Midterm Response of Understory Plant Communities after Different Regeneration Treatments in Temperate Hardwood Forests of Quebec, Canada

Romain Jaeger, Sylvain Delagrange, Isabelle Aubin, Gilles Joanisse, Patricia Raymond, and David Rivest[1]

Abstract.—Short-term effects of disturbances intensity on understory plant communities are well documented, however, only few studies have examined longer term effects. While increased intensity of soil and canopy disturbances tend to increase species richness in the short term due to early seral-species establishment, those competitive-pioneer species emerging from early stages of succession can become recalcitrant, which can alter patterns of natural regeneration especially by being detrimental to rarer species and such functional groups associated with closed forest habitats. We measured taxonomic and functional diversity indices and soil properties using four levels of disturbance intensity in six temperate hardwood forests of Quebec distributed along a longitudinal gradient. Reference forests—i.e., control forests with no silvicultural treatment known for ≥80 years (control: CON, n=21)—were compared to 20-year-old single-tree selection cuts (SIN, n=13), 20-year-old group-selection cuts (GRP, n=15), and 20-year-old group-selection cuts with soil scarification (GRPS, n=17). Species richness in group-selection treatments was higher than that in reference forests. Plant equitability and beta diversity among sites in GRP and GRPS were lower than in SIN and CON forests. More intense treatments (i.e., GRP and GRPS) contributed to the midterm persistence of early-successional competitor species (i.e., *Rubus idaeus*, *Prunus pensylvanica*) whereas sensitive species (e.g., *Monotropa uniflora*, *Dryopteris spinulosa*) occurred less often in stands with soil scarification. Of the 20-year-old treatments studied, single-tree selection cutting appears to be the most appropriate silvicultural treatment for maintaining heterogeneous understory plant communities with compositions and structures like natural forests—while more intense treatments maintain and expand for at least 20 years—species that are better adapted to a wider range of environmental conditions, including open environments.

INTRODUCTION

Within temperate forest ecosystems, the diversity of understory plant communities is a key determinant of forest dynamics. These communities play important roles in the occurrence and maintenance of several key ecological processes (e.g., nutrient recycling, regeneration; Gracia et al. 2007, Moisan-De Serres et al. 2018). Yet, these communities exhibit increased environmental sensitivity that could be exacerbated by repeated harvesting pressures that disturb the soil and forest cover (Ellum 2009, Roberts and Zhu 2002). Since the 1990s, researchers have been interested in relationships between the intensity of forest management (Foley et al. 2005), forest productivity, and biodiversity (Brockerhoff et al. 2008, Gilliam and Roberts 1995, Paquette and Messier 2010). To date, the relationships among understory plant communities' diversity, soil properties, and

[1] Université du Québec en Outaouais and Institut des sciences de la forêt tempérée (RJ, DS, DR), 58 rue Principale, J0V1V0, Ripon, QC, Canada; Natural Resources Canada (IA), Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON, Canada; Centre d'enseignement et de recherche en foresterie de Sainte-Foy Inc (GJ), Québec, QC, Canada; Direction de la recherche forestière (PR), Ministère des Forêts, de la Faune et des Parcs, Québec, QC, Canada. RJ is corresponding author: to contact, call 873-651-6900 or email jaer01@uqo.ca.

the intensity of canopy and soil disturbances remain unclear. In fact, different levels of soil and canopy disturbance intensity—relative to the size of canopy openings and the nature of machinery that is used—can have contrasting effects on biotic and abiotic conditions (Duguid and Ashton 2013, Siemion et al. 2011), therefore modifying plant community composition and soil properties (Roberts 2004). In the short term, hardwood forests that are disturbed by logging tend to have higher species richness than unmanaged forests but exhibit a lower degree of heterogeneity (Falk et al. 2008, Markgraf et al. 2020).

This response is particularly due to the establishment of competitive pioneer species that specialize in openings within communities that are composed primarily of species that are associated with late-successional forests (Archambault et al. 1998, Moola and Vasseur 2008, Naaf and Wulf 2007). During ecological succession, the coexistence of pioneer and late-successional species is generally considered to be transient, i.e., lasting less than 20 years (Moola and Vasseur 2008). However, for a given disturbance, the functional traits of competitive pioneer species and their spatio-temporal capacities to exploit available resources may allow them to remain in the community longer and, ultimately, slow down successional trajectories (Roxburgh et al. 2004, Wyatt and Silman 2010). In recent decades, management of North American hardwood forests has evolved toward alternative regeneration processes that aim to maintain some type of continuous canopy cover (Seymour et al. 2002), multi-aged stands to maintain forest resilience to global change and better integrate biodiversity conservation objectives (Messier et al. 2015).

For instance, harvest practices that promote permanent forest cover and uneven-aged structure have negligible negative impacts on abiotic conditions and vegetation diversity (Raymond et al. 2018), allowing the natural dynamics of regeneration to be maintained. The mid-lasting effects of harvesting intensity on soil properties and understory vegetation over approximately 20 to 30 years have not been assessed in a well documented manner in temperate deciduous forest of northeastern America. Thus, it is important to verify whether regeneration treatments that stay at the margin of the range of natural canopy gaps (i.e., group-selection cuts; Seymour et al. 2002) contribute to longer persistence of these competitive species and to the decrease in structural and functional heterogeneity of understory plant communities, or whether they allow a convergence of plant communities toward the attributes of unmanaged forests (Duguid and Ashton 2013, Paillet et al. 2010).

METHODS

We compared key soil chemical properties and diversity of understory plant communities along a gradient of canopy opening and soil disturbance in six deciduous forests located in the yellow birch-sugar maple bioclimatic domain (Saucier et al. 2009) in Quebec, Canada. The sites were selected with the aim of comparing reference forests (i.e., control forests that were not logged for at least 80 years (CON, n = 21) to three regeneration treatments, applied once about 20 years ago and representing a gradient of canopy and soil disturbance intensity). These are: (1) single-tree selection cuts (SIN, n = 13), an uneven-aged low-intensity treatment removing about 30 percent of average basal area; (2) group-selection cuts (GRP, n = 15), an uneven-aged moderate-intensity treatment alternative to clearcuts and resulting in openings ranging in area from 1500 m^2 to 2500 m^2; (3) group-selection cuts with soil scarification (GRPS, n = 17), an uneven-aged moderate-intensity alternative treatment with the additional purpose of creating soil microsites for some commercial tree species such as yellow birch.

Each site consisted of 3 to 5 randomized complete blocks in which regeneration treatments were compared. Blocks and sites were used as random variables in our linear-mixed model analyses. Within each sampling unit, chemical properties of forest floor and surface mineral soil (i.e., pH,

total C and N, extractable P, and exchangeable basic cations) and different understory plant diversity indices (i.e., species richness, evenness index, and functional dispersion) were assessed about 20 years after the application of the treatments. To compare functional redundancy between the treatments, we determined the community weighted means (CWM) for three environmental performance traits (sensu Violle et al. 2007); namely (1) biological type, (2) reproductive mode, and (3) shade tolerance. These traits were selected for the analyses because of their links with competitive abilities (i.e., biological type) and potential for colonization following disturbance (i.e., shade tolerance and reproduction mode). Finally, to assess the conservation potential of the different regeneration treatments, we also tested the responses of species identified in the literature as potentially sensitive (Haeussler et al. 2002, Moola and Vasseur 2008) and potentially recalcitrant (Bell et al. 2011, Royo and Carson 2006).

RESULTS AND DISCUSSION

First, the geographic location of sites explained a much more substantial proportion of the variation of soil properties than regeneration treatments. The regeneration treatments considered in our study had more limited, longer-term effects on soil properties than we had anticipated, although other studies have shown medium-term recovery of soil chemical properties following forest harvesting and soil scarification treatments (Hope 2007). However, our results indicate group-selection cuts with a soil scarification treatment in temperate hardwood forests can leave a legacy effect on soils that persists in the medium term, especially in the surface horizon. Twenty years after the application of group-selection cuts and soil scarification, FH-horizon thickness in CON was significantly higher (i.e., almost twofold) than in the GRPS. C:N ratio of the organic horizon in the control stands were higher than in the GRPS. The decrease of FH-horizon thickness and C:N ratio in the group-selection cuts can be attributed to the extraction of forest biomass and subsequently lower inputs of fresh litter (Clarke et al. 2015, Saint-Laurent et al. 2000, Thiffault et al. 2011), higher litter decomposition rates from early-successional species compared to late-stage species (Kazakou et al. 2009), and the burial of surface organic matter in the soil-mineral horizon (Henneb et al. 2019). Concurrently, species richness and composition differed weakly among canopy opening treatments, being almost similar between the SIN and the CON forests (Fig. 1). These results are consistent with other studies that have measured negligible effects of single-tree selection cuts on environmental conditions and understory-plant communities' diversity (Raymond et al. 2018, Smith et al. 2008). Twenty years after the application of the regeneration treatments, species richness was slightly higher and species-equitability index was lower in the group-selection cuts due to the presence of a greater number of species that are associated with open habitats (Table 1; Deconchat and Balent 2001, Hilmers et al. 2018). When considering species abundance or community-weighted means of functional groups, our results showed that increasing the intensity of disturbance tended to favor biotic-homogenization processes (Brewer et al. 2012, Falk et al. 2008, Markgraf et al. 2020). Although control forests and SINs in our study had fewer understory species on average, they were associated with higher beta diversity between sites compared to GRPS, indicating more heterogeneous plant communities across study sites. Our study suggests increasing canopy-opening intensity may increase the potential for the installation of colonizer and "recalcitrant" species that are present in the medium term (Royo and Carson 2006), such as *Rubus idaeus* and *Prunus pensylvanica* (Table 2), while being detrimental to rarer species and such functional groups associated with closed forest habitats.

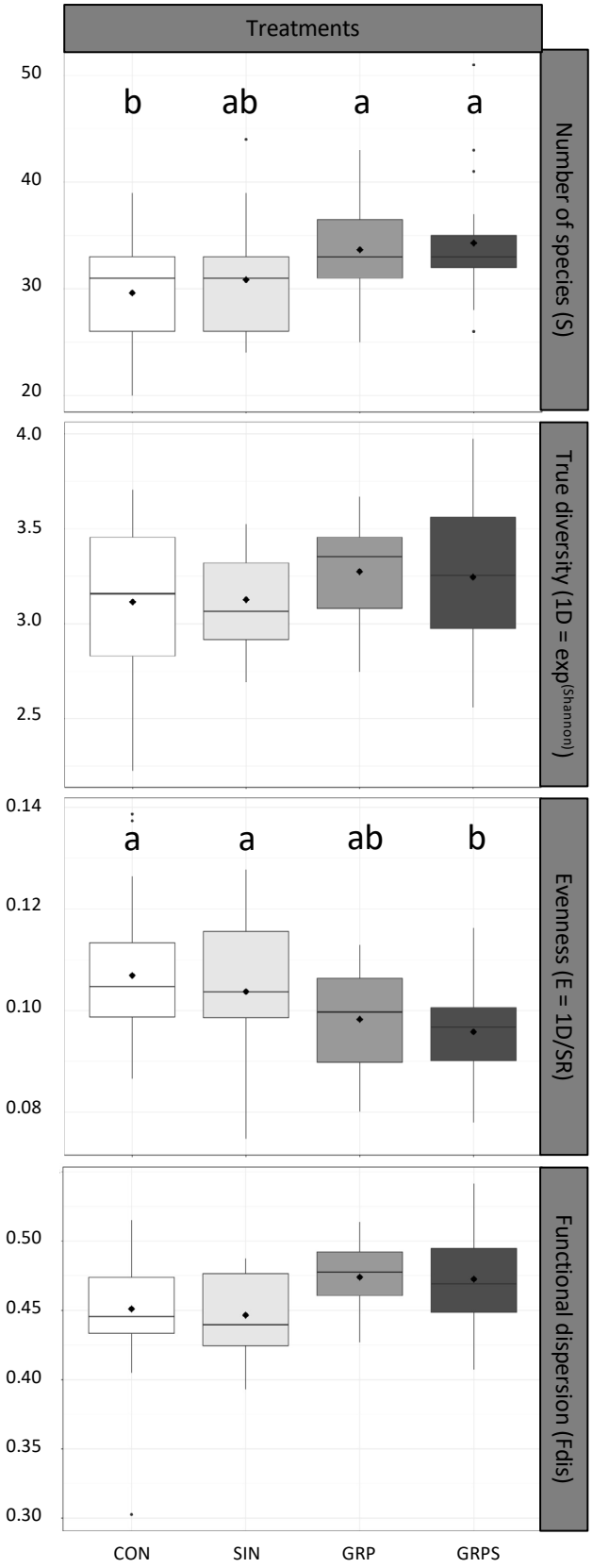

Figure 1.—Species richness (*S*), true diversity (*1D*), evenness index (*E*), and functional dispersion index (*Fdis*) of understory plant communities in southern Quebec, as a function of regeneration treatments. Means with different letters significantly differ following pairwise Tukey's tests (P <0.05). Box-and-whisker plots in each panel display 25th and 75th percentiles (the inter-quartile range from the lower and upper edges of the box), the horizontal lines within boxes indicate the 50th percentiles (i.e., medians), and bullets within boxes indicate means; whiskers below and above boxes indicate 10th and 90th percentiles, respectively, beyond which dots indicate outliers (i.e., values > 1.5 x IQR).

Legend:
CON: controls
SIN: single-tree selection cut
GRP: group-selection cut
GRPS: group-selection cut with scarification

Table 1.—Functional diversity (Rao index), mean species richness (S), and mean relative occurrence (F) of environmental performance traits as a function of regeneration treatments

Biological type	Index	CON	SIN	GRP	GRPS
Functional diversity	Rao	0.40	0.41	0.41	0.42
Evergreen	S	1.7 (1.0)	1.5 (1.1)	1.4 (0.9)	1.3 (1.3)
	F	0.34 (0.25)	0.31 (0.22)	0.28 (0.30)	0.27 (0.32)
Deciduous	S	3.2 (0.8)	3.2 (0.9)	3.8 (0.9)	3.5 (1.3)
	F	0.46 (0.33)	0.46 (0.45)	0.54 (0.33)	0.50 (0.33)
Shrubs	S	5.2 (1.7)	4.3 (1.4)	5.7 (1.9)	6.0 (1.9)
	F	0.43 (0.27)	0.36 (0.25)	0.48 (0.29)	0.50 (0.28)
Bushes	S	**1.3 (0.9) b**	**1.8 (0.9) b**	**1.7 (1.0) b**	**2.1 (0.9) a**
	F	**0.33 (0.23) b**	**0.44 (0.29) b**	**0.43 (0,.5) b**	**0.53 (0.28) a**
Asterales	S	1.3 (0.9)	1.1 (1.1)	1.6 (1.1)	1.1 (0.8)
	F	0.32 (0.25)	0.27 (0.18)	0.40 (0.26)	0.28 (0.22)
Graminaceae	S	**0.9 (0.8) b**	**0.8 (0.8) b**	**1.3 (0.6) b**	**1.6 (0.6) a**
	F	**0.45 (0.24) b**	**0.42 (0.16) b**	**0.63 (0.42) a**	**0.79 (0.12) a**
Monocots	S	4.5 (1.6)	4.2 (1.6)	4.3 (1.7)	4.9 (1.6)
	F	0.50 (0.27)	0.54 (0.26)	0.48 (0.26)	0.55 (0.34)
Sporophytes	S	4.1 (1.6)	3.4 (1.5)	4.5 (1.6)	4.9 (1.6)
	F	0.37 (0.28)	0.32 (0.26)	0.41 (0.27)	0.45 (0.27)
Other flowering plants	S	5.5 (2.9)	6.6 (2.1)	6.2 (2.0)	6.3 (1.9)
	F	0.26 (0.25)	0.32 (0.25)	0.30 (0.25)	0.30 (0.28)
Reproductive mode					
Functional diversity	Rao	0.33	0.34	0.34	0.33
Vegetative	S	**14.3 (4.1) b**	**15.3 (2.9) b**	**15.4 (3.2) b**	**16.6 (2.0) a**
	F	0.36 (0.27)	0.38 (0.28)	0.39 (0.29)	0.41 (0.33)
Sexual & vegetative	S	**10.0 (2.2) ab**	**9.3 (2.4) b**	**11.8 (2.6) a**	**12.7 (3.5) a**
	F	0.41 (0.28)	0.38 (0.29)	0.47 (0.26)	0.48 (0.25)
Sexual	S	2.5 (0.7)	2.2 (1.3)	2.6 (1.0)	2.7 (1.1)
	F	0.31 (0.18)	0.27 (0.15)	0.33 (0.25)	0.32 (0.29)
Shade tolerance					
Functional diversity	Rao	0.30	0.28	0.32	0.32
Shade intolerant	S	**1.0 (1.3) b**	**0.6 (0.9) b**	**2.0 (1.1) a**	**2.5 (1.3) a**
	F	**0.15 (0.09) ab**	**0.09 (0.09) b**	**0.29 (0.18) ab**	**0.35 (0.20) a**
Intermediate tolerance	S	6.9 (1.9)	6.9 (2.6)	7.5 (2.2)	8.1 (2.0)
	F	0.34 (0.25)	0.34 (0.26)	0.37 (0.27)	0.41 (0.27)
Shade tolerant	S	19.8 (5.3)	20.2 (4.6)	21.1 (4.9)	21.2 (3.1)
	F	0.41 (0.27)	0.42 (0.27)	0.44 (0.29)	0.44 (0.32)

Values in parentheses are standard deviations of the means. Within rows, means followed by the same letter do not differ significantly at $\alpha = 0.05$ according to pairwise Tukey's tests. CON: control; SIN: single-tree selection cut; GRP: group-selection cut; GRPS: group-selection cut with scarification.

Table 2.—Taxon-specific responses of potentially sensitive and potentially recalcitrant species to regeneration treatments

		Relative Occurrence				ANOVA
		CON	SIN	GRP	GRPS	p-value
Sensitive						
	Athyrium filix-femina	1.12	0.55	1.11	1.27	0.7947
	Circeae alpina	0.37	0.23	0.26	0.06	0.7173
	Coptis trifolia	4.96	6.52	3.69	2.65	0.5869
	Cypripedium acaule	0.64	0.70	0.59	0.18	0.6244
	Dryopteris spinulosa	**31.46 a**	**27.94 a**	**26.28 a**	**11.03 b**	**0.0154**
	Lycopodium spp.	1.97	1.20	1.66	1.09	0.8245
	Monotropa uniflora	**0.42 a**	**0.47 a**	**0.58 a**	**0.13 b**	**0.0016**
	Oxalis acetosella ssp. *montana*	15.40	9.61	11.79	6.01	0.0849
Recalcitrant						
	Acer spicatum	25.41	29.27	27.51	21.15	0.6159
	Corylus cornuta	5.52	5.32	5.14	6.71	0.9206
	Populus tremuloides	0.05	0.01	0.36	0.44	0.1056
	Prunus pensylvanica	**0.04 b**	**0.29 b**	**2.24 a**	**3.56 a**	**0.0441**
	Pteridium aquilinum	1.25	1.20	0.40	0.42	0.6335
	Rubus idaeus	**0.41 b**	**0.44 b**	**3.52 a**	**2.83 a**	**0.0370**

Mean relative occurrence values (%) are presented and two-way permutation ANOVA p-values. Significant treatment effects are represented by a *P*-value in bold ($P < 0.05$). Within rows, means followed by the same letter do not differ significantly from one another at $\alpha = 0.05$ according to pairwise Tukey's tests. CON: controls; SIN: single-tree selection cut; GRP: group-selection cut; and GRPS: group-selection cut with scarification.

CONCLUSION

Our results confirm sites' locations, and therefore their specific abiotic conditions, are responsible for much of the variation in plant communities and soil properties. Our results also suggest that, in temperate hardwood forests, there is a legacy of regeneration treatments with soil scarification on soil properties, particularly in the surface horizon. This legacy, in turn, can affect the composition and diversity of understory-plant communities. The most intense silvicultural treatments we investigated (i.e., GRP and GRPS) not only resulted in slightly increased species richness in the medium term, but also a decrease in understory plant communities' heterogeneity between sites. Indeed, these treatments contributed to a greater-relative occurrence of shade-intolerant competitive species adapted to disturbed environments and potentially recalcitrant in the longer term, which could compete with commercial species and alter plant community composition. Among the studied treatments, SIN appeared to be the most appropriate silvicultural treatment for maintaining soil functions and understory plant communities of unmanaged forests. On the other hand, more intense treatments tended to favor species adapted to a wider range of abiotic conditions, including open environments. Therefore, at the landscape level, the guarantee of maintaining the highest biodiversity of understory plant communities will lie in the search for adequate spatial representativeness of the different silvicultural treatments by considering the functions of the species that they favor over the long term.

ACKNOWLEDGMENTS

We would like to thank Hélène Lalande and Eve-Marie Hébert for their technical assistance. Thanks to the Canadian Trait Network and Laura Boisvert-Marsh for making the functional trait data available. William F.J. Parsons revised the English.

LITERATURE CITED

Archambault, L.; Morissette, J.L.; Bernier-Cardou, M. 1998. **Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Quebec, Canada.** Forest Ecology and Management. 102: 61–74. https://doi.org/10.1016/S0378-1127(97)00109-6.

Bell, F.W.; Kershaw, M.; Aubin, I.; Thiffault, N.; Dacosta, J.; Wiensczyk, A. 2011. **Ecology and traits of plant species that compete with boreal and temperate forest conifers: an overview of available information and its use in forest management in Canada.** Forestry Chronicle. 87(02): 161–174. https://doi.org/10.5558/tfc2011-006.

Brewer, J.; Bertz, C.; Cannon, J.; Chesser, J.; Maynard, E. 2012. **Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities?** Ecological Applications. 22(2): 442–458. https://doi.org/10.1890/11-0386.1.

Brockerhoff, E.G.; Jactel, H.; Parrotta, J.A. 2008. **Plantation forests and biodiversity: oxymoron or opportunity?** Biodiversity and Conservation. 17: 925–951. https://doi.org/10.1007/978-90-481-2807-5_1.

Clarke, N.; Gundersen, P.; Jönsson-Belyazid, U.; Kjønaas, O.J.; Persson, T. [et al.]. 2015. **Influence of different tree-harvesting intensities on forest soil carbon stocks in boreal and northern temperate forest ecosystems.** Forest Ecology and Management. 351: 9–19. https://doi.org/10.1016/j.foreco.2015.04.034.

Deconchat, M.; Balent, G. 2001. **Vegetation and bird community dynamics in fragmented coppice forests.** Forestry. 74(2): 105–118. https://doi.org/10.1093/forestry/74.2.105.

Duguid, M.C.; Ashton, M.S. 2013. **A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests.** Forest Ecology and Management. 303: 81–90. https://doi.org/10.1016/j.foreco.2013.04.009.

Ellum, D.S. 2009. **Floristic diversity in managed forests: demography and physiology of understory plants following disturbance in southern New England forests.** Journal of Sustainable Forestry. 28(1–2): 132–151. https://doi.org/10.1080/10549810802626431.

Falk, K.J.; Burke, D.M.; Elliott, K.A.; Holmes, S.B. 2008. **Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario.** Forest Ecology and Management. 255(7): 2486–2494. https://doi.org/10.1016/j.foreco.2008.01.033.

Foley, J.A.; Defries, R.; Asner, G.P.; Barford, C.; Bonan, G. [et al.]. 2005. **Global consequences of land use.** Science. 309: 570. https://doi.org/10.1126/science.1111772.

Gilliam, F.S.; Roberts, M.R. 1995. **Impacts of forest management on plant diversity.** Ecological Applications. 5(4): 911–912. https://doi.org/10.2307/2269342.

Gracia, M.; Montané, F.; Piqué, J.; Retana, J. 2007. **Overstory structure and topographic gradients determining diversity and abundance of understory shrub species in temperate forests in central Pyrenees (NE Spain).** Forest Ecology and Management. 242(2-3): 391–397. https://doi.org/10.1016/j.foreco.2007.01.056.

Haeussler, S.; Bedford, L.; Leduc, A.; Bergeron, Y.; Kranabetter, J.M. 2002. **Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest.** Silva Fennica. 36(1): 307–327. https://doi.org/10.14214/sf.565.

Henneb, M.; Valeria, O.; Thiffault, N.; Fenton, N.J.; Bergeron, Y. 2019. **Effects of mechanical site preparation on microsite availability and growth of planted black spruce in Canadian paludified forests.** Forests.10(8): 670. https://doi.org/10.3390/f10080670.

Hilmers, T.; Friess, N.; Bässler, C.; Heurich, M.; Brandl, R. [et al.]. 2018. **Biodiversity along temperate forest succession.** Journal of Applied Ecology. 55(6): 2756–2766. https://doi.org/10.1111/1365-2664.13238.

Hope, G.D. 2007. **Changes in soil properties, tree growth, and nutrition over a period of 10 years after stump removal and scarification on moderately coarse soils in interior British Columbia.** Forest Ecology and Management. 242(2-3): 625–635. https://doi.org/10.1016/j.foreco.2007.01.072.

Kazakou, E.; Violle, C.; Roumet, C.; Pintor, C.; Gimenez, O.; Garnier, E. 2009. **Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply.** Annals of Botany. 104(6): 1151–1161. https://doi.org/10.1093/aob/mcp202.

Markgraf, R.; Doyon, F.; Kneeshaw, D. 2020. **Forest landscape heterogeneity increases shrub diversity at the expense of tree seedling diversity in temperate mixedwood forests.** Forests. 11(2): 160. https://doi.org/10.3390/f11020160.

Messier, C.; Puettmann, K.; Chazdon, R.; Andersson, K.P.; Angers, V.A. [et al.]. 2015. **From management to stewardship: viewing forests as complex adaptive systems in an uncertain world.** Conservation Letters. 8: 368–377. https://doi.org/10.1111/conl.12156.

Moisan-De Serres, A.; Gélinas, N.; Marcotte, P. 2018. **Les produits forestiers non ligneux: une opportunité de développement touristique régional.** Journal of Rural Community Development. 12(2–3): 168–185.

Moola, F.M.; Vasseur, L. 2008. **The maintenance of understory residual flora with even-aged forest management: a review of temperate forests in northeastern North America.** Environmental Reviews. 16: 141–155. https://doi.org/10.1139/A08-005.

Naaf, T.; Wulf, M. 2007. **Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps.** Forest Ecology and Management. 244(1-3): 141–149. https://doi.org/10.1016/j.foreco.2007.04.020.

Paillet, Y.; Bergès, L.; Hjältén, J.; Ódor; P.; Avon C. [et al.] 2010. **Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe**. Conservation Biology. 24(1): 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.

Paquette, A.; Messier, C. 2010. **The role of plantations in managing the world's forests in the Anthropocene.** Frontiers in Ecology and the Environment. 8(1): 27–34. https://doi.org/10.1890/080116.

Raymond, P.; Royo, A.A.; Prévost, M.; Dumais, D. 2018. **Assessing the single-tree and small group selection cutting system as intermediate disturbance to promote regeneration and diversity in temperate mixedwood stands.** Forest Ecology and Management. 430: 21–32. https://doi.org/10.1016/j.foreco.2018.07.054.

Roberts, M.R. 2004. **Response of the herbaceous layer to natural disturbance in North American forests.** Canadian Journal of Botany. 82(9): 1273–1283. https://doi.org/10.1139/b04-091.

Roberts, M.R.; Zhu, L. 2002. **Early response of the herbaceous layer to harvesting in a mixed coniferous–deciduous forest in New Brunswick, Canada.** Forest Ecology and Management. 155(1–3): 17–31. https://doi.org/10.1016/S0378-1127(01)00544-8.

Roxburgh, S.H.; Shea, K.; Wilson J.B. 2004. **The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence.** Ecology. 85(2): 359–371. https://doi.org/10.1890/03-0266.

Royo, A.A.; Carson, W.P. 2006. **On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession.** Canadian Journal of Forest Research. 36(6): 1345–1362. https://doi.org/10.1139/x06-025.

Saint-Laurent, S.; Ouimet, R.; Tremblay, S.; Archambault, L. 2000. **Évolution des stocks de carbone organique dans le sol après coupe dans la sapinière à bouleau jaune de l'est du Québec.** Canadian Journal of Soil Science. 80: 507–514. https://doi.org/10.4141/S99-083.

Saucier J.-P.; Robitaille, A.; Grondin, P. 2009. **Cadre bioclimatique du Québec.** In: Doucet, R.; Côté, M., eds. Manuel de foresterie. Quebec, QC: Multi-mondes: 186–205.

Seymour, R.S.; White, A.S.; DeMaynadier, P.G. 2002. **Natural disturbance regimes in northeastern North America—Evaluating silvicultural systems using natural scales and frequencies.** Forest Ecology and Management. 155: 357–367. https://doi.org/10.1016/s0378-1127(01)00572-2.

Siemion, J.; Burns, D.A.; Murdoch, P.S.; Germain, R.H. 2011. **The relation of harvesting intensity to changes in soil, soil water, and stream chemistry in a northern hardwood forest, Catskill Mountains, USA.** Forest Ecology and Management. 261(9): 1510–1519. https://doi.org/10.1016/j.foreco.2011.01.036.

Smith, K.J.; Keeton, W.S.; Twery, M.J.; Tobi, D.R. 2008. **Understory plant responses to uneven-aged forestry alternatives in northern hardwood–conifer forests.** Canadian Journal of Forest Research. 38(6): 1303–1318. https://doi.org/10.1139/X07-236.

Thiffault, E.; Hannam, K.D.; Paré, D.; Titus, B.D.; Hazlett, P.W. [et al.]. 2011. **Effects of forest biomass harvesting on soil productivity in boreal and temperate forests—a review.** Environmental Reviews. 19: 278–309. https://doi.org/10.1139/a11-009.

Violle, C.; Navas, M.L.; Vile, D.; Kazakou, E.; Fortunel, C. [et al.] 2007. **Let the concept of trait be functional.** Oikos. 116: 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Wyatt, J.L.; Silman, M.R. 2010. **Centuries-old logging legacy on spatial and temporal patterns in understory herb communities.** Forest Ecology and Management. 260: 116–124. https://doi.org/10.1016/j.foreco.2010.04.010.

CITATION: Jaeger, Romain; Delagrange, Sylvain; Aubin, Isabelle; Joanisse, Gilles; Raymond, Patricia; Rivest, David. 2023. **Midterm Response of Understory Plant Communities after Different Regeneration Treatments in Temperate Hardwood Forests of Quebec, Canada.** In: Kern, Christel C.; Dickinson, Yvette L., eds. Proceedings of the first biennial Northern Hardwood Conference 2021: Bridging science and management for the future. Gen. Tech. Rep. NRS-P-211. Madison, WI: U.S. Department of Agriculture, Forest Service, Northern Research Station: 203–211. https://doi.org/10.2737/NRS-GTR-P-211-paper41.