Aspects of ecological development in managed stands of jack pine and black spruce in northern Ontario: Understory vegetation and nutrient relations

by S.L. Hunt¹, A.M. Gordon¹ and D.M. Morris²

ABSTRACT

This study investigated relationships between understory vegetation and nutrient pools in managed stands of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP) in the Lake Nipigon region of northern Ontario. The species composition, biomass, and nutrient pool sizes in the understory vegetation, as well as biomass and nutrient pools in trees and soils, were determined in 16 managed stands ranging in age from 10 to 53 years since establishment and one mature, natural stand. Patterns of above-ground biomass accumulation in understory vegetation varied with overstory tree species and general site type (dry, sandy soils, or mesic, finer-textured soils). Understory vegetation contributed little (0.3 to 2.6%) to total above-ground organic matter (live biomass plus forest floor) but accounted for higher proportions of total above-ground nutrient pools (e.g., 0.7 to 3.4% of N; 3.2 to 11.7% of K) and net primary productivity (1.2 to 21.2%). The species composition of the understory vegetation was strongly related to stand basal area as well as to concentrations of nutrients (N, P, K, Ca, Mg) in the forest floor and mineral soil. The greatest amount of change in vegetation community composition occurred from the pre- to post-canopy closure stages of stand development; fewer differences were observed among stands of a given species and site type 35 to 50 years after establishment. The effects of silvicultural practices were detected in certain stands 35 years after establishment; for example the most severely treated (bladed and thinned) jack pine stand differed from other stands of similar age and soils with its *Cladina/Vaccinium*-dominated understory, and large amounts of biomass in the moss/lichen stratum. The understory vegetation communities in other managed jack pine stands, by 35 to 50 years, were similar to that of the mature, natural stand, indicating resilience to silvicultural disturbances. Silviculture may have lasting effects on understory vegetation biomass and species composition through its effects on stand basal area, overstory species, and soil nutrients. This research serves as baseline information for further studies into the ecology of managed stands in northern Ontario.

Key words: understory, nutrients, managed forests, jack pine, black spruce, canonical correspondence analysis

RÉSUMÉ

Cette étude s'attarde aux relations entre la végétation en sous-étage et les sources d'éléments nutritifs dans des peuplements aménagés de pin gris (*Pinus banksiana* Lamb.) et d'épinette noire (*Picea mariana* [Mill.] BSP) de la région du Lac Nipigon du nord de l'Ontario. La composition en fonction des espèces, de la biomasse et de la taille des sources d'éléments nutritifs a été relevée dans 16 peuplements aménagés dont l'âge variait de 10 à 53 ans depuis l'établissement et dans un peuplement mûr naturel. Les modèles d'accumulation de la biomasse au-dessus du sol de la végétation en sous-étage variaient en fonction des espèces d'arbres du couvert et du type général de la station (sec, sols sableux ou sols secs à texture fine). La végétation en sous-étage contribuait pour peu (0,3 à 2,6 %) à la matière organique totale au-dessus du sol (biomasse vivante plus litière), mais comptait en plus grandes proportions au niveau des sources d'éléments nutritifs au-dessus du sol (p. ex., 0,7 à 3,4 % de N; 3,2 à 11,7 % de K) et de la productivité primaire nette (1,2 à 21,2 %). La composition des espèces au niveau de la végétation en sous-étage était fortement reliée à la surface terrière du peuplement ainsi qu'aux concentrations d'éléments nutritifs (N, P, K, Ca, Mg) de la litière et du sol minéral. La plus importante modification dans la composition floristique de la végétation se retrouvait au niveau des stades de pré- et de post-fermeture du couvert dans le développement du peuplement; les différences les plus faibles ont été observées dans les peuplements d'une espèce et d'un type de station donné, entre 35 et 50 ans après l'établissement. Les effets des pratiques sylvicoles ont été détectés dans certains peuplements de 35 ans après l'établissement; à titre d'exemple, le peuplement le plus sévèrement traité (sol dégagé par un buteur et éclairci) de pin gris était différent des autres peuplements d'âge semblable et sur sol similaire avec son sous-étage dominé par *Cladina/Vaccinium* et les grandes quantités de biomasse dans la strate de mousse et de lichen. Les communautés floristiques en sous-étage dans les autres peuplements aménagés de pin gris âgés de 35 à 50 ans, étaient semblables à celles du peuplement mûr naturel, indiquant une résilience aux perturbations sylvicoles. La sylviculture pourrait engendrer des effets durables sur la biomasse floristique et la composition des espèces par ses effets sur la surface terrière du peuplement, sur les espèces du couvert et sur les éléments nutritifs du sol. Cette recherche représente une base d'information pour d'autres études sur l'écologie des peuplements aménagés du nord de l'Ontario.

Mots clés : sous-étage, éléments nutritifs, forêts aménagées, pin gris, épinette noire, analyse de correspondance canonique

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Introduction

Managed, second-growth forests (including plantations and naturally regenerated post-harvest stands subjected to precommercial thinning and/or other treatments) are increasingly becoming a common feature on the northern Ontario landscape. However, little is known about the ecological structure and function of these stand types, especially in

mid- to late-rotation. The creation of an information base that can be drawn upon when assessing the impacts of intensive silviculture is important in light of the current need for ecosystem-based management strategies. One little-studied component of managed forests in North America is understory vegetation. Often the target of control measures early in the rotation of a new forest, understory vegetation is nevertheless an important part of the boreal ecosystem in terms of its contribution to biodiversity (Qian *et al.* 1998), wildlife habitat (Johnson *et al.* 2003), nutrient dynamics (Wurtz 1995), net primary productivity (NPP) (O'Connell *et al.* 2003), and even site mycorrhizal status (Hagerman *et al.* 2001). The successional changes in understory vegetation in several northern Ontario jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP) stands from 1978 to 1998 were studied by Hunt *et al.* (2003). The current study encompasses a larger number of stands for which data on both species composition and nutrient pools (soil and vegetation) were collected in 1998 and 1999. The study had the following main objectives: 1. to determine the amounts of biomass and nutrients held in the understory vegetation, evaluate changes in these pools over time, and compare stands of different species and site types; 2. to estimate the contribution of the understory vegetation to above-ground stand biomass, nutrient pools and NPP; 3. to characterize the species composition of understory vegetation communities and its relationship to soil nutrients and other environmental variables.

This study was carried out in managed stands subjected operationally to various silvicultural treatments at the discretion of forest managers, rather than as part of a controlled experimental design. We acknowledge that the vari-

ety of different silvicultural treatments applied to the stands in this study makes it impossible to conclusively determine the effects of specific practices on the structure of the understory vegetation communities, except in a small subset of stands similar in age, soils, and location. This study, therefore, serves as a first look into understory vegetation and site nutrient relations in managed stands of different ages, for which little information is currently available, especially in managed boreal forests. This study can provide forest managers with information about the general implications of management-induced alteration of environmental factors (such as soil nutrient concentrations and crop tree basal area) for understory vegetation communities. This information also provides a basis for monitoring activities as well as hypothesis generation for future research in the managed forests of northern Ontario.

Site Description

Study sites were located to the east of Lake Nipigon, near the town of Beardmore, Ontario (49.5° N; 88° W). Included in this portion of the study were five black spruce stands, ranging in age from 12 to 38 years since establishment, and 11 jack pine stands, ranging in age from 10 to 53 years since establishment, all on well-drained, upland sites (soils ranged from pure sands to silty clays). Stands were divided into groups based on species and general site type (dry, sandy soils, or mesic, finer-textured soils). One mature, natural jack pine stand in the area was included as a general reference stand. Stand management histories varied, ranging in intensity from precommercial thinning of naturally regenerated post-fire stands, to post-harvest site preparation, planting, and vegetation control (Table 1).

Materials and Methods

In each plantation, four 15 m X 15 m plots were established to obtain mensurational data and to measure selected ecological variables, including soil nutrient concentrations (N, P, K, Ca, Mg; forest floor and top 15 cm of mineral soil) used in the analysis of links between understory vegetation community dynamics and environmental factors. Within each plot, five 1 m X 1 m quadrats were located by treating the plot as a grid and drawing random numbers to determine the coordinates of each quadrat (resulting in 20 quadrats per stand; these were used to inventory understory vegetation). The presence and percent cover of each species of understory vegetation (lichens and mosses, herbaceous plants, shrubs, and tree seedlings) were noted and recorded. Nomenclature of lichens, mosses, and vascular plants followed Brodo *et al.* (2001), Crum (1976), and Gleason and Cronquist (1991), respectively. Vegetation inventories were conducted in mid-summer (mid-July to mid-August), 1998 and 1999.

Destructive sampling was carried out on one quadrat per plot over the course of one week in late July, 1999, to measure the above-ground biomass of each layer of understory vegetation. The size of the area sampled depended on the vegetation stratum: 1 m X 1 m for shrub biomass, 0.5 m X 0.5 m for herbaceous biomass (prostrate shrubs, e.g., *Epigaea repens* L., were included in this category), and 0.25 m X 0.25 m for moss/lichen biomass. Shrub biomass was divided into leaves and stems. All above-ground biomass within each sampling category was clipped and stored in

Table 1. Stand identification codes, management histories and general stand information for managed second-growth stands of jack pine (P) and black spruce (S) in the Lake Nipigon area of northern Ontario.

Stand	Management history	Stand age (years since establishment)	Mean tree height (m)	Basal area (m ² · ha ⁻¹)	Soil texture ¹ and site-type group
P2	Harvested, planted, some natural regeneration	31	14	34	fS (dry)
P3	Harvested, site prepared by blading, seeded, thinned (precommercial)	34	11	23	fS (dry)
P4	As in P3, but not thinned	34	14	32	fS (dry)
P5	Harvested, planted, competing vegetation controlled	36	15	32	LvfS (mesic)
P7	Original stand burned (wildfire), salvage harvested, natural regeneration thinned (precommercial), competing vegetation controlled	38	15	30	SivfS (mesic)
P8	Original stand burned (wildfire), salvage harvested, planted, some natural regeneration	39	16	32	SiL (mesic)
P10	Harvested, burned (escaped prescribed burn), planted	47	18	25	fS (mesic)
P11	Original stand burned (escaped prescribed burn?), natural regeneration thinned (precommercial)	53	19	34	SiL (mesic)
P13	Salvage harvested (after budworm infestation), burned (prescribed), planted	10	4	7	vfS (dry)
P14	Natural reference stand (natural regeneration after 1920s wildfire)	~ 75	19	35	Si
P15	Harvested, planted	35	16	28	Si (mesic)
P16	Harvested, planted	14	7	14	SivfS (mesic)
S1	Harvested, burned (wildfire), planted	37	11	34	Si (mesic)
S2	Harvested, burned (escaped prescribed burn?), planted, competing vegetation controlled	38	11	44	SiS (mesic)
S5	As in S2	37	8	32	SiC (mesic)
S7	As in P5	36	10	32	SiS (mesic)
S10	Harvested, planted 1986	12	4	4	SivfS (mesic)

¹texture of the top 15 cm layer of mineral soil: fS=fine sand; LvfS=loamy very fine sand; Si=silt; SiC=silty clay; SivfS=silty fine sand; SiL=silty loam; SiS=silty sand; SivfS=silty very fine sand; vfS=very fine sand

paper bags before being oven dried at 65°C, cooled in a desiccator, and weighed. For determination of nutrient content (N, P, K, Ca, Mg), tissues of the dominant species (i.e., with the highest percent cover) within each stratum were then ground in a Wiley mill to pass through a 2-mm mesh screen. Directly prior to chemical analysis ground samples were dried again at 65°C and cooled in a desiccator. Total N and P content was determined by Kjeldahl digestion (Nelson and Sommers 1980), followed by colorimetric analysis on a Technicon II Autoanalyser. Total K, Ca, and Mg were determined by H₂O₂/H₂SO₄ digestion (Parkinson and Allen 1975) followed by atomic absorption (Ca and Mg) or flame emission (K) spectrophotometry (AAS Model 251, Instrument Laboratories, Inc.). Ca and Mg analyses were conducted in the presence of lanthanum oxide (Parkinson and Allen 1975, Simard 1993). Concentrations of the measured elements were combined with understory biomass measurements to estimate nutrient pool sizes. Nutrient analyses of understory vegetation were performed only on samples of the dominant species from each stratum in order to obtain information about the nutrient content of important individual species while providing a reasonable

estimate of total above-ground nutrient pools in each stratum of the understory vegetation.

Sampling of the forest floor (O horizon) and top 15 cm of the mineral soil (samples were taken from the B-horizon to represent the surface mineral soil) was conducted in mid-summer 1999. Three samples each of the forest floor and mineral soil were taken from randomly selected points within each 15 m X 15 m plot. One sample each of the forest floor and mineral soil within each plot was collected volumetrically for bulk density determinations. Samples were kept frozen until processing in the lab. Samples were then air dried and ground to pass through a 1-mm mesh, after the removal of visible roots.

Total N and P were determined for both mineral soil and forest floor samples by Kjeldahl digestion and colorimetric analysis using a Technicon II Autoanalyser. Total K, Ca, and Mg content of forest floor samples were determined on H₂O₂/H₂SO₄ digests, while exchangeable K, Ca, and Mg in mineral soil were determined on neutral NH₄OAc (ammonium acetate) extracts. Digests and extracts were analysed for K, Ca, and Mg by atomic absorption or flame emission spectrophotometry as described above.

Basal area was calculated for each plot using diameter at breast height (dbh) and stem density measurements. Above-ground biomass of the crop trees was estimated from dbh measurements and biometric equations. Above-ground tree nutrient pool sizes were determined by applying values of nutrient concentrations in tree tissues (obtained from nine destructively sampled trees per plot, tissues of which were analysed for total N, P, K, Ca and Mg as described above) to tree biomass estimates. Estimates of above-ground net primary productivity (ANPP) were obtained in a subset of stands (two black spruce stands and six jack pine stands) chosen to represent the range of ages and site types encountered in the full set of stands. ANPP was estimated as the sum of annual wood production (calculated from tree dbh measurements and biomass equations), foliar production (derived from measurements of foliar litterfall over a three-year collection period), and the above-ground biomass of shrub foliage and herbs (assumed to represent annual production, but results in a conservative estimate as mosses, lichens, and shrub stems were not included).

Standard univariate statistics (ANOVA, Duncan's Multiple Range Test) were used to investigate differences in understory biomass and nutrient pools among stands of different site types. An alpha level of 0.05 was chosen to represent statistical significance. A chronosequence approach (using stands of different ages as a surrogate for stand development over time) was used to investigate temporal trends within each of three species/site type groups: jack pine on dry sites (10 to 47 years since establishment), jack pine on mesic sites (14 to 53 years), and black spruce on mesic sites (12 to 38 years). One mature, natural jack pine-dominated stand in the area was used for general comparison with the managed stands. While we acknowledge that it would be valuable to include a suite of naturally disturbed and regenerated stands for more direct and meaningful comparisons with the managed stands, this was not possible within the scope of the study, as our objective was to include as many managed stands as possible, covering a range of ages, species and site types. Future research in this area should involve replicate stands stratified by management history, as well as age and site type; this will only become possible as more managed stands at different rotation stages become available in northern Ontario (mid- to late-rotation managed stands are still rare in northern Canada). Coupled with a suite of natural stands with a similar age range, direct comparisons of the effects of natural versus silvicultural disturbance could then be made (Haeussler *et al.* 2002).

Relationships between understory species composition and site nutrition variables (concentrations of N, P, K, Ca, Mg in the forest floor and top 15 cm layer of mineral soil) were explored using multivariate analysis (Canonical Correspondence Analysis (CCA), Kovach 1998). Although the purpose of this part of the study was to determine the importance of soil nutrients in explaining the variation seen in understory community composition among stands, we also included other environmental variables known to be important to the distribution of species in forest understories, namely basal area (as a surrogate measure of light availability; Okland *et al.* 1999), and soil texture (as a surrogate for moisture availability). Only species present in at least 5% of all quadrats were included in the ordination analysis, as

rare species have a disproportionately large effect on the outcome of the analysis that may obscure ecological relationships (Gauch 1982). Analyses were performed on various configurations of the data. First, all stands were subjected to the analysis, then a subset of three adjacent jack pine stands of similar age and soils but differing in management history were analysed separately to investigate differences due to silvicultural treatment. The relative positions of stands did not change whether ordinations were done on individual plots or stand averages, so for ease of interpretation, stand averages were used in the presentation of results from the all-stands ordination, while individual plots were used in the three-stand ordination to allow for finer-scale interpretation of this small subset of stands.

Results

Biomass and nutrient pools in above-ground understory vegetation
Above-ground biomass of understory vegetation (mosses, lichens, herbs, shrubs) in managed jack pine and black spruce stands ranged from 387 to 2231 kg · ha⁻¹, and contained 5 to 19 kg N · ha⁻¹, 0.9 to 5 kg P · ha⁻¹, 5 to 30 kg K · ha⁻¹, 3 to 20 kg Ca · ha⁻¹, and 0.7 to 4 kg Mg · ha⁻¹. Understory biomass and nutrient pools in the mature, natural jack pine stand also fell within these ranges, and were most similar to those in the 53-year-old jack pine stand in the mesic group. Among mid-aged stands (31–39 years of age) grouped by species and site type, average above-ground understory vegetation biomass was significantly smaller ($P = 0.011$) in the black spruce stands on mesic sites (Fig. 1a). No significant difference was found between jack pine stands on mesic versus dry sites, although the contributions of the different vegetation strata to the total differed among stand groups. Jack pine stands on mesic sites contained more herb and shrub biomass and less biomass in the moss/lichen stratum than jack pine stands on dry sites.

Pools of nutrients (N, P, K, Ca, Mg) in the above-ground understory vegetation did not differ significantly (P values ranged from 0.053 for K to 0.781 for Mg) among species/site type groups in the ~35 year old category (Fig. 1 b–f). Concentrations of nutrients were generally higher in the tissues of species dominating the black spruce stands (e.g., *Aster macrophyllus* L., *Rubus pubescens* Raf.) than in those dominating the mesic jack pine stands (*Cornus canadensis* L., *Diervilla lonicera* Mill.) and dry jack pine stands (*Cladina* spp., *Epigaea repens* L., *Vaccinium* spp.) (Table 2), resulting in similar nutrient pools sizes in the mid-aged stands despite the significant differences in biomass.

Understory vegetation biomass and nutrient pools in the 53-year-old jack pine stand and the mid-aged black spruce stands, all on mesic sites, were similar to those in the mature, natural jack pine stand (Fig. 1 a–f).

Temporal trends in above-ground understory vegetation biomass depended on stand species and site type (Fig. 1a). In mesic jack pine stands, understory biomass increased from 10 to 35 years, then declined from 35 to 50 years. The youngest stand in this group was approaching canopy closure, and, thus, competition with the overstory for resources (light, moisture, nutrients) appears to have resulted in the relatively low understory biomass. By mid-age, the canopies in these stands were more open, due in part to a precommercial thinning that occurred in at least two of the four stands. This likely resulted in the increase in understory

Fig. 1. Biomass (a) and N (b), P (c), K (d), Ca (e), and Mg (f) in the understory vegetation of managed jack pine and black spruce stands grouped by species ("Pj" = jack pine, "Sb" = black spruce), age (years since establishment), and site type (dry or mesic). Data from a mature, natural jack pine stand ("ntrl Pj") is given for comparison. Standard errors are shown for categories consisting of more than one stand. Bars marked with different letters are significantly different ($P < 0.05$) based on ANOVA (GLM) and Duncan's multiple range test.

biomass in the 35-year-old stands. The higher shrub biomass in the oldest stand likely resulted in the shading out of herbaceous and moss/lichen strata, effectively lowering the overall biomass of the understory. In jack pine on dry sites, understory vegetation declined from 10 to 35 years, as early-successional shrubs such as *Rubus idaeus* L. succumbed to increasing shade, then increased from 35 to 50 years, due to the increasing biomass of both the moss/lichen and herbaceous vegetation strata (including prostrate shrubs such as *Epigaea repens* L., a prominent species in the oldest dry jack pine stand). In black spruce stands on mesic sites, understory vegetation declined from 10 to 35 years, as herb biomass remained low and the biomass of the moss/lichen and shrub strata declined, coinciding with the development of densely closed canopies in these stands.

Patterns of change over time in understory vegetation nutrient pools within each species/site type group were similar to the biomass patterns, with the exception of N, K, Ca and Mg in the dry jack pine group and Ca in the mesic black spruce group. In these stands, Ca pools changed little over time. In the jack pine stands on dry sites, N, K, and Mg pool sizes exhibited a distinct U-shaped pattern over time, decreasing from 10 to 35 years, then increasing from 35 to 50 years. Large nutrient pools in the oldest dry jack pine stand were the result of a high accumulation of low-nutrient biomass, while in the youngest dry jack pine stand, moderate amounts of biomass with high nutrient concentrations also resulted in relatively large nutrient pools. The vegetation species first to become established on disturbed sites (i.e., post-harvest) are generally opportunistic and

Table 2. Nutrient concentrations of the tissues of dominant species of understory vegetation in jack pine and black spruce stands. Where samples of a given species from more than one stand were analysed, standard errors are given in parentheses. Species within each stratum are listed in order of nitrogen concentration (lowest to highest). Species with the lowest nutrient concentrations are most common in jack pine stands on dry sites, while those with the highest concentrations are most common in black spruce stands on mesic sites.

Species	Tissue nutrient concentrations (%)					
	N	P	K	Ca	Mg	
Moss/lichen layer						
<i>Cladina rangiferina</i>	0.44 (0.09)	0.11 (0.04)	0.56 (0.36)	0.26 (0.19)	0.04 (0.02)	
<i>Dicranum polysetum</i>	0.85	0.21 (0.02)	0.74 (0.05)	0.35 (0.02)	0.11 (0.01)	
<i>Pleurozium schreberi</i>	0.99 (0.07)	0.24 (0.01)	0.91 (0.05)	0.33 (0.02)	0.11 (0.00)	
<i>Polytrichum commune</i>	1.15 (0.01)	0.17 (0.00)	0.92 (0.16)	0.27 (0.01)	0.14 (0.02)	
<i>Polytrichum juniperinum</i>	1.38	0.16	0.64	0.28	0.10	
Herb layer						
<i>Lycopodium clavatum</i>	0.67 (0.24)	0.17 (0.05)	1.09 (0.18)	0.10 (0.05)	0.09 (0.03)	
<i>Epigaea repens</i>	0.95 (0.04)	0.15 (0.00)	0.87 (0.00)	0.42 (0.03)	0.18 (0.01)	
<i>Cornus canadensis</i>	0.98 (0.21)	0.29 (0.02)	1.29 (0.07)	2.37 (0.13)	0.44 (0.02)	
<i>Clintonia borealis</i>	1.26	0.32	6.15	0.90	0.21	
<i>Lycopodium obscurum</i>	1.46	0.19	0.92	0.09	0.12	
<i>Hieracium auranticum</i>	1.53	0.27	4.35	1.36	0.54	
<i>Fragaria virginiana</i>	1.75	0.46	2.04	1.72	0.79	
<i>Aralia nudicaulis</i>	2.13	0.19	1.11	2.08	0.59	
<i>Aster macrophyllus</i>	2.22	0.45	4.69	2.41	0.34	
<i>Maianthemum canadense</i>	na	0.17	3.38	1.76	0.62	
Shrub layer						
<i>Vaccinium angustifolium</i>	(fol.) ¹	1.29 (0.05)	0.17 (0.01)	0.97 (0.09)	0.71 (0.05)	0.20 (0.03)
	(stem)	0.75 (0.04)	0.14 (0.001)	0.74 (0.06)	0.44 (0.02)	0.07 (0.00)
<i>Diervilla lonicera</i>	(fol.)	1.53 (0.14)	0.40 (0.07)	2.37 (0.15)	1.14 (0.05)	0.42 (0.07)
	(stem)	0.76 (0.05)	0.11 (0.00)	1.21 (0.11)	0.29 (0.01)	0.13 (0.01)
<i>Rubus idaeus</i>	(fol.)	1.78	0.31	1.50	1.05	0.68
	(stem)	0.86	0.14	0.39	0.52	0.16
<i>Vaccinium myrtilloides</i>	(fol.)	1.80	0.18 (0.04)	1.09 (0.55)	0.61 (0.04)	0.23 (0.07)
	(stem)	0.94	0.10 (0.00)	0.72 (0.02)	0.27 (0.03)	0.04 (0.01)
<i>Rubus pubescens</i>	(fol.)	2.04	0.55	2.24	1.13	0.87
	(stem)	1.15	0.34	1.50	0.48	0.30

¹fol. = foliage

more nutrient-demanding than later-successional species, and their tissues more rich in nutrients. Early-successional species such as *Polytrichum juniperinum* Hedw., *Hieracium* spp., and *Rubus idaeus* L. were common in the youngest stands in this study, and contained relatively high concentrations of nutrients (Table 2).

Contribution of the understory vegetation to above-ground organic matter, nutrient pools, and NPP

Understory vegetation (above-ground) generally comprised less than 1% of above-ground stand organic matter (sum of tree biomass, understory vegetation biomass, and forest floor mass; MacLean and Wein 1977) with proportions greater than 1% in the youngest and oldest jack pine stands on dry sites, and the youngest black spruce stand (Table 3). Proportions of above-ground organic matter contained in the understory vegetation generally followed the same patterns over time as the understory vegetation biomass pools: decreasing then increasing in dry jack pine stands, increasing then decreasing in mesic jack pine stands, and decreasing in black spruce stands.

However, understory vegetation contributed proportionally more to above-ground nutrient pools compared to organic matter pools, due to relatively high concentrations of nutrients in tissues, especially herbaceous plants and shrub foliage (Table 2). The proportion of above-ground stand N (total of N in trees, understory vegetation and forest floor) contained in the understory vegetation of the managed stands ranged from 0.8 to 3.4% (Table 3), with the highest values found in the youngest black spruce stand, in which canopy closure had not yet begun, and the oldest dry jack pine stand, a relatively open stand with an understory dominated by feathermoss and lichen. Proportions of above-ground stand P in understory vegetation resembled those of N, ranging from 0.7 to 3.7%, and exhibiting similar patterns among stands. Understory vegetation K contributed 3.2–11.7% of above-ground stand K capital, the highest of all nutrients in this study, and up to 10 times the contribution to above-ground stand organic matter, similar to the amount of K in tree crowns in some cases. As with organic matter, the proportions of stand K in the understory were greatest in the youngest and oldest jack pine stands on

Table 3. Contributions of understory vegetation (lichen, moss, herbs, shrubs) to above-ground stand biomass and nutrient pools, expressed as percentages of total above-ground stand biomass and nutrient capital (estimated as the sum of tree, understory vegetation, and forest floor pools), in managed jack pine and black spruce stands in northern Ontario. Contributions of understory vegetation to above-ground net primary productivity (ANPP) (expressed as percentages of total measured ANPP, estimated as the sum of wood production, foliar litterfall, and herb and shrub foliar biomass). Stands are grouped by average age (years since establishment), crop tree species (jack pine or black spruce), and site type (dry or mesic).

	Jack pine – dry			Jack pine – mesic			Black spruce – mesic		Jack pine – natural
	10	33	47	14	37	53	12	37	75
Biomass	1.1	0.7	1.4	0.6	0.7	0.4	2.6	0.4	0.3
N	1.9	1.3	2.7	1.3	1.5	0.8	3.4	1.2	0.7
P	1.4	1.7	3.1	0.8	1.6	0.7	3.7	1.2	0.6
K	11.5	6.2	10.2	4.3	8.1	4.4	11.7	3.2	3.5
Ca	2.2	2.5	2.6	0.8	2.3	2.1	3.8	1.1	1.3
Mg	2.8	2.7	6.2	1.2	3.4	2.6	2.6	1.9	2.0
ANPP	11.4	10.1	21.2	1.2	11.0	na1	13.1	5.5	7.4

¹na = data not available

dry sites, and in the youngest black spruce stand. Ca in understory vegetation represented 0.8–3.8% of above-ground stand Ca, while understory Mg comprised 1.2–6.2% of the above-ground stand capital of that nutrient.

At most, the understory vegetation contribution amounted to 21% of above-ground net primary productivity (ANPP) (in the oldest dry jack pine stand), with the smallest value (1.2%) found in the youngest mesic jack pine stand (Table 3). In any case, the contribution of understory vegetation to ANPP was greater than its contribution to above-ground stand capital of organic matter and most nutrients.

The contributions of understory vegetation to above-ground organic matter and nutrient capital and ANPP in the mature, natural jack pine stand were below or near the low end of the ranges seen in the managed stands.

Relationships between understory vegetation communities and environmental variables

Multivariate analysis (CCA) of all stands detected variation in species composition related to a basal area/soil nutrient gradient (Fig. 2). Eigenvalues of axes 1 and 2 were 0.32 and 0.072, respectively, indicating that most of the variation in species composition occurred along axis 1. This axis was most highly correlated with basal area, as indicated by the length of the basal area vector, and its small angle with axis 1. This axis separated the young (pre-canopy closure) stands from the older stands, and also separated the poorest jack pine stand (P3) from other mid-aged jack pine stands, as well as separating spruce from pine stands (except for P5). All soil nutrients (except forest floor Mg) also increased along axis 1, with forest floor N and Ca most highly correlated with the variation in species composition along this axis.

The weaker gradient along axis 2 separated S5 (the one stand with a significant clay component to its soil) from the rest of the stands along a gradient of forest floor Mg concentration (axis 2 is also correlated with mineral soil cations and K in the forest floor). In addition, the dry jack pine stands are slightly separated from the mesic jack pine stands along this axis.

The length of axis 1 (just over 2.6 units) indicates that there is a substantial degree of species turnover from one end of the axis to the other, but also that some species are present in all stands (an axis length of 4 would indicate that stands at opposite ends of the axis have no species in common). Species such as *Pleurozium schreberi* (Brid.) Mitt., *Cornus canadensis* L., *Maianthemum canadense* Desf. and *Vaccinium angustifolium* Aiton were ubiquitous in these upland stands, though their relative frequency differed among stands.

The youngest stands (group i; Fig. 2a) were found at the low end of axis 1, and were dominated by early successional and shade-intolerant species such as *Rubus idaeus* L., *Hieracium caespitosum* Dumort., *Epilobium angustifolium* L., and *Polytrichum commune* Hedw. (Fig. 2b). The mid-aged and older jack pine stands on dry sites (group ii) were characterized by ericaceous low shrubs (*Epigaea repens* L., *Vaccinium angustifolium* Aiton, *V. myrtilloides* Michx.) along with reindeer lichen (*Cladonia rangiferina* (L.) Nyl. and *C. mitis* (Sandst.) Hustich) and herbs common to dry sites such as *Melampyrum lineare* Desr. and *Cypripedium acaule* Aiton. The jack pine stands on mesic sites, slightly higher in basal area and mineral soil nutrients than their counterparts on dry soils, contained more shade-tolerant, late-seral species such as *Aralia nudicaulis* L., *Goodyera repens* (L.) R. Br., and *Streptopus roseus* Michx. The mid-aged black spruce stands, clustered at the high end of axis 1, were characterized by species with affinity for moister, richer sites, such as *Mertensia paniculata* (Aiton) G. Don, *Petasites palmatus* (Aiton) Cronq., and *Aster macrophyllus* L.

Successional development in the managed stands progressed from the early successional species found in the 10- to 14-year-old stands to species characteristic of closed forest (or open jack pine forest in the case of the stands on deep sands) by 35 to 50 years, with many of the mid-aged and older jack pine stands exhibiting a species composition similar to that of the natural 75-year-old stand (Fig. 2a).

The lasting effects of different silvicultural regimes were investigated by ordinating plots within a smaller subset of stands. Stands P2, P3, and P4 were close in age, adjacent to

Fig. 2. Ordination of 16 managed jack pine and black spruce stands (plus one mature, natural jack pine stand) using canonical correspondence analysis (CCA), based on species composition of the understory vegetation. Species present in at least 5 % of all inventory quadrats were included in the analysis, which was constrained by a suite of environmental variables (soil nutrient concentrations and stand basal area). a) Each stand is represented by one data point (stand codes are given in Table 1). Arrows indicate the direction of increase of a given variable. Clusters of similar stands are delineated within ovals on diagram: i) Young stands (pre-canopy closure); ii) Jack pine stands on dry sites; iii) Jack pine stands on mesic sites; iv) Black spruce stands on mesic sites. b) Species scientific names, represented in short form on the species ordination diagram, are as follows: *Aralia nudicaulis* L., *Aster ciliolatus*, *Aster macrophyllus*, *Cladonia mitis* (Sandst.) Hustich, *Cladonia rangiferina* (L.) Nyl., *Cladonia chlorophaea* (Florke ex Sommerf.), *Cladonia coniocrea* (Florke) Sprengel, *Cladonia gracilis* (L.) Willd., *Clintonia borealis* Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Cypripedium acaule* L., *Dicranum fuscescens* Turn., *Dicranum polysetum* Sw., *Diervilla lonicera* Miller, *Epigaea repens* L., *Epilobium angustifolium* L., *Fragaria virginiana* Duchesne, *Gaultheria hispidula* (L.) Muhl., *Goodyera repens* L. (R.) Br., *Herzogiella turfacea* (Lindb.) Iwats., *Hieracium caespitosum* Dumort., *Ledum groenlandicum* Oeder., *Linnaea borealis* L., *Lycopodium clavatum* L., *Lycopodium obscurum* L., *Maianthemum canadense* Desf., *Melampyrum lineare* Desr., *Mertensia paniculata* (Aiton) G. Don, *Petasites palmatus* (L.) Fries., *Picea mariana* (Mill.) B.S.P. (seedlings), *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum juniperinum* Hedw., *Polytrichum commune* Hedw., *Ptilidium ciliare* (L.) Hampe, *Ptilium crista-castrensis* (Hedw.) De Not., *Rosa acicularis* Lindley., *Rubus idaeus* L., *Rubus pubescens* Raf., *Streptopus roseus* Michx., *Thuidium delicatulum* (Hedw.) B.S.G., *Trientallis borealis* Raf., *Vaccinium angustifolium* Aiton., *Vaccinium myrtilloides* (Michx.), *Viola renifolia* A. Gray.

Fig. 3. Ordination (by canonical correspondence analysis, or CCA) of a subset of 3 managed jack pine stands (P2, P3, P4; see Table 1 for stand codes) based on understory vegetation species composition. These 3 stands were similar in age, soil, and location, but were subjected to different silvicultural treatments. Species present in at least 5 % of inventory quadrats were included in the analysis, which was constrained by a suite of environmental variables (soil nutrient concentrations and stand basal area). a) Each data point represents one sample plot (4 plots per stand, 5 quadrats per plot). Arrows indicate the direction of increase of a given variable. Clusters of plots within stands are delineated within ovals on diagram. b) Species scientific names, represented in short form on the species ordination diagram, are as follows: *Alnus rugosa* L. Moench., *Apocynum androsaemifolium* L., *Aralia nudicaulis* L., *Aster ciliolatus*, *Ceratodon purpureus* (Hedw.) Brid., *Cetraria pinastri* (Scop.) Gray, *Cladina mitis* (Sandst.) Hustich, *Cladina rangiferina* (L.) Nyl., *Cladonia chlorophaea* (Florke ex Sommerf.), *Cladonia coniocrea* (Florke) Sprengel, *Cladonia cornuta* (L.) Hoffm., *Cladonia furcata* (Huds.) Schrad., *Cladonia gracilis* (L.) Willd., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Cypripedium acaule* L., *Dicranum fuscescens* Turn., *Dicranum polysetum* Sw., *Diervilla lonicera* Miller, *Epigaea repens* L., *Epilobium angustifolium* L., *Fragaria vesca* L., *Fragaria virginiana* Duchesne, *Gaultheria hispidula* (L.) Muhl., *Geocaulon lividum* (Richardson) Fern., *Goodyera repens* L. (R.) Br., *Herzogiella turfacea* (Lindb.) Iwats., *Ledum groenlandicum* Oeder., *Linnaea borealis* L., *Lycopodium clavatum* L., *Maianthemum canadense* Desf., *Melampyrum lineare* Desr., *Petasites palmatus* (L.) Fries., *Picea mariana* (Mill.) B.S.P. (seedlings), *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum piliferum* Hedw., *Ptilium crista-castrensis* (Hedw.) De Not., *Pyrola virens* Swartz., *Rosa acicularis* Lindley., *Trientalis borealis* Raf., *Vaccinium angustifolium* Aiton., *Vaccinium myrtilloides* (Michx.).

each other, and on similar soils, yet were separated in ordination space (Fig. 3a). These three sites were subjected to different silvicultural regimes of varying intensity. P2 was harvested and replanted, with some natural regeneration. P4 was harvested, site-prepared by blading, then seeded. P3 was harvested and site-prepared as in P4, but was also thinned to a 1.2 m X 1.2 m spacing at five years after seeding. It is likely that the blading treatment was more severe (removing some topsoil as well as the forest floor) in P3, as some areas within this stand remained devoid of any forest floor or vegetation besides sparse lichen and moss cover.

When plots within these three stands only were subjected to CCA, basal area, mineral soil K and mineral soil Mg were the variables most closely correlated with the main axis of variation in the vegetation composition data. The eigenvalues for axes 1 and 2 were 0.412 and 0.104, respectively. The length of axis 1 indicated considerable turnover of species from one end to the other; with the P3 plots dominated by lichens and ericaceous shrubs (*Vaccinium* spp.), the P2 plots characterized by herbaceous species such as *Petasites palmarum* (Aiton) Cronq. and *Fragaria virginiana* Duchesne, and the P4 plots containing more *Diervilla lonicera* Mill. and *Clintonia borealis* Aiton than the other stands (Fig. 3b). Differences in dominant vegetation type among these three stands could also be seen by looking at the estimates of biomass represented by each stratum. P3 contained more than twice the moss/lichen biomass of the other two stands, while P2 had slightly more herb biomass than P3 and P4, and P4 contained more than twice the shrub biomass of the other two stands (not shown). Overall, P3 contained more understory vegetation biomass than either P4 or P2, mainly accounted for by *Cladina* spp. and *Pleurozium schreberi* (Brid.) Mitt.

Discussion

The amount of biomass contained in understory vegetation was small, relative to total above-ground biomass, similar to findings from other studies in upland, closed canopy forests in the boreal region, whether of natural or plantation origin (Alban *et al.* 1978, Rutkowski and Stottlemeyer 1993). The greater contribution of understory vegetation to nutrient pools compared to biomass pools has also been well documented in forests (e.g., Maclean and Wein 1977, Alban *et al.* 1978) and is due to the relatively high plant tissue nutrient concentrations in understory vegetation. The higher-quality litter from some understory plants may play an important role in nutrient cycling, especially in coniferous forests where overstory litter is low in nutrients (Foster and Morrison 1976).

Contributions of the understory vegetation to above-ground nutrient pools in the mid-aged jack pine stands in our study were considerably higher, both as proportions and absolute amounts, than those reported by Foster and Morrison (1976) in a 30-year-old natural jack pine stand on sandy soil in the Great Lakes – St. Lawrence region, except for N, which was only slightly higher in our study. MacLean and Wein (1977) found similar amounts of understory vegetation biomass and nutrients in 40- to 60-year-old natural jack pine stands on sandy loam in New Brunswick, compared to similarly aged stands in our study. However, the understory vegetation in their study accounted for a much higher proportion of total above-ground biomass and

nutrient pools, due to lower amounts of tree biomass in their stands.

Our findings of the proportions of above-ground nutrients stored in understory vegetation were similar to those of Alban *et al.* (1978) in 40-year-old jack pine plantations on sandy loam in northern Minnesota, even though our absolute amounts were different. Greater amounts of understory vegetation were found in their study than in our 35- to 50-year-old plantations, although amounts of N and P were similar, and amounts of cations were smaller in their study. This further illustrates the influence of species composition, and species-specific nutrient requirements and uptake, on nutrient pool sizes in the understory vegetation. Nutrient transfers from the canopy to the understory vegetation in throughfall can also have an influence on nutrients in understory vegetation, particularly feathermosses (Okland *et al.* 1999).

At 35 years, the densely planted spruce stands, high in soil nutrients, supported a relatively small understory vegetation biomass, while understory biomass was greater in the more open-canopied jack pine stands, and highest in the 50-year-old, nutrient-poor jack pine stand on sandy soil. Vegetation communities also differed between these two extreme stand types, which were found at the opposite ends of the gradient of variation in species composition. The availability of site resources can have both direct and indirect effects on the composition and productivity of the understory vegetation. Understory species vary in their ability to tolerate environmental stresses, so species composition is in part a direct reflection of nutrient and moisture availability. Nutrients and moisture are also drivers of overstory productivity, which in turn determines the amount of light reaching the understory, and hence influences understory productivity and composition in an indirect fashion as well (Hanley and Brady 1997). The crown structure of the overstory species also influences light regimes in the understory (Légaré *et al.* 2001). Alban *et al.* (1978) also found larger amounts of understory biomass in jack pine versus white spruce (*Picea glauca* [Moench] Voss) plantations of the same age, even when planted on the same soils. The effects of light and moisture limitation on understory vegetation can be difficult to separate, and the vegetation responses to increased moisture availability in canopy openings can be mistaken for responses to increased light (Anderson *et al.* 1969). However, in this study, the greater amount of understory vegetation biomass in the open jack pine stands on sandy sites was driven mainly by light availability as shade-intolerant reindeer lichens accounted for a large proportion of understory biomass in these stands.

Invasive, non-native understory species were found to be a very common component of understory vegetation communities in red pine (*Pinus resinosa* Aiton) plantations in southern Ontario (Parker *et al.* 2001), causing concern about the displacement of native species. On the contrary, in our study, non-native species (e.g., *Taraxacum officinale* Weber ex Wiggers, *Hieracium caespitosum* Dumort) were uncommon, and confined mainly to the youngest (pre-canopy closure) stands. The managed stands in our study contained a suite of species common to natural forests on similar sites in northwestern Ontario. For example, all but one of the understory vegetation species noted as common to stands on deep, fresh to moist, loamy, silty, and sandy soils in the

Northwestern Ontario Forest Ecosystem Classification guide (Sims *et al.* 1989) (not including those confined to the Quetico/Rainy River area) were found in the Beardmore stands. The lone exception was *Arctostaphylos uva-ursi* (L.) Spreng., a trailing shrub with an affinity for sandy sites, but not found in our stands; interestingly, another ericaceous species, *Epigaea repens* L., was abundant in stands on sandy soils in our study, but not noted as common by Sims *et al.* (1989). Encouragingly, from the standpoint of biodiversity maintenance in managed forests, the vegetation community composition in the managed stands approached that of the natural stand by 35 to 50 years after stand establishment. Also, species considered infrequent in northwestern Ontario (e.g., *Cypripedium acaule* Aiton, *Pyrola asarifolia* Michx., *Moneses uniflora* (L.) Gray, *Polygala paucifolia* Willd.; Baldwin and Sims 1989) were present (infrequently) in the managed stands, as were species considered potentially sensitive to silvicultural treatments (e.g., *Goodyera repens* (L.) R. Br., *Chimaphila umbellata* L. Bart, and *Corallorhiza trifida* Chat.) (Haeussler *et al.* 2002). However, it is difficult to definitively detect the loss of particular species, especially when the composition of the pre-harvest vegetation is unknown. More research is needed to identify sensitive understory vegetation species and to determine to what extent local or regional occurrence in northern Ontario is threatened by silvicultural treatments.

Strong relationships between understory community composition and soil nutrient variables have been detected in both managed and natural forests (Ferris *et al.* 2000, Wang 2000, Wilson *et al.* 2001). In coniferous plantations in Britain, Ferris *et al.* (2000) found that available N, available Ca, and soil pH corresponded closely with change in understory vegetation. Understory vegetation composition has been investigated as an indicator of site nutrient status by many authors (e.g., Payandeh 1986, Strong *et al.* 1991), and is used in forest ecosystem classification and interpretation systems, including those in use in Ontario (e.g., Racey *et al.* 1989). Certain types of vegetation, such as ericaceous shrubs, may influence soil nutrient dynamics (e.g., N mineralization and forest floor dynamics; Prescott *et al.* 2000, and Krause 1998 respectively) to a degree that belies their relatively small contribution to total biomass in forests. In the current study, the strong relationships between site nutrition variables and understory community composition suggest that in these plantation ecosystems, the understory community can provide a means of detecting management-related changes in site nutrient regimes.

More than 30 years after stand establishment, the effects of different combinations and intensities of silvicultural treatments can still be seen in these stands when other factors are controlled. Among stands P2, P3, and P4, the main cause of the differences in understory vegetation composition appears to be the influence of management on soil organic matter and its associated nutrient content, as well as overstory basal area and, hence, light regimes. The most severely bladed plots are found at one end of the main gradient, while at the other end lie the bladed, unthinned plots, and the planted plots not subjected to blading. It seems that the severe blading treatment plus thinning of P3 resulted in an excessive removal of organic matter and nutrients from the site, causing low basal area to be attained due to poor tree

growth, and very nutrient-poor soils. These factors have led to an understory vegetation dominated by reindeer lichens, feathermoss, and ericaceous species, while nearby stands on similar soils subjected to less intense organic matter removal have higher overstory basal area, higher soil nutrients, and more herb and shrub-rich understory vegetation. While *Cladina* spp. and *Vaccinium* spp. are important for wildlife (Racey *et al.* 1989), and stands rich in these species are valuable to the forest landscape as a whole, their proliferation in managed stands may signal site degradation. An understory rich in lichen and ericaceous vegetation may indicate sites that are susceptible to organic matter and nutrient loss and unsuitable for intensive management (Mallik 1995, Szwaliuk and Strong 2003).

Conclusions

Silvicultural treatments manipulate stand basal area and overstory species composition, and have the potential to affect soil nutrient content. These variables influence understory vegetation biomass, as well as species composition, which dictates the concentrations of nutrients in understory vegetation, and in turn affects the nutrient pool sizes in this ecosystem component. These characteristics of the understory vegetation (species composition, biomass and nutrient pools) determine the value of this ecosystem component as wildlife food and habitat, as well as its contribution to nutrient cycling and overall stand productivity. Insofar as these factors vary with different silvicultural treatments and the interactions of these treatments with site characteristics, variety in management prescriptions should result in the occurrence of a structurally and functionally diverse array of vegetation communities on the landscape. Many of the managed stands in this study developed an understory vegetation species composition similar to that expected in natural stands on similar sites. However, certain stands were obviously showing lasting effects of silvicultural treatments on both species composition and biomass of the understory vegetation. More research and monitoring are needed to assess the long-term effects of particular treatments and treatment combinations on sensitive species and sites, as well as on whole communities of understory vegetation and their pattern over the forest landscape, to ensure that the important ecological role played by the understory vegetation is maintained in Ontario's managed forests. Future research into the dynamics of understory vegetation in managed stands should involve pre-harvest data and comparisons with naturally disturbed stands at various developmental stages.

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