencil or a thumbnail could penetrate readily. This corresponds to decay classes #3 and #4 in Fraver et al. (2002).
7. Rock: Exposed rocks of various sizes.
8. Live tree base: Area occupied by live trees or saplings.

In selection cuts, we recorded whether or not a quadrat was located in a skid trail. We considered the area in a skid trail as the one including and between the two wheel tracks left by the wheeled skidder, as well as the narrow area on each side where soil disturbance was more pronounced. Obviously, the older the cuts, the more difficult it was to locate the skid trails. The following criteria were considered to help in locating skid trails: location of stumps, injuries at the base of residual trees, constraints for the passage of a skidder and bole manoeuvring, and general concordance with the skid trail network (Hartmann et al., 2009).

2.3. Statistical analyses

The proportion of quadrats located in a skid trail was calculated for each transect in harvested stands. These transect-level proportions were analyzed with a mixed-model analysis of variance (ANOVA) using the GLIMMIX procedure of SAS (version 9.22, SAS Institute Inc., 2010) with time since harvesting as a fixed effect, and stand and transect as random effects. Denominator degrees of freedom were adjusted using the Kenward–Roger method. Time since harvesting was expressed in number of years, with year 1 corresponding to the first growing season after harvesting.

The dataset composed of seedbed proportions recorded in individual quadrats ($n = 3600$ per seedbed type) contained many zero values in certain categories, which made it difficult to meet linear model assumptions, even with data transformations. Seedbed proportions were therefore averaged by transect and by stand, as well as by location (in or outside of a skid trail); analyses were performed on the resulting mean proportions ($n = 88$ per seedbed type).

In selection cuts, to determine whether seedbed proportions outside skid trails differed from those observed in unharvested stands, a mixed model ANOVA was performed with harvest status (harvested or not) and location (in or outside a skid trail) as fixed effects, and stand and transect as random effects. A planned contrast was then used to specifically test the difference between seedbed proportions observed in unharvested stands and those observed outside skid trails, in harvested stands.

To assess the effects of time since harvesting and location in selection cuts, seedbed proportions were analyzed with a mixed model ANOVA, with time since harvesting and location as fixed effects, and stand and transect as random effects. For a given seedbed type, when a significant interaction was found between the two fixed factors, post hoc least-square means comparisons were used to further investigate how the effect of location varied with time since harvesting. For these seedbed types, we also modeled how seedbed proportions varied as a function of time since harvesting, using non-linear regression with the SAS NLMIXED and MODEL procedures. A number of functions were considered (e.g., power, logistic), but we present only the one that provided the best fit, based on values of adjusted R^2 and Akaike information criterion corrected for small sample size (AIC_c).

An angular transformation ($\arcsin(x^{0.5})$) was performed on seedbed proportions to improve the residual distribution in mixed model ANOVA and regression analyses. No transformation was required for the proportions of quadrats in skid trail data. All tests were considered significant at an alpha level of 0.05, except the multiple comparisons, for which a corrected alpha level was used ($0.05/n_c$ where n_c is the number of comparisons simultaneously tested).

3. Results

Among substrates in unharvested stands, undisturbed litter was found in the highest proportion (87.3 ± 1.0%, mean ± 1 SE). Rotten wood and fresh wood covered 4.9% and 3.0% of the forest floor, respectively (Fig. 1). Humus, rocks and live tree bases occupied between 1% and 2% the forest floor, while mineral soil and moss covered less than 1% (Fig. 1).

In selection cuts, 24.1 ± 1.3% of the quadrats were in skid trails. This proportion did not vary as a function of time since harvesting ($P = 0.337$). Seedbed proportions observed outside skid trails did not vary from those observed in unharvested stands (P ranging from 0.097 to 0.950 for all seedbed types). Proportions of moss, fresh wood and rock did not vary as a function of location in or outside skid trails, nor as a function of time since harvesting (Table 1A). Proportions of rotten wood and live tree bases varied as a function of location ($P = 0.002$ and <0.001, respectively), but not as a function of time since harvesting (Table 1A); both were lower in skid trails (1.8 ± 0.4% for rotten wood and 0 for live tree bases in skid trails, compared to 3.0 ± 0.3% and 1.1 ± 0.2%, outside skid trails). Proportions of undisturbed litter, mineral soil and humus varied between locations in interaction with time since harvesting ($P < 0.001$ for litter and mineral soil, and $P = 0.026$ for humus, Table 1A). The proportion of undisturbed litter was significantly lower in skid trails for the first 2 years after selection cuts, but not later on (Table 1B). The proportion of mineral soil in skid trails reached 18.8% after 1 year, 7.2% after 2 years and 5.7% after 3 years, which was significantly higher than outside skid trails (Table 1B). In older cuts, the proportion of mineral soil returned to less than 1% (Fig. 1) and differences between locations were no longer significant (Table 1B). Finally, the proportion of disturbed humus briefly increased in skid trails following selection cutting, reaching 9.4% in 1-year-old cuts (Fig. 1), but the effect of location was no longer significant thereafter (Table 1B).

Proportions of undisturbed litter, mineral soil and humus varied non-linearly as a function of time since harvesting, in a manner that was best described by power functions (Fig. 2, Table 2). The proportion of undisturbed litter was the lowest the first year after harvest, and increased thereafter; the proportions of mineral soil and disturbed humus followed the opposite trend (Fig. 2).

4. Discussion

4.1. Seedbed proportions in unharvested stands and outside skid trails in selection cuts

The seedbed proportions observed in unharvested stands were consistent with values reported in the literature for northern hardwood stands. Leaf litter is clearly the predominant substrate (Barras and Kellman, 1998; Caspersen and Saprunoff, 2005), while the proportion of mineral soil is very small (⩽1%) (Barras and

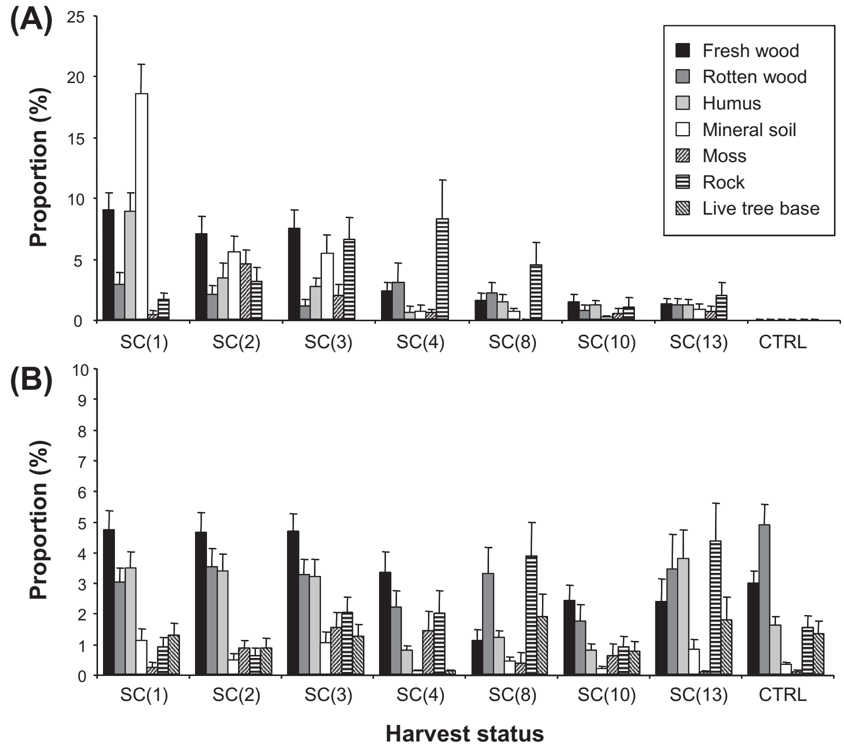

Fig. 1. Mean proportions (±1 SE) of different seedbed types (A) in skid trails and (B) outside skid trails in selection cuts (SC) and unharvested control (CTRL) stands. Selection cuts labels also include the time since harvesting (number of years). Undisturbed litter proportions are not shown on the figures but they represent the remaining proportions. Note that the scale of the *y*-axis differs between pannels A and B.

Table 1
Results of (A) ANOVA on seedbed proportions[a] recorded in stands submitted to selection cutting 1–13 years prior to sampling, and (B) multiple comparison tests to further investigate significant Time × Location interactions. To simplify table presentation, only fixed effects are presented, although stand and transect random effects were accounted for in the analysis.

Effet	d.f.	Litter		Mineral soil		Humus		Moss		Fresh wood		Rotten wood		Rock		Live tree base	
		F	*P*[b]	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
(A) ANOVA results[c]																	
Time since harvesting	6	0.95	0.565	1.42	0.417	0.72	0.664	2.60	0.231	0.77	0.641	0.38	0.853	1.56	0.190	1.68	0.360
Location in skid trail	1	7.11	**0.010**	26.78	**<0.001**	0.33	0.566	0.28	0.600	0.15	0.701	11.81	**0.002**	2.39	0.132	95.49	**<0.001**
Time × Location	6	7.98	**<0.001**	8.63	**<0.001**	2.59	**0.026**	2.07	0.083	1.66	0.145	0.99	0.448	0.97	0.463	1.87	0.116
(B) Multiple comparison results[c]																	
Skid trail (yr 1)	1		**<0.001**		**<0.001**		**0.002**										
Skid trail (yr 2)	1		**0.002**		**<0.001**		0.526										
Skid trail (yr 3)	1		0.024		**0.005**		0.270										
Skid trail (yr 4)	1		0.232		0.639		0.570										
Skid trail (yr 8)	1		0.712		0.845		0.987										
Skid trail (yr 10)	1		0.361		0.806		0.990										
Skid trail (yr 13)	1		0.018		0.895		0.075										

[a] An angular transformation (arcsin($p^{0.5}$)) was applied on all seedbed proportions (*p*).
[b] Significant *P* values are emphasized in bold.
[c] An alpha level of 0.05 was used for the ANOVA results, while a corrected alpha level of 0.007 (0.05/7 comparisons) was used for multiple comparison tests.

Kellman, 1998). The 5% cover of rotten wood observed in this study is in agreement with coarse woody debris cover of 4–6% observed in primary hemlock–hardwood forests in Upper Michigan (McGee and Birmingham, 1997; Marx and Walters, 2008).

There was no difference in seedbed proportions between unharvested stands and areas outside skid trails in selection cuts. This indicates that the influence of harvesting on seedbed proportions is concentrated in the skid trails. A localized pattern of forest floor and soil disturbance (e.g. compaction), almost exclusively restricted to skid trails, has also been reported elsewhere (McGee and Birmingham, 1997; Caspersen and Saprunoff, 2005; Puettmann et al., 2008; Malo and Messier, 2011).

4.2. Effects of skid trails on seedbed proportions in selection cuts

Skid trails covered almost one fourth of the area in the sampled selection cuts, which is within the range of values reported for various selection cuts (9–25% in Angers, 2004; Hartmann et al., 2009; Malo and Messier, 2011). The trails, which included a disturbed area on each side of the wheel tracks, were typically 4–5 m wide and separated by a distance of about 20 m (M. Beaudet, pers. obs). Skid trails not only covered a significant proportion of managed areas, but also differed in seedbed proportions from areas located outside skid trails, at least for the first few years following harvesting.

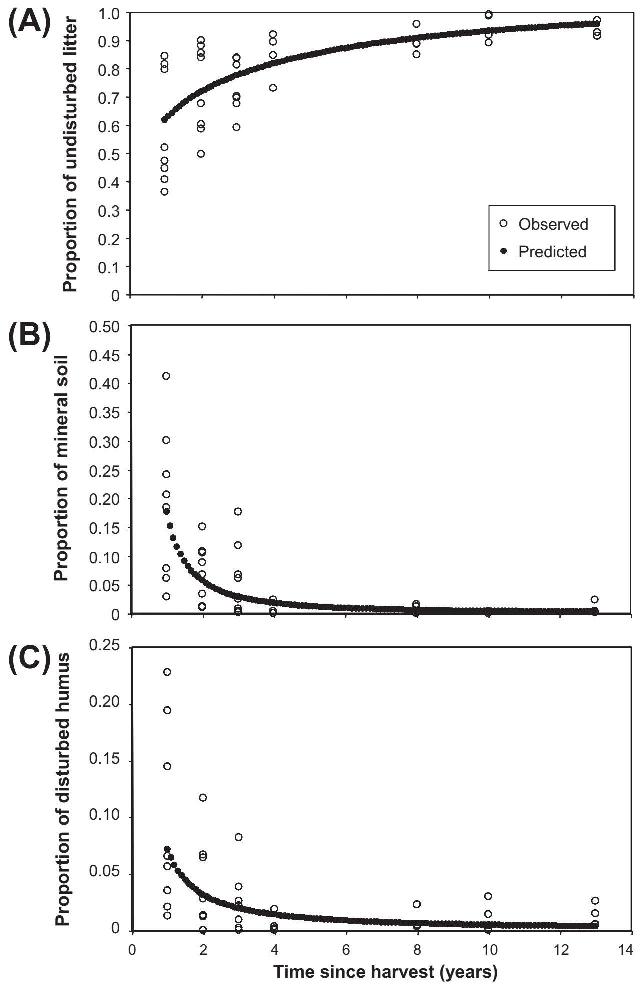

Fig. 2. Proportion of (A) undisturbed litter, (B) mineral soil and (C) disturbed humus observed in skid trails as a function of time since selection cutting. Fitted regression lines correspond to the equation and parameters provided in Table 2 (but note that to improve clarity, untransformed proportions are presented on the graphs). Each of the observed data point corresponds to seedbed proportion averaged by transect ($n_p = 40$).

4.2.1. Effects on mineral soil and disturbed humus proportions

The most important change in seedbed proportions in skid trails was a sharp increase in mineral soil and disturbed humus observed immediately after harvest (17.1-fold and 2.7-fold, respectively). Despite the initial marked impact of skid trails on the proportions of mineral soil and disturbed humus, their effect was only temporary to substrates. The proportions of mineral soil and humus rapidly decreased and returned within 3 years and 1 year, respectively, to the levels observed in undisturbed conditions. A rapid covering of exposed mineral soil and disturbed humus by falling leaves is consistent with the abundant input of leaf litterfall expected in deciduous stands with relatively high residual basal area (Ruel et al., 1988; Greene and Johnson, 1998).

In partially harvested stands, exposed mineral soil and disturbed humus are mostly restricted to skid trails, while in undisturbed forests such substrates are generally associated with tip-up mounds resulting from windthrow (Ruel et al., 1988). Differences can be expected between the spatio-temporal pattern of such seedbeds availability in harvested stands compared to undisturbed forests. While our results showed that the increased proportions of mineral soil and disturbed humus were short-lived following harvesting, Ruel et al. (1988) reported a relatively slow litter accumulation on mounds, associated with the microtopography created by tip-up mounds. A brief availability of suitable substrates, such as that observed for mineral soil after selection cutting, may not coincide with the occurrence of a mast year (or one with sufficient seed input) for desired species such as yellow birch (Erdmann, 1990). On the other hand, a longer term availability of suitable substrates, such as that observed on tip-up mounds (Ruel et al., 1988), can be expected to favor the successful establishment of desired species.

While the increased availability of mineral soil and disturbed humus in skid trails can favor regeneration establishment, there are several reasons why it could be risky to rely on these microsites to address the seedbed requirements of desired species. While the mounds associated with tip-up mounds can be considered as safe sites for regeneration (Grubb, 1977; Nakashizuka, 2001), establishment of tree seedlings in skid trails might be more risky. This would be the case, for instance, if the same skid trails are used when the next cut is performed. Sapling cohorts established in the trails after the first cut would then be put at risk of being destroyed by the passage of harvesting machinery (McGee and Birmingham, 1997; Lambert, 2013). A careful planning of skid trails layout is necessary to preserve regeneration cohorts established following a prior harvest, while accounting for physical constraints (topography, boulder, etc.) and the need to avoid excessive soil compaction (Nyland, 2002; Puettmann et al., 2008; Hartmann et al., 2009; Malo and Messier, 2011).

4.2.2. Effects on dead wood

Another difference between areas in and outside skid trails is that the proportion of rotten wood was lower in the trails. Such a trend was also noted by McGee (2001). This effect is likely caused by logs collapsing under passing machinery, since they are in an advanced stage of decay and very brittle. The magnitude of the effect is not very large, with cover of dead wood of 1.8% in skid trails compared to 3.0% outside skid trails, but the potential implications in terms of regeneration dynamics are worth considering.

Deadwood is a favorable substrate for the establishment of many tree species in different forest ecosystems, hence the term nurse logs used to refer to some types of dead wood (Harmon et al., 1986; Christie and Armesto, 2003; Marx and Walters,

Table 2
Fitted regression describing the variation in proportion of (A) undisturbed litter, (B) mineral soil, and (C) humus in skid trails, as a function of time since harvesting. A power model ($y = a$ year^b) provided the best fit, where $y = \arcsin(p^{0.5})$ and p is seedbed proportion (as a fraction ranging from 0 to 1) observed in 20 cm × 20 cm quadrats, averaged by transect ($n_p = 40$).

Seedbed	Parameter	Estimate (SE)	Test	P	AIC$_c$	$R^2_{adj.}$
(A) Undisturbed litter	a	0.9012 (0.036)	$a = 0$	<0.001	−36.5	0.530
	b	0.1604 (0.024)	$b = 1$	<0.001		
(B) Mineral soil	a	0.4322 (0.040)	$a = 0$	<0.001	−52.6	0.565
	b	−0.8510 (0.152)	$b = 1$	<0.001		
(C) Humus	a	0.2705 (0.033)	$a = 0$	<0.001	−65.6	0.301
	b	−0.6056 (0.154)	$b = 1$	<0.001		

2008; Sanchez et al., 2009; Iijima and Shibuya, 2010; Yano and Shibuya, 2010; Bače et al., 2012). Rotten wood offers better moisture retention, easy rooting conditions and, because of its elevation, a competitive advantage over surrounding vegetation (Harmon et al., 1986; McGee and Birmingham, 1997; Cornett et al., 2000; McGee, 2001). Moreover, though deadwood generally covers only a small proportion of the forest floor (less than 5%), its availability over time is more stable than that of mineral soil and disturbed humus. Deadwood could therefore play an important role in longer term seedling and sapling recruitment (Lambert, 2013). In northeastern American temperate forests, studies have documented that deadwood is used more often as a tree seedling establishment site than would be expected, based on its relative coverage of the forest floor. This has been observed for various species such as yellow birch, eastern hemlock and red spruce (McGee and Birmingham, 1997; Caspersen and Saprunoff, 2005; Marx and Walters, 2008; Bolton and D'Amato, 2011; Lambert, 2013).

However, the proportion of coarse woody debris is often reduced by forest management interventions (McGee and Birmingham, 1997; Goodburn and Lorimer, 1998; Hale et al., 1999). In temperate forests, partial harvesting systems usually aim to reduce residual tree mortality by harvesting trees that are at high risk of dying. There are concerns that this could eventually reduce the input of deadwood in managed stands. In addition, logs in an advanced stage of decay (a high-quality seedbed type, Bolton and D'Amato, 2011) easily collapse under passing machinery. We observed this as well, since the proportion of rotten wood was lower in than outside skid trails. Moreover, the decreased proportion of rotten wood did not recover over time, at least not during the first 13 years after harvesting. The recruitment of fresh wood from logging slash may constitute a future input of rotten wood (Vanderwel et al., 2010), but in the stands we studied, fresh wood was mainly composed of branches and of small diameter pieces of wood. Reduced availability of coarse woody debris following harvesting is already a concern regarding various aspects of biodiversity (e.g., McKenny et al., 2006); its potential implications for the availability of germination substrates should not be neglected (Christie and Armesto, 2003; Marx and Walters, 2008; Lambert, 2013). Specific guidelines are needed, aimed at retaining dying and dead trees during harvesting operations, and at preserving highly decayed woody debris already on site (Marx and Walters, 2008; Bolton and D'Amato, 2011). Intentional creation of nurse logs could also be considered (McGee and Birmingham, 1997).

5. Conclusion

We showed that selection cutting significantly modified substrate proportions for many seedbed types, but that its effects were concentrated in skid trails and very short-term (1–3 years) for mineral soil and disturbed humus. By contrast, the slight but significant decrease in rotten wood observed in skid trails remained noticeable for more than a decade. The increase in the proportions of mineral soil and disturbed humus should favor yellow birch establishment. However, given the very short-term increase in the proportions of these substrates, the fact that these effects were only observed in skid trails and the possibility for skid trails to be re-utilized when the next harvest is performed, it is not known whether such microsites can be considered as safe sites for longer term recruitment of desired species. Moreover, although the decrease in rotten wood we observed in skid trails was of small magnitude, the effect lasted for more than 10 years. Since such a substrate is known to be favorable to yellow birch establishment, our observations suggest that because of decreased cover of rotten wood, skid trails could also have a negative impact on the longer term recruitment of the species. Clearly, longer-term studies (i.e., over a whole rotation or more) are required to determine how the observed modifications in seedbed proportions will relate with regeneration patterns at later stages of development (e.g., saplings). Moreover, a longer-term perspective would help assess the effect of selection cutting on rotten wood availability as a germination substrate, over one rotation or more. In addition to longer-term field studies, using spatially explicit models that can simulate spatio-temporal variations in the availability of substrates would be useful to assess the long-term implications of harvesting on seedbed proportions and regeneration patterns (Coates et al., 2003).

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