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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

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Abstract

Changes in forest floor properties and nutrient availability along a boreal post-fire sere succession covering a time span of 231 years were assessed using soil analysis and exchange resins. A decline in pH (from 5.5 to 3.65), effective cation exchange capacity (CEC) (from 72.5 to 39.6 cmol(+) kg^{-1}), exchangeable cation concentrations, as well as in Ca, Mg, K and PO_4 concentrations on resin was observed. Contrary to what has been reported so far for boreal forests, NO_3 and NH_4 concentrations did not decrease in the course of succession. Ammonium concentrations remained constant while those of NO_3 reached their highest values at age 27, decreased abruptly between ages 27 and 47, and started to increase in older stands. No correlation was found between NO_3 availability and pH, P concentrations or C/N ratio. Interactive effects of stand age and stand composition on nutrient concentrations on resins were evaluated using path analysis. While it is not possible to fully disentangle the contribution of single factors, the results showed a positive effect of aspen on Ca concentrations. These results stressed the need to evaluate the long term impacts of successive rotations of softwood species coupled with the elimination of hardwood competition on the soil base status of plantations.

Keywords: Succession; Nitrate; Ammonium; Nutrient cycling; Soil acidity

1. Introduction

In boreal forests, the forest floor constitutes an important nutrient pool (Krause et al., 1978) and is the soil layer that best reflects species composition and stand age with respect to N dynamics (Fyles and McGill, 1987). Accumulation of organic matter and nitrogen immobilization commonly occur over the course of natural boreal forest succession (Van Cleve and Nooman, 1975; Van Cleve and Viereck, 1981), whereas nitrification is often considered to be absent (Krause et al., 1978). Several studies have documented the changes in soil nutrient availability along successional gradients in the boreal forest (Van Cleve and Viereck, 1981; Van Cleve et al., 1983). They have shown a decline in nutrient availability, espe-

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cially of N, which was related to succession to coniferous trees.

Modifications of forest floor properties that parallel changes in the forest cover from broadleaf deciduous species to conifers can include: (i) a decrease in the nutrient concentration of the litterfall (Gosz, 1981); (ii) a decrease in soil respiration (Flanagan and Van Cleve, 1983); (iii) reduction of the availability of macro and micro-nutrients (Bormann and Sidle, 1990); (iv) an increase in C/N ratio (Bormann and Sidle, 1990); (v) an increase in forest floor biomass (Gosz, 1981); (vi) a decline in soil temperature (Van Cleve and Yarie, 1986). In addition, differences among succession species in canopy geometry and nutrient requirements can affect overall nutrient availability: e.g. conifers are considerably more efficient than broadleaf plants at trapping aerosols, and thus increase atmospheric nutrient inputs, but typically have lower nutrient requirements (Gosz, 1981; Carlyle, 1986).

In northwestern Quebec, two intolerant pioneer hardwood species, aspen (*Populus tremuloides* Michx) and white birch (*Betula papyrifera* Marsh.), are the dominant species following fire on mesic clayey sites. They remain part of the forest cover, although in diminishing importance, for more than 200 years while the late successional coniferous species, white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and white cedar (*Thuja occidentalis* L.) gradually attain stand dominance (Bergeron and Dubuc, 1989). Fire is the dominant natural disturbance while forests aged 150 years and older are periodically affected by outbreaks of spruce budworm (*Choristoneura fumiferana*) (Morin et al., 1993). A previous study (Paré et al., 1993), conducted on forests of 47,144 and 231 years, has shown that changes in forest floor properties were influenced by time since fire, insect disturbance and, forest composition. The principal objective of this study was to assess general trends in forest floor properties and nutrient availability in the southern boreal forest, along a post-fire sere succession covering a time span of 231 years, using conventional soil analysis and in situ resin bag methods. Fire intervals were roughly 30 years. A second objective was to assess the interactive effects of stand age and stand composition on these properties using path analysis. The study is part of a larger research program on succession dynamics following fire in northwestern Quebec.

2. Study area

The study area is located 30 km northwest of Rouyn-Noranda, in northwestern Quebec (48°30′N, 79°20′W). The climate is continental with a mean annual temperature of 0.6°C. Annual precipitation is 823 mm, of which 78% occurs as rain from April to November. The mean frost-free period is 64 days (Environment Canada, 1982). Soils on all sites are grey luvisols (Canada Soil Survey Committee, 1987), originating from glacio-lacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). The region belongs to the southern part of the boreal forest and is characterized by forests of balsam fir, white birch and white spruce on mesic clayey sites (Bergeron et al., 1983). Succession on these sites has been described by Bergeron and Dubuc (1989) and the fire history for the study area has been researched by Bergeron (1991) and Dansereau and Bergeron (1993), using fire scars and tree dating.

3. Methods

Stands of fire origin aged 27, 47, 75, 121, 144, 168, 194 and 231 years have been located in the course of other studies (Bergeron, 1991; Dansereau and Bergeron, 1993). All stands are within 11 km of each other. Two 20 m × 20 m quadrats per age were sampled for basal area determination of all trees over 10 cm diameter at breast height (DBH). Distance between the quadrats varied between 50 and 900 m.

Forest floor nutrient availability was assessed through soil analysis and through exchange resins. For sites 47 years old and older, with a Mor humus, two grab samples of the FH horizon were collected beside each quadrat, a few meters apart from one other. At each sample location (two per quadrat), five bags of both cation (Biorex 70 CER, 20–50 mesh, 7.8 meq per bag) and anion (Biorad AG3-X4A, 20–50 mesh, 7.3 meq per bag) exchange resins were placed within this horizon. At the 28-year-old site, characterized by a Moder humus, the Hi horizon was sampled and the resin bags were placed between the L and the Hi horizons. Exchange resins were left on site for 1 year.

Forest floor samples were air dried and ground. Samples were analyzed for organic matter (OM) by loss on ignition (organic C = 0.58 × OM) (McKeague, 1976), for Kjeldahl N, including NO_2 and NO_3 (Bremmer and Mulvaney, 1982), and for exchangeable cations ($_eCa$, $_eMg$, $_eK$) (inductively coupled plasma atomic emission (ICP), Perkin Elmer Plasma 40) and exchangeable acidity (titration, Metler DL-40) after extraction with 1 M NH_4NO_3 (Stuanes et al., 1984). Soil pH was determined in 0.01 M $CaCl_2$ (McKeague, 1976). Effective cation exchange capacity (CEC_E) was estimated by summing base and acid cations. Cation resins were extracted with 0.1 M HCl and anion resins with 0.05 M Na_2CO_3. Ammonium and NO_3 concentrations on resins were determined by flow injection analysis (Tecator FIAstar 5020 Analyzer) and PO_4 and cation concentrations (Ca, Mg, K) by ICP.

3.1. Data analysis

Results from forest floor analyses were averaged over each quadrat as were the median values for each of the two sets of five cation and anion exchange resins bags, in order to minimize the effect of extreme values. Homogeneity of variance was tested using Bartlett's procedure (Steel and Torrie, 1980). All variables met the requirement. Significance of linear and quadratic effects of stand age on nutrient concentrations were tested by means of orthogonal polynomials (Steel and Torrie, 1980).

As stand composition and age are highly correlated, it becomes difficult to distinguish their respective effects. Path analysis is a powerful analytical tool which can be used for the construction and evaluation of alternative structural models or theory testing (Sokal and Rohlf, 1981; Legendre and Legendre, 1983). As an extension of multiple linear regression, it allows the evaluation of the contribution of various factors (predictors) to one or two criterion variables in complicated interaction systems (Sokal and Rohlf, 1981). Direct and indirect contributions are estimated by way of correlation and partial regression coefficients, between the standardized predictor and criterion variables. The main emphasis is to estimate magnitude and directions of interactions rather than the significance of individual coefficients.

Path analysis was used to explore relationships between selected nutrient concentrations (NO_3, PO_4, K, Mg, Ca) on exchange resins and stand composition and time. Total covariance between variables was decomposed into direct or indirect causal variation, and non causal or spurious correlation as suggested by Legendre and Legendre (1983). The ORTHOREG procedure of the Statistical Analysis System Institute Inc. (1988) was used to evaluate regression coefficients; this procedure is recommended when variables are collinear with each other. Individual species representation, expressed as percent of total basal area, and time since fire were used as predictor variables. All combination of predictor variables were considered and models yielding the highest R^2 values were retained. All predictor variables were significant at the $P = 0.15$ level.

4. Results

4.1. Changes along the chronosequence

Changes in stand composition along the chronosequence are depicted in Fig. 1. Only species present in at least four quadrats were considered for analysis.

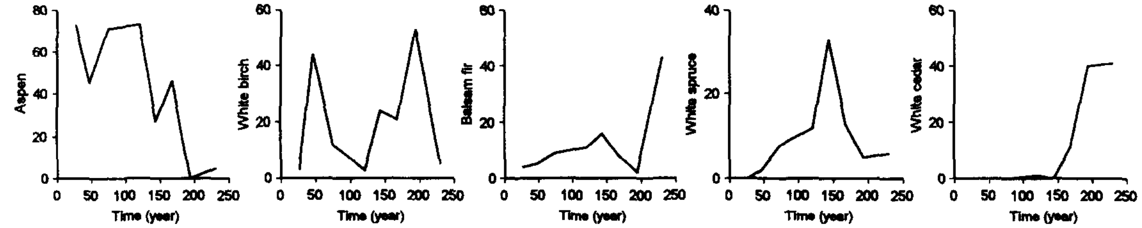

Fig. 1. Changes in species composition along a successional gradient. Values are expressed as a percentage of total basal area.

Aspen representation remained high in stands of up to 121 years and declined thereafter but white birch representation showed no clear pattern. Effects of the latest outbreak (1973–1987) of spruce budworm on balsam fir representation were still apparent as its basal area remained low everywhere except in the oldest stands. Proportion of total basal area occupied by white spruce was higher in stands aged 121–168 years, while white cedar was present only in the oldest stands.

Organic carbon increased along the age gradient but the C/N ratio showed no significant relationship with age (Fig. 2, Table 1). Ammonium concentrations on exchange resins remained constant as well (Fig. 3, Table 1), while NO_3 concentrations reached their highest values at age 27, decreased abruptly between age 27 and 47, and started to increase in older stands from 168 years and over, the quadratic function being significant (Table 1). Phosphorus concentrations on exchange resins decreased linearly but more or less regularly (Fig. 3, Table 1).

Forest floor pH decreased by one unit, between age 27 and 75 (Fig. 2). Thereafter, it decreased more slowly but continuously and linearly with an increase in stand age. Both polynomials were significant (Table 1). Exchangeable acidity increased linearly (Fig. 4, Table 1). Exchangeable Ca and $_eMg$ concentrations decreased linearly with stand age (Fig. 4, Table 1), although the $_eMg$ decrease was more pronounced at the beginning of the chronosequence. Calcium and Mg concentrations on exchange resins also decreased linearly (Table 1) and were correlated with values for $_eCa$ and $_eMg$ ($r = 0.611$, $P = 0015$ and $r = 0.922$, $P < 0.001$, respectively).

Exchangeable K showed a different pattern from that of $_eCa$ and $_eMg$. Concentrations increased until age 75 and thereafter decreased until age 231 (Fig. 4). The quadratic function was significant (Table 1). However, K concentrations on exchange resins decreased abruptly between ages 27 and 47 and more slowly thereafter (Fig. 3). Both polynomials were significant (Table 1). Correlation between exchangeable K and resins K was non significant ($r = 0.311$, $P = 0.260$). CEC_E decreased linearly with time (Fig. 4, Table 1).

4.2. Effects of time and species composition

Changes in NO_3 concentrations are related to time and changes in aspen and birch representation (Fig. 5). The causal (direct and indirect) covariation between each species and NO_3 was higher than indicated by the value of the correlation (total covariation) (Table 2). Both species had a negative effect on NO_3 concentrations but the decrease of aspen abundance with stand age positively affected nitrate availability, while time had a negative direct effect on NO_3 that cannot be related to species composition.

Magnesium concentrations were positively affected by white cedar and negatively so by white birch (Fig. 5, Table 2). Time through its positive correlation with cedar had a positive indirect effect on concentrations but its direct effect was negative and stronger resulting in negative total causal covariation between time and Mg concentrations. Both aspen and cedar had a positive effect on Ca concentrations, but, with increasing stand age, these effects counteracted one another; aspen representation decreased while that of cedar increased (Fig. 5, Table 2). Stand age had a direct negative effect on Ca concentrations which was independent of stand composition. Effects of time on K concentration on exchange resins were related to changes in stand composition (Fig. 5, Table 2). All species had a

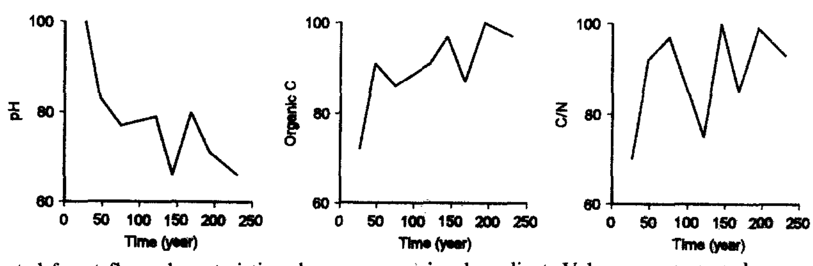

Fig. 2. Changes in selected forest floor characteristics along a successional gradient. Values are expressed as a percentage of maximum value. Maximum values are: pH, 5.5; organic C, 433 g kg^{-1}; C/N ratio, 29.0.

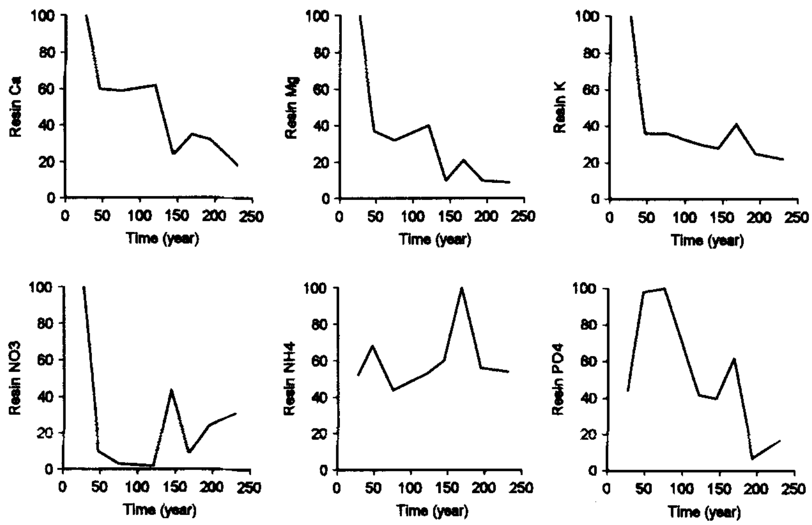

Fig. 3. Changes in selected nutrient concentrations on exchangeable resins along a successional gradient. Values are expressed as a percentage of maximum value. Maximum values are: resin Ca, 7393 mg kg^{-1}; resin Mg, 1651 mg kg^{-1}; resin K, 494 mg kg^{-1}; resin NO_3, 157 mg kg^{-1}; resin NH_4, 33 mg kg^{-1}; resin PO_4, 11 mg kg^{-1}.

negative effect on K concentrations and the overall effect of time was indirect and negative. Species composition did not directly impact on PO_4 concentrations (model not shown).

5. Discussion

Among the numerous causes underlying changes in nutrient availability along successional gradients (Odum, 1969; Vitousek and Reiners, 1975; Bormann and Likens, 1979; Gorham et al., 1979; Reiners, 1981) some are of particular relevance to the southern part of the boreal forest. Among these are the direct effect of fire on nutrient distribution and cycling (MacLean et al., 1983), pattern of biomass accumulation (Vitousek and Reiners, 1975) and insect disturbance (Paré et al., 1993). Changes in forest composition influence the overall nutrient availability owing to differential patterns among plants species in rooting (Alban, 1982), nutrient accumulation (Alban et al., 1978), litter return (Gosz, 1981), canopy geometry and nutrient requirement (Carlyle, 1986).

While it is not possible to fully disentangle the contribution of single factors, the trends observed here indicated a general linear decline for pH, P and base cations but not for both forms of mineral N as measured by resin bags (Table 1). However, the form and strength of the relationship between age and nutrient availability differed considerably among

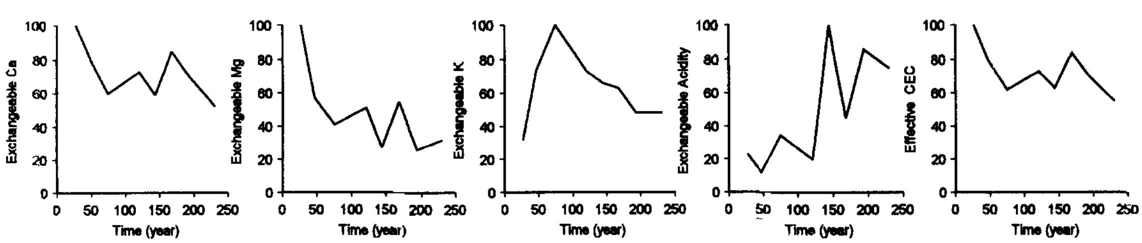

Fig. 4. Changes in selected nutrient concentrations and CEC_E along a successional gradient. Values are expressed as a percentage of maximum value. Maximum values are: $_e$Ca, 57.6 cmol(+) kg^{-1}; $_e$Mg, 11.9 cmol(+) kg^{-1}; $_e$K, 4.1 cmol(+) kg^{-1}; $_e$Acidity, 4.8 cmol(+) kg^{-1}; CEC_E, 72.5 cmol(+) kg^{-1}.

nutrients. $_eK$, $_eMg$ and $_eCa$ decreased with time, although $_eK$ concentrations showed an initial increase and the $_eCa$ decrease was less pronounced than that of $_eMg$ and $_eK$. Some of these changes were related to species composition, as was indicated by path analysis. The positive effect of aspen and white cedar on $_eCa$ concentrations (Fig. 5) may be caused by a rapid cycling of Ca in litter (Gosz, 1981; Alban, 1982) and throughfall (Mahendrappa, 1983).

Acidification of the forest floor in this study may be partly explained by biomass accumulation at the onset of succession, resulting in base cation sequestration in plant biomass and increased inputs of H (Binkley and Richter, 1987). This is seen in the effect of age on $_eCa$ and $_eMg$ concentrations that could not be accounted for by changes in species composition (Fig. 5) and may explain the abrupt drop in pH between ages 27 and 75 which coincided with the last part of the forest aggradation phase which was completed by age 75 (Paré and Bergeron, 1995). Increase in cation leaching due to higher NO_3 concentrations in older stands may have contributed to the decrease in pH in these stands.

Table 1
Effects of time on forest floor characteristics and nutrient concentrations on exchange resins. Analysis of variance, first- and second-degree polynomials

Variable	Source	R^2	$Pr > F$
Forest floor characteristics			
pH	Model	0.91	0.003
	1 degree		< 0.001
	2 degree		0.021
C organic	Model	0.65	0.221
	1 degree		0.033
	2 degree		0.261
CIN	Model	0.59	0.322
	1 degree		0.223
	2 degree		0.518
$_eCa$	Model	0.70	0.142
	1 degree		0.053
	2 degree		0.450
$_eMg$	Model	0.92	0.002
	1 degree		< 0.001
	2 degree		0.006
$_eK$	Model	0.79	0.052
	1 degree		0.297
	2 degree		0.017
$_e$Acidity	Model	0.93	0.001
	1 degree		< 0.001
	2 degree		0.195
CEC_E	Model	0.71	0.128
	1 degree		0.044
	2 degree		0.388
Concentrations on exchange resins			
Ca	Model	0.61	0.286
	1 degree		0.027
	2 degree		0.399
Mg	Model	0.83	0.027
	1 degree		0.003
	2 degree		0.044
K	Model	0.74	0.096
	1 degree		0.025
	2 degree		0.076
NO_3	Model	0.77	0.064
	1 degree		0.236
	2 degree		0.028
NH_4	Model	0.38	0.734
	1 degree		0.706
	2 degree		0.640
PO_4	Model	0.73	0.107
	1 degree		0.018
	2 degree		0.511

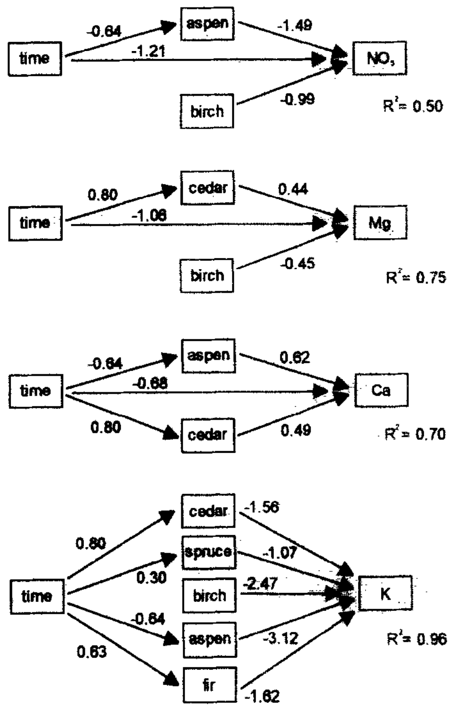

Fig. 5. Path analysis of relationships between time, species composition and, selected nutrient concentrations on exchange resins. Causal relationships between predictor and criterion variables are depicted by arrows with the magnitude of the contribution or path coefficient given next to the arrow.

In this study, concentrations of NH_4 in soil solution remained low and constant along the gradient. However, NO_3 concentrations were highest at age 27, decreased abruptly thereafter and increased in stands aged 168 and older. Conditions favoring mineralization at the onset of succession, such as high pH and availability of other nutrients, may explain high initial NO_3 concentrations. If NO_3 concentrations were linked to NH_4 availability, as suggested by Purchase (1974), Robertson and Vitousek (1981), Robertson (1982), and Montagnini et al. (1986), then, the subsequent decrease in NO_3 concentrations may be due to a stronger demand for NH_4 from the growing stand and less NH_4 being available to nitrifiers. Finally, as biomass accumulation ceases and aspen abundance decreases, NH_4 ought to be in lower demand. At both ends of the gradient, surpluses of NH_4 are available to and utilized by nitrifier populations, thus maintaining a low level of NH_4 in the soil solution.

Phosphate availability has been reported as a factor controlling nitrification (Melillo, 1977; Pastor et al., 1984) and experimental manipulation of incubated soils and laboratory testing on pure cultures of nitrifiers have contributed to the widespread belief that low pH limits nitrification (Robertson, 1982; Schmidt, 1982; Haynes, 1986). However, working with previously published data on nitrification, Robertson (1982) has shown that the relationship between relative nitrification and pH can be rather weak. In our study, there was no significant correlation between NO_3 concentrations and pH ($r = 0.342$, $P = 0.213$), PO_4 availability ($r = -0.288$, $P = 0.298$) as measured by the exchange resins, or C/N ratio ($r = -0.218$, $P = 0.436$).

Nitrogen availability and nitrification in relation to succession have received considerable attention (Melillo, 1977; Robertson and Vitousek, 1981; Thibault et al., 1982; Montagnini et al., 1986; Pastor et al., 1987) in the wake of Rice and Pancholy's hypothesis on nitrification inhibition by late successional species (Rice and Pancholy, 1972). Although inhibition of nitrification by phenolic compounds has been reported (Olson and Reiners, 1983), inhibition of nitrification by late successional species is not a general trend (Robertson and Vitousek, 1981; Montagnini et al., 1986) and, in our study, NO_3 concentrations were at their lowest level during periods of early successional species dominance. In a parallel study, Paré et al. (1993) found no relationship be-

Table 2
Path analysis of relationships between age, vegetation and selected nutrient concentrations on exchange resins

Relationship	Total covariation	Causal covariation			Spurious correlation
		Direct	Indirect	Total	
Time–Aspen	−0.64	−0.64	0	−0.64	0
Time–White birch	0	0	0	0	0
Time–Balsam fir	0.63	0.63	0	0.63	0
Time–White spruce	0.31	0.31	0	0.31	0
Time–White cedar	0.80	0.80	0	0.80	0
Time–NO_3	−0.26	−1.21	0.95	−0.26	0
Aspen–NO_3	−0.09	−1.49	0	−1.49	1.40
White birch–NO_3	−0.04	−0.99	0	−0.99	0.95
Time–Mg	−0.71	−1.06	0.35	−0.71	0
White birch–Mg	−0.41	−0.45	0	−0.45	0.04
White cedar–Mg	−0.43	0.44	0	0.44	−0.87
Time–Ca	−0.69	−0.68	−0.01	−0.69	0
Aspen–Ca	0.73	0.62	0	0.62	0.11
White cedar–Ca	−0.46	0.49	0	0.49	−0.95
Time–K	−0.56	0	−0.59	−0.59	−0.03
Aspen–K	0.46	−3.12	0	−3.12	2.66
White birch–K	−0.34	−2.47	0	−2.47	2.13
White spruce–K	−0.35	−1.07	0	−1.07	0.72
Balsam fir–K	−0.42	−1.62	0	−1.62	1.20
White cedar–K	−0.31	−1.52	0	−1.52	1.21

tween mineralizable N values, obtained by laboratory incubation, and stand age. Nitrates in the soil solution could also have originated from atmospheric deposition which amounts 14 kg ha^{-1} $year^{-1}$ NO_3-N for the region (Jacques and Boulet, 1990).

6. Conclusion

A general decline in nutrient availability was observed along a successional gradient in the southern part of the boreal forest, the only exception being that of N availability. Both time since succession initiation and modification to forest composition have contributed to the observed changes. Nitrification does take place in this boreal ecosystem despite conditions of low soil pH. More studies are currently under way to assess the effect of man-made and natural disturbances on N availability and nitrification.

Although the results of path analysis have little predictive value, considering the number of samples, they raise interesting questions concerning the effect of early successional species, especially aspen, on forest floor Ca availability. Long term impacts on soil base status of successive rotations of softwood species coupled with the elimination of hardwood competition should receive more attention.

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