

Influence of Forest Composition on Understory Cover in Boreal Mixed-wood Forests of Western Quebec

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Forest overstory composition influences both light and nutrient availability in the mixed boreal forest. The influence of stand composition on understory cover and biomass was investigated on two soil types (clay and till deposits). Four forest composition types were considered in this study: aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.) and a mixture of balsam-fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). The cover of all understory species was recorded while the biomass of two important and ubiquitous species was measured: mountain maple (*Acer spicatum* Lam.) of the shrub layer and large-leaved aster (*Aster macrophyllus* L.) of the herb layer. Soil analyses were conducted to evaluate the influence of overstory composition on understory biomass through its influences on soil characteristics. Analyses of variance showed a significant effect of forest canopy type on mountain maple biomass, understory cover and shrub cover but not on herb cover and large-leaved aster biomass. Path analysis was performed to explore the relationships between canopy type, nutrient availability and understory biomass. Contrary to what was expected, the variation in plant biomass associated with forest composition was weakly related to soil nutrient availability and more strongly related to stand structural attributes.

Keywords understory, composition, canopy, nutrient availability, biomass

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1 Introduction

The forest understory is an important component of forest biodiversity, and is where competition for light, water and nutrients strongly affects the initial success of tree species (Abrams and Dickmann 1982, Brumelis and Carleton 1989, George and Bazzaz 1999, Kabzems and Lousier 1992, Lieffers and MacDonald 1993). The prediction of the effect of forest management activities on forest biodiversity, regeneration and productivity requires a better understanding of the factors controlling the composition and growth of the understory layer. It is well established that there are interactions between overstory and understory vegetation (Carleton and Maycock 1980, Gagnon and Bradfield 1986, Host and Pregitzer 1992, Gilliam et al. 1995, Sagers and Lyon 1997, Légaré et al. 2001), mediated by relationships among light, water and nutrients (Paré et al. 1993, Longpré et al. 1994, Brais et al. 1995, Paré and Bergeron 1996, Messier et al. 1998).

It has long been recognized that understory biomass increases with an increase in incident solar energy (Zavitkovski 1976). In fact, the understory layer is affected by a reduction of light, when canopy is closed and stratified, and by nutrient availability (Gilliam and Turrill 1993). Also, more light is transmitted to the understory of stands composed predominantly of shade intolerant species such as aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and white birch (*Betula papyrifera* Marsh.), than stands composed of shade tolerant species such as balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and white cedar (*Thuja occidentalis* L., Messier et al. 1998).

The different nutrient requirements of the species in a stand and their relative contributions to the chemistry of the forest litter affect soil nutrient availability and other soil properties such as pH and net nitrification (Paré et al. 1993, Longpré et al. 1994, Brais et al. 1995, Paré and Bergeron 1996, Ste-Marie and Paré 1999). The relationship between overstory and understory is complex and also dependant on permanent site factors such as surface deposit. This is illustrated in the use of understory species as indicators of site quality or site productivity (Spies and Barnes

1985, Nieppola and Carleton 1991). It has been demonstrated that canopy type, through its influence on nutrient availability, affects understory composition (Légaré et al. 2001). Our general hypothesis was that forest composition influences understory cover and biomass despite similar edaphic conditions.

The principal objective of this study was to determine the influence of forest canopy composition on understory. More precisely, we studied the effect of forest composition on: i) the abundance (i.e., per cent cover) of tree, shrub, and herbaceous species in the understory; and, ii) the biomass (g/m^2) of the indicator species mountain maple (*Acer spicatum* Lam.) and large-leaved aster (*Aster macrophyllus* L.). A secondary objective was to investigate the interactions among canopy type, nutrient availability and understory biomass using path analysis.

2 Materials and Methods

2.1 Study Area

The area studied is located at Lake Duparquet Research and Teaching Forest, in northwestern Quebec ($48^{\circ}30'N$, $79^{\circ}20'W$). This area is part of the western *Abies balsamea* (balsam fir)–*Betula papyrifera* (paper birch) bioclimatic domain (Groncin 1996). This domain covers a part of the clay belt of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial Lakes Barlow and Ojibway at the time of their maximum expansion during the post-Wisconsinian (Vincent and Hardy 1977). The closest weather station to the study area is located at La Sarre, 35 km north of Lake Duparquet. The average annual temperature is 0.8°C , daily mean temperature for January is -17.9°C and 16.8°C for July, and the average annual precipitation is 856.8 mm (Environnement Canada 1993).

In the early stages of succession, paper birch, aspen, or jack pine dominate the forests in our study area. If stands are not subjected to any major disturbances such as fires (Bergeron 1991, Dansereau and Bergeron 1993) or spruce budworm outbreaks (Morin et al. 1993), they develop

into forests dominated by balsam fir and white cedar (Bergeron and Dubuc 1989). However, several different successional pathways are possible, and in some cases fir and spruce return immediately after a fire (Bergeron and Dubuc 1989). Pioneer understory species such as *Solidago rugosa* Mill. and *Rubus idaeus* L. disappear soon after canopy closure. Later, shade tolerant species such as *Cornus canadensis* L., *Linnaea borealis* L. and *Taxus canadensis* Marsh. appear, while dominance of *Aster macrophyllus* L., *Aralia nudicaulis* L. and *Acer spicatum* Lam. decreases (De Grandpré et al. 1993).

2.2 Sampling Methods

Ninety-four plots, each measuring 10 m × 10 m, were selected with particular care to ensure that the site conditions (slope and drainage) among plots were similar. The small size of these plots enabled us to avoid areas that had been disturbed by spruce budworm outbreaks. Plots were chosen on two different types of surface deposits; well to moderately drained clay and till. Four categories of forest composition were considered: aspen, paper birch, jack pine, and spruce-fir (balsam fir, white cedar, white spruce). One of these categories was assigned to each plot as a function of the species or group of species that exceeded 75% of the total basal area of the stand (Table 1). Sampled stands originated from fires that occurred in: 1870, 1916, 1919, 1923, 1944, 1964 (Table 2). Except for the aspen stand originating from the 1870 fire, which corresponds to a second cohort of aspen, dominant trees established immediately after the fire in all stands (Bergeron 2000). The

Table 1. Mean basal area of each tree species, mean stand height and mean stand density for each canopy type.

	Forest canopy			
	White birch	Spruce-fir	Aspen	Jack pine
Basal area (m ² /ha)				
White birch	28.0	4.4	1.5	2.1
Spruce-fir	2.3	23.5	1.5	0.9
Aspen	1.0	1.8	44.8	0.0
Jack pine	0.0	0.4	0.2	36.6
Total	31.3	30.1	48.0	39.6
Stand height (m)	13.6	11.9	16.5	18.0
Stand density (number of stems (dbh ≥ 5cm)/ha)	2025.9	2148.2	2100.0	1600.0

stand type and surface deposits selected represent the common forests and soils in the region (Bergeron et al. 1983). There were several replicates for each combination of soil and forest composition (Table 2). Some combinations had fewer replicates than others because of the difficulty of finding sites undisturbed by human activity and on the desired soil type.

2.2.1 Vegetation Sampling Methods

Herb, shrub and tree species less than 1 m high, or of a diameter at breast height less than 1 cm (Appendix 1) were sampled in the summer of 1998. Ten randomly distributed subplots (1 m × 1 m) were installed in each 10 m × 10 m plot. The per cent cover of each species was estimated in each subplot. For each plot, the mean cover of

Table 2. Sampling plan.

Forest composition	Clay				Till			
	130	77-84	56	Time since fire (yr)				
				36	130	77-81	56	36
Aspen	4	4	4	4	4	4	4	4
White birch	4	3	4	0	4	5	4	3
Jack pine	0	4	0	0	0	4	0	0
Spruce-fir	4	4	4	0	4	4	4	3
Number of plots	12	15	12	4	12	17	12	10

each species was calculated, as well as total herb cover, shrub cover and total understory cover (i.e., all species).

Following the observations of preliminary sampling in 1997, two understory species (mountain maple for its dominance in the shrub layer and large-leaved aster in the herb layer) were selected as indicator species of their respective understory layer biomass. Mountain maple and large-leaved aster biomass in each plot (10 m × 10 m) were assessed with allometric equations established for the Lake Duparquet Research and Teaching Forest (Appendix 2 and 3).

2.2.2 Soil Sampling

Eight samples were taken from two soil horizons: four samples from FH horizon and four samples from the first 10 cm of the mineral soil (Ae horizon and the top of the B horizon) in each plot. The samples were pooled by horizon and were air dried and ground. FH layer pH was analyzed in distilled water (McKeague 1977). Mineral N (NH₄ and NO₃) was extracted with 2M KCl and analyzed by flow injection analysis (Tecator FIA Star 5020). Exchangeable calcium in the humus layer was extracted with 0.1M BaCl₂ and determined by atomic absorption (Hendershot et al. 1993). Percentages of silt and clay in the mineral soil were determined by granulometric analysis (McKeague 1977).

2.2. Light Measurements

Available light for herb species was assessed using a LAI-2000 plant canopy analyzer (LICOR Inc., Lincoln, NE), which measured photosynthetic photon flux density (PPFD). PPFD was measured at 50 cm above forest floor at eight systematically selected places in each plot. Simultaneously, reference measures, which corresponded to full light, were recorded every 15 seconds in an open field near the study stand. Light measured at 50 cm above the forest floor was associated with the appropriate reference measures by the C-2000 computer program (LICOR Inc., Lincoln, NE), and light ratio transmitted at 50 cm above the forest floor was calculated.

2.2. Statistical Analysis

To maintain a balanced experimental design, jack pine stands were not included in the preliminary analyses of variance (ANOVA). Preliminary ANOVAs, with three fixed factors (canopy type, time since fire and surface deposit), were performed for the following dependant variables: shrub cover, herb cover, total understory cover, mountain maple biomass, and large-leaved aster biomass. Analyses were conducted on ranked cover and ranked mountain maple biomass data (Conover and Iman 1981). Biomass data for large-leaved aster was log transformed to satisfy the assumption of normality. The principal objective of these analyses was to ensure that there was no interaction between forest composition and time since fire. Therefore, data of only the 77, 81 and 84 year-old stands, which include all canopy types, were subjected to analysis of variance testing the effects of forest composition type and surface deposit. Herb cover, shrub cover, understory cover and large-leaved aster biomass were subjected to Tukey's multiple comparison tests to identify the significant differences among cover types. Because there is a significant interaction between forest composition type and surface deposit for the mountain maple biomass, two other Tukey's multiple comparison tests between canopy types were conducted for each surface deposit. All statistical analyses were performed using SAS (SAS Institute Inc. 1985)

It is difficult to distinguish the respective effects of nutrient and light availability on understory cover and biomass. Path analysis, by way of correlation and partial regression coefficients, can be used to estimate direct and indirect contributions between the standardized predictor and criterion variables (Sokal and Rohlf 1981, Legendre and Legendre 1983). The first path analysis was performed to explore relationships between understory cover, forest composition type (spruce-fir basal area), surface deposit (silt-clay percentage), nutrient availability (NH₄ and silt-clay percentage), and light availability (stand height and spruce-fir basal area). The second path analysis was performed to observe relationships between mountain maple biomass, canopy type (spruce-fir basal area and aspen basal area), surface deposit (silt-clay percentage), nutrient availability

(exchangeable Ca) and light availability (stand height and spruce-fir basal area). The third path analysis was performed to explore the relationship between herb biomass (large-leaved aster biomass), canopy type (spruce-fir basal area), surface deposit (silt-clay percentage), and nutrient availability (NH_4 available). Light availability was removed from the model because its influence on large-leaved aster biomass was not significant. These path analyses were performed on Piste 3.1.1 (Université de Montréal (A. Vaudor), Montreal, Quebec), by way of Spearman correlation (SAS Institute Inc 1985).

3 Results

3.1 Effects of Forest Cover Type on Indicator Species Biomass and on Total Understory, Shrub and Herb Cover

Total understory cover was affected by forest canopy type, being lower under spruce-fir stand than under any other forest composition (Table 3, Fig. 1). There was a strong effect of forest composition on shrub cover, which was also lower under shade-tolerant coniferous stands than under white birch, aspen and jack pine stands (Fig. 2). Total herb cover and large-leaved aster biomass were unaffected by forest composition and surface deposit (Table 4). Mountain maple biomass was significantly affected by forest composition, surface deposit and the interaction of these factors. On clay, its biomass was significantly lower under spruce-fir stand than under jack pine and aspen stands. However, on till deposits, mountain

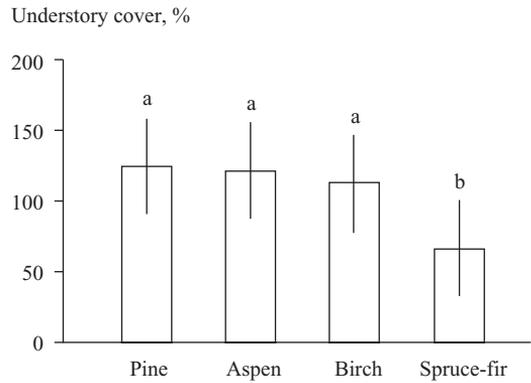


Fig. 1. Tukey's multiple comparison tests of understory cover rank mean among forest composition types. Note: Columns with same letter are not significantly different according to Tukey's test. Bars indicate standard deviation.

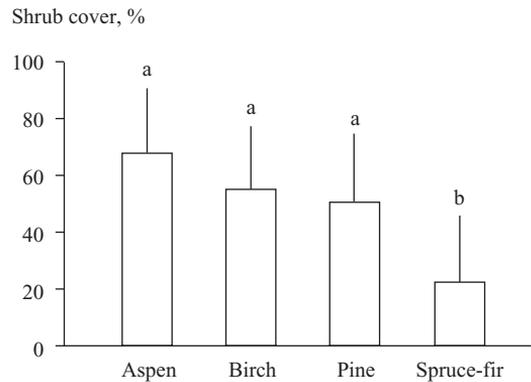


Fig. 2. Tukey's multiple comparison tests of shrub cover rank mean among forest composition types. Note: Columns with same letter are not significantly different according to Tukey's test. Bars indicate standard deviation.

Table 3. Analysis of variance performed, on 77, 81 and 84 year old stands, on understory cover rank, shrub cover rank and herb cover rank including all canopy types.

	Understory cover ($R^2 = 0.49$)			Shrub cover ($R^2 = 0.53$)			Herb cover ($R^2 = 0.31$)		
	DF	MS	F value	DF	MS	F value	DF	MS	F value
Model	7	189.48	3.24*	7	207.94	3.92**	7	118.92	1.51
Error	24	58.40		24	53.01		24	78.90	
Forest composition	3	411.93	7.05**	3	439.07	8.28**	3	202.08	2.56
Surface deposit	1	0.16	0.00	1	21.21	0.40	1	160.23	2.03
Interaction	3	27.04	0.46	3	33.18	0.63	3	21.42	0.27

Table 4. Analysis of variance performed, on 77, 81 and 84 year old stands, on mountain maple biomass rank and on large-leaved aster biomass including all canopy types.

	Mountain maple biomass (R ² = 0.64)			Large-leaved aster biomass (R ² = 0.25)		
	DF	MS	F-value	DF	MS	F-value
Model	7	247.50	5.97**	7	4.46	1.13
Error	24	41.48		24	3.95	
Forest composition	3	266.41	6.42**	3	3.52	0.89
Surface deposit	1	271.60	6.55 *	1	13.55	3.43
Interaction	3	199.58	4.81**	3	2.33	0.59

* = 0.01 < p < 0.05 ; ** = 0.001 < p < 0.01 ; *** = p < 0.001, DF: Degree of freedom, MS: Mean square

maple biomass was lower in spruce-fir stands than in both deciduous stands and it was also lower in jack pine stands than in white birch stands (Fig. 3).

3.2 Effects of Forest Composition, Nutrients and Light Availability

Total understory cover was positively related to NH₄ availability, which was negatively associated to spruce-fir basal area. It was also positively related to stand height, which was negatively related to spruce-fir basal area. Spruce-fir basal area also had a direct negative relationship with understory cover (Table 5, Fig. 4). The silt-clay percentage is positively related to stand height but it had no causal relation with understory cover. The availability of calcium had a positive direct relationship with mountain maple biomass and exchangeable calcium was positively related to aspen basal area and silt-clay percentage. Mountain maple biomass was positively associated to stand height, which was related to aspen (positive effect) and spruce-fir (negative effect) basal area and silt-clay percentage. Aspen and spruce-fir basal area also had a direct negative relationship with mountain maple biomass (Table 6, Fig. 5). For clarity (Figs. 4 and 5), stand height was related to silt-clay percentage instead of calcium availability and to the acidity of the mineral soil, which had a strong direct relationship with stand height (model not shown). Large-leaved aster biomass was positively associated to available NH₄

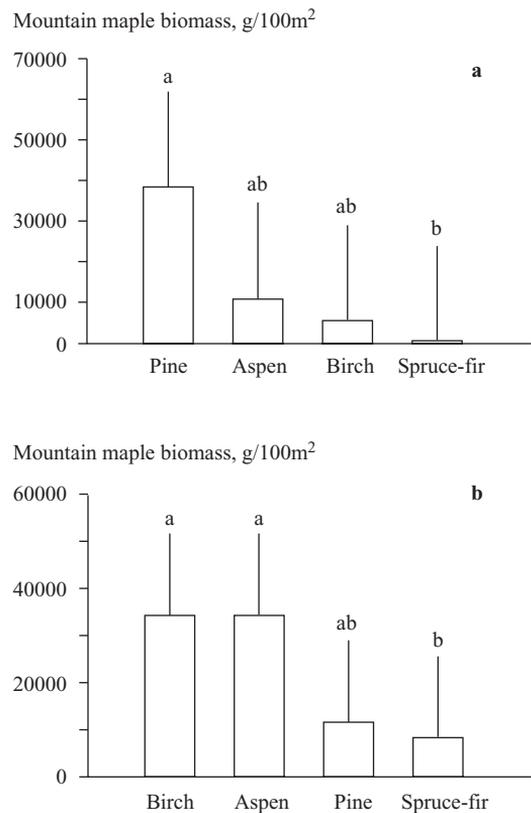


Fig. 3. Tukey’s multiple comparison tests of mountain maple biomass rank mean among forest composition types over two surface deposits: a) clay and b) till. Note: Columns with same letter are not significantly different according to Tukey’s test. Bars indicate standard deviation.

Table 5. Path analysis performed on spruce-fir basal area (BAsf), percent silt-clay (Clay), stand height (Height), available ammonium (NH₄) and understory cover (cover).

Relationship	Total covariation	Causal covariation direct	Causal covariation indirect	Causal covariation total	Spurious correlation
BAsf-Height	-0.32	-0.32	0.00	-0.32	0.00
BAsf-NH ₄	-0.29	-0.29	0.00	-0.29	0.00
BAsf-cover	-0.65	-0.52	-0.13	-0.65	0.00
Clay-Height	0.22	0.22	0.00	0.22	0.00
NH ₄ -cover	0.36	0.19	0.01	0.20	0.15
Height-cover	0.42	0.22	0.00	0.22	0.20

Table 6. Path analysis performed on aspen basal area (BAa), spruce-fir basal area (BAsf), percent silt-clay (Clay), stand height (Height), exchangeable calcium (Ca) and mountain maple biomass (maple).

Relationship	Total covariation	Causal covariation direct	Causal covariation indirect	Causal covariation total	Spurious correlation
BAsf-maple	-0.42	-0.42	-0.04	-0.46	0.04
BAa-maple	0.10	-0.23	0.17	-0.06	0.16
Height-maple	0.30	0.20	0.00	0.20	0.10
Ca-maple	0.23	0.28	0.00	0.28	-0.05
BAa-Ca	0.42	0.40	0.00	0.40	0.02
Clay-Ca	0.52	0.51	0.00	0.51	0.01
BAsf-Height	-0.32	-0.22	0.00	-0.22	-0.10
BAa-Height	0.38	0.30	0.00	0.30	0.08
Clay-Height	0.22	0.21	0.00	0.21	0.01

Table 7. Path analysis performed on spruce-fir basal area, silt-clay percent, available ammonium and large-leaved aster biomass (aster).

Relationship	Total covariation	Causal covariation direct	Causal covariation indirect	Causal covariation total	Spurious correlation
BAsf-aster	-0.36	-0.30	-0.06	-0.36	0.00
NH ₄ -aster	0.24	0.20	0.00	0.20	0.04
Clay-aster	0.33	0.36	0.00	0.36	-0.03
BAsf-NH ₄	-0.29	-0.29	0.00	-0.29	0.00

and silt-clay percentage, and negatively related to spruce-fir basal area (Table 7, Fig. 6). Light availability at 50 cm above the forest floor had no direct relationship with aster biomass (model not shown). Light availability at 50 cm above the

forest floor cannot be considered as a predictive variable for the model of total understory cover and mountain maple biomass because shrub species grow higher than 50 cm.

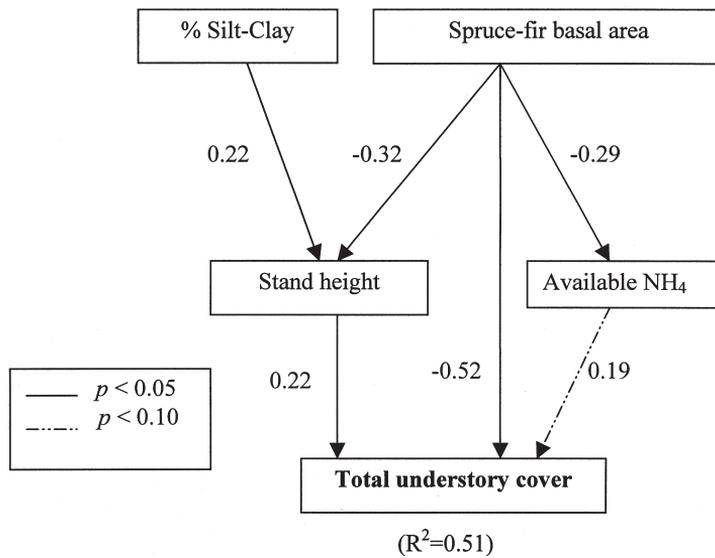


Fig. 4. Path analysis performed on spruce-fir basal area (BASf), percent silt-clay (Clay), stand height (Height), available ammonium (NH₄) and understory cover (cover). Causal relationships between predictor and criterion variables are depicted as arrows with the magnitude of the contribution (path coefficient) next to the arrow.

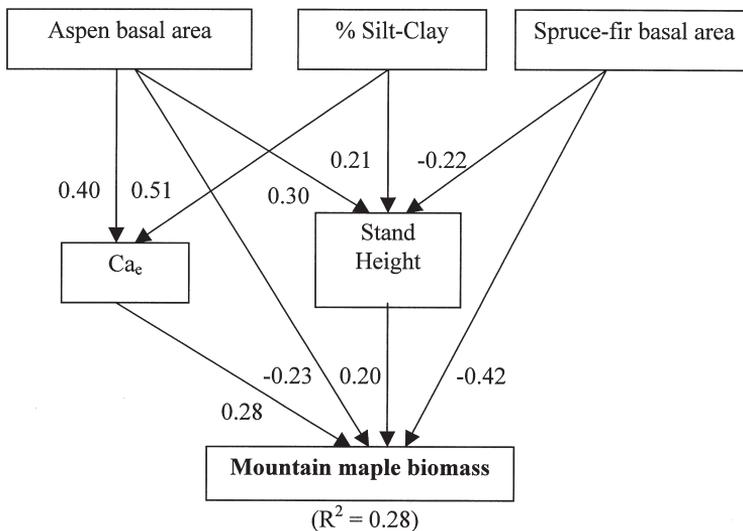


Fig. 5. Path analysis performed on aspen basal area (BAa), spruce-fir basal area (BASf), silt-clay percent (Clay), stand height (Height), exchangeable calcium (Ca) and mountain maple biomass (maple). Causal relationships between predictor and criterion variables are depicted as arrows with the magnitude of the contribution (path coefficient) next to the arrow.

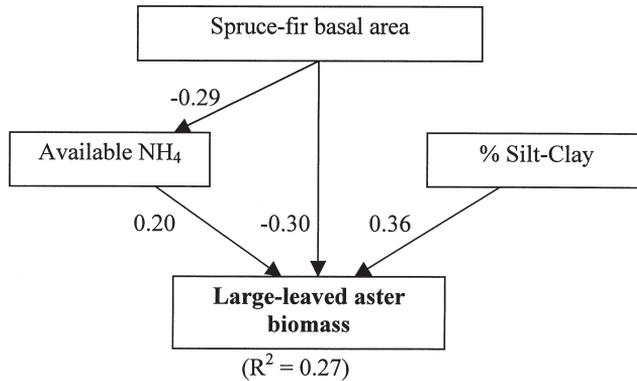


Fig. 6. Path analysis performed on spruce-fir basal area, silt-clay percent, available ammonium and large-leaved aster biomass. Causal relationships between predictor and criterion variables are depicted as arrows with the magnitude of the contribution (path coefficient) next to the arrow.

4 Discussion

The variation seen in the effect of forest composition on understory biomass suggests an influence of the stand structure. Our work seems to be consistent with that of Gilliam and Turrill (1993), who showed that understory layer is more limited by light availability when canopy is closed and stratified. Messier et al. (1998) found that shade intolerant tree species such as aspen, white birch and jack pine, transmit more light than shade tolerant tree species such as balsam fir and white spruce. The direct negative effect of spruce-fir basal area on total understory could be explained by the light attenuation of the forest canopy. Furthermore, stand height, a factor positively related to light availability (Messier et al. 1998) has a direct influence on understory cover. Above-ground biomass is often related to light availability and to the structure of the canopy cover (Zavitkovski 1976, González-Hernández et al. 1998) and it is generally accepted that understory biomass is negatively affected by increasing tree canopy cover (Ohmann and Grigal 1985, Tappeiner and Zasada 1993, Huffman et al. 1994). The absence of significant variation of herb layer (herb cover and large-leaved aster biomass) related to forest composition could be explained by the fact that light availability at the

forest floor level and at 50 cm above the forest floor is not significantly different between stands of different composition (Messier et al. 1998, Légaré et al. 2001).

The influence of spruce-fir basal area on the herb layer as well as the lower total understory and shrub cover in spruce-fir stands could also be explained by the competition for water and nutrients between understory species and late-successional trees. Fine and small roots of aspen and white birch are well distributed in the soil profile, whereas for late-successional trees such as balsam fir and white spruce, the fine roots are concentrated in the humus layer and in the surface mineral soil (Grier et al. 1981, Gale and Grigal 1987, Finér et al. 1997), close to the roots of understory species. Interception of precipitation by the forest canopy could also contribute to the direct effect of spruce-fir basal area on understory composition (Anderson et al. 1969).

Légaré et al. (2001) showed that through its influence on nutrient availability (Paré et al. 1993, Longpré et al. 1994, Brais et al. 1995, Paré and Bergeron 1996), forest composition affects understory composition and Turner and Franz (1986) suggest that soil heterogeneity associated with tree species would influence the spatial distribution of understory species. The negative relationship between available ammonium and spruce-fir

basal area and the positive relationship with total understory cover observed in the present study, suggests an influence of nitrogen availability on understory cover. However, a significant difference in understory cover between conifer stands (jack pine and spruce-fir) of lower soil fertility and deciduous stands of higher soil fertility was not observed.

The effect of forest composition on mountain maple biomass varied with surface deposit. In jack pine stands, a greater biomass of mountain maple on clay deposits, which contains high available Ca, suggests that nutrient availability has an important influence. Mountain maple is a relatively nutrient demanding species (Vincent 1965, Jobidon 1995) and is often nutrient limited (Aubin 1999). On till, the smaller biomass of mountain maple in jack pine stands among early-successional species stands can be explained by the negative influence of jack pine on available nutrients (Longpré et al. 1994). Thus, mountain maple could be replaced, to some extent, by another species that are better adapted to infertile soil (e.g., green alder (*Alnus crispa* (Ait.) Pursh.)). Other studies have indicated an influence of forest composition on understory composition through an effect on soil nutrient availability (Bergeron and Bouchard 1983, Légaré et al. 2001). On clay, the differences observed among forest compositions was also linked to stand structure variables such as total basal area, stand height and stand density, which affect light availability. The smaller biomass of mountain maple in aspen and white birch stands on clay deposits, could be related to the leaf area index (LAI) which is influenced by soil fertility (Zobel et al. 1976, Long and Smith 1988).

5 Conclusion

In this study, stand structure variables seems to explained variation in understory biomass among stands of different composition and availability of soil nutrients does not appear to be an important factor. In contrast, a companion study indicated that changes in understory composition among forests of different composition were strongly related to nutrient availability (Légaré et al. 2001).

The lack of a strong effect of nutrient availability on understory biomass suggests that understory species present in a given stand are well adapted to soil characteristics and that their growth is largely linked to light and water availability. However, in full light conditions, when the canopy is removed, or on poor site, nutrient availability may become more critical to the understory and the better adapted species should be more competitive and productive.

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References

- Abrams, M.D. & Dickmann, D.I. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Canadian Journal of Botany* 60: 946–954.
- Anderson, R.C., Loucks, O.L., & Swain, A.M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50: 255–263.
- Aubin, I. 1999. Végétation de sous-bois et disponibilité de la lumière dans la forêt boréale du sud-ouest québécois. Mémoire de maîtrise en biologie. Université du Québec à Montréal, Montréal, Québec. 85 p.
- Bergeron, Y. 1991. The influence of lake and mainland landscapes on fire regime of the boreal forest. *Ecology* 72: 1980–1992.
- 2000. Species and stand dynamics in the mixed-woods of Quebec's southern boreal forest. *Ecology* 81: 1500–1516.
- & Bouchard, A. 1983. Use of ecological groups in analysis and classification of plant communities in a section of western Quebec. *Vegetatio* 56: 45–63.

- & Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. *Vegetatio* 79: 51–63.
- , Bouchard, A., Gangloff, P. & Camiré, C. 1983. La classification écologique des milieux forestiers de la partie ouest des cantons d'Hébécourt et de Roquemaure, Abitibi, Québec. *Études écologiques*. Université Laval, Québec. 169 p.
- Brais, S., Camiré, C., Bergeron, Y. & Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. *Forest Ecology and Management* 76: 181–189.
- Brumelis, G. & Carleton, T.J. 1989. The vegetation of post-logged black spruce lowlands in central Canada. II. Understorey vegetation. *Journal of Applied Ecology* 26: 321–339.
- Carleton, T.J. & Maycock, P.F. 1980. Vegetation of the boreal forest south of James Bay: non-centered component analysis of the vascular flora. *Ecology* 61: 1199–1212.
- Conover, W.J. & Iman, R.L. 1981. Rank transformation as a bridge between parametric and nonparametric statistics. *The American Statistician* 35: 124–129.
- Dansereau, P.-R. & Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. *Canadian Journal of Forest Research* 23: 25–32.
- De Grandpré, L., Gagnon, D. & Bergeron, Y. 1993. Changes in understory of Canadian southern boreal forest after fire. *Journal of Vegetation Science* 4: 803–810.
- Environnement Canada. 1993. Normales climatiques au Canada. Service de l'environnement atmosphérique, Ottawa. 157 p.
- Finér, L., Messier, C. & De Grandpré, L. 1997. Fine-root dynamics in mixed boreal conifer-broad-leaved forest stands at different successional stages after fire. *Canadian Journal of Forest Research* 27: 304–314.
- Gagnon, D. & Bradfield, G.E. 1986. Relationships among forest strata and environment in southern coastal British Columbia. *Canadian Journal of Forest Research* 16: 1264–1271.
- Gale, M.R. & Grigal, D.F. 1987. Vertical root distribution of northern species in relation to successional status. *Canadian Journal of Forest Research* 17: 829–834.
- George, L.O. & Bazzaz, F.A. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80: 833–845.
- Gilliam, F.S. & Turrill, N.L. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bulletin of the Torrey Botanical Club* 120: 445–450.
- , Turrill, N.L. & Adams, M.B. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications* 5: 947–955.
- González-Hernández, M.P., Silva-Pando, F.J. & Casal Jiménez, M. 1998. Production patterns of understory layers in several Galician (NW Spain) woodlands: seasonality, net productivity and renewal rates. *Forest Ecology and Management* 109: 251–259.
- Grier, C.C., Vogt, K.A., Keyes, M.R. & Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* 11: 155–167.
- Grondin, P. 1996. *Écologie forestière*. In: Manuel de foresterie. Presse de l'Université Laval, Québec. p. 135–279.
- Hendershot, W.H., Lalande, H. & Duquette, M. 1993. Ion exchange and exchangeable cations. In: Carter, M.R. (ed.). *Soil sampling and methods of analysis*. Canadian Society of Soil Science. p. 167–176.
- Host, G.E. & Pregitzer, K.S. 1992. Geomorphic influences on ground-flora and overstory composition in upland forests of northwestern lower Michigan. *Canadian Journal of Forest Research* 22: 1547–1555.
- Huffman, D.W., Tappeiner II, J.C. & Zasada, J.C. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. *Canadian Journal of Forest Research* 24: 39–51.
- Jobidon, R. 1995. *Érable à épis*. In: *Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec*. Revue de la littérature. Mémoire de recherche forestière 117. Gouvernement du Québec, Québec. p. 54–61.
- Kabzems, R. & Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the boreal white and black spruce zone. FRDA research program, research branch, BC ministry of forest. FRDA report 176. Victoria, Canada. 35 p.

- Légaré, S., Bergeron, Y. & Paré, D. 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. *Canadian Journal of Botany* 79: 1019–1027.
- Legendre, L. & Legendre, P. 1983. *Numerical ecology*. 2nd edition. Elsevier, New York. 197 p.
- Lieffers, V.J. & MacDonald, S.E. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. *Canadian Journal of Forest Research* 23: 2070–2077.
- Long, J.N. & Smith, F.W. 1988. Leaf area – sapwood area relations of lodgepole pine as influenced by stand density and site index. *Canadian Journal of Forest Research* 18: 247–250.
- Longpré, M.H., Bergeron, Y., Paré, D. & Béland, M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). *Canadian Journal of Forest Research* 24: 1846–1853.
- McKeague, J.A. (ed.). 1977. *Manuel de méthodes d'échantillonnage et d'analyse des sols*. Comité canadien de pédologie, Ottawa, Ontario. 223 p.
- Messier, C., Parent, S. & Bergeron, Y. 1998. Effects of overstory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9: 511–520.
- Morin, H., Laprise, D. & Bergeron, Y. 1993. Chronology of spruce budworm outbreaks in the Lake Duparquet region, Abitibi, Québec. *Canadian Journal of Forest Research* 23: 1497–1506.
- Nieppola, J.J. & Carleton, T.J. 1991. Relation between understory vegetation, site productivity, and environmental factors in *Pinus sylvestris* L. stands in southern Finland. *Vegetatio* 93: 57–72.
- Ohmann, L.F. & Grigal, D.F. 1985. Biomass distribution of unmanaged upland forests in Minnesota. *Forest Ecology and Management* 13: 205–222.
- Paré, D. & Bergeron, Y. 1996. Effect of colonizing tree species on soil nutrient availability in clay soil of the boreal mixedwood. *Canadian Journal of Forest Research* 26: 1022–1031.
- , Bergeron, Y. & Camiré, C. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. *Journal of Vegetation Science* 4: 811–818.
- Sagers, C.L. & Lyon, J. 1997. Gradient analysis in a riparian landscape: contrast among forest layers. *Forest Ecology and Management* 96: 13–26.
- SAS Institute. 1985. *SAS user's guide: statistics*. 5th edition. SAS Institute, NE. 956 p.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W.H. Freeman and Co., San Francisco, California. 859 p.
- Spies, T.A. & Barnes, B.V. 1985. A multifactor ecological classification of the northern hardwood and conifer ecosystems of Sylvania Recreation Area, Upper Peninsula, Michigan. *Canadian Journal of Forest Research* 15: 949–960.
- Ste-Marie, C. & Paré, D. 1999. Soil, pH, and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biology and Biochemistry* 31: 1579–1589.
- Tappeiner, J.C. & Zasada, J.C. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. *Canadian Journal of Forest Research* 23: 1775–1780.
- Vincent, A.B. 1965. Growth habits of mountain maple in the Ontario claybelt. *Forestry Chronicle* 41: 330–344.
- Vincent, J.S. & Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. *Géographie Physique du Quaternaire* 31: 357–372.
- Zavitkovski, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. *Ecology* 57: 694–706.
- Zobel, D.B., McKee, W.A., Hawk, G.M. & Dyrness, C.T. 1976. Relations of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs* 46: 135–156.

Total of 51 references

Appendix 1. Understory species status.

Shrub species	Herb species		
<i>Abies balsamea</i> (L.) Mill.	<i>Actae rubra</i> (Ait.) Willd.	<i>Goodyera tessellata</i> Lodd.	<i>Prunella vulgaris</i> L.
<i>Acer rubrum</i> L.	<i>Apocynum androsaemifolium</i> L.	Graminée spp.	<i>Pteridium aquilinum</i> (L.) Kuhn
<i>Acer spicatum</i> Lam.	<i>Aralia nudicaulis</i> L.	<i>Dryopteris disjuncta</i> (Ledeb.) Morton	<i>Pyrola asarifolia</i> Michx.
<i>Alnus crispa</i> (Ait.) Pursh.	<i>Aster acuminatus</i> Michx.	<i>Impatiens capensis</i> Meerb.	<i>Pyrola elliptica</i> Nutt.
<i>Alnus rugosa</i> (DuRoi) Spreng.	<i>Aster macrophyllus</i> L.	<i>Kalmia angustifolia</i> L.	<i>Pyrola virens</i> Scheigger
<i>Amélanchier</i> spp.	<i>Athyrium filix-femina</i> (L.) Roth	<i>Linnaea borealis</i> L.	<i>Ribes glandulosum</i> Grauer
<i>Betula papyrifera</i> Marsh.	<i>Carex</i> spp.	<i>Lonicera canadensis</i> Bartr.	<i>Ribes lacustre</i> (Pers.) Poir.
<i>Cornus alternifolia</i> L.	<i>Chenopodium album</i> L.	<i>Lycopodium lucidulum</i> Michx.	<i>Ribes triste</i> Pallas
<i>Cornus stolonifera</i> Michx.	<i>Chiogenes hispidula</i> (L.) T. & G.	<i>L. annotinum</i> L.	<i>Rosa acicularis</i> Lindl.
<i>Corylus cornuta</i> Marsh.	<i>Circaea alpina</i> L.	<i>L. clavatum</i> L.	<i>Rubus idaeus</i> L.
<i>Nemopanthus mucronatus</i> (L.) Trel.	<i>Clintonia borealis</i> (Ait.) Raf.	<i>L. complanatum</i> L.	<i>Rubus pubescens</i> Raf.
<i>Picea glauca</i> (Moench)Voss	<i>Cornus Canadensis</i> L.	<i>L. obscurum</i> L.	<i>Solidago rugosa</i> Mill.
<i>Picea mariana</i> (Mill.) BSP.	<i>Coptis groenlandica</i> (Oeder) Fern.	<i>Maianthemum canadense</i> Desf.	<i>Streptopus roseus</i> Michx.
<i>Populus tremuloides</i> Michx.	<i>Corallorhiza maculata</i> Raf.	<i>Mertansia paniculata</i> (Ait.) G Don.	<i>Thelypteris noveboracensis</i>
<i>Prunus</i> spp.	<i>Diervilla lonicera</i> Mill.	<i>Mitella nuda</i> L.	<i>Dryopteris phegopteris</i> (L) C. Chr.
<i>Salix</i> spp.	<i>Dryopteris spinulosa</i> (O.F.Muel.) Watt.	<i>Monotropa uniflora</i> L.	
<i>Sorbus americana</i> Marsh.	<i>Epilobium angustifolium</i> L.	<i>Osmunda claytoniana</i> L.	
<i>Taxus canadensis</i> Marsh.	<i>Equisetum sylvaticum</i> L.	<i>Oxalis Montana</i> Raf.	
<i>Thuja occidentalis</i> L.	<i>Fragaria virginiana</i> Duchesne	<i>Petasites palmatus</i> (Ait.) Gray	
<i>Viburnum cassinoides</i> L.	<i>Galium triflorum</i> Michx.		

Appendix 2. Mountain maple biomass equations according to Aubin et Hély.

Total biomass (gram)

$$\ln(\text{total biomass}) = -2.7348 + 2.7071 \cdot \ln(\text{diameter}) [R^2 = 0.9793]$$

Correction factor = 1.034

Appendix 3. Large-leaved aster biomass equations according to Légaré.

Total biomass (gram/1 m²)

$$\log_{10}(\text{aster biomass}) = -0.18 + 0.69 \log_{10}(\text{percentage cover of aster/1 m}^2) [R^2 = 0.9000]$$

Correction factor = 1.02