Understorey plant community characteristics and natural hardwood regeneration under three partial harvest treatments applied in a northern red oak (*Quercus rubra* L.) stand in the Great Lakes-St. Lawrence forest region of Canada

Jeffery P. Dech [a,b], Lisa M. Robinson [a], Peter Nosko [a,*]

[a] *Department of Biology, Nipissing University, 100 College Drive, North Bay, ON, Canada P1B 8L7*
[b] *Forestry Research Partnership, PO Box 430, 6905 Highway 17, Mattawa, ON, Canada P0H 1V0*

ABSTRACT

Throughout eastern North America, stands of northern red oak (*Quercus rubra* L.) are undergoing successional replacement by shade-tolerant competitors. In the Great Lakes-St. Lawrence (GLSL) forest region, *Q. rubra* approaches the northern limit of its distribution, and ecosystem-specific silvicultural directives are needed to promote regeneration. We used an inductive, ordination-based approach to explore patterns in understorey plant community composition and microenvironment under different partial harvest treatments applied in a GLSL hardwood stand, and related these to characteristics of natural seedlings of *Q. rubra* and its competitors *Acer rubrum* and *Acer saccharum*.

Two years after harvest, we established 2 m × 2 m plots in a stratified random design under 70% ($n = 20$) and 50% ($n = 19$) crown closure uniform shelterwood, group selection ($n = 15$), and uncut upper slope ($n = 10$) and lower slope ($n = 10$) areas. Percent cover of understorey vascular plant species, and a suite of microclimatic and edaphic variables were measured in each plot. Density, mean diameter and mean height of seedlings in the understorey (height <1 m) were determined in each plot for *Q. rubra*, *A. rubrum* and *A. saccharum*.

Correspondence analysis (CA) ordination extracted two major axes explaining 21.6% of the total inertia in the species cover by plot matrix. Axis one separated uncut plots from the 50% shelterwood along a gradient of canopy cover associated with partial harvest treatments. Plot scores on axis one (13.2%) reflected a shift in dominance of the understorey from shade-tolerant *Acer* spp. to shade-intolerant colonizers, *Rubus idaeus* and *Carex* spp. Plot scores on axis one were directly ($p < 0.05$) associated with total understorey plant cover, litter depth, soil temperature and pH, but not with measures of plant diversity. Axis two (8.4%) separated plots from upper slope and lower slope areas, and plot scores were inversely associated ($p < 0.05$) with soil pH, phosphorus and nitrogen levels. Along axis two there was a shift in dominance from competitive (e.g. *A. saccharum*) to stress-tolerant (e.g. *A. rubrum*) species as soil fertility declined. Stepwise linear regression indicated seedling diameter in *Q. rubra*, *A. rubrum* and *A. saccharum* was inversely related to canopy cover. This suggests all three species benefited from partial harvest, although the relationship was strongest in *Q. rubra*. Patterns in understorey composition, microenvironment and seedling characteristics provide the basis to identify the main competitors of *Q. rubra* seedlings and adjust regeneration efforts along gradients of canopy closure and soil fertility under partial harvest systems within the GLSL forest region.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Oaks (*Quercus* spp.) provide significant ecological and economic value to the Eastern Deciduous forests of North America; however, in the absence of adequate disturbance *Quercus* dominated stands are being replaced by other species assemblages, except on the poorest sites (Abrams, 1996; Johnson et al., 2002). The failure of some *Quercus* species to regenerate is a phenomenon that has also been reported in Europe (Watt, 1919; Shaw, 1968) and Asia (Masaki et al., 1992; Vetaas, 2000). In North America, the trend of diminishing regeneration is exemplified by *Quercus rubra* L. (northern red oak), which is undergoing successional replacement by shade-tolerant species throughout its range (Crow, 1988; Abrams, 1992). Long-term studies indicate that competing shade-

tolerant species (e.g. *Acer saccharum*, *Acer rubrum*) dominate the understorey and gradually replace the overstorey of *Q. rubra* as minor disturbances create small canopy gaps (Christensen, 1977; Lorimer, 1984; Parker et al., 1985; Nowacki et al., 1990; Spetich and Parker, 1998; Schuler and Gillespie, 2000; Silvius et al., 2003). The failure of *Q. rubra* to regenerate has been attributed to a lack of seedling establishment or reduced competitive ability and mortality of seedlings in the understorey of undisturbed forests (Crow, 1988; Loftis, 1988; Lorimer et al., 1994). Natural regeneration of *Q. rubra* typically depends on periodic fires, which increase light penetration through the canopy and reduce interspecific competition in the understorey (Abrams, 1992, 2005). Historically, *Quercus* spp. achieved greatest densities in association with frequent disturbance, including natural and anthropogenic fire, and timber harvesting (Johnson et al., 2002). Adaptations to disturbance such as re-sprouting increase the fire tolerance of *Quercus* spp. relative to shade-tolerant competitors (Huddle and Pallardy, 1999; Dolan and Parker, 2004), and provide an opportunity for vigorous growth of stump sprouts after harvest (Johnson et al., 2002). Suppression of fire has been suggested as a major cause of the failure of *Q. rubra* stands to regenerate (Crow, 1988; Abrams, 1992, 2005). In Ontario, fire has declined since the 1920s, promoting the replacement of *Q. rubra* in the canopy by shade-tolerant species (Dey and Guyette, 2000). Currently, there is a paucity of *Q. rubra* dominated stands under 60 years of age on the managed land base in Ontario, with the majority of stands falling into the 81–100 year age class (OMNR, 2006). These stands originated under the more frequent disturbance regime of the early 1900s, when anthropogenic fires and logging reduced the dominance of *A. saccharum*, and *Q. rubra* seedlings recruited into the overstorey during a subsequent period of reduced fire activity (Dey and Guyette, 2000). These events were part of a larger pattern of disturbance that increased the dominance of *Q. rubra* throughout the Eastern Deciduous forest (Abrams, 1992, 2005).

Throughout the Eastern Deciduous forest region, a recommended approach to regenerating *Q. rubra* is to combine an overstorey manipulation (e.g. uniform shelterwood harvest) with understorey vegetation control (Hannah, 1987; Crow, 1988; Loftis, 1990). This strategy is derived from the ecological niche of *Q. rubra* as a mid-tolerant, transitional species (Sander, 1990; Abrams, 1992). Seedlings of *Q. rubra* often have high mortality and poor growth when both canopy and understorey shade are present (Lorimer et al., 1994; Dey and Parker, 1997a). The light compensation point for *Q. rubra* is reached at approximately 2–5% of full sun (Hanson et al., 1987); however, positive shoot growth rates require 20% of full sun (Gottschalk, 1994). In Ontario, the recommended harvest methods to maintain or regenerate *Q. rubra* are uniform shelterwood or group selection (OMNR, 1998). Various studies in the Eastern Deciduous forest region have shown that overstorey reduction through uniform shelterwood improved the survival and growth of *Q. rubra*, especially when understorey vegetation cover was also reduced (e.g. Hill and Dickmann, 1988; Johnson et al., 1989; Crow, 1992; Teclaw and Isebrands, 1993).

The success of different approaches to regenerate *Quercus* spp. depends on site conditions and the specific competitors present in a given stand (Johnson et al., 1989), and ecosystem-specific information is needed to manage individual stands and promote the recruitment of *Q. rubra* seedlings (Crow, 1988; Dey and Parker, 1996, 1997a; Johnson et al., 2002). Plant community responses to clear-cut and group selection harvest treatments differed between dry-mesic and mesic slopes in southern Indiana, with *Quercus* spp. achieving greater importance in the postharvest communities of dry-mesic sites than mesic sites (Jenkins and Parker, 1998). In general, soil moisture and nutrients are important drivers of forest tree distributions on the landscape (Whitney, 1991; Host and

Pregitzer, 1992), although relationships of species abundances to edaphic gradients may differ according to life stage (Collins and Carson, 2004). The initial stages of stand development are perhaps most critical from a management perspective, as silvicultural treatments can have significant effects on growth within 2-years after harvest (Romagosa and Robison, 2003). Canopy removal through partial harvest treatments can create additional micro-environmental gradients by changing light (Dey and Parker, 1996), temperature and soil moisture (Laporte et al., 2003), litter depth and soil nutrients (Kim et al., 1996); however, these environmental effects of harvesting can be seasonally inconsistent (Laporte et al., 2003) and site-specific (Elliot and Knoepp, 2005).

Populations of *Q. rubra* in the GLSL forest region approach the current northern limits of the species range, and studies of the understorey plant communities and natural hardwood seedling competition under managed *Q. rubra* stands are lacking. Studies of regeneration at the northern margins of species ranges could provide important baseline information for tree species that shift their distributions in response to climate change. For *Q. rubra* in the GLSL forest region, understanding the regeneration niche (Grubb, 1977) requires information on competition and environmental conditions in the understorey immediately following harvest. We used an inductive, ordination-based approach to identify the type of competition for *Q. rubra* seedlings under three different partial harvest treatments compared to uncut portions of a *Q. rubra* dominated stand in central Ontario. The specific objectives of our study were (i) to explore patterns in the composition and microenvironment of the understorey plant community related to partial harvest treatments and site conditions, and (ii) to relate these differences to the growth of natural seedlings of *Q. rubra* and its main competitors *A. rubrum* and *A. saccharum*.

2. Methods

2.1. Site description

The study was conducted at the Phelps Township red oak research site (46°22′N, 79°6′W), located approximately 29 km northeast of North Bay, Ontario, Canada. This site is located within the GLSL forest region of Canada, which stretches from southeastern Manitoba to Prince Edward Island, and has a significant portion of its area contained within central Ontario (Rowe, 1972). The regional climate is continental, with warm summers and cold winters. Annual mean daily temperature for North Bay is 3.8 °C. Mean daily temperature of the coldest month (January) is −13.0 °C and of the warmest month (July) is 18.6 °C. Mean annual rainfall is 774.6 mm, snowfall is 273.4 cm and total precipitation is 1007.7 mm (Environment Canada, 2007).

The site was situated within the Laurentian Highlands division of the Canadian Shield, with glacial till surface materials underlain by Precambrian metamorphic rocks. Topography on the site was rolling to steep, and elevation ranged from 345 to 360 m above sea level. Soils on the site were deep loamy sands with a dry to fresh moisture regime. The site was classified as ecosite 23.1/23.2 (oak and other hardwoods with dry to fresh or fresh to moist soils) under the central Ontario forest ecosystem classification scheme (Chambers et al., 1997). Over the 61 ha stand area, *Q. rubra* was the dominant overstorey species (50% of stand basal area), with *Populus* spp (20%) being sub-dominant, and presence of *A. saccharum*, *A. rubrum* and *Pinus strobus* (Kovacs, 2003). Stand age was estimated at 90 years, and some minor, isolated harvesting of *Q. rubra* for fuel wood has periodically taken place (Kovacs, 2003).

In 2004, the stand was harvested under three different partial harvest treatments. Areas within the stand were harvested in the uniform shelterwood system to 50 and 70% crown closure. In both

shelterwood intensities, harvests were conducted by thinning from below and preferentially retaining large, high-quality *Q. rubra* trees (OMNR, 2004). Group selection circular canopy openings with diameters of 24 and 36 m were also established. Areas where no harvesting took place were retained within the stand. The harvest coincided with a mast year crop of acorns. All data presented here were collected during the 2006 growing season, representing the conditions 2 years postharvest.

2.2. Sampling design

Seventy-four 2 m × 2 m plots were located throughout the stand in a stratified random sampling design. Sample plots were established under four different canopy conditions; 50 and 70% shelterwood, group selection openings, and two separate uncut portions of the stand representing upper slope and lower slope (*sensu* Chambers et al., 1997) areas, respectively. The designations for uncut areas refer to topographic position along a minor slope gradient that spanned the entire site. The two uncut areas represented the ends of this edaphic gradient from dry to fresh soils on the upper slope to fresh to moist soils on the lower slope. All canopy treatments were applied along the portion of this gradient lying between the uncut end points. The contiguous area occupied by each canopy condition was stratified into multiple sampling frames to provide complete spatial coverage. Sample plots were randomly established within these sampling frames under the 50% (19 plots) and 70% (20 plots) shelterwood, group selection (15 plots) and each of the uncut areas (10 × 2 = 20 plots). Only three group selection openings were available for sampling, constraining the number of plots established under this canopy condition.

2.3. Vegetation measurements

On each 2 m × 2 m sample plot, percent cover values of each understorey vascular plant species were determined during June–July, 2006. Percent cover of each plant species was determined based on a standard scale: 1 = <5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 80–95%, and 6 = >95% (Daubenmire, 1968). All species nomenclature followed Gleason and Cronquist (1991). Prior to all analyses, the percent cover of each species in each plot was converted to the mid-point of the assigned cover class. Voucher specimens of all species observed within sample plots were deposited in the Nipissing University Herbarium.

We defined the understorey layer as stems <1 m in height, and refer to these hereafter as seedlings. Measurements of the height and basal diameter of each *Q. rubra*, *A. rubrum* and *A. saccharum* seedling were taken within the plots. Total seedling density of each of these species within the plot was also determined.

2.4. Environmental measurements

Within each sample plot, environmental measurements were taken over the course of the 2006 growing season. The total percent canopy cover above each plot was determined after leaves had fully expanded (26–27 July, 2006), using a spherical crown densiometer (Model A, Forestry Suppliers, Jackson, MS, USA). Canopy cover for each plot was based on the average of eight readings (one taken facing each cardinal direction from the centre of the plot by two independent observers). Total leaf litter depth (mm) was measured at the centre of each of four 50 cm × 50 cm quarters to calculate an average depth for each 2 m × 2 m plot. Two pairs of soil samples were obtained from each plot; the first pair was taken on 26 July, 2007, immediately after a rainfall event producing 56.2 mm of precipitation, and the second pair on 31

August, 2007, following a period of 11 days with a total rainfall of only 5 mm. Soil samples were obtained by removing surface litter and collecting soil to a depth of 15 cm using a soil corer. Soil moisture content for all samples was determined gravimetrically; however, to avoid redundancy only the percent moisture data from the latter (dry) sampling period were included in further analyses of the suite of environmental factors presented here. The July and August soil samples for each plot were subsequently combined and analyzed for pH, total nitrogen and plant-available phosphorus, potassium and magnesium at the University of Guelph Soil Laboratory (Guelph, Ontario, Canada). On 23 August 2007, soil temperature loggers (Watch Dog Model 100, Spectrum Technologies, East Plainfield, IL, USA) were inserted to a depth of 5 cm at a distance of 10 cm from the north side of the centre of each plot. The loggers were programmed to obtain temperature readings at 30 min intervals and were left in the plots for a period of 42 days. Mean daily maximum, minimum and mean temperatures were calculated for each plot over the measurement period. Growing degree days above 5 °C for the measurement period were calculated from the daily temperature record in each plot, to provide a relative comparison of the thermal regime under the different canopy conditions.

2.5. Data analyses

We used correspondence analysis (reciprocal averaging procedure, PC-ORD for Windows, version 4.20) to produce an indirect ordination of the species cover by plot matrix, and elucidate patterns of plant community composition latent within the multivariate data set. Correspondence analysis (CA) was chosen because it is an appropriate multivariate technique for plant community data, which typically include many zero entries where species are absent, and patterns of species abundance that represent non-linear relationships to environmental gradients (Kenkel et al., 2002; Legendre and Legendre, 1998). Rare species in the data matrix (species with a frequency ≤ the maximum frequency in the data set divided by five) were downweighted in proportion to their frequency (McCune and Mefford, 1999) to address the problem of outliers and idiosyncratic plot-species associations influencing the overall ordination (Kenkel et al., 2002). Our objective in this analysis was first to describe the variation (if any) in plant community composition associated with the gradient of different canopy conditions, and then relate any pattern detected to the environmental variables we measured. We calculated Spearman non-parametric correlation coefficients for all species cover values and environmental variables to the first two ordination axes, and produced overlay plots for the dominant species and environmental variables in the data set.

To examine the characteristics of the plant community across the canopy conditions established at the site, species richness, Shannon's diversity index and evenness were calculated from species cover values for each plot (PC ORD for Windows version 4.20, McCune and Mefford, 1999). Understorey cover was calculated as the sum total of the assigned cover values for all species in a given plot, and total cover was calculated as the sum of understorey and overstorey cover for each plot. Spearman's correlation coefficients for all diversity and cover variables to axes one and two of the CA ordination were determined.

Relationships between the characteristics of *Q. rubra*, *A. rubrum* and *A. saccharum* seedlings in the plots and environmental conditions were examined in a series of stepwise multiple linear regression analyses (SPSS for Windows, Version 11.5.0). Seedling density, height and diameter were analyzed as dependent variables and the suite of environmental variables were entered as independents. To account for the effects of interspecific

competition in the understorey, the density of each of the three main species (*Q. rubra*, *A. rubrum*, *A. saccharum*) were entered into regressions as environmental factors, excluding the situation where the density of a given species was the dependent variable. Adjusted coefficients of determination for each term in the regression models were assessed to make comparisons among relationships, and plots of residuals were analyzed to ensure that assumptions of linearity and homoscedascity were met (Zar, 1999). Where necessary, dependent variables were log-trans-formed ($y' = \log_{10}(y + 1)$) to rectify violations of the assumptions of the analyses. Outliers beyond three standard deviations from the predicted values were removed from the data set prior to producing the final regression analysis for a given dependent variable. The selected model for each dependent variable was chosen based on the explained variance and significance, conformity to the assumptions of the stepwise regression analysis, and retention of the original data structure over transformed variables wherever possible.

3. Results

3.1. Ordination of the understorey plant community

Understorey plant community composition varied considerably across the different canopy conditions and microenvironments represented in the sample plots. Correspondence analysis (CA) of the species cover by plot matrix produced two major axes that explained 21.6% of the total inertia (variance) in the data set. Axis one (13.2%) separated plots in uncut areas (low plot scores) from those in the 50% shelterwood area (high plot scores). Plots from the group selection and 70% shelterwood areas occupied intermediate positions on axis one (Fig. 1). Axis two (8.4%) separated plots from upper slope (high scores) and lower slope areas (low scores), in the uncut portions of the stand, but also illustrated considerable spread within the canopy treatments themselves (Fig. 1).

A total of 60 vascular plant taxa were observed within the plots, and many species showed patterns of abundance related to the first two axes extracted by the ordination (Table 1). Species with cover values exhibiting significant positive correlations to axis one included a group of shade-intolerants represented by several sedges (*Carex arctata*, *Carex intumescens*, and *Carex praticola*), an epiphytic vine (*Polygonum cilinode*) and two shrub species (*Prunus pensylvanica*, *Rubus idaeus*). Generally, these species reached peak abundance and frequency under the 50% uniform shelterwood canopy (Table 1). Species with significant negative associations to axis one included shade-tolerant club moss (*Lycopodium dendroi-deum*) and understorey shrubs (*Acer pensylvanicum*, *Acer spicatum*). These species tended to reach peak abundance and frequency under the uncut canopy (Table 1). Cover values for *Q. rubra* and *A. saccharum* were not significantly associated with plot scores on axis one; however, those of *A. rubrum* had a significant negative correlation to axis one (Table 1).

Several species had significant correlations to the second ordination axis; however, plot scores on axis two were mainly associated with the cover values of *Acer* spp. (Table 1). Both *A. pensylvanicum* and *A. rubrum* had significant positive correlations to axis two and reached peak abundance and frequency in the upper slope uncut area. Cover values of *A. saccharum* and *A. spicatum* were negatively correlated to this axis, and reached peak abundance in the lower slope uncut area. There was no association between cover values for *Q. rubra* and plot scores on axis two (Table 1).

There was a clear pattern of variation in the microenvironment that suggested the first two axes extracted by the CA ordination of the understorey plant community were related to canopy cover
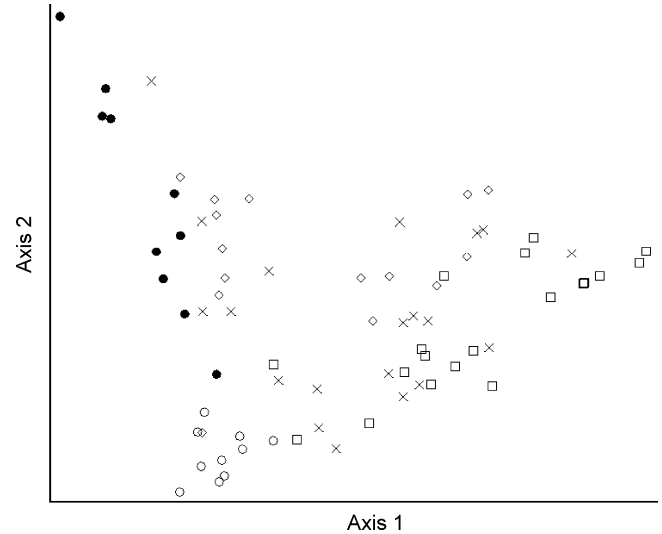

Fig. 1. Correspondence analysis ordination of plot scores derived from understorey plant species cover values. Data collected during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by *Quercus rubra* (northern red oak) near North Bay, Ontario, Canada. (○) Lower slope, uncut; (●) upper slope, uncut; (◇) group selection; (□) 50% shelterwood; (×) 70% shelterwood.

and soil fertility, respectively (Table 2). Canopy cover and litter depth decreased from the uncut areas to the 50% shelterwood areas, and both of these variables had significant negative correlations to plot scores on axis one of the ordination. The mean and standard deviation of soil temperature were largest in the more open canopy cover treatments, such as group selection and the 50% shelterwood. Growing degree days (soil) accumulated during the measurement period were highest in the 50% shelter-wood, and decreased in the uncut and 70% shelterwood plots. Mean daily maximum and mean temperature, accumulation of growing degree days and soil pH had significant positive correlations to plot scores on axis one (Table 2).

In general, soil nutrient levels were highest in the lower slope uncut area, and lowest in the upper slope uncut area (Table 2). The greatest differences in soil nutrients among plots were for plant-available phosphorus and total nitrogen; these variables had significant negative correlations to axis two of the ordination. This gradient of soil fertility had some spatial continuity. The upper slope uncut, 70% shelterwood and group selection plots, were all situated in close proximity and at slightly higher elevation than the 50% shelterwood and the lower slope uncut area. Although the canopy cover gradient established by the partial harvesting treatments was superimposed on this topographical soil fertility gradient, plot scores on axes one and two extracted by the ordination were not related (Spearman's $\rho = -0.027$, $p > 0.05$), and represented independent variation in the plant community associated with light or nutrients, respectively.

Plant species diversity characteristics were similar among the different canopy conditions established by the partial harvest treatments (Table 3). The mean species richness in the sample plots varied from a low of 11.8 in the 50% shelterwood area to a peak of 14.1 in the 70% shelterwood area. The Shannon diversity index showed a similar pattern of variation across the canopy conditions. The evenness index was relatively constant for all canopy conditions, with the notable exception of the low evenness value for the lower slope uncut site, which was strongly dominated by *A. saccharum* (Table 3). None of the indices of plant species richness and diversity were significantly related to plot scores for axes one or two (Table 3).

Table 1
Mean cover (%) and frequency (%) of understorey vascular plant species observed during the 2006 growing season on plots under uncut areas and three different partial harvest treatments within a forest stand dominated by *Quercus rubra* (northern red oak) near North Bay, Ontario, Canada

Species	Upper slope-uncut (n = 10)		Lower slope-uncut (n = 10)		70% Shelterwood (n = 20)		Group selection (n = 15)		50% Shelterwood (n = 19)		Axis one (ρ)	Axis two (ρ)
	Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency		
Ferns and fern allies												
Lycopodium annotinum	–	–	0.25	10.0	–	–	–	–	–	–	-0.079	-0.195
Lycopodium clavatum	–	–	0.25	10.0	–	–	0.16	6.7	–	–	-0.144	-0.242*
Lycopodium obscurum	5.00	100.0	4.25	70.0	1.50	60.0	1.67	33.3	1.05	42.1	-0.449**	-0.271*
Dryopteris carthusiana	–	–	4.00	60.0	1.00	15.0	0.17	6.7	0.26	10.5	-0.105	-0.298**
Dryopteris intermedia	–	–	–	–	–	–	–	–	0.26	10.5	0.176	-0.016
Dryopteris marginalis	–	–	0.25	10.0	–	–	–	–	0.13	5.3	-0.016	-0.215
Pteridium aquilinum	–	–	–	–	0.13	5.0	3.83	26.7	–	–	-0.085	-0.082
Graminoids												
Carex spp.[a]	1.50	60.0	–	–	1.75	45.0	1.67	33.3	0.53	21.1	-0.269*	0.187
Carex arctata	–	–	0.50	20.0	10.25	55.0	11.50	46.7	20.00	89.5	0.690**	-0.102
Carex intumescens	–	–	–	–	0.13	5.0	2.83	20.0	6.45	31.6	0.445**	0.155
Carex praticola	–	–	–	–	1.13	20.0	–	–	13.16	73.7	0.632**	0.055
Poa pratensis	–	–	–	–	–	–	–	–	0.13	5.3	0.200	0.096
Herbs												
Aralia nudicaulis	4.00	60.0	0.50	20.0	3.25	35.0	6.33	86.7	0.53	21.1	-0.266*	0.275*
Aster macrophyllus	–	–	–	–	–	–	–	–	0.13	5.3	0.178	0.019
Clintonia borealis	0.25	10.0	1.50	60.0	4.25	70.0	0.5	20.0	0.53	21.1	0.078	-0.247*
Epilobium angustifolium	–	–	–	–	–	–	–	–	0.13	5.3	0.074	-0.047
Galium triflorum	–	–	0.25	10.0	–	–	–	–	–	–	-0.129	-0.184
Maianthemum canadense	2.00	80.0	1.00	40.0	4.25	95.0	2.33	93.3	1.71	68.4	-0.030	0.299**
Medeola virginiana	–	–	–	–	0.25	10.0	0.17	6.7	–	–	0.024	-0.082
Monotropa uniflora	0.50	20.0	–	–	–	–	0.17	6.7	–	–	-0.213	0.191
Polygonum cilinode	–	–	–	–	21.00	75.0	15.17	66.7	13.42	57.9	0.610**	0.238*
Polygonatum pubescens	0.25	10.0	0.75	30.0	0.75	30.0	0.50	20.0	0.66	26.3	0.171	-0.268*
Pyrola elliptica	–	–	0.25	10.0	–	–	–	–	–	–	-0.079	-0.195
Smilacina racemosa	0.50	20.0	0.50	20.0	1.13	45.0	2.17	53.3	1.18	21.1	0.008	-0.134
Streptopus roseus	–	–	1.75	20.0	–	–	–	–	0.13	5.3	-0.143	-0.270*
Trientalis borealis	3.75	100.0	2.00	80.0	3.00	70.0	2.50	100.0	2.37	68.4	-0.300**	0.148
Trillium spp.[a]	0.50	20.0	1.25	50.0	1.13	45.0	0.67	26.7	0.79	31.6	-0.041	-0.363**
Viola sp.[a]	–	–	0.25	10.0	0.13	5.0	0.17	6.7	–	–	0.018	-0.085
Shrubs												
Acer pensylvanicum	22.50	90.0	0.25	10.0	4.50	35.0	3.33	33.3	–	–	-0.587**	0.521**
Acer spicatum	0.50	20.0	5.00	50.0	2.00	30.0	–	–	–	–	-0.340**	-0.322**
Amelanchier laevis	0.25	10.0	–	–	–	–	0.17	6.7	–	–	-0.172	0.179
Amelanchier sanguinea	–	–	–	–	–	–	1.17	13.3	–	–	0.179	0.171
Cornus alternifolia	1.00	40.0	3.25	30.0	0.13	5.0	0.67	26.7	–	–	-0.358**	-0.081
Corylus cornuta	–	–	–	–	4.50	55.0	–	–	5.92	36.8	-0.369**	-0.172
Diervilla lonicera	11.50	80.0	13.50	60.0	0.25	10.0	3.67	46.7	0.26	10.5	0.145	-0.143
Gaultheria procumbens	1.75	20.0	–	–	0.13	5.0	0.17	6.7	–	–	-0.223	0.107
Lonicera canadensis	0.50	20.0	0.75	30.0	0.25	10.0	0.17	6.7	0.13	5.3	-0.260*	-0.127
Mitchella repens	0.75	30.0	0.75	30.0	0.38	15.0	0.17	6,7	–	–	-0.252*	-0.104
Prunus pensylvanica	–	–	–	–	8.88	65.0	10.83	46.7	10.26	100.0	0.732**	0.157
Prunus virginiana	0.50	20.0	4.00	60.0	1.13	20.0	1.33	20.0	1.05	15.8	-0.084	-0.246*
Rubus allegheniensis	–	–	–	–	–	–	0.17	6.7	–	–	-0.145	0.173
Rubus idaeus	–	–	–	–	4.00	60.0	1.00	40.0	16.58	84.2	0.720**	0.094
Rubus canadensis	–	–	0.25	10.0	–	–	0.5	20.0	–	–	-0.056	-0.042
Sambucus canadensis	–	–	–	–	–	–	–	–	1.97	5.3	0.189	0.052
Sambucus racemosa	–	–	–	–	–	–	–	–	1.05	15.8	0.280*	0.070
Vaccinium angustifolium	–	–	–	–	0.13	5.0	0.17	6.7	–	–	-0.168	-0.105
Viburnum alnifolium	–	–	4.25	30.0	4.63	20.0	0.17	6.7	0.13	5.3	-0.109	-0.085
Viburnum cassinoides	0.25	10.0	0.25	10.0	–	–	–	–	–	–	-0.125	-0.199
Trees												
Abies balsamea	–	–	1.00	40.0	0.38	15.0	4.17	6.7	–	–	-0.117	-0.426**
Acer saccharum	15.75	90.0	54.75	100.0	11.88	90.0	13.50	93.3	19.74	84.2	-0.220	-0.627**
Acer rubrum	25.00	90.0	5.25	60.0	10.50	80.0	24.00	100.0	5.79	57.9	-0.388*	0.441*
Betula alleghaniensis	–	–	4.00	20.0	0.88	10.0	0.17	6.7	1.05	15.8	0.201	-0.031
Betula papyrifera	–	–	–	–	0.13	5.0	–	–	–	–	0.173	0.079
Ostrya virginiana	5.75	40.0	1.75	20.0	2.00	10.0	0.17	6.7	1.97	5.3	-0.287*	0.044
Picea glauca	–	–	0.25	10.0	–	–	–	–	–	–	-0.047	-0.151
Pinus strobes	3.00	20.0	–	–	0.25	10.0	–	–	0.13	5.3	-0.240*	0.231*
Populus grandidentata	0.50	20.0	0.50	20.0	0.88	10.0	5.33	53.3	–	–	-0.319**	0.294*
Populus tremuloides	0.75	30.0	0.25	10.0	18.75	65.0	3.00	53.3	18.29	52.6	0.324**	-0.296*
Prunus serotina	0.75	30.0	2.00	30.0	1.63	15.0	1.00	6.7	0.26	10.5	-0.238*	-0.151
Quercus rubra	1.75	70.0	2.00	80.0	6.75	80.0	2.67	73.3	1.97	52.6	-0.145	-0.112

Spearman's nonparametric correlation coefficients (ρ) for the association of cover values of each species to plot scores on the first two axes of the correspondence analysis ordination of the understorey plant community are shown.

* $p < 0.05$.
** $p < 0.01$.
[a] Specimens in a vegetative state that could not be identified beyond the Genus level.

Table 2
Mean ± 1 S.D. for microenvironmental variables measured during the 2006 growing season on plots under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* (northern red oak) near North Bay, Ontario, Canada

Variable	Upper slope-uncut ($n = 10$)	Lower slope-uncut ($n = 10$)	70% Shelterwood ($n = 20$)	Group selection ($n = 15$)	50% Shelterwood ($n = 19$)	Axis one (ρ)	Axis two (ρ)
Canopy cover (%)	99 ± 1	98 ± 1	69 ± 14	61 ± 18	59 ± 21	−0.642**	−0.225
Litter depth (mm)	17 ± 3	17 ± 5	14 ± 7	11 ± 5	11 ± 8	−0.476**	−0.169
Maximum soil temperature[a] (°C)	13.1 ± 0.3	13.0 ± 0.6	13.3 ± 0.5	14.1 ± 1.2	14.5 ± 1.3	0.470**	0.194
Minimum soil temperature[a] (°C)	11.6 ± 0.4	11.4 ± 0.7	11.1 ± 0.5	11.6 ± 0.7	11.2 ± 0.5	−0.060	0.242*
Mean soil temperature[a] (°C)	12.3 ± 0.3	12.2 ± 0.6	12.2 ± 0.4	12.9 ± 0.7	12.7 ± 0.6	0.321**	0.281*
Growing degree days[a,b]	341.8 ± 11.0	336.8 ± 24.7	332.6 ± 81.3	384.2 ± 49.1	399.1 ± 55.3	0.442**	0.207
Soil moisture (%)	17.58 ± 1.75	25.07 ± 6.06	19.21 ± 5.31	23.46 ± 10.94	21.13 ± 6.07	−0.007	−0.083
pH	4.6 ± 0.1	4.9 ± 0.2	4.8 ± 0.2	4.6 ± 0.2	4.8 ± 0.3	0.418**	−0.332**
Soil P[c] (mg L^{-1})	9.5 ± 2.7	25.6 ± 6.5	8.25 ± 3.3	11.4 ± 3.4	16.3 ± 10.2	0.020	−0.239*
Soil K[c] (mg L^{-1})	32.6 ± 6.8	42.6 ± 7.3	31.3 ± 6.7	42.8 ± 13.4	38.5 ± 10.6	−0.167	−0.135
Soil Mg[c] (mg L^{-1})	16.7 ± 3.7	19.2 ± 3.0	14.2 ± 2.3	18.4 ± 4.3	17.0 ± 6.0	−0.256*	−0.108
Total Soil N (%)	0.11 ± 0.02	0.20 ± 0.05	0.15 ± 0.04	0.16 ± 0.09	0.18 ± 0.06	0.071	−0.282*

Spearman's nonparametric correlation coefficients (ρ) for the association of each variable to plot scores on the first two axes of the correspondence analysis ordination of the understorey plant community are shown.
* $p < 0.05$.
** $p < 0.01$.
[a] Mean daily and cumulative temperature statistics are calculated based on a measurement period of 23 August–2 October, 2007.
[b] Growing degree days are calculated at $>5\ °C$.
[c] Plant available concentrations.

Table 3
Plant community compositional and structural characteristics (mean ± 1 S.D.) observed during the 2006 growing season on plots under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* (northern red oak) near North Bay, Ontario, Canada

Variable	Upper slope-uncut ($n = 10$)	Lower slope-uncut ($n = 10$)	70% Shelterwood ($n = 20$)	Group selection ($n = 15$)	50% Shelterwood ($n = 19$)	Axis one (ρ)	Axis two (ρ)
Composition							
Species richness	12.1 ± 2.1	12.4 ± 3.0	14.1 ± 3.2	13.5 ± 3.0	11.8 ± 2.1	−0.096	−0.203
Diversity (Shannon's H)	1.85 ± 0.28	1.66 ± 0.36	2.02 ± 0.32	1.98 ± 0.34	1.88 ± 0.23	0.016	−0.043
Evenness (J)	0.75 ± 0.09	0.66 ± 0.11	0.77 ± 0.07	0.76 ± 0.08	0.77 ± 0.07	0.128	0.072
Structure							
Canopy cover (%)	99 ± 1	98 ± 1	69 ± 14	61 ± 17	59 ± 21	−0.644**	−0.225
Understorey cover (%)	111 ± 25	124 ± 29	140 ± 47	130 ± 54	150 ± 48	0.361**	0.034
Total cover (%)	210 ± 25	222 ± 29	209 ± 48	191 ± 57	209 ± 55	0.027	−0.060

Spearman's nonparametric correlation coefficients (ρ) for the association of each variable to plot scores on the first two axes of the correspondence analysis ordination of the understorey plant community are also shown.
** $p < 0.01$.

Partial harvesting treatments produced changes in both the overstorey and understorey cover on sample plots (Table 3). Uncut areas had the lowest understorey cover, which increased in 70% shelterwood and group selection, and peaked in 50% shelterwood plots. Among the two uncut areas, the nutrient-rich lower slope site had greater understorey cover than the upper slope site. Overstorey cover had a significant negative correlation to plot scores on axis one, whereas understorey cover had a significant positive correlation to this axis (Table 3). There were no significant correlations between overstorey or understorey cover values and plot scores on axis two. The sum of overstorey and understorey cover (total cover) was very similar for the upper slope uncut, 70 and 50% shelterwood areas (Table 3). The peak mean total cover was observed in lower slope uncut plots, and the lowest total cover was observed in-group selection plots. Total cover was not significantly related to axes one or two (Table 3).

The most important change in plant community characteristics across the canopy and soil fertility gradients represented by axes one and two of the ordination, was a difference in the identity of the species potentially competing with regenerating *Q. rubra* seedlings. There was no pattern of abundance in *Q. rubra* related to either axis one or two (Fig. 2, Table 1); however, the nine species with the highest overall mean cover for the entire data set showed clear patterns of abundance related to the
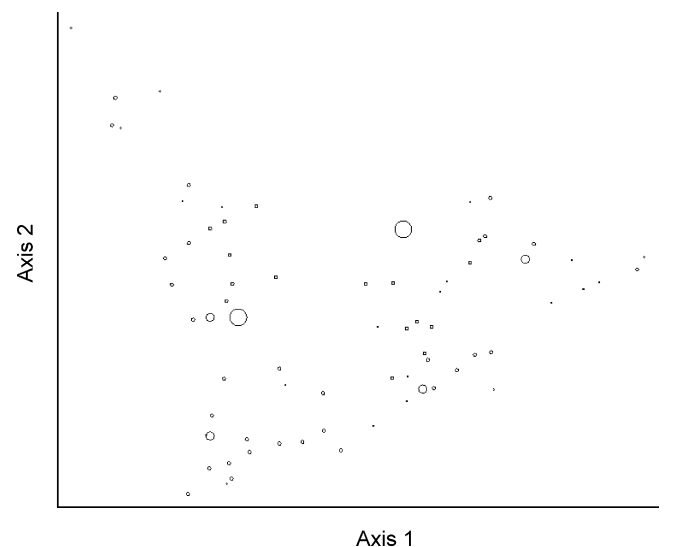

Fig. 2. Overlay of total cover values for *Q. rubra* (northern red oak) on a correspondence analysis ordination of plot scores derived from understorey plant species cover values. Data collected during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* near North Bay, Ontario, Canada. Symbol sizes are proportional to the magnitude of the plotted variable.
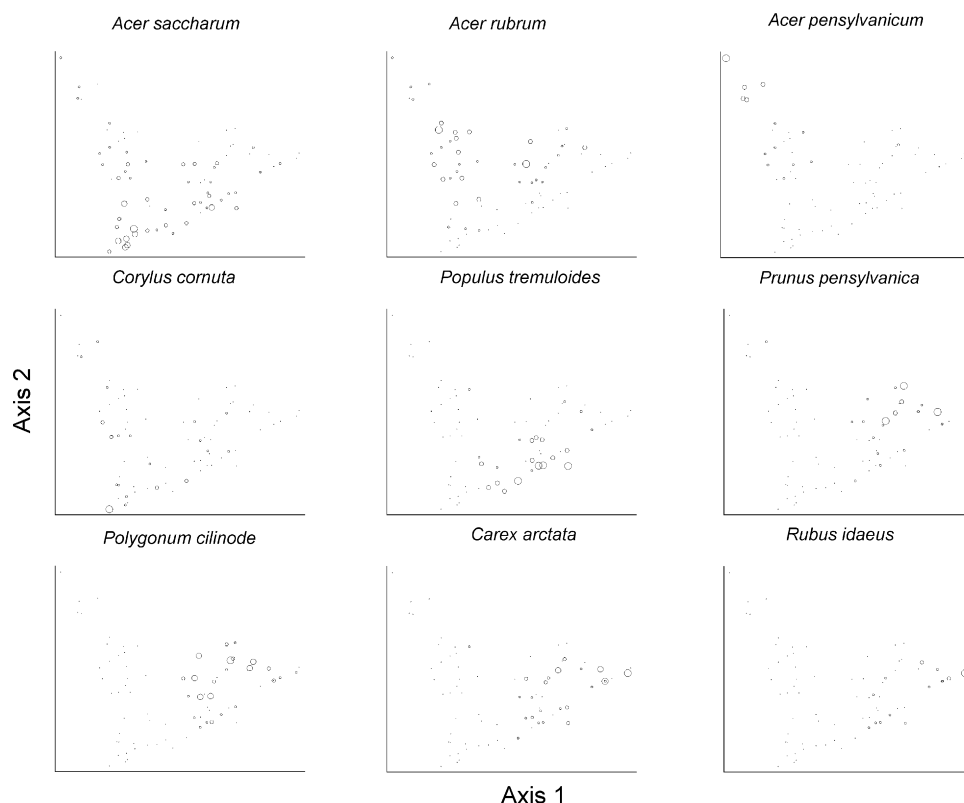
Fig. 3. Overlay of cover values for the nine most abundant understorey vascular plant species on a correspondence analysis ordination of the understorey plant community. Data collected during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by Q. rubra (northern red oak) near North Bay, Ontario, Canada. Symbol sizes are proportional to the magnitude of the plotted variable.

gradients of canopy cover and/or soil fertility (Fig. 3, Table 1). The zonation of competitors along axis one reflected the strong dominance of *Acer* spp. in uncut plots with high canopy cover, deep litter and lower soil temperatures, and the emergence of *R. idaeus* and several *Carex* spp. as major competitors in the more open, shallow litter, warmer soil of the 50% shelterwood (Fig. 4). *Populus tremuloides* also exhibited an increase in cover related to the greater canopy openness under the partial harvest treatments. The strong zonation of dominance within *Acer* spp. along axis two involved a shift from *A. saccharum* in the fertile zone characterized by high pH and relatively high levels of soil phosphorus and nitrogen, to *A. rubrum* at moderate levels of these variables, and *A. pensylvanicum* at lower levels.

3.2. Analyses of seedling density and size

The density of seedlings in the understorey varied considerably with respect to canopy cover, soil fertility and species (Table 4). The peak mean density of *Q. rubra* seedlings was observed in the 70% shelterwood plots; however, this was influenced by a few outlier plots with very high seedling densities (e.g. 22–72 stems m^{-2}), which were all in close spatial proximity and likely represented areas of unusually high seed deposition density during the mast crop of 2004. The only environmental factor significantly related to *Q. rubra* seedling density was litter depth, with higher seedling densities occurring on plots having greater litter depths (Table 5, Fig. 5). The density of *A. rubrum* seedlings was high in the upper slope uncut and group selection plots, and

Table 4
Population characteristics (mean ± 1 S.D.) for regeneration layer of Q. rubra, A. rubrum and A. saccharum observed during the 2006 growing season on plots under uncut areas and three different partial harvest treatments within a forest stand dominated by Q. rubra (northern red oak) near North Bay, Ontario, Canada

| Variable	Upper slope-uncut (n = 10)	Lower slope-uncut (n = 10)	70% Shelterwood (n = 20)	Group selection (n = 15)	50% Shelterwood (n = 19)
Density (stems m^{-2})					
Q. rubra	0.2 ± 0.3	0.4 ± 0.2	2.0 ± 4.4	0.4 ± 0.7	0.1 ± 0.1
A. rubrum	2.9 ± 2.1	1.0 ± 1.7	1.2 ± 1.4	2.4 ± 2.0	0.3 ± 0.4
A. saccharum	1.5 ± 1.5	80.1 ± 35.9	1.8 ± 2.2	0.6 ± 0.8	5.2 ± 7.3
Diameter (mm)					
Q. rubra	1.5 ± 0.6	2.5 ± 1.3	2.8 ± 1.2	2.6 ± 1.5	4.6 ± 1.6
A. rubrum	3.2 ± 2.9	2.6 ± 2.3	4.0 ± 3.1	4.4 ± 2.9	4.0 ± 2.0
A. saccharum	2.6 ± 1.9	1.5 ± 0.9	2.6 ± 2.3	5.3 ± 3.8	2.9 ± 2.1
Height (cm)					
Q. rubra	12.5 ± 4.7	24.6 ± 8.9	19.9 ± 10.1	16.6 ± 8.2	27.4 ± 6.5
A. rubrum	27.8 ± 22.3	22.4 ± 8.9	33.4 ± 28.3	40.6 ± 26.4	36.4 ± 23.3
A. saccharum	25.6 ± 22.9	13.0 ± 7.1	13.8 ± 12.9	34.2 ± 22.7	20.3 ± 17.6
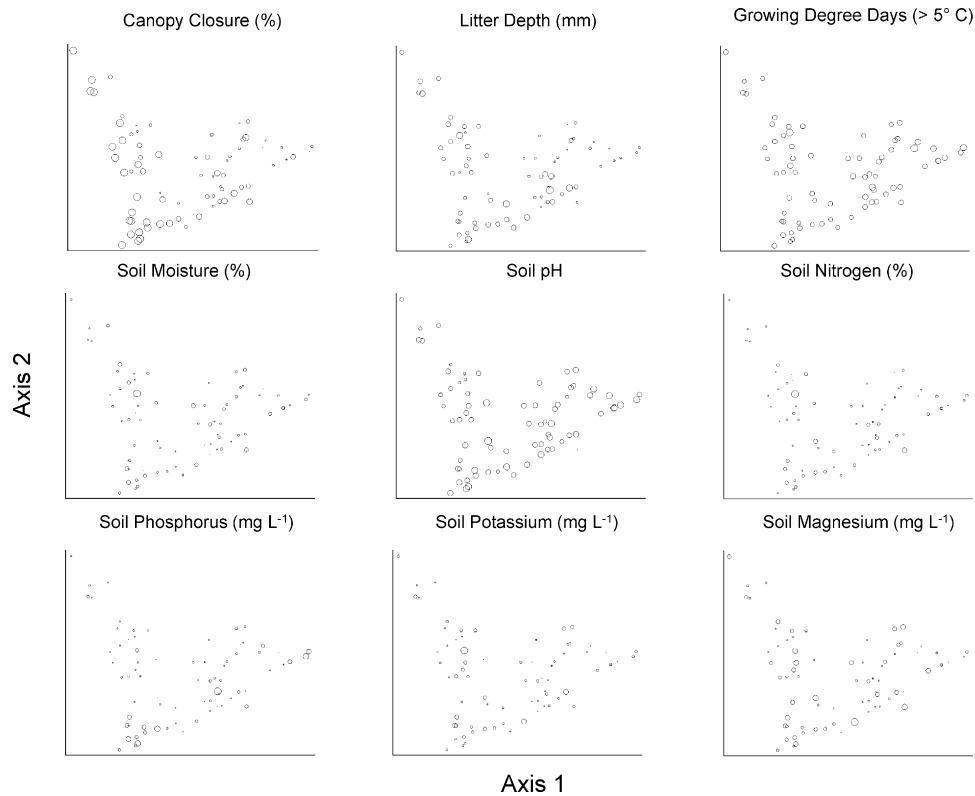
Fig. 4. Overlay of microenvironmental variables on a correspondence analysis ordination of the understorey plant community. Data collected during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* (northern red oak) near North Bay, Ontario, Canada. Symbol sizes are proportional to the magnitude of the plotted variable.

Table 5
Regression statistics for density, diameter and height of regeneration layer of *Q. rubra*, *A. saccharum* and *A. rubrum* related to environmental variables observed during the 2006 growing season on plots under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* (northern red oak) near North Bay, Ontario, Canada

Variable (y)	Predictor(s)	r^2	Equation	F	N
Q. rubra					
Density (stems m^{-2})	1. Litter depth (x)	0.21	$\log_{10}y = 0.017(x) - 0.004$	19.56**	70
Diameter (mm)	1. Canopy closure (x)	0.32			
	2. Density *A. rubrum* (y)	0.43			
	3. Maximum temperature (z)	0.54			
	4. Minimum temperature (a)	0.61	$y = -0.017x - 0.049y + 0.612z - 0.606a + 3.01$	17.11**	41
Height (cm)	1. Density *A. rubrum* (x)	0.20			
	2. Maximum temperature (y)	0.30			
	3. Soil phosphorus (z)	0.38	$y = -0.419x + 2.74y - 0.24z - 16.41$	7.77**	42
A. rubrum					
Density (stems m^{-2})	1. Soil phosphorus (x)	0.07			
	2. Canopy closure (y)	0.13	$\log_{10}y = -0.018x + 0.0054y + 0.807$	6.25**	74
Diameter (mm)	1. Canopy closure (x)	0.08	$y = -0.002x + 0.83$	5.30*	53
Height (cm)	1. Canopy closure (x)	0.11	$y = -0.346x + 60.57$	7.21**	53
A. saccharum					
Density (stems m^{-2})	1. Soil phosphorus (x)	0.25			
	2. Canopy closure (y)	0.39			
	3. Soil pH (z)	0.44			
	4. Soil nitrogen (a)	0.48			
	5. Density *Q. rubra* (b)	0.51			
	6. Soil moisture (c)	0.54	$\log_{10}y = 0.032x + 0.017y + 0.757z + 4.07a - 0.018b - 0.024c - 4.41$	15.19**	74
Diameter (mm)	1. Canopy closure (x)	0.19	$y = -0.025x + 4.75$	13.17**	54
Height (cm)	1. Soil moisture (x)	0.08			
	2. Soil nitrogen (y)	0.15	$\log_{10}y = 0.012x - 0.861y + 1.08$	5.52**	55

Note: Cumulative r^2 (adjusted) values are presented for the addition of each significant predictor. F and p values are for the model including all significant predictors.
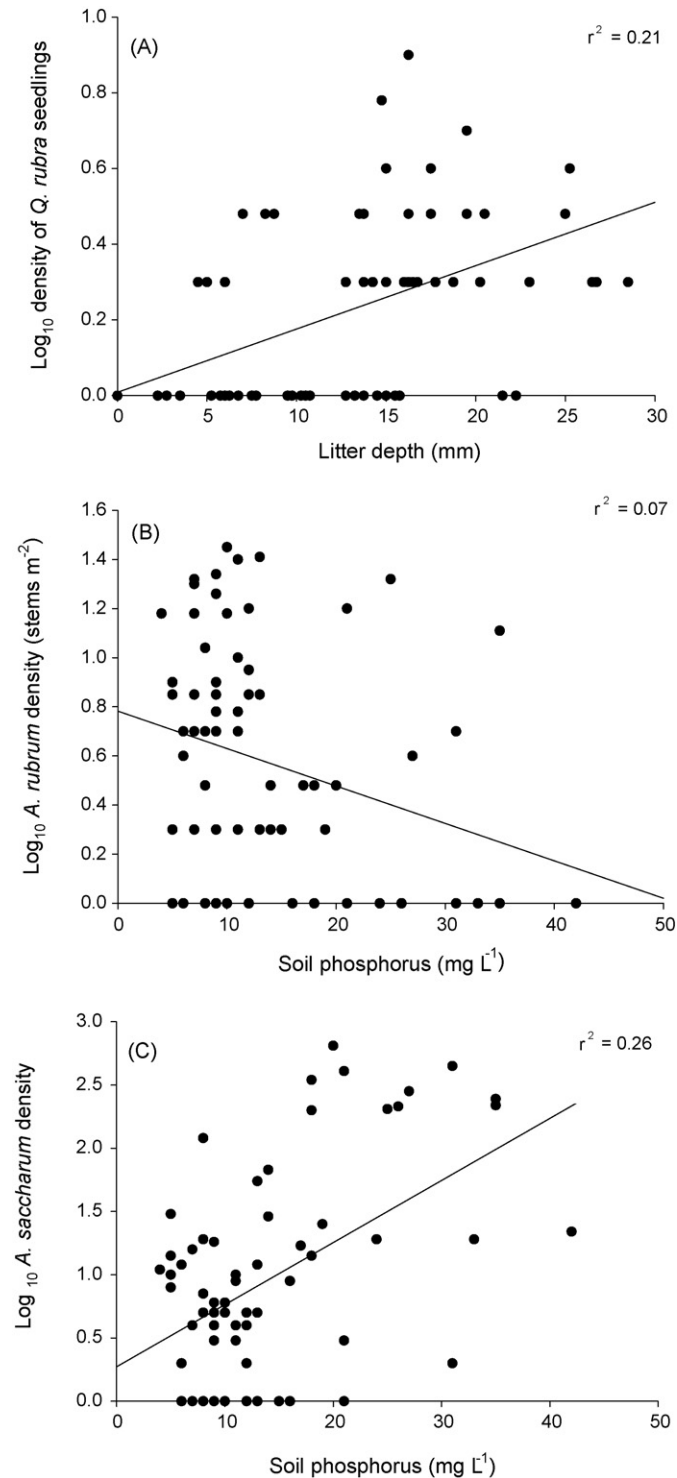* $p < 0.05$.
** $p < 0.01$.

Fig. 5. Scatterplots of seedling densities (stems m^{-2}) and the primary environmental variable extracted by stepwise linear regression analyses. Data collected from sample plots during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by Q. rubra (northern red oak) near North Bay, Ontario, Canada. (A) Q. rubra (n = 70); (B) A. rubrum (n = 74); (C) A. saccharum (n = 74).
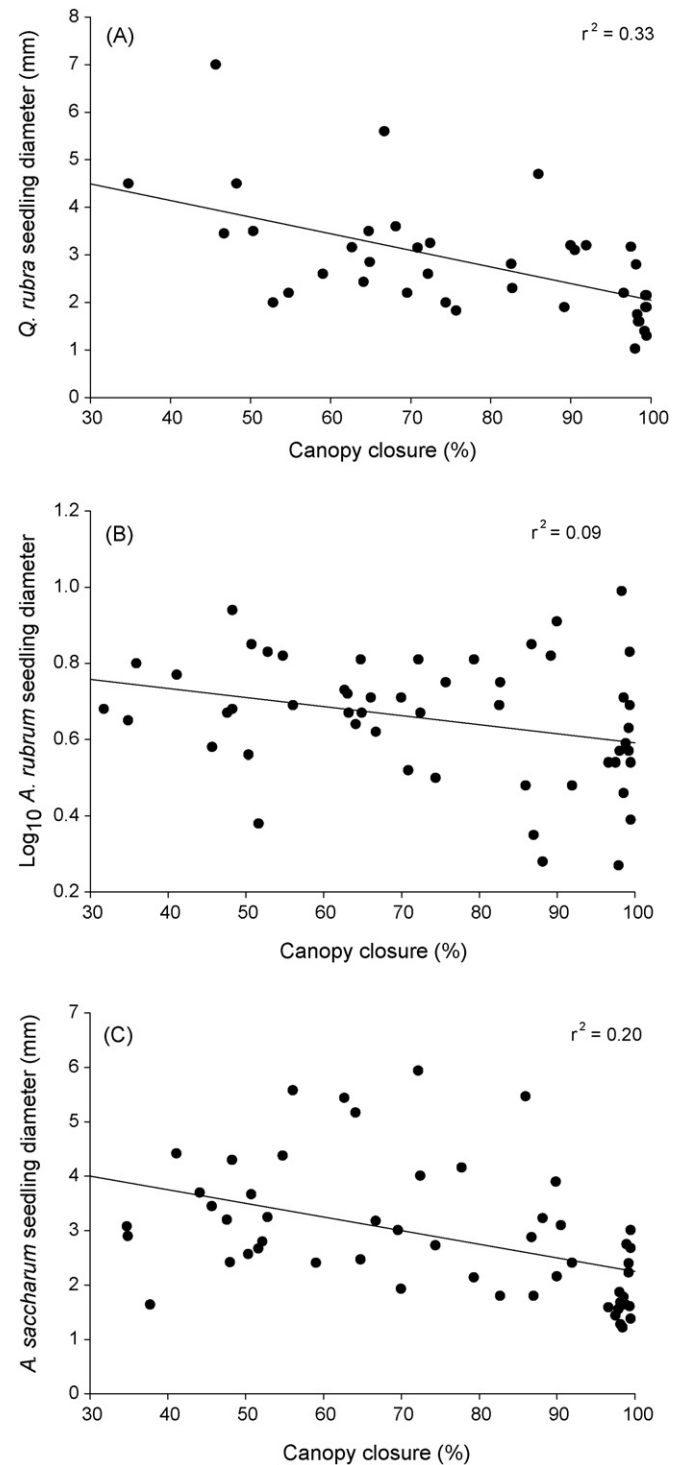

Fig. 6. Scatterplots of mean seedling diameters (mm) and the primary environmental variable extracted by stepwise linear regression analyses. Data collected from sample plots during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by Q. rubra (northern red oak) near North Bay, Ontario, Canada. (A) Q. rubra (n = 41); (B) A. rubrum (n = 53); (C) A. saccharum (n = 54).

lower in the lower slope uncut and shelterwood plots (Table 4). Density of A. rubrum seedlings was primarily related to soil phosphorus, such that higher densities occurred on plots with lower soil phosphorus levels (Table 5, Fig. 5). As a significant secondary factor, some of the residual variance in A. rubrum density unaccounted for by soil phosphorus was positively related to canopy cover (Table 5). A. saccharum reached extremely high densities in the uncut lower slope site (e.g. 80 stems m^{-2}), and was less abundant under all of the remaining conditions. Soil phosphorus was the primary significant environmental factor

related to *A. saccharum* densities, which peaked in plots with relatively high concentrations of this nutrient (Table 5, Fig. 5). A number of additional factors were related to the residual variance in *A. saccharum* densities, which were included in the regression model in the following order of importance: canopy cover

Fig. 7. Scatterplots of mean seedling height (cm) and the primary environmental variable extracted by stepwise linear regression analyses. Data collected from sample plots during the 2006 growing season under uncut areas and three different partial harvest treatments within a forest stand dominated by *Q. rubra* (northern red oak) near North Bay, Ontario, Canada. (A) *Q. rubra* (*n* = 42); (B) *A. rubrum* (*n* = 53); (C) *A. saccharum* (*n* = 55).

(positive), soil pH (positive), soil nitrogen (positive), density of *Q. rubra* (negative) and soil moisture (negative) (Table 5).

Seedlings of all three species had greater diameters under canopies of lower cover. The largest mean seedling diameters were observed under the 50% shelterwood treatment for *Q. rubra*, and under the group selection treatment for both *A. rubrum* and *A. saccharum*. In all species, the diameters of seedlings under an uncut canopy were lower than those under any of the partial harvest treatments (Table 4). Seedling diameters in *Q. rubra* were primarily related to canopy cover (negative), with density of *A. rubrum* (negative), mean daily maximum soil temperature (positive), and mean daily minimum temperature (negative) as additional significant factors listed in order of importance (Table 5). Diameters of seedlings of both *A. rubrum* and *A. saccharum* had significant relationships only with canopy cover (Table 5, Fig. 6). The negative relationship in seedling diameters of all three species with canopy cover suggests that the increased light availability in partial harvest treatments was associated with larger diameter growth of seedlings (Fig. 6). Among the three species, the slope of the regression line relating seedling diameter and canopy cover was greatest for *Q. rubra*, suggesting that this species benefited more than *A. rubrum* or *A. saccharum* under reduced canopy cover (Fig. 6).

Seedling heights did not exhibit a consistent pattern of variation among species across the canopy cover and soil fertility gradients (Table 4). Each species varied in height under the different canopy conditions according to relationships with different environmental factors. Mean seedling height in *Q. rubra* peaked in the 50% shelterwood plots, and exhibited a primary negative relationship with the density of *A. rubrum* seedlings (Tables 4 and 5, Fig. 7). Mean daily maximum soil temperature (positive) and soil phosphorus (negative) were significant secondary and tertiary factors respectively (Table 5). The largest mean seedling heights of *A. rubrum* were observed in the group selection plots (Table 4). The height of *A. rubrum* seedlings had a significant relationship (negative) with canopy cover (Table 5, Fig. 7). The largest mean seedling heights of *A. saccharum* also occurred in the group selection plots (Table 4); however, the primary factor significantly related to seedling height for this species was soil moisture. Plots with higher levels of soil moisture had taller *A. saccharum* seedlings (Fig. 5). Soil nitrogen was a significant secondary factor negatively related to *A. saccharum* seedling height (Table 5).

4. Discussion

Two years following the application of partial harvest treatments in a stand dominated by *Q. rubra* in the GLSL forest region of Canada, patterns of understorey plant community composition and the identity of potential competitors for *Q. rubra* seedlings were driven by gradients of canopy cover and soil fertility. Changes in plant community composition and microenvironment immediately following harvest have been observed for hardwood stands with a *Q. rubra* component in the Eastern Deciduous forest region (Elliot and Knoepp, 2005; Jackson et al., 2006). In our study, *A. saccharum* and *A. rubrum* reached high cover in all treatments; however, several early successional species colonized or expanded into the 50% uniform shelterwood to create a different suite of competitors for *Q. rubra*. The largest increase in cover we observed under the 50% shelterwood was in a group of *Carex* species (e.g. *C. arctata*, *C. praticola*). Leckie et al. (2000) found the seed bank of an old growth deciduous forest in Quebec was dominated in frequency and abundance by *Carex* spp. In a 50-year study of understorey dynamics in upland forests of Wisconsin and the upper peninsula of Michigan, Wiegmann and Waller (2006) found
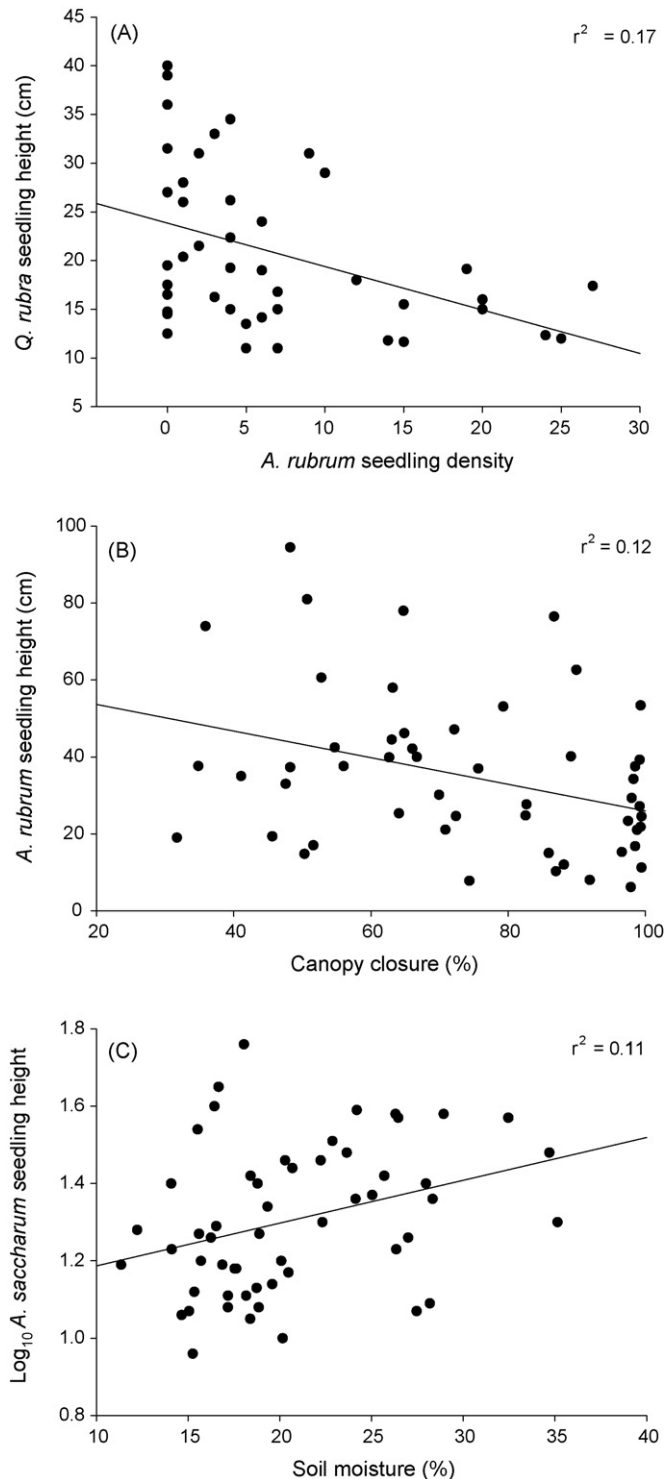
that *Carex* spp. increased in frequency by 286%, and attributed this colonization success to abiotic pollination mechanisms and clonal reproduction. Increases in understorey plant cover in clear-cut and shelterwood treatments in *Quercus* stands of lower Michigan largely involved the expansion of existing populations of *Carex* spp. and other graminoids (Buckley et al., 1998). We found that *Carex* spp. colonized plots with lower residual canopy cover (e.g. 50% shelterwood), and these were also the plots where the diameter of *Q. rubra* seedlings was greatest. This relationship suggests that the benefits of canopy reduction on graminoid-dominated plots are not negated by understorey competition for light, as they may be on plots with abundant shrub cover or advanced regeneration. Buckley et al. (1998), found a significant increase in the photon flux density of photosynthetically active radiation under harvested *Quercus-Pinus* stands when the shrub layer (>25 cm height) was removed in comparison to removal of the herb-layer (<25 cm height). We also observed a large increase in the cover of *R. idaeus* on the more open 50% shelterwood plots. *R. idaeus* regenerates from a high-longevity seed bank (Marks, 1974), and commonly colonizes (Peterson and Carson, 1996) or expands (Palmer et al., 2000) into areas shortly following disturbance. Roberts and Dong (1993) found that the competitive effect of *R. idaeus* on *Betula* seedlings in a 4-year old clear-cut site in New Brunswick was lower than that of advanced regeneration of other tree species (e.g. *A. saccharum*). Competitive effects on the regeneration of *Q. rubra* will be influenced by relative height of understorey species. In a concomitant study of planted *Q. rubra* seedlings on similar plots at this research site, the main competing vegetation was approximately 180, 165 and 127 cm in 50% shelterwood, group selection and 70% shelterwood, respectively (A.E. Morneault, unpublished data). Therefore, natural oak seedlings we measured were below the main competing vegetation in all treatments, although less so in the 70% shelterwood. However, the relative position of *Q. rubra* seedlings was improved in plots dominated by graminoids that ranged in height from 25 to 70 cm, compared to plots dominated by *Populus* spp. that ranged in height from 50 to 400 cm (A.E. Morneault, Unpublished Data). Ultimately, competitors with lesser effects may explain why *Q. rubra* seedlings in open canopy conditions had larger diameters, even though total understorey cover was greater in these plots.

Reducing the canopy releases vigorous shade-tolerant species already present in the understorey (Beck and Hooper, 1986; Jenkins and Parker, 1998). Despite increases in total understorey cover following canopy reduction, our results indicate plant species richness and diversity were similar in uncut and partial harvest plots. Jackson et al. (2006) observed an increase in herbaceous plant diversity under shelterwood treatments, which they attributed to the environmental heterogeneity associated with partial canopy removal. In our study, there was greater variation in environmental conditions as canopy openness increased; however, species richness and diversity peaked in the 70% shelterwood. The only clear difference in diversity among the treatments was associated with the strong dominance of *A. saccharum* in the more fertile, lower slope uncut area. Elliot and Knoepp (2005) studied oak-dominated forests in the southern Appalachians of North Carolina and found that uncut sites had lower diversity than partial harvest treatments 1 year after harvest, but differences in diversity indices were not significant 3 years after harvest. The results of our study, indicate compositional differences in understorey plant communities between partial harvest treatments and uncut areas were not associated with large differences in plant species richness or diversity, and suggest that reorganization of existing species (e.g. *Acer* spp., *Populus* spp.) and new species establishment (e.g. *Carex* spp., *R. idaeus*) were important mechanisms of change (*sensu* Marks, 1974).

The main competing species in the understorey of *Quercus*-dominated stands throughout the Eastern Deciduous forest are *A. saccharum* and *A. rubrum* (Abrams, 1992, 1996). In our study, mean seedling diameters of these competitors were negatively related to canopy cover; however, the relationship was stronger in *Q. rubra* than *A. rubrum* or *A. saccharum*. Larger diameter *Q. rubra* seedlings holds ecological significance, as basal diameter is significantly related to future growth and competitive success (Dey and Parker, 1997b; Spetich et al., 2002). Nine years after partial harvest treatments were applied in North Carolina, *Q. rubra* seedling diameter was positively related to basal area reduction in shelterwood stands thinned from below (Loftis, 1990). Nevertheless, responses of *Q. rubra* to canopy reduction can be confounded by understorey competition (Schuler and Miller, 1995).

In the GLSL forest region, *P. tremuloides* and *P. grandidentata* can also contribute significantly to the postharvest understorey cover through suckering. We observed a marked increase of *Populus* spp. cover on plots under partial harvest canopies, often in high-density pockets surrounding a felled *Populus* stem. In the GLSL forest region, *P. tremuloides*. can produce sucker densities ranging from 25,000 to 75,000 per hectare (Perala, 1990). Huffman et al. (1999) found that *P. tremuloides* sucker densities were inversely related to residual canopy cover. Furthermore, increased soil temperatures following a disturbance are considered the most important environmental factor controlling sucker initiation (Frey et al., 2003). The influence of these factors on the suckering response of *Populus* spp. suggests that the competitive threat suckers pose to *Q. rubra* seedlings should be most important in more open partial harvest treatments (e.g. 50% shelterwood). We found that the percent cover of *P. tremuloides* was positively related to plot scores on axis one, indicating that *Populus* competition was most intense on the plots under low canopy cover that had higher soil temperatures. Suckers are highly competitive due to their rapid height growth and the large amount of space occupied by their lateral roots (Carey, 1994). The presence of *Populus* spp. may have negated the advantage of partial harvesting to *Q. rubra* seedlings on many of the plots with low residual canopy cover.

In our study, there was a gradient in the ratio of canopy to understorey cover from the uncut upper slope (99:111) to the 50% shelterwood (59:150). In *Quercus* and *Pinus*-dominated stands in Michigan, canopy treatments (uncut, shelterwood at 25 and 75% crown closure, clear-cut) had a stronger effect on *Q. rubra* seedling growth than understorey competition control treatments, suggesting that canopy shade was the critical factor (Buckley et al., 1998). Alternatively, the improved survival and growth of *Q. rubra* seedlings established under a closed canopy with tall understorey competition removal led Lorimer et al. (1994), to conclude that understorey shade has a strong influence on recruitment. Dey and Parker (1996) found that light levels in shelterwood harvests at 50 and 70% canopy cover were sufficient to increase net CO_2 assimilation relative to *Q. rubra* seedlings in uncut areas, but the step from 70 to 50% crown closure produced relatively small increases in photosynthesis. Despite the positive relationship between canopy openness and seedling diameter we observed, seedling growth may have been dampened by increased understorey cover. *Q. rubra* seedlings show peak height and diameter at approximately 30% full sun (Phares, 1971a; Gottschalk, 1994). However, increases in total and root biomass are made up to 100% full sun (Phares, 1971a; Gottschalk, 1987).

We observed that *Acer* spp. in the understorey were stratified along a soil fertility gradient, such that *A. saccharum* and *A. spicatum* reached peak abundance on the fresh, rich portions of the site, whereas *A. rubrum* and *A. pensylvanicum* were more abundant on the drier, poorer portions of the site. *A. rubrum* has been

classified as a super-generalist with low resource requirements; however, it is typically out-competed by *A. saccharum* on rich, mesic sites (Abrams, 1998). Our regression analyses indicated that *A. rubrum* seedling density was negatively related to soil phosphorus, whereas *A. saccharum* seedling densities exhibited a positive relationship with this variable. Phosphorus may be an important limiting nutrient in GLSL forests given that nitrogen input via atmospheric deposition region is relatively high, and that recent variation in the diameter increment of *A. saccharum* trees can be mostly (74%) explained by available soil phosphorus (Gradowski and Thomas, 2006). Phares (1971b) observed that growth of potted *Q. rubra* seedlings was more responsive to phosphorus than nitrogen addition. In our study, relationships of cover or seedling variables for *Q. rubra*, *A. saccharum* and *A. rubrum* to total soil nitrogen were weaker than those for plant available soil phosphorus. Although our characterizations of nitrogen (total) and phosphorus (plant-available) are different, total nitrogen levels have been correlated to various measures of available nitrogen (Dou et al., 2000; Antep, 1997). Elliot and Knoepp (2005) observed no significant difference in total soil nitrogen among shelterwood, group selection and uncut areas in a hardwood stands 3 years after harvest, and found few harvest effects on physical or chemical soil properties. The major nutrient differences (e.g. phosphorus) among our plots existed between the two uncut sites. This suggests that the change in dominance from *A. saccharum* to *A. rubrum* we observed was associated with pre-existing variation in the soils across the stand. Phosphorus availability has been positively associated with pH in soils of *A. saccharum* forests in central Ontario (Gradowski and Thomas, 2006). In our study, the highest phosphorus availability occurred in the lower slope uncut plots which had higher soil pH, and both variables had negative relationships to axis two of the ordination. The implications of this pattern of dominance in *Acer* spp. to *Q. rubra* regeneration are not clear, as there is a lack of information on the relative competitive effects of *A. rubrum* and *A. saccharum* on the establishment and growth of *Q. rubra* seedlings across a nutrient gradient. Within the range of canopy openness and soil fertility observed in this study, there was a decline in the mean height and diameter of *Q. rubra* seedlings related to increases in the density of *A. rubrum*, and no such relationships to the density of *A. saccharum*. The cover, density or size of *Q. rubra* seedlings had few, weak relationships with soil nutrients, suggesting that light levels were insufficient to support growth increases for seedlings in high nutrient microenvironments (Phares, 1971a; Latham, 1992). Instead, it is likely that nutrients had an indirect effect on *Q. rubra* seedlings, by determining the main species they competed with.

At the landscape level, *Q. rubra* seedlings in stands throughout northern Michigan and Wisconsin are being competitively excluded from rich, mesic sites by *A. saccharum* and from poorer, dry-mesic sites by *A. rubrum* (Host et al., 1987; Nowacki et al., 1990). We observed this pattern of competitor identity repeated along a microenvironmental gradient. Much of our understanding of tree species distributions on the landscape is largely based on relationships developed between characteristics of adult trees and environmental gradients, with less emphasis placed upon the relationships at the seedling stage (Johnson et al., 2002; Collins and Carson, 2004). Differences in plant community composition of forests may be the result of processes that operate during the regeneration stage, when resources are limiting and patchy (Grubb, 1977; Latham, 1992; Johnson et al., 2002). For example, in undisturbed forest stands in Virginia, seedling densities of *Q. rubra* were not related to adult tree abundance, but had significant relationships to site aspect and elevation (Collins and Carson, 2004). The patterns in understorey plant community composition

observed in this study provide the ecological basis for identifying the major competitors of *Q. rubra* seedlings along gradients of canopy cover and soil fertility within stands, and illustrate the need to direct regeneration efforts (e.g. vegetation control) toward these two key sources of variation in early stand development.

This study was established after the harvest had taken place, and is therefore limited in scope to a snapshot of conditions 2-years after harvest. Given the variation that we detected in soil nutrients across the entire site, we must address the question of potential differences in the forest understorey prior to the cut, and the role such differences may have played in the differences we observed among the different canopy conditions we studied. There were no data collected prior to the harvest that would be suitable for a comparative analysis to our data. However, we suggest that any differences in the pre-harvest conditions across the stand would not explain the pattern of postharvest plant community composition and seedling characteristics we observed among the canopy treatments. We base this assertion on three lines of evidence; (i) uncut stands represented the extremes of the natural variation in soil fertility at the site, yet both were very similar with respect to ordination scores on axis one which we interpret as the influence of the partial harvest treatments on plant community composition, (ii) the second ordination axis summarizes the differences related to soil fertility among the plots, and plot scores for axis one were not related to those for axis two, (iii) all three species had greater diameters under lower canopy cover, which we interpreted as the main relationship of the regenerating seedlings with the partial canopy treatments. This interpretation is supported by the fact that stepwise regression models did not identify direct measurements of soil nutrients as predictors of seedling diameter in any of the three species examined.

In conclusion, composition of understorey plant communities of managed *Q. rubra* dominated stands in the GLSL forest region was primarily associated with canopy cover, and secondarily with soil fertility. From the perspective of *Q. rubra* regeneration, the importance of the main competing species can be predicted based on the intensity of canopy removal and the soil conditions typically related to topographical variation. Reductions in canopy cover from partial harvesting were balanced by increases in the cover of understorey species potentially competing with *Q. rubra*; however, seedlings of *Q. rubra* and its competitors *A. saccharum* and *A. rubrum* were all larger in diameter in plots under the lowest residual canopy cover. This suggests some early benefit may be provided to seedlings in the understorey after harvest alone. The association between greater *Q. rubra* diameter and lower canopy cover, tended to occur on plots with a specific suite of competitors including *Carex* spp. and *R. idaeus*. This suggests that competitor identity may influence the competitive ability of *Q. rubra* seedlings early after harvest, and that woody vegetation competition may be more critical to regenerating *Q. rubra* in these stands. Long-term monitoring of the plots established in this study coupled with experimental studies of the competitive effect the dominant species in the understorey have on *Q. rubra* will further elucidate the most effective way to regenerate this species in the GLSL forest region.

References

Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42, 346–353.

Abrams, M.D., 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Ann. For. Sci. 53, 487–512.

Abrams, M.D., 1998. The red maple paradox. Bioscience 48, 355–364.

Abrams, M.D., 2005. Prescribing fire in eastern oak forests: is time running out? North. J. Appl. For. 22, 190–196.

Antep, S., 1997. Evaluation of some chemical methods of soil nitrogen available based on ^{15}N technique. Commun. Soil Sci. Plant. 28, 537–550.

Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. 10, 168–172.

Buckley, D.S., Sharik, T.L., Isebrands, J.G., 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. Ecology 79, 65–78.

Carey, J.H. 1994. *Populus grandidentata*. In: Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/popgra/all.html (March 12, 2008).

Chambers, B.A., Naylor, B.J., Nieppola, J., Merchant, B., Uhlig, P., 1997. Field Guide to the Forest Ecosystems of Central Ontario. Queen's printer for Ontario, Toronto.

Christensen, N.L., 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. Am. Mid. Nat. 97, 176–188.

Collins, R.J., Carson, W.P., 2004. The effects of environment and life stage on Quercus abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients. For. Ecol. Manage. 201, 241–258.

Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. For. Sci. 34, 19–40.

Crow, T.R., 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91, 192–200.

Daubenmire, R.F., 1968. Plant Communities: A Textbook of Synecology. Harper and Row, New York.

Dey, D.C., Guyette, R.P., 2000. Anthropogenic fire history and red oak forests in south-central Ontario. For. Chron. 76, 339–347.

Dey, D.C., Parker, W.C., 1996. Regeneration of red oak (*Quercus rubra* L.) using shelterwood systems: ecophysiology, silviculture and management recommendations. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie, Ontario, Forest Research Information Paper No. 126, 59 p.

Dey, D.C., Parker, W.C., 1997a. Overstorey density affects field performance of underplanted red oak (*Quercus rubra* L.) in Ontario. North. J. Appl. For. 14, 120–125.

Dey, D.C., Parker, W.C., 1997b. Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. New Forest 14, 145–156.

Dou, H., Alva, A.K., Appel, T., 2000. An evaluation of plant-available soil nitrogen in selected sandy soils by electro-ultrafiltration, KCl, and $CaCl_2$ extraction methods. Biol. Fertil. Soils 30, 328–332.

Dolan, B.J., Parker, G.R., 2004. Understorey response to disturbance: an investigation of prescribed burning and understorey removal treatments. In: Spetich, M.A. (Ed.). Upland oak ecology symposium, history, current conditions, and sustainability. General Technical Report SRS-73, Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station. 311 pp.

Elliot, K.J., Knoepp, J.D., 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. For. Ecol. Manage. 211, 296–317.

Environment Canada, 2007. Canadian Climate Normals 1971–2000. North Bay. Available from http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html (cited August 23, 2007).

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169–1179.

Gleason, H.A., Cronquist, A., 1991. Manual of Vascular Plants of the Northeastern United States and Adjacent Canada. New York Botanical Garden, New York.

Gottschalk, K.W., 1987. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. II. Biomass partitioning and prediction. In: Proceedings of the Central Hardwood Forest Conference VI. University of Tennessee: 53-58, Knoxville, TN, February 24–20, 1987 pp. 99–110.

Gottschalk, K.W., 1994. Shade, leaf growth and crown development of *Quercus rubra, Quercus velutina, Prunus serotina* and *Acer rubrum* seedlings. Tree Physiol. 14, 735–749.

Gradowski, T., Thomas, S.C., 2006. Phosphorus limitation of sugar maple growth in central Ontario. For. Ecol. Manage. 226, 104–109.

Grubb, P.J., 1977. The maintenance of species richness in plant communities: importance of the regeneration niche. Biol. Rev. 52, 107–145.

Hannah, P.R., 1987. Regeneration methods for oaks. North. J. Appl. For. 4, 97–101.

Hanson, P.J., Isebrands, J.G., Dickson, R.E., 1987. Carbon budgets of *Quercus rubra* L. seedlings at selected stages of growth: influence of light. In: Proceedings of the Central Hardwood Forest Conference VI. University of Tennessee: 53-58, Knoxville, TN, February 24–20, 1987 pp. 269–276.

Hill, J.P., Dickmann, D.I., 1988. A comparison of three methods for naturally reproducing oak in southern Michigan. North. J. Appl. For. 5, 113–117.

Host, G.E., Pregitzer, K.S., 1992. Geomorphic influences on ground-flora and overstory competition in upper slope forests of northwestern lower Michigan. Can. J. For. Res. 22, 1547–1555.

Host, G.E., Pregitzer, K.S., Ramm, C.W., Hart, J.B., Cleland, D.T., 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern lower Michigan. For. Sci. 33, 445–457.

Huddle, J.A., Pallardy, S.G., 1999. Effect of fire on survival and growth of *Acer rubrum* and *Quercus* seedlings. For. Ecol. Manage. 118, 49–56.

Huffman, R.D., Fajvan, M.A., Wood, P.B., 1999. Effects of residual overstory on aspen development in Minnesota. Can. J. For. Res. 29, 284–289.

Jackson, S.W., Harper, C.A., Buckley, D.S., Miller, B.F., 2006. Short-term effects of silvicultural treatments on microsite heterogeneity and plant diversity in mature Tennessee oak-hickory forests. North. J. Appl. For. 23, 197–203.

Jenkins, M.A., Parker, G.R., 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. For. Ecol. Manage. 109, 57–74.

Johnson, P.S., Jacobs, R.D., Martin, A.J., Godel, E.D., 1989. Regenerating northern red oak: three successful case histories. North. J. Appl. For. 6, 174–178.

Johnson, P.S., Shifley, S.R., Rogers, R., 2002. The Ecology and Silviculture of Oaks. CABI Publishing, Wallingford, UK.

Kenkel, N.C., Derksen, D.A., Thomas, A.G., Watson, P.R., 2002. Multivariate analysis in weed research. Weed Sci. 50, 281–292.

Kim, C., Sharik, T.L., Jurgensen, M.F., 1996. Literfall, nitrogen and phosphorus inputs at various levels of canopy removal in oak and pine stands in northern lower Michigan. Am. Midl. Nat. 135, 195–204.

Kovacs, I., 2003. Forest Operations Prescription, Phelps Township Stand 686786. Nipissing Forest Resource Management Inc., Callander, Ontario.

Laporte, M.F., Duchesne, L.C., Morrison, I.K., 2003. Effect of clearcutting, selection cutting and microsites on soil surface CO_2 efflux in a tolerant hardwood ecosystem of northern Ontario. For. Ecol. Manage. 174, 565–575.

Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73, 2129–2144.

Leckie, S., Vellend, M., Bell, G., Lechowicz, M.J., 2000. The seed bank in an old-growth, temperate deciduous forest. Can. J. Bot. 78, 181–192.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.

Loftis, D.L., 1988. Regenerating oaks on high-quality sites: an update. In: Guidelines for Regenerating Appalachian Hardwood Stands: Workshop Proceedings. SAF Publication, 88-03 pp. 199–209.

Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. 36, 917–929.

Lorimer, C.G., 1984. Development of the red maple understorey in northeastern oak forests. For. Sci. 30, 3–22.

Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82, 227–237.

Marks, P.L., 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. 44, 73–88.

Masaki, T., Suzuki, W., Niiyama, K., Iida, S., Tanaka, H., Nakashikuza, T., 1992. Community structure of a species rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98, 97–111.

McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4.0. MjM Software Design, Gleneden Beach, Oregon.

Nowacki, G.J., Abrams, M.D., Lorimer, C.G., 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36, 276–292.

Ontario Ministry of Natural Resources (OMNR), 1998. A Silvicultural Guide for the Tolerant Hardwood Forest in Ontario. Queen's Printer for Ontario, Toronto, 500 pp.

Ontario Ministry of Natural Resources (OMNR), 2004. Ontario tree marking guide. Queen's Printer for Ontario, Toronto, 252 pp.

Ontario Ministry of Natural Resources (OMNR), 2006. The Forest Resources of Ontario.

Palmer, M.W., McAlister, S.D., Arévalo, J.R., DeCoster, J.K., 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. J. Veg. Sci. 11, 841–854.

Parker, G.R., Leopold, D.J., Eichenberger, J.K., 1985. Tree dynamics in an old-growth, deciduous forest. For. Ecol. Manage. 11, 31–57.

Perala, D.A., 1990. *Populus tremuloides* Michx. Quaking aspen. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 2. Hardwoods. Forest Service, United States Department of Agriculture, Washington, D.C., pp. 555–569.

Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Can. J. For. Res. 26, 45–52.

Phares, R.E., 1971a. Growth of red oak seedlings in relation to light and nutrients. Ecology 52, 669–672.

Phares, R.E., 1971b. Fertilization Tests With Potted Red Oak Seedlings. Research Note NC-114. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Roberts, M.R., Dong, H., 1993. Effects of organic layer removal on regeneration after clear-cutting a northern hardwood stand in New Brunswick. Can. J. For. Res. 23, 2093–2100.

Romagosa, M.A., Robison, D.J., 2003. Biological constraints on the growth of hardwood regeneration in upland Piedmont forests. For. Ecol. Manage. 175, 545–561.

Rowe, J.S., 1972. Forest regions of Canada. Canadian Forestry Service, Publication No. 1300, Ottawa.

Sander, I.L., 1990. *Quercus rubra* L. Northern Red Oak. In: Burns, R.M., Honkala, B.H. (Technical Co-ordinators), Silvics of North America, vol. 2, Hardwoods. Agricultural Handbook No. 654, USDA Forest Service, Washington, DC.

Schuler, T.M., Gillespie, A.R., 2000. Temporal patterns of woody species diversity in a central Appalachian forest from 1856–1997. B. Torrey Bot. Club 127, 149–161.

Schuler, T.M., Miller, G.W., 1995. Shelterwood treatments fail to establish oak reproduction on mesic forest sites in West Virginia. In: Gottschalk, K.W., Fosbroke, S.L.C. (Eds.), Proceedings of the Tenth Central Hardwood Conference, Morgantown, WV, USDA Forest Service, General Technical Report NE-197, March 5–8, 1995, pp. 375–387.

Shaw, M.W., 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales: I. A preliminary study of acorn production, viability and losses. J. Ecol. 56, 565–583.

Silvius, J.E., Lowell, C.A., Knickerbocker, C., 2003. The Tawawa Woods natural landmark. II. Plant species composition and recovery from disturbance. Ohio J. Sci. 103, 12–18.

Spetich, M.A., Parker, G.R., 1998. Distribution of biomass in an Indiana old-growth forest from 1926 to 1992. Am. Midl. Nat. 139, 90–107.

Spetich, M.A., Dey, D.C., Johnson, P.S., Graney, D.L., 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. For. Sci. 48, 504–517.

Teclaw, R.M., Isebrands, J.G., 1993. An artificial regeneration system for establishing northern red oak on dry-mesic sites in the lake states. USA. Ann. Sci. For. 50, 543–552.

Vetaas, O.R., 2000. The effect of environmental factors on the regeneration of *Quercus semecarpifolia* Sm. in Central Himalaya, Nepal. Plant Ecol. 146, 137–144.

Watt, A.S., 1919. On the causes of failure of natural regeneration in British oak-woods. J. Ecol. 7, 173–203.

Whitney, G.G., 1991. Relation of plant-species to substrate, landscape position, and aspect in North Central Massachusetts. Can. J. For. Res. 21, 1245–1252.

Wiegmann, S.M., Waller, D.M., 2006. Fifty years of change in northern upland forest understories: identity and traits of "winner" and "loser" plant species. Biol. Cons. 129, 109–123.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Englewood Cliffs, New Jersey.