Forest Ecology and Management 432 (2019) 748–760

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Managing conservation values and tree performance: Lessons learned from 10 year experiments in regenerating eastern white pine (*Pinus strobus* L.)

Kierann Santala[a], Isabelle Aubin[a,*], Michael Hoepting[b], Marianne Bachand[c], Doug Pitt[b]

[a] Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, 1219 Queen St E, Sault Ste. Marie, ON P6A 2E5, Canada
[b] Canadian Wood Fibre Centre, Canadian Forest Service, Natural Resources Canada, 1219 Queen St E, Sault Ste. Marie, ON P6A 2E5, Canada
[c] Hydrology and Ecohydraulic Section, National Hydrological Services, Environment and Climate Change Canada, 801-1550 avenue d'Estimauville, Québec, QC G1J 5E9, Canada

ARTICLE INFO

Keywords:
Competition
Plant trait
Recalcitrant layer
Silviculture
Sustainable forest management
Understory plants
Vegetation management
White pine

ABSTRACT

Multiple-use land management is an important aspect of sustainable forest management and requires strategies that both promote sustainable fiber production and conserve biodiversity. Studies formally integrating these two aspects of forest management are needed to develop silviculture prescriptions capable of maintaining the delivery of multiple ecosystem goods and services. Techniques used to suppress vegetation that competes with young pine seedlings have become standard practice in the regeneration of eastern white pine (*Pinus strobus* L.), but they can cause changes in plant community composition. We compared white pine performance to understory development under five vegetation suppression treatments within three experimental white pine plantations. White pine performance was assessed in terms of basal stem diameter and the percentage of trees reaching an age 10 height target. Understory development was characterized in terms of understory plant functional composition using a complementary set of functional and taxonomic diversity metrics. Plantations included one clearcut site and two sites managed under a uniform shelterwood system. Our results show that after 10 years, plots treated with a single, second-season application of herbicide that temporarily suppressed both woody and herbaceous vegetation favoured rapid white pine growth, increased pine canopy cover, and allowed the understory community to recover towards a mature functional and taxonomic composition. Repetitive suppression of either only herbaceous or woody vegetation caused major shifts in community composition that were still evident after 10 years. These shifts were due to the prevalence of competitive species that formed dominant layers in these treatments. Impacts of treatments on tree performance and understory development observed in this study have important implications for forest management. Some treatments might create problems in the long-term by delaying understory maturation, while others appear capable of balancing multiple management objectives.

1. Introduction

Eastern white pine (*Pinus strobus* L.) has been historically one of the most economically, socially, and culturally important tree species in Eastern North America (Uprety et al., 2014). However, in the centuries since European settlement, harvesting, fire and pest damage have caused its steady decline (Beaulieu et al., 1996). Early efforts to improve white pine regeneration using then standard silvicultural techniques produced inconsistent results that generated poor growth and low survival due to plant competition, white pine blister rust infection (*Cronartium ribicola* J.C. Fisch.), and white pine weevil attack (*Pissodes strobi* Peck) (Hosie, 1953; Stiell, 1985). Although a move to a uniform shelterwood system in the 1970s helped mitigate losses from white pine blister rust and weevil (De Groot et al., 2005; Hannah, 1988; Ostry et al., 2010), achieving successful white pine regeneration still remains a significant challenge, largely due to the effects of competing vegetation. Consequently there is a need for research that focuses on methods to mitigate competition (Carleton et al., 1996; Pitt et al., 2009).

Vegetation management has long been used to raise performance of desired tree species and its direct positive effects on tree growth are well documented (Pitt et al., 2016, 2015, Wagner et al., 2006). These practices usually involve the suppression of herbaceous and woody competitive species through herbicide application and/or manual removal (Wagner et al., 2006; Wiensczyk et al., 2011), providing crop

* Corresponding author.
E-mail addresses: kierann.santala@canada.ca (K. Santala), isabelle.aubin@canada.ca (I. Aubin), michael.hoepting@canada.ca (M. Hoepting), marianne.bachand@canada.ca (M. Bachand), doug.pitt@canada.ca (D. Pitt).

https://doi.org/10.1016/j.foreco.2018.09.038
Received 3 May 2018; Received in revised form 16 August 2018; Accepted 21 September 2018
0378-1127/

trees with greater access to limited resources. Developing vegetation management strategies for white pine is particularly challenging because successful regeneration often relies on both managing understory environmental conditions to help mitigate weevil and blister rust damage while maintaining light levels that do not overly suppress regenerating seedlings (Hodge et al., 1989; Pitt et al., 2016; Stiell, 1985).

It can be difficult to predict the long-term outcomes that vegetation suppression will have on complex and dynamic understory communities. Vegetation suppression can be detrimental to interior forest species of the understory by altering community composition and contributing to a loss of species and plant diversity (Gauthier et al., 2015; Miller et al., 1995; Noble and Dirzo, 1997). Disturbances associated with vegetation suppression can also provide colonization opportunities by freeing up space and increasing resource availability for previously non-dominant opportunistic species (Balandier et al., 2006; Davis et al., 2000). This may lead to the formation of a dense competitive layer (or "recalcitrant layer") that has the potential to limit forest regeneration by preventing the colonization of more desirable, late successional species (Mallik, 2003; Meier et al., 1995; Royo and Carson, 2006; Young and Peffer, 2010). The persistence of competitive species could also lead to increased silvicultural efforts, and therefore costs, to ensure success of the current crop and to initiate subsequent rotations. For example, early dominance of bracken fern (*Pteridium aquilinum* (L.) Kuhn) can pose significant challenges to regenerating tree seedlings; and once it dominates a site it is very difficult to eradicate (Griffiths and Filan, 2007; Milligan et al., 2016). Since multiple-use land management is a fundamental aspect of sustainable forest management (Wang and Wilson, 2007), it requires management strategies that both promote sustainable fiber production and the conservation of biodiversity (Eriksson and Hammer, 2006; Spence, 2001; Work et al., 2003). It is of central importance for land managers seeking to ensure the sustainability and ecological integrity of commercial forests to have access to research that address the potential trade-off that exists between these two interrelated objectives so they can make informed decisions (Urli et al., 2017).

This paper aims to compare understory development to gains in crop tree performance under contrasting vegetation suppression treatments. To explore this topic we took advantage of three experimental sites initiated in 2000 to evaluate the effects of timing and duration of vegetation suppression treatments on planted white pine survival and growth. Our objective was to address the following questions: (1) How do vegetation suppression treatments alter the trajectory of understory development over time? (2) How do understory communities respond to these treatments after 10 years? (3) What are the responses of competitive species and interior forest species? (4) What are the effects of these treatments on planted white pine performance? We used a trait-based approach in addition to traditional taxonomic information to provide a comprehensive assessment of understory community development. This approach is particularly useful because it provides greater comparability among geographically distant sites (Garnier et al., 2016). Another aspect of our study is that it included vegetation suppression treatments designed to isolate the response from removal of specific understory components (i.e. suppression of either herbaceous-only or woody-only vegetation). Only a few studies have looked at the response of understory vegetation and crop tree performance to suppression of specific competitive components (e.g. Little et al., 2018; Miller et al., 2003) and, to our knowledge, none have been conducted in Eastern North America.

Our intent is to identify vegetation suppression approaches and intensities (i.e., duration of suppression in years) that provide adequate resources for successful white pine regeneration in terms of stem diameter and height, with minimal effects on understory plant community composition. These results can provide an empirical basis on which to develop vegetation suppression prescriptions designed to optimize investment both in the short- and long-term.

2. Methods

The study was conducted in three planted white pine sites – two in Ontario, Canada (henceforth: Clearcut-ON and Shelterwood-ON) and one in New Brunswick, Canada (henceforth: Shelterwood-NB). All three sites are part of the White Pine Competition Study (Pitt et al., 2016, 2011, 2009). The sites were harvested using either one of two conventional silviculture systems: clearcut or uniform shelterwood. Both create conditions for even-aged regeneration, but the clearcut system generally involves the harvest of all overstory trees from an area at one time. The uniform shelterwood system consists of harvesting overstory trees in two or more successive cuts, depending on the management objective, with the primary intent of managing the understory environment – in the case of white pine, to mitigate damage from white pine weevil and white pine blister rust (Hodge et al., 1989; Stiell, 1985). Site histories and characteristics of these sites are summarized in Table 1; for more details on white pine response and ecophysiology effects of treatments from previous investigations within these sites, see Pitt et al. (2016, 2011, 2009) and Parker et al. (2012, 2010, 2009).

2.1. Study sites

2.1.1. Climate and soil conditions

Clearcut-ON (World Geodetic System; WGS 84: 46°42′44.3″ N; 79°22′14.4″ W) and Shelterwood-ON (WGS 84: 46°43′50.7″ N; 79°22′46.1″ W) are located 2.2 km apart in the Great-Lakes-St. Lawrence forest region (Rowe, 1972), northeast of the city of North Bay. Shelterwood-NB (WGS 84: 46°24′30″ N; 66°04′26″ W) is located in the Acadian forest region (Rowe, 1972) of central New Brunswick, near the city of Doaktown. The Ontario sites had mean annual, January, and July temperatures of 4.4 °C, −12.2 °C, and 18.8 °C, respectively, with 1574 annual growing degree days and 475 mm of precipitation from May to September. The New Brunswick site had a similar climate with mean annual, January, and July temperatures of 5.0 °C, −10.5 °C, and 18.9 °C, respectively, with 1559 annual growing degree days and 480 mm precipitation during May to September.

Both Ontario sites represent Ecosite G033 (Ontario Ministry of Natural Resources, 2009) and are typical of white and red pine-dominated (*Pinus resinosa* Aiton) mixedwood forests. Shelterwood-NB is located within the transitional zone between the Castaway and Bantalor ecodistricts of the Eastern Lowlands Ecoregion and is classified as an Ecosite 5 (Zelazny et al., 2007). Both Ontario sites have approximately 10 cm of fine loamy sands that overlay deep, medium- to coarse-textured sands, with a rooting depth of about 60 cm and no signs of mottling or gleying. By contrast, Shelterwood-NB has less than 10 cm of fine loamy sand soil underlain by formations of grey lithic and feldspar sandstone (Colpitts et al., 1995; Loucks, 1962).

2.1.2. Site history

Prior to harvesting, sites were mature stands likely of fire origin (approximately 86 years old for the Clearcut site and 100 years old for the Shelterwood sites). Clearcut-ON was full-tree harvested in spring 2000 with subsequent manual felling of all remaining residual trees to emulate a true clearcut harvest condition. No advanced regeneration remained following harvest. Shelterwood-ON was partially harvested in 1999 following a prescription for the regeneration cut phase of the uniform shelterwood system. This harvest left an overstory of high quality *Pinus strobus* L. and *Pinus resinosa* Aiton, along with many subordinate stems of *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Acer rubrum* L., and *Populus tremuloides* Michx. that had been marked for harvest but left standing due to poor market conditions. To achieve the intended silvicultural prescription, these remaining marked subordinate stems were manually felled in 2000 and removed with a grapple skidder. The result was an overstory of relatively evenly spaced dominant and co-dominant trees (basal area 18 m^2/ha, 71% white pine). In 1998, Shelterwood-NB was partially harvested for the

Table 1
Treatment history and residual stand characteristics of the three white pine (*Pinus strobus)* study sites.

Site	Harvesting system	Site preparation	Planting	2002 Post-harvest and 2012 (Year 10) stand characteristics					
				Density (stems ha^{-1})	Height (m)	DBH (cm)	Basal area[a] (m^2 ha^{-1})	Gross total volume[b] (m^3 ha^{-1})	Canopy closure[c] (%)
Clearcut-ON	2000: full-tree overstory harvest using clearcut system	None	2001: Multipot 67 white pine seedlings planted at 2 m spacing	–	–	–	–	–	–
Shelterwood-ON	1998: regeneration harvest using shelterwood system 2000: manual felling and grapple skidder used to remove subordinate stems to meet basal area targets	2001: chain scarification with two perpendicular passes	2002: Multipot 67 white pine seedlings planted at 2 m spacing	***2002*** 133	27	40.4	18.1	217	61
				2012 120	29.2	45.9	20.8	263	66
Shelterwood-NB	1998: regeneration harvest using shelterwood system	1999: chain scarification with single pass	2002: Jiffy 36 white pine seedlings planted at 2 m spacing	***2002*** 100	25.3	45.1	17.5	197	60
				2012 98	26.7	49.5	20.5	245	66

[a] Total cross-sectional area of stems at 1.3 m per hectare.
[b] Calculated following Eq. (14) in Honer et al. (1983).
[c] Canopy closure calculated from residual basal area using a relationship developed by Parker (2014).

regeneration cut phase of the uniform shelterwood system. Like the Shelterwood-ON site, the residual overstory was dominated by large white pine, but these trees tended to be of lower overall quality (e.g., poor form) due to early white pine weevil damage (basal area 17.5 m^2/ha, 92% white pine). Post-harvest stand volume, basal area, and light transmittance were similar within the Shelterwood-ON and Shelterwood-NB sites, but more variable within Shelterwood-NB due to the more irregular spacing of fewer and larger diameter residual trees. To encourage natural regeneration, both Shelterwoods were mechanically site prepared using chains pulled by a skidder. Site history, including site preparation and planting details, are described in Table 1. Seedlings at all three sites were initially the same size when planted (Table 1).

2.2. Vegetation suppression treatments

The original White Pine Competition Study had 14 treatments consisting of various levels and timing of woody and non-woody species suppression, including a single broadcast herbicide treatment to emulate operational practices (Pitt et al., 2016, 2011, 2009). Our investigation focused on 5 of the original 14 treatments (Table 2).

Herbaceous suppression in *4-yr herb-only* and *4-yr herb and woody* treatments was maintained for the first four growing seasons after planting via repeated directed foliar applications of 3% solution of Vision® herbicide (a.i. glyphosate; see Pitt et al., 2016 for details). Woody stem removal in *10-yr woody-only* was achieved by basal bark treatment using the herbicide Release® (a.i. trycolpyr) just before planting. Subsequent woody stem regeneration was manually clipped each year during the first ten years. The intent of these treatments was to achieve the four different vegetation conditions as a 2^2 factorial (Herb (0, 1) x Woody (0, 1)), and not test any specific operational treatments or means of achieving these conditions. The *1-yr herb and woody* treatment was intended to emulate an operational treatment and was achieved by a single broadcast application of 2% Vision® applied at the end of the second growing season. This treatment targeted both woody and herbaceous vegetation, with no subsequent follow-up treatment. All herbicides were applied using Solo® backpack sprayers with either 8004 nozzles for Vision® or SS1502 nozzles for Release®.

Table 2
Vegetation suppression treatments.[a]

Treatment name		Growing season[c]										
	N plots[b]	1	2	3	4	5	6	7	8	9	10	Description
No suppression	9	–	–	–	–	–	–	–	–	–	–	No vegetation suppression
1-yr herb and woody	9	–	–	hw	–	–	–	–	–	–	–	1-yr of both herbaceous and woody vegetation suppression at end of year 2 (corresponding to operational practices)
4-yr herb-only	9	h	h	h	h	–	–	–	–	–	–	4-yr of herbaceous-only suppression
4-yr herb and woody	3	hw	hw	hw	hw	w	w	w	w	w	w	4-yr of both herbaceous and woody vegetation suppression followed by woody-only suppression
10-yr woody-only	3	w	w	w	w	w	w	w	w	w	w	10-yrs of woody-only suppression

[a] Letters indicate the specific competitive components to which the treatment was applied to: h – herbaceous suppression, w – woody suppression, "-" no treatment.
[b] The original design of the White Pine Competition Study included an additional stem density treatment that consisted of three levels of regenerating deciduous hardwoods. However, these density treatments were subsequently found to have non-significant effects (Pitt et al., 2016) so these density treatments were kept as additional replicates for vegetation suppression treatments in the present study.
[c] Growing season refers to the number of growing seasons for planted white pine. Growing season 1 was 2001 for Clearcut-ON site and 2002 for both Shelterwood sites.

Each vegetation suppression treatment was replicated three times at each site in a randomized complete block design. The original design of the White Pine Competition Study also included an additional stem density treatment that consisted of three levels of regenerating deciduous hardwoods (5000, 10000, 15,000 stems per hectare). However, these density treatments were subsequently found to have non-significant effects on understory vegetation and planted tree performance (Pitt et al., 2016; $p > 0.1$), so these density treatments were kept as additional replicates for vegetation suppression treatments in the present study. Hence, vegetation suppression treatments were replicated either three (*4-yr herb and woody*, *10-yr woody-only*) or nine times (*no suppression*, *1-yr herb and woody*, and *4-year herb*) (Table 2). Each treatment was randomly assigned to an 18-m × 18-m plot separated by at least 2-m corridors.

2.3. Tree performance indicator

Each treatment plot consisted of 9 rows of 9 planted white pine at 2-m spacing. The inner 10 m × 10 m area of each treatment plot, coinciding with 5 rows of 5 planted trees, was established as the measurement plot. Basal stem diameter (5 cm above the ground line) and the percentage of trees meeting or exceeding a target height of 2.5 m height (henceforth: P250), a standard target height for a 10-year-old stand, were used as practical indicators of planted pine performance (Pitt et al., 2016). P250 and basal stem diameter was determined through total height and basal stem diameter measurements of the surviving planted trees and was measured at the end of the tenth growing season.

2.4. Vegetation survey

Non-crop vegetation was assessed during July or early August of growing seasons one, three, six and ten from five 2 m × 2 m subplots randomly located within each treatment plot. Cover (%) of all non-crop vascular species was visually estimated to the nearest one percent. Identification was done to the species level following the nomenclature of the Database of Vascular Plants of Canada (VASCAN), with the exception of 13 genera (*Actaea* L., *Alnus* Mill., *Amelanchier* Medik, *Aster* L., *Hieracium* L., *Lactuca* L., *Pyrola* L., *Ribes* L., *Salix* L., *Solidago* L., *Vaccinium* L., *Viburnum* L., *Viola* L.) that were identified to the genus level. Grass cover was pooled to include both grasses and *Carex spp*. Total cover of natural conifer regeneration was assessed and apportioned to each species based on stem density. We did not include cover values of planted white pine in our analysis of plant community response, as we were interested in the response of naturally regenerating species to the competition suppression treatments.

2.5. Species traits

Plant traits were obtained from the TOPIC database (Aubin et al., 2012) and from field observations. We use the term "trait" in its broader sense, which includes morphological, physiological or phenological features of the plant, as well as performance traits related to individual fitness (Violle et al., 2007). Traits were selected for analysis because of their relation to the competitive ability (Raunkiaer lifeform, maximum height, foliage architecture) and colonization potential following disturbance (lateral extension, seed weight, seed production, seed dispersal distance, shade tolerance; Table 3).

2.6. Analyses

Analyses were designed to test for similarities in plant community response and planted white pine performance to treatments across the three study sites. We based the analyses on four distinct matrices to answer our four research questions: (1) matrix *L* (plots by species) containing cover data, (2) matrix *Q* (traits by species) containing mixed species traits data, (3) matrix *R* consisting of ordinal variables representing vegetation suppression treatment (Table 2), and (4) a matrix containing pine performance (plots by performance indicator). All statistical analyses and graphics were conducted using the open-source statistical package R (R Core Team, 2017).

2.6.1. How do vegetation suppression treatments alter the trajectory of community composition development over time?

To explore the effect of treatment on species composition over time, we used the principal response curve method (PRC) (Van den Brink and Ter Braak, 1999) on the L and R matrices. PRCs are a special case of redundancy analysis (RDA) that uses a multivariate approach based on constrained ordination techniques to test the interaction between time and a given treatment ($\alpha = 0.05$), relative to the change between a given treatment and an *a priori* determined baseline for comparison. Preliminary analyses found the two shelterwood sites responded similarly to treatments, therefore the clearcut was analyzed separately (see Appendix, Fig. S1). Prior to analysis, a Hellinger transformation was performed on the L matrix (Legendre and Gallagher, 2001) using the "decostand" function of the "vegan" package (Oksanen et al., 2008). We considered treatment and year as factors. The *no suppression* treatment was used as the *a priori* baseline for comparison. Since the vegetation in this treatment was not disturbed, other than by harvesting, it was considered the most appropriate baseline condition against which to assess the impact of suppression treatments on community composition. Significance for the overall PRC was assessed using Monte-Carlo permutations (n = 999). To test for differences among treatments in the 10th year, the PRC included a Tukey's post-hoc comparison of site scores, which were evaluated against a multivariate t-distribution using the "multcomp" package (Hothorn et al., 2008). To avoid bias introduced by multiple comparisons between treatments, a Bonferroni correction was applied when significant effects were detected.

2.6.2. How do understory communities respond after 10 years?

We used a complementary set of functional and taxonomic metrics to assess understory response in year 10. To investigate how understory functional composition is related to vegetation suppression treatments, we first generated a Community-Weighted Mean (CWM) matrix using matrix *L* and matrix *Q*. The CWM matrix was generated by calculating the mean of the trait value present in the community, weighted by its percent cover for each species (Garnier et al., 2004). We then conducted a Principal Component Analysis (PCA) on the CWM matrix to relate patterns of co-occurring traits to experimental treatments. Seed weight and typical maximum height were both skewed in distribution and each were log-transformed to obtain a normal distribution (Májeková et al., 2016).

Taxonomic and functional diversity metrics were calculated and compared between vegetation suppression treatments. Taxonomic diversity was measured using species richness (S; i.e. the number of species per site) computed on matrix L. Functional diversity was calculated using Rao's quadratic entropy index (FD; Rao, 1982). Rao's index is calculated as the sum of pairwise distances between species weighted by their relative abundance, and describes the variation of species trait composition within the community. Using the matrices L and Q, FD was computed as a univariate index (i.e. the mean value of each trait FD). To asses the response of diversity indices between vegetation suppression treatments (i.e. alpha diversity) we used one-way ANOVAs with Monte Carlo tests with 999 permutations, followed by a Bonferonni post hoc test for multiple tests when significant treatment effects were detected. FD Rao's quadratic entropy were calculated using the library 'FD' (Laliberte and Legendre, 2010). For computational details and definition of CWM and FD, see Ricotta and Moretti (2011).

2.6.3. What are the responses of competitive species and interior forest species?

We tested differences in the 10th year mean cover of competitive

Table 3
Traits included in the analyses.

Trait	Code	Trait value description
Raunkiaer Lifeform	RA	Qualitative variable: *mg, mega or meso-phanerophyte* (height ≥ 8 m); *mc, micro or nano-phanerophyte* (25 cm to 8 m); *ch, chamaephyte*, herb or shrub with buds between 0.1 and 25 cm above ground; *h, hemicryptophyte*, herb with bud at the ground surface; *hf, hemicryptophyte fern*, fern with bud at the ground surface; *g, geophyte*, herb with underground bud; *gf, geophyte fern*, fern with underground bud; *t, therophyte*, annual
Typical Maximum Height	HT	Quantitative variable: 38–4850 cm
Foliage Architecture	FOL	Qualitative variable: *Phanerophytes* m, mono-stem; mu, multi-stem. *Other life forms without stems;* r, rosette and semi-rosette; e, erect leaves. *Other life forms with stems;* el, erect leafy stem; de, decumbent or prostrate stem; h, horizontal stem bend in an arch or umbel-shaped stem
Lateral Extension	LE	Semi-quantitative variable: Defined as lateral spread by means of vegetative organs. *For Phanerophytes:* pl, limited; pcc, compact; pci, intermediate; pce, extensive. *For other life forms:* l, limited; cc, compact; ce, extensive
Seed Weight*	SDWT	Quantitative variable: 1200–100000000 seeds or spores kg^{-1}. Seeds and spores are defined as generative units of reproduction
Seed Production	SPRO	Semi-quantitative variable: f, few(< 20 seeds ind^{-1} yr^{-1}); s, semi-abundant (20–1000 seeds ind^{-1} yr^{-1}); a, abundant (> 1000 seeds ind^{-1} yr^{-1})
Seed Dispersal Distance	DD	Semi-quantitative variable: short, gravity and ant dispersed; short wind, dispersed but lack seed structures that facilitate long distance dispersal; intermediate, dispersed by animals through internal or external transport; long wind, seeds dispersed by birds or specialized seed structures that facilitate long dispersal
Shade Tolerance	LI	Semi-quantitative variable: s, shade tolerant; m, mid-tolerant; i, shade intolerant

* Reciprocal transformation applied to assist in visual interpretation of results.

species between treatments for each of the three study sites separately using one-way ANOVAs with permutations (n = 999) (Anderson, 2001; Borcard et al., 2011; Legendre, 2007). Post-hoc pairwise t-tests were used to test for differences between treatments. When significant effects were detected with post-hoc tests, a Bonferroni correction was applied to avoid bias introduced by multiple comparisons between treatments. Eleven species in this dataset were identified as competitive species: *Acer rubrum* L., *Acer spicatum* Lam., *Betula papyrifera* Marshall, *Corylus cornuta* Marshall, *Epilobium angustifolium* L., *Kalmia angustifolia* L., *Populus tremuloides* Michx., *Prunus pensylvanica* L.f., *Pteridium aquilinum* (L.) Kuhn, *Rubus* spp., and Grass. These species are known in Eastern Canada for their ability to suppress crop tree survival and growth, and for their potential to form dense “recalcitrant understory layers” that can dominate the understory community and inhibit the colonization of later successional species (Bell et al., 2011; Jobidon, 1995; Young and Peffer, 2010). Because woody species were actively suppressed throughout the experiment in *10-yr woody-only* and *4-yr herb and woody* suppression treatments, we only included non-woody species (*P. aquilinum*, *E. angustifolium, and* Grass) in the analysis for these two treatments.

Ten species known to be typical of interior forest habitats were identified in our dataset: *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Dryopteris* spp., *Maianthemum canadense* Desf., *Mitchella repens* L., *Polygaloides paucifolia* (Willdenow) J.R. Abbott, *Rubus pubescens* Raf., *Lysimachia borealis* (Rafinesque) U. Manns & Anderberg *and Trillium undulatum* Willd. These species tend to be shade tolerant, less nutrient demanding, with known sensitivity to frequent and/or intense disturbances (Avon et al., 2010). We were interested in the recovery of interior forest species because there is a growing interest in using management strategies and practices that produce forest ecosystems that are structurally and functionally similar to ecosystems that would result from a natural disturbance (Long, 2009; Urli et al., 2017). We compared cover of species typical of interior forest habitats among treatments as an indication that later successional species are beginning to colonize the plot. These species have low cover values therefore we used an average percent cover for all ten interior forest species to test differences between vegetation suppression treatments for each of the three study sites separately. One-way ANOVAs with permutations (n = 999) were used for these analyses, followed by a post-hoc pairwise *t*-test to test for differences between treatments (Anderson, 2001; Borcard et al., 2011; Legendre, 2007). To avoid bias introduced by multiple comparisons between treatments, a Bonferroni correction was applied when significant effects were detected for post-hoc tests.

2.6.4. What are the treatment effects on white pine performance?

To assess the effects of vegetation suppression treatments on white pine performance, we tested for differences in stem diameter, cover, and percentage of trees reaching year the 10 height target of 2.5 m, between treatments. Each site was analysed separately using one-way ANOVAs with permutations (n = 999; Anderson, 2001; Borcard et al., 2011; Legendre, 2007) followed by post-hoc pairwise Bonferroni comparison to test for differences between treatments.

3. Results

3.1. How do vegetation suppression treatments alter the trajectory of community composition development over time?

3.1.1. Clearcut – ON

A total of 19 woody species and 24 herbaceous species were identified in the Clearcut site. Principal response curves for the site revealed that all treatments led to changes in species composition over the 10-year monitoring period when compared to plots that received *no suppression* treatment (RDA axis 1 = 64.8%, F = 217.41, p = 0.01) (Fig. 1a). Time explained 11% of the variance and the treatment × time interaction explained 67% of the variance. Changes were most pronounced between years one and three, after which composition remained relatively stable until year 10 (Fig. 1a). Post-hoc comparisons revealed significant differences between all vegetation suppression treatments relative to the *no suppression* treatment (Appendix Table S2a, $p < 0.001$). The species composition within *4-yr herb-only* treatment developed differently over time from that of the *10-yr woody-only*, *1-yr herb and woody*, and *4-yr herb and woody* suppression treatments (Fig. 1a, Appendix Table S2a). Positive scores for *Pteridium aquilinum*, Grass, and *Comptonia peregrina* indicate that these species benefited from conditions generated by treatments consisting of *10-yr woody-only* suppression, *1-yr herb and woody* suppression, and *4-yr herb and woody* suppression (Fig. 1a). *Populus tremuloides* became more prevalent in the *4-yr herb-only* treatment (Fig. 1a).

3.1.2. Shelterwood sites

A total of 32 woody species and 41 herbaceous species were identified at the two Shelterwood sites. At these sites, all vegetation suppression treatments altered species composition over time (RDA axis 1 = 52.9%, F = 76.96, p = 0.001) relative to the *no suppression* treatment. Time explained 11% of the variance and the treatment × time interaction explained 33% of the variance. Like Clearcut-ON, changes in species composition were most pronounced between years one and three

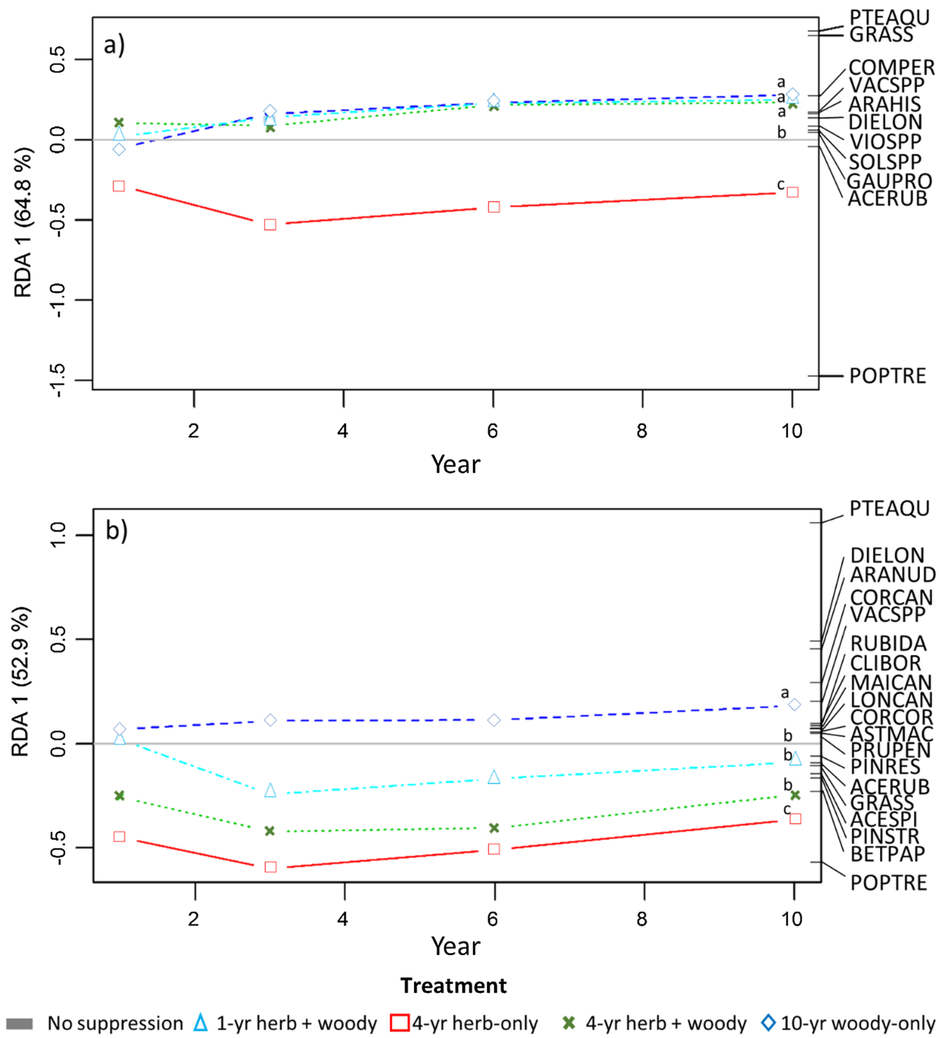

Fig. 1. Principal response curves (PRC) for the first axis of the RDA testing the effect of treatment × time on species composition, representing the dominant temporal trajectory the three planted white pine (*Pinus strobus*) sites, (a) Clearcut-ON and (b) Shelterwood sites. See Table 2 for treatment code and descriptions. Response curves for each treatment are presented, with the zero line representing the baseline condition (*No suppression*). PRCs with the same lowercase letter were not significantly different at year 10 (Significance based on Tukey post-hoc test, with Bonferroni correction). Species scores of the dominant species are displayed along the right-side vertical axis (species scores $\geq |0.05|$). Scores indicate how strongly each species is correlated with the temporal patterns displayed by the curves, and thus illustrate the main drivers of the temporal trajectories (positive score = positive correlation, 0 = no correlation, negative score = negative correlation). See Species codes in Appendix Table S4.

(Fig. 1b). Although the species composition of the treatments appear to converge towards the *a priori* baseline for comparison (i.e. *no suppression* treatment) over time, some significant differences between treatments remained in year 10 (Fig. 1b, Appendix Table S2b). Plots receiving *4-yr of herb-only* suppression or *10-yr woody-only* suppression were found to differ significantly from the *a priori* baseline and from each other, whereas *1-yr both herb and woody* and *4-yr herb and woody* suppression treatments did not (Fig. 1b, Appendix Table S2b). Species scores for *Pteridium aquilinum*, *Diervilla lonicera*, and *Aralia nudicaulis* indicate that these species benefited from conditions generated by treatments with *10-yr woody-only* suppression (Fig. 1b). *Populus tremuloides* and *Betula papyrifera* became more frequent throughout the experiment when compared to the *no suppression* treatment and were more prevalent in the *4-yr herb-only* treatment (Fig. 1b).

3.2. How do understory communities respond after 10 years?

3.2.1. Clearcut-ON

The two PCA axes of the Community-Weighted Mean (CWM) show trait distribution in relation to their relative importance for each treatment (Clearcut-ON site: Fig. 2a; Shelterwood sites: Fig. 2b). For Clearcut-ON, the first two axes explained 87.2% of the total variation (Fig. 2a). The first axis clearly separates the treatments, with the *no suppression* and the *10-yr woody-only* treatments on the left and the other treatments on the right. The *no suppression* treatment showed a high prevalence of tall (HT), shade intolerant species (LI), abundant seed producers (SDPRO), with small seeds (SDWT), and long dispersal ability (DI). Geophyte ferns (Ra_gf) with erect stems (Fol_e) spreading extensively though vegetative means (LE) were prevalent in the *10-yr woody-only* treatment. Multi-stemmed (Fol_mu), micro-phanerophytes (Ra_mc) were also associated with this treatment. Traits associated with the *1-yr* and the *4-yr herb and woody* suppression treatments included large seed size (SDWT), shade tolerance (LI), short stature (HT), low seed production (SDPR), and low dispersal ability (DD). The *4-yr herb-only* treatment tended to be associated with mono-stemmed (Fol_m) and meso-phanerophytes (Ra_mg).

3.2.2. Shelterwood sites

The first two axes of the PCA explained 86% of the total variation for the two shelterwood sites (Fig. 2b). Similar to Clearcut-ON, the first axis shows a clear separation in treatments with *no suppression* and *10-yr woody-only* treatments on the left and the other treatments on the right. Traits of species associated with the *no suppression* treatment included tall (HT), shade intolerant (LI), abundant seed producers (SDPRO), with small seeds (SDWT), and good dispersal ability (DI). Geophyte ferns (Ra_gf) with erect stems (Fol_e) spreading extensively though vegetative means (LE) were prevalent in the *10-yr woody-only* treatment. This treatment was also associated with multi-stemmed (Ra_mu) micro-phanerophytes (Ra_mc). Traits associated with the *1-yr* and the *4-yr herb and woody* suppression treatments included shade tolerant species (LI) that produce few large seeds (SDPRO, SDWT), with low dispersal ability (DI). The *4-yr herb and woody* suppression treatment was also associated with mono-stemmed (Fol_m) meso-phanerophytes (Ra_mg).

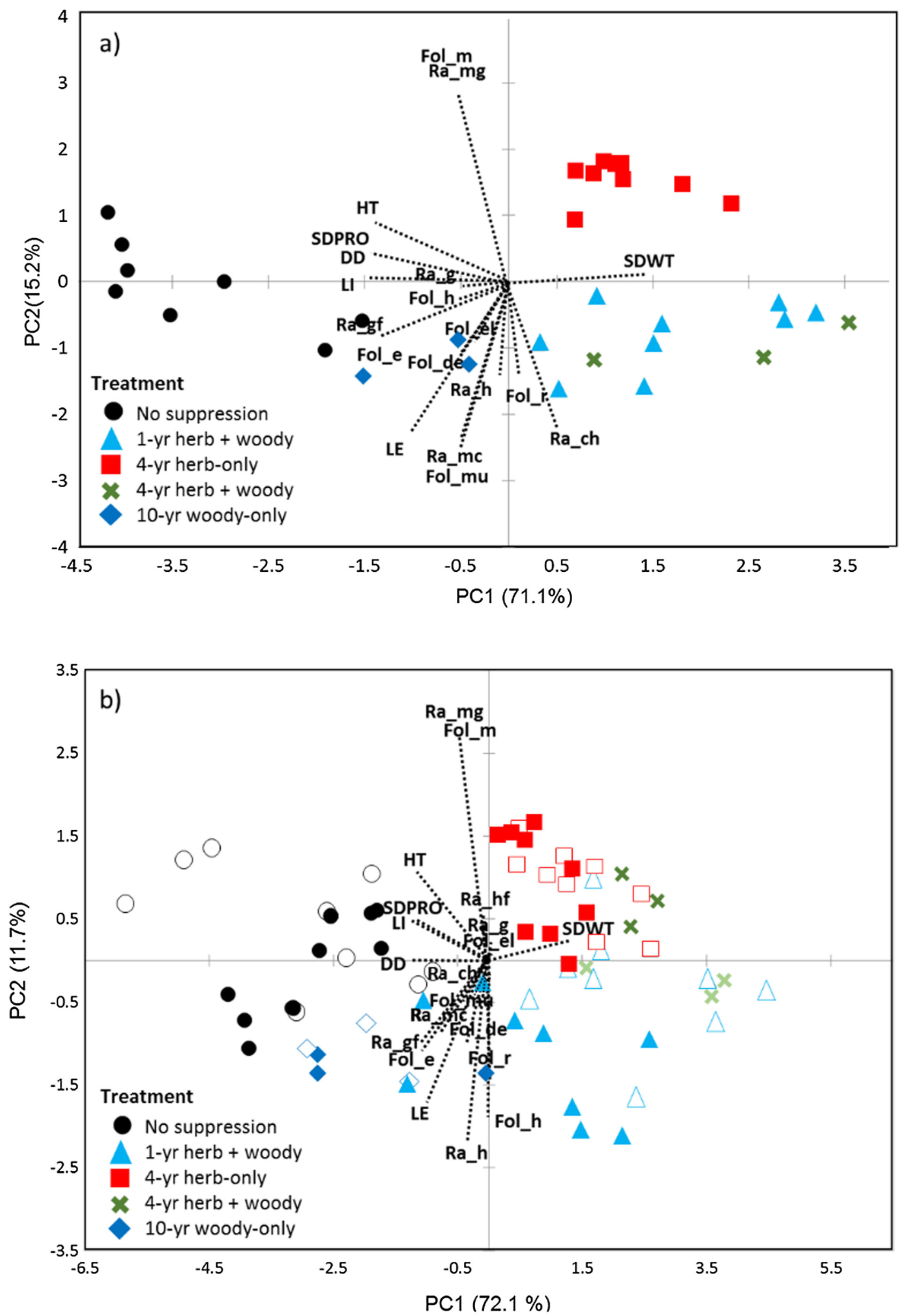

Fig. 2. Patterns in trait occurrences for the (a) Clearcut-ON site and (b) Shelterwood sites in Ontario (solid/dark), and New Brunswick (open/light) at year 10. See Table 2 for treatment code and description and Table 3 for trait code description. First two axes of the PCA conducted on the CWM trait × site matrix.

3.2.3. *Clearcut-ON*

The taxonomic and functional diversity indices responded similarly to the suppression treatments (ANOVA; Table 4). The taxonimic and functiona diversity were greatest in the *1-yr herb and woody suppression* treatment (S:15; FD:0.53), *no suppression* and the *4-yr herb and woody* suppression (S:14, 13; FD:0.51, 0.52, respectively) treatments. The *4-yr herb-only* treatment had the lowest taxonomic (S: 8) and functional diversity (FD: 0.15).

3.2.4. *Shelterwood sites*

For the shelterwood sites, taxonomic and functional diversity responses deferred from that of functional diversity (ANOVA; Table 4). Plots that received *no suppression*, *1-yr herb and woody*, or *10-yr woody-only* suppression treatments, had the highest values for taxonomic diversity (S:15.5, 13.5, 13.5 respectively). Plots that received *4-yr herb and woody,* and *4-yr herb-only* suppression treatments had the lowest taxonomic diversity (S:11 and 11.5 respectively). In terms of functional diversity, the *4-yr herb-only*, the *no suppression*, and the *1-yr herb and woody* suppression treatments had greatest values (FD: 0.49, 0.46, 0.44 respectively). The *4-yr herb and woody* and the *10-yr woody-only* suppression treatments had the lowest values (FD: 0.31 and 0.38 respectively).

Table 4
Diversity metrics: species richness (S) and Rao univariate index (FD). A different letter indicates a significant difference at $p < 0.05$ (one-way permutations ANOVAs with followed by a multiple comparison Bonferonni post-hoc test). FD level of significance was corrected for multiple testing using Holm's procedure.

Site	Diversity indices	Mean					ANOVA	
		No suppression	1-yr herb + woody	4-yr herb-only	4-yr herb + woody	10-yr woody-only	p-value	p-corrected
Clearcut-ON	S	14^{a}	15^{a}	8^{b}	13^{ab}	10^{ab}	< 0.001	**< 0.001**
Shelterwood-ON and Shelterwood-NB		15.5^{a}	13.5^{ab}	11.5^{b}	11^{b}	13.5^{ab}	< 0.001	**< 0.001**
Clearcut-ON	FD	0.51^{a}	0.53^{a}	0.15^{b}	0.52^{a}	0.46^{a}	< 0.001	**< 0.001**
Shelterwood-ON and Shelterwood-NB		0.46^{ab}	0.44^{b}	0.49^{a}	0.31^{c}	0.38^{bc}	< 0.001	**< 0.001**

Table 5
Statistical differences between mean percent cover for species identified as recalcitrant the three planted *Pinus strobus* L. sites (Clearcut-ON, Shelterwood-ON, Shelterwood-NB) 10 years following initiation of competition suppression treatments. Each site was tested separately using one-way ANOVAs with permutations (n = 999) with a post-hoc pairwise *t*-test to test for differences between treatments. See Table 2 for treatment codes and description. Bold text denotes statistical significance. [1]Treatment only included in analysis when testing herbaceous species because these treatments controlled for woody species for the duration of experiment. df = 4.

Species	Site	Mean cover					ANOVA		
		No suppression	1-yr herb + woody	4-yr herb-only	4-yr herb + woody[1]	10-yr woody-only[1]	Mean square	F value	p - value
Acer rubrum	Clearcut-ON	0.13	0.00	0.53	0.00	0.07	0.69	0.79	0.727
	Shelterwood-ON	30.53^{a}	7.57^{b}	36.51^{a}	0.06	0.64	2099.98	15.36	**< 0.001**
	Shelterwood-NB	27.28^{a}	7.57^{b}	30.83^{a}	0.40	0.86	1412.55	7.87	**0.004**
Acer spicatum	Clearcut-ON	0.83	0.13	0.03	0.00	0.53	1.70	4.38	0.019
	Shelterwood-ON	1.13	0.15	7.42	0.00	0.00	140.15	3.83	0.03
	Shelterwood-NB	–	–	–	–	–	–	–	–
Betula papyrifera	Clearcut-ON	–	–	–	–	–	–	–	–
	Shelterwood-ON	0.36	7.46	0.18	0.13	0.00	310.41	2.71	0.042
	Shelterwood-NB	27.87^{a}	7.77^{b}	30.60^{a}	1.19	0.00	1399.60	7.54	**0.005**
Corylus cornuta	Clearcut-ON	0.82	0.00	0.00	0.00	0.00	2.03	1.00	0.973
	Shelterwood-ON	7.9	2.66	0.30	0.00	1.33	136.52	11.23	**0.002**
	Shelterwood-NB	0.11	0.51	0.29	0.33	0.00	0.36	0.57	0.674
Epilobium angustifolium	Clearcut-ON	0.0	0.42	0.00	0.33	0.00	0.31	3.21	0.043
	Shelterwood-ON	0.0	0.03	0.00	0.00	0.50	0.17	2.93	0.062
	Shelterwood-NB	0.32	0.67	0.28	1.70	2.30	3.39	2.77	0.061
Kalmia angustifolia	Clearcut-ON	4.04^{a}	0.24^{b}	0.11^{b}	0.00	0.00	44.89	16.02	**< 0.001**
	Shelterwood-ON	–	–	–	–	–	–	–	–
	Shelterwood-NB	0.32	0.67	0.28	1.70	2.30	0.40	0.63	0.565
Populus tremuloides	Clearcut-ON	52.11^{a}	1.02^{c}	72.11^{b}	0.13	0.00	12095.56	77.65	**< 0.001**
	Shelterwood-ON	30.36^{a}	2.50^{b}	25.93^{a}	0.00	0.00	2017.13	14.77	**< 0.001**
	Shelterwood-NB	0.97	0.02	1.64	0.00	0.00	5.97	2.49	0.066
Prunus pensylvanica	Clearcut-ON	0.11	0.00	0.00	0.00	0.00	0.04	1.00	0.968
	Shelterwood-ON	0.1	4.57	0.03	0.07	0.00	60.76	4.09	0.003
	Shelterwood-NB	3.4	0.09	0.22	0.00	0.00	31.62	2.48	0.04
Pteridium aquilinum	Clearcut-ON	75.47^{a}	17.91^{b}	2.27^{b}	3.13^{b}	61.67^{a}	9714.07	64.34	**< 0.001**
	Shelterwood-ON	40.22^{a}	12.11^{b}	0.02^{b}	0.06^{b}	60.53^{a}	4222.83	25.50	**< 0.001**
	Shelterwood-NB	44.77^{a}	4.20^{b}	0.24^{b}	1.23^{b}	52.13^{a}	4792.47	72.03	**< 0.001**
Rubus allegheniensis	Clearcut-ON	0.0	0.36	0.00	0.00	0.00	0.38	1.33	0.307
	Shelterwood-ON	0.0	0.68	0.00	0.00	0.00	1.39	1.00	0.353
	Shelterwood-NB	0.0	0.40	0.00	0.00	0.00	0.48	1.91	0.096
Rubus idaeus	Clearcut-ON	0.0	0.36	0.00	0.00	0.00	0.38	1.33	0.302
	Shelterwood-ON	0.1	5.17	0.00	0.56	5.80	78.70	2.63	0.03
	Shelterwood-NB	0.89	1.86	0.00	2.49	8.35	7.75	2.46	0.076
Grass	Clearcut-ON	10.46	21.33	3.04	24.73	9.33	505.71	2.60	0.052
	Shelterwood-ON	0.67	0.64	0.27	0.33	0.73	0.29	0.73	0.586
	Shelterwood-NB	0.08	0.84	0.06	0.06	0.00	0.99	0.83	0.353

Table 6
Mean[1] treatment responses of planted white pine (*Pinus strobus* L.) at the three sites 10 years following initiation of competition suppression treatments. Each site was tested separately using one-way ANOVAs with permutations (n = 999). A post-hoc pairwise *t*-test with Bonferroni correction was used to test for differences between treatments. df = 4. See Table 2 for treatment description.

Variable	Site	Mean					ANOVA		
		No suppression	1-yr herb + woody	4-yr herb-only	4-yr herb + woody	10-yr woody-only	Mean Squared	F value	p-value
Stem diameter (mm) 5 cm AGL[3]	Clearcut-ON	30^{a}	56^{b}	52^{b}	82^{c}	37^{a}	1839.43	33.91	< **0.001**
	Shelterwood-ON	22^{a}	54^{b}	29^{a}	71^{c}	43^{b}	1708.60	34.52	< **0.001**
	Shelterwood-NB	29^{a}	60^{c}	50^{b}	74^{c}	42^{ab}	6730.44	25.32	< **0.001**
Percentage of Trees reaching 10 year target (P250)	Clearcut-ON	5^{a}	2^{a}	36^{b}	21^{ab}	0^{a}	1819.39	9.49	**0.002**
	Shelterwood-ON	20^{a}	70^{b}	31^{a}	97^{b}	59^{ab}	5464.40	11.98	< **0.001**
	Shelterwood-NB	21^{a}	70^{c}	59^{bc}	73^{c}	36^{ab}	3546.10	17.22	< **0.001**
Percent Cover	Clearcut-ON	13^{a}	22^{a}	42^{b}	56^{b}	10^{a}	1827.76	13.68	< **0.001**
Planted	Shelterwood-ON	12^{a}	37^{c}	17^{a}	54^{bc}	24^{ab}	1522.94	18.32	< **0.001**
White Pine	Shelterwood-NB	13^{a}	38^{bc}	34^{b}	53^{c}	18^{ab}	1419.45	13.30	< **0.001**
n		9	9	9	3	3			

[1] Values are averaged from surviving planted white pine (up to 25 trees) in each of n treatment plots at each site.

3.3. What are the responses of competitive species and interior forest species?

The *no suppression* treatment had greater cover of tall woody competitive species (*Acer rubrum*, *Betula papyrifera*, *Populus tremuloides*) than the *1-yr herb and woody* treatments (Table 5). The *4-yr herb-only* and the *10-yr woody-only* treatments also tended to have greater cover of tall woody competitive species than the *1-yr herb and woody* suppression treatment (Table 5). *Pteridium aquilinum* cover was greatest in the *no suppression* and *10-yr woody-only* treatments (Table 5). Although total cover of interior forest herb species was less than 5% in all sites and treatments, interior forest herbs were found to have greatest cover at Shelterwood-ON in the *1-yr herb and woody* treatment ($F_{4,28} = 16.93$, $p < 0.001$; Appendix Table S3).

3.4. What are the treatment effects on planted white pine performance?

There was a strong treatment effect on basal stem diameter at all sites ($p = 0.001$; Table 6). The smallest stem diameters in year 10 were consistently found in the *no suppression treatment* (22–30 mm). A moderate diameter growth response was achieved at each site in the *4-yr herb-only* suppression, *10-yr woody-only* suppression, and 1-*yr herb and woody* suppression treatments. For the *4-yr herb and woody* suppression treatment, stem diameters were more than double those of the *no suppression* treatment at each site (Table 6).

The percentage of trees reaching the year 10 height target of 2.5 m (P250) was affected by treatment at each of the three sites ($p \le 0.002$; Table 6). Only shelterwood sites had treatments that exceeded the year 10 height target for over 50% of stems. Plots with *no suppression* had the poorest performance, with the lowest P250 across the three sites (5 to 21%). At the shelterwood sites, intermediate heights were achieved in treatments with either *4-yr herb-only* (31–59%) or *10-yr woody-only* suppression (36–59%). The highest P250 values were achieved within the *4-yr herb and woody* suppression treatment (70–97%; Table 6). Overall, Clearcut-ON had the lowest P250 values (< 36%). At this site, the greatest P250 values were found in the *4-yr herb-only* (36%) and the *4-yr herb and woody* suppression treatments (21%).

Treatments caused differences in the cover of planted white pine at each of the three sites ($p = 0.001$) (Table 6). Plots with *no suppression* had the lowest white pine cover values across the three sites (12–13%). At the shelterwood sites, intermediate cover results were achieved with *4-yr herb-only* and with *10-yr woody-only* treatments. The greatest cover of planted white pine was found in the *1-yr* and *the 4-yr herb and woody* suppression treatments within the shelterwood sites (37–54%) (Table 6).

4. Discussion

In this study, we quantify understory response and white pine performance to a range of vegetation suppression treatments that varied in duration and intensity. By comparing three geographically distant sites managed under two harvest systems, we were able to find common patterns in response to the different treatments, allowing us to go beyond the limits of a regional context when informing silvicultural prescriptions. We identified treatments beneficial for tree performance and with minimal effect on understory community composition - a central goal of current silviculture.

An ideal treatment would release white pine from competition while allowing the understory community to recover quickly enough to converge toward the functional composition of a mature forest. Within the range of experimental treatments compared in this investigation, a single, second-season suppression of herbaceous and woody vegetation, which emulates current practices, was the most effective treatment in these regards (Tables 5 and 6). This treatment in the shelterwood sites provided white pine performance close to that of the more intense 4-yr suppression of both herb and woody vegetation where virtually all competition was eliminated for four growing seasons. Although it is generally accepted that conifer performance is positively related to the duration of vegetation suppression treatments (Wagner et al., 2006), several studies have found, similar to ours, that an early one-time treatment can produce comparable growth and performance in *Picea engelmannii, Picea glauca*, *Pinus banksiana* to those produced in suppression treatments applied annually over several years (Biring et al., 2003; MacDonald and Thompson, 2003).

Analysis of the trait distribution at year 10 (Fig. 2b) showed contrasting impacts of treatments on the understory plant functional composition. The *1-yr* and the *4-yr herb and woody* vegetation suppression treatments within the shelterwood sites had a greater prevalence of species with traits that included: shade tolerant, production of a few large seeds, and low seed dispersal ability (Fig. 2b). These traits are associated with interior habitats in several ecosystems (Dölle et al., 2008; Knapp et al., 2016; Messier et al., 2009). The 1-yr treatment also had higher taxonomic and functional diversity (Table 4). Several studies have reported that a single application of herbicide at initial stand development in conifer forests has only minor short-term effects on plant communities due to adaptation to disturbance-prone environments (Miller and Miller, 2004). Seed banks in the soil and crown, effective seed dispersal and re-sprouting ability, are all traits contributing to the resilience of boreal forest species that can rebound quickly provided no other compounding disturbance follows (Hart and Chen, 2006; Seidl et al., 2014).

By contrast, intensive, annual suppression of competing vegetation for several years can emulate short intervals of multiple disturbances that can have drastic effects on understory development (Donato et al., 2009; Pidgen and Mallik, 2013). Multiple disturbances can exert a strong filter on species capacity to survive, colonize and establish, promoting the establishment of species that are adapted to disturbances (i.e. fast-growing, pioneer species with small wind-dispersed seeds) to the competitive disadvantage of interior forest herbs (Haeussler et al., 2002). In our investigation the *4-yr herb and woody* suppression treatment was similar in terms of functional composition to the 1-yr treatment, but had lower taxonomic and functional diversity (Table 4; Fig. 2b). Several factors may explain the similarity between these two treatments. Good survival and growth of large seeded white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) seedlings that performed well in both the 4-yr and 1-yr treatments that provided suitable competition free growing conditions. Greater canopy cover of planted and naturally regenerating pine species found within this more intense treatment (Table 6) also resulted in a rapid recovery of understory environmental conditions (i.e. light availability and microclimate) that were more suitable for interior forest species. Other studies have also found faster recovery of interior forest species in previously harvested sites following canopy closure (Jones et al., 2012; Scheller and Mladenoff, 2002). Low taxonomic and functional diversity observed within the 4-yr treatment may be the result of shifts in community composition in response to environmental filters imposed by a reduction in light availability that converged composition to a more functionally similar community better adapted to these conditions (Mayfield et al., 2010; Sabatini et al., 2014). These findings could have management implications as there is a growing consensus that biodiversity can play a key role in promoting ecosystem stability and resilience to disturbance on the basis that more functionally diverse systems will be more likely to compensate for the environmentally driven decline of other species (Hallett et al., 2017).

Treatments that suppressed only one specific competitive component, the *10-yr woody-only* or the *4-yr herb-only* suppression treatments, appeared to cause major shifts in community composition. This was due to the prevalence of competitive species that were favoured in these treatments at the end of our 10 year study (Fig. 1, Table 6). We found that *Pteridium aquilinum* tended to dominate treatments with *10-yr woody-only* suppression at all three sites, whereas the *4-yr herb-only* suppression treatment tended to be dominated by competitive trees and tall shrubs, primarily *Populus tremuloides*, *Betula papyrifera* and *Acer rubrum* in both shelterwood sites (Fig. 1, Table 5).

Other studies have also shown that suppression of non-woody species increases abundance and cover of competitive woody species, while the suppression of woody species alone typically favours the release of competitive herbaceous species (de la Cretaz and Kelty, 1999; Miller et al., 2003). Minimal gains and some volume losses have been observed in *Pinus taeda* plantations in the Southeastern United states when either herbaceous-only or woody-only vegetation were suppressed as a result of severe competition from remaining vegetation (Miller et al., 2003). In contrast, reductions in mean growth were not observed when either herbaceous-only or woody-only vegetation were suppressed within *Pinus patula* and *Pinus tecunumanii* plantations within a South African study because vegetation was never found to have reached competitive levels in this study (Little et al., 2018). Disturbances such as logging and vegetation suppression can increase colonization potential by freeing up space and increasing availability of light and soil moisture for opportunistic species (Balandier et al., 2006; Davis et al., 2000). The establishment of competitive species into disturbed areas, either woody or herbaceous, means that positive effects on crop trees can be only temporary (Balandier et al., 2006). These competitive species can then become a management problem themselves, by forming a recalcitrant layer, reducing not only crop tree growth but also limiting successional development of the overall plant community (Royo and Carson, 2006).

In the present study we also found high taxonomic diversity but low functional diversity following *10-yr woody-only* suppression in the shelterwood sites (Table 4). Differences in taxonomic and functional response to this treatment may be the result of intense light competition from a dense fern layer that is limiting species composition to a more functionally similar community (Mayfield et al., 2010; Sabatini et al., 2014). We found the opposite response in the *4-yr herb-only* suppression treatment within shelterwood sites where we observed the lower taxonomic diversity but the highest functional diversity compared to other treatments. This difference in response could be the result of an initial suppression of species that then allowed for recolonization of species with more diverse functional types (Mayfield et al., 2010). Due to the roles functional composition and diversity play in the regulation and maintenance of key ecosystem processes, the use of these complementary taxonomic and functional metrics can provide important information on the potential impacts of vegetation suppression on the long-term stability of ecosystem function (Chillo et al., 2018; Díaz and Cabido 2001; Sabatini et al., 2014).

The release and dominance of *P. aquilinum* in the *10-yr woody-only* suppression treatment and the dominance of deciduous tree species in the *4-yr herb-only* suppression treatment are of particular concern because both can remain locally dominant for several decades (Balandier et al., 2006; Douterlungne et al., 2013). Success of *P. aquilinum* as a competitor is attributed to its extensive rhizomes containing considerable carbon stores, nutrients and dormant buds. Rapid growth allows this species to quickly develop dense understory layers that compete aggressively for light with other forest herbs. *P. aquilinum* also causes the accumulation of a thick litter layer containing potentially phytotoxic compounds that can limit establishment of other species (Dolling, 1996; Milligan et al., 2016). By comparison, competitive overstory tree species are considered one of the longest persisting competitive groups (Balandier et al., 2006). Traits that make *P. tremuloides*, *B. papyrifera*, and *A. rubrum* strong competitors include their ability to colonize quickly through abundant seed production, effective resprouting ability, and rapid juvenile growth that allows them to overtake neighbouring trees quickly following establishment (Johnson et al., 1987; Landhäusser and Lieffers, 1998; Lavertu et al., 1994; Safford et al., 1990). The strong competitive nature of *P. aquilinum* and of deciduous trees along with their ability to dominate communities for long periods of time, suggest that beyond the challenges they pose at stand initiation, they may create longer term issues that affect future rotations. These changes in community composition can also cascade into changes in ecological services and functions that these systems provide (Milligan et al., 2016; Mori et al., 2017).

Although we did not attempt to statistically compare the two harvest systems (clearcut vs. shelterwood), we observed differences in responses to the treatments within them. The Clearcut-ON site remained dominated by competitive, shade intolerant species, including *P. aquilinum*, Grass, *Comptonia peregrina* and *P. tremuloides* (Fig. 1, Table 5). In contrast, we observed a more rapid convergence of plant community composition in the vegetation suppressed treatments at shelterwood sites towards similar composition of the *no suppression* treatment. Lower tree retention in clearcuts than in shelterwoods is likely to affect understory development (Macdonald and Fenniak, 2007). Clearcuts are known to be colonized quickly by fast growing, early successional species because these species can more efficiently utilize newly available resources (Parker et al., 2009; Thompson and Pitt, 2003). *No suppression*, *1-yr* and *4-yr herb and woody suppression* treatments had higher taxonomic and functional diversity in the clearcut site. However, white pine suffered from strong competition combined with increased occurrence of weevil attack that resulted in stunted height and poor form (Pitt et al., 2016). This suggests that clearcut harvesting may be unsuitable for the effective regeneration of white pine unless additional measures are taken to mitigate effects of both weevil and competition (Hébert and Thiffault, 2015; Parker et al., 2010, 2009; Pitt et al., 2016)

5. Conclusions

There is growing support in the literature that biodiversity can play a key role in promoting ecosystem stability. Diverse forests can support a greater number of ecosystem services (Hallett et al., 2017; Hisano et al., 2018); can be more resistant to insect pests and disease (Carnus et al., 2006); and can recover more quickly following extreme drought events (Sousa-Silva et al., 2018; Van Ruijven and Berendse, 2010). Furthermore, changes in functional composition in response to vegetation suppression can have a strong influence on key ecosystem processes such as biogeochemical cycles, decomposition, as well as food availability and habitat for wildlife and insect pollinators (Lindenmayer et al., 2006; Sabatini et al., 2014). Since silviculture prescriptions will need to be capable of providing sustainable yield while mitigating the risks of climate change and evolving societal needs (Franklin et al., 2018), studies investigating the impacts of vegetation suppression practices on both crop tree productivity and biological conservation are needed to improve management options available.

Findings from our study suggest a balance can be struck between sustainable fiber production and conserving plant biodiversity within managed forests. For regenerating white pine, management practices that provide early release from competition and conserve enough canopy cover are necessary to favour white pine seedling survival and growth while allowing the understory community to recover. Comparing the magnitude of change in understory community to gains in crop tree performance will help identify future vegetation suppression strategies that manage competitive vegetation, minimize the effects on plant community composition, and enhance crop tree performance. Our use of a complementary set of taxonomic and functional metrics provides a mechanistic understanding of understory recovery that may serve as an empirical basis on which to develop silviculture prescriptions. The use of functional metrics also provides unique insights regarding disturbance intensity that support understory recovery in areas with similar forest composition and may also allow for future comparisons (Scolastri et al., 2017). Forest managers could use this information to define management objectives and create similar outcomes using the tools available to them

Acknowledgements

This research was made possible by funding from the Canadian Forest Service and the Ontario Ministry of Natural Resources and Forestry, and project support from SERG International. We would like to thank L. Boisvert-Marsh who performed data structuring, assisted with data analysis, and reviewed the manuscript. Thanks to N. Thiffault, K. Chapman, and F. Cardou, and two anonymous reviewers for providing useful suggestions for improving this manuscript. This investigation would not have been possible without the infrastructure of the original white pine competition studies, which were financially supported by the Canadian Ecology Centre-Forestry Research Partnership (Tembec, Canadian Forest Service, Ontario Ministry of Natural Resources and Forestry); Living Legacy Trust; Canada Foundation for Innovation; Enhanced Forest Productivity Science Program-Forestry Futures Trust Ontario; Ontario Innovation Trust Fund; Monsanto Canada Inc.; Dow AgroSciences Canada Inc.; Collège Boréal; Domtar Corporation; Nipissing Forest Resource Management Inc.; J.D. Irving Limited; Forest Protection Limited; SERG International; Upper Lakes Environmental Research Network; and the U.S. Forest Service. During the establishment years, W. Bell and M. Irvine were instrumental in facilitating OMNRF funding and support. Thanks to A. Morneault and L. Lanteigne who led vegetation surveys.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.09.038.

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