



A cyclical but asynchronous pattern of fine root and woody biomass production in a hardwood forest of southern Quebec and its relationships with annual variation of temperature and nutrient availability

Benoît Côté^{1,3}, Nicolas Bélanger¹, François Courchesne², James W. Fyles¹ & William H. Hendershot¹

¹Department of Natural Resource Sciences, Macdonald campus of McGill University, Ste-Anne-de-Bellevue, Québec, Canada H9X 3V9. ²Département de géographie, Université de Montréal, Montréal, Québec, Canada H3C 3J7. ³Corresponding author*

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Abstract

In contrast to the well-documented seasonal variation in growth of below- and above-ground components of trees, the annual variation in below- and aboveground production is not well understood. In this study, we report on the monitoring of an unmanaged hardwood forest ecosystem in a small watershed of southern Quebec between 1993 and 1999. Below- and above-ground biomass production, leaf and soil solution chemistry, and air temperature were measured at different regular intervals and are reported on an annual basis. The objective of the study was to describe the annual dynamics of carbon partitioning between below- and above-ground tree components and to gain a better understanding of the soil and climatic factors that govern it. Fine root production peaked one year earlier than woody biomass production and years with high production of fine roots had low woody biomass production. All models that included May temperature in the calculation of the predicting/independent variables were significant predictors of total tree biomass production ($r > 0.87$). Fine root production was associated negatively with the previous year average growing season temperature ($r < -0.84$). Soil solution NO_3^- , NH_4^+ and $\text{NO}_3^- + \text{NH}_4^+$ concentrations were positively correlated with fine root production ($r > 0.72$) and negatively correlated with woody biomass production ($r < -0.84$). Leaf N and P concentrations were negatively correlated ($r = -0.99$ and $r = -0.98$, respectively) with fine root production for the period of 1994–1998. Our results suggest that a cool growing season, and in particular a cool month of October, is likely to result in low fine root production and nutrient uptake the following year and, therefore, to increase soil N availability and decrease leaf N. This initial response is thought to be the first step of a feedback loop involving plant N nutrition, soil N availability, fine root growth and aboveground biomass production that led to a cyclical (3–4 years) but asynchronous production of fine roots and aboveground biomass production.

Introduction

The seasonal pattern of root and stem growth in hardwood forests of eastern Canada and northeastern USA is relatively well known. Fine root production usually resumes before or during leaf expansion in the spring

(Burke and Raynal, 1994; Fahey and Hughes, 1994; Hendrick and Pregitzer, 1993; Lyr and Hoffmann, 1967), typically peaks in late spring to early summer (Hendrick and Pregitzer, 1992, 1996; McClaugherty et al., 1982), and usually stops or decreases rapidly with leaf fall in autumn (Burke and Raynal, 1994; Fahey and Hughes, 1994; Hendrick and Pregitzer, 1996). Growth in diameter and height typically resumes with

* FAX No: +1-514-398-7990.
E-mail: coteb@nrs.mcgill.ca

leaf expansion, peaks early in the growing season for height in fixed-growth species, and diameter growth usually stops with the onset of leaf senescence or leaf fall in late summer or autumn (Kozlowski et al., 1991).

Factors affecting aboveground biomass production have been studied extensively. Numerous studies in dendroclimatology have linked diameter growth to various climatic variables (e.g. monthly, seasonal or annual temperature or precipitation) of current and previous year (Rubino and McCarthy, 2000; Zarnovican, 2000). For the most part, the growth response to climatic variables seems to be site-specific. One exception could be made for the prevalent negative effect of severe/prolonged droughts on tree diameter growth (Abrams et al., 1998; Brooks et al., 1998; Lebourgeois, 2000; Rolland et al., 2000; Ruffner and Abrams, 1998; Splechtna et al., 2000). Both temperature and precipitation regime have a strong influence on soil fertility which in turn affects root growth dynamics. Canadian forests growing on recently glaciated sites have been shown to be generally N-limited (Krause et al., 1987). Recent evidence suggests, however, that many forests of northeastern America could be becoming limited by other nutrients such as K (Bernier and Brazeau, 1988), Ca (Moore et al., 2000) and Mg (Horsley et al., 2000).

Numerous factors are known to affect root growth dynamics. Soil temperature is a key variable for root growth with minimum and optimum temperatures of most temperate woody trees ranging from 0 to 5 °C, and 20 to 25 °C, respectively (Kozlowski et al., 1991). The fact that substantial root growth can occur early in spring when soil temperature is low (Côté et al., 1998; Kuhns et al., 1985; Morrow, 1950; Taylor and Dumbroff, 1975) suggests that other factors, such as soil nutrients and water, or internal physiological processes are controlling the dynamics of root production. Root growth generally responds positively to increased water availability when soil temperature is conducive for growth (Bartsch, 1987; Bevington and Castle, 1985; Kuhns et al., 1985; Teskey and Hinckley, 1981). As for soil fertility, root growth has been widely referenced to respond positively to soil-P fertility and negatively to soil-N fertility (Tisdale et al., 1985). Such a response, however, has been established mainly in agricultural and horticultural systems where soil fertility is usually determined by the episodic application of fertilizers. The relationships between available soil-P and soil-N, and root growth in unmanaged deciduous hardwood forests, where soil fertility

depends on natural cycling of elements, may not be as clear (Burke et al., 1992; Côté et al., 1998).

In contrast to the well-documented seasonal variation in growth of below- and above-ground components of trees, the annual variation in below- and above-ground production is not well understood. Few field studies have considered concomitantly root and stem growth, and the external and internal factors that control them. The production of above-ground biomass can be higher when root production is low (Axelsson and Axelsson, 1986) and be asynchronous with fine root production (Côté et al., 1998). Given the high demand for nitrogen during the production of new foliage, it is possible that the above-/below-ground source/sink relationship is modified by the availability of soil nitrogen. Seasonal carbon allocation pattern in sugar maple was shown to be associated with soil nitrogen availability (Burke et al., 1992) whereas carbon allocation to roots of black spruce seedlings was mediated by foliar N (Campagna and Margolis, 1989). Through its effect on both soil N and leaf N, elevated atmospheric deposition was recently suggested as a condition that could decrease forest fine root biomass but stimulate their turnover and production (Nadelhoffer, 2000).

In this study, we report on the monitoring of an unmanaged hardwood forest ecosystem in a small watershed of southern Quebec between 1993 and 1999. Below- and above-ground biomass production, leaf and soil solution chemistry, and climatic variables were measured at different regular intervals and are reported on an annual basis. The objective of the study was to describe the annual dynamics of carbon partitioning between below- and above-ground and to gain a better understanding of the soil and climatic factors that govern it.

Materials and methods

Study site

The study site is located in the Hermine watershed at the Station de Biologie des Laurentides of Université de Montréal, Québec, in the Lower Laurentians, 80 km north of Montréal (45°50'N, 74°01'W). Thirty-year average precipitation at the station is 1100 mm, with 30% falling as snow. Mean annual temperature is 3.6 °C. The forest has a mean basal area of 28 m² ha⁻¹. The lower slope is dominated by sugar maple (*Acer saccharum* Marsh.) with more than 90% of the

total basal area. The proportion of red maple (*Acer rubrum* L.) increases with elevation and peak around 50% in some upper slope plots. Part of the topmost section of the southern hillslope is dominated (>50% total basal area) by paper birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and largetooth aspen (*Populus grandidentata* Michx.). Beech (*Fagus grandifolia* Ehrh.) is omnipresent in the watershed but accounts for less than 10% of the total basal area. The bedrock is Precambrian anorthosite of the Morin series. The soils at the site are sandy loams derived from well to imperfectly drained rocky glacial till with a mineral composition similar to that of the anorthosite. The forest floor is a moder humus form and the soils are classified as Orthic Humo-Ferric Podzols and Gleyed Ferro-Humic Podzols (Expert Committee on Soil Survey of Agriculture Canada, 1987). One commercial harvest can be documented in the area, but operations were executed so that only large trees were harvested (Savage, 2001). Traces of charcoal in the watershed suggest a fire. In the lower Laurentians of Quebec, many hardwood stands typical of the climax of sugar maple forests were disturbed by fire in the mid-1920s and this led mostly to the establishment of largetooth aspen and yellow birch (Lortie, 1979).

Sampling

In September of 1993, nine plots representative of the different forest types of the forest mosaic created by the fire were selected. Plots were 300 m² and covered together approximately 10% of the whole surface area of the southern slope of the watershed. All trees with a stem diameter greater than 9 cm at 1.3 m above-ground within a plot were measured for their diameter at breast height (DBH). The height of at least ten trees per species was determined and used to model tree height with DBH as the independent variable.

In each plot, five or six dominant or co-dominant trees representative of the species found in the plot were marked and sampled in mid-August of each year for the determination of leaf chemistry. Sampling was done with a 15-m telescopic pole-pruner. Leaves exposed to direct sun light and located in the upper half of the canopy were sampled. Thirty to forty leaves from 2 to 3 branches were collected and stored in paper bags in the field before drying at 65 °C for 48 h. Leaf nutrient concentrations were determined from analyses on H₂O₂–H₂SO₄ digested samples (Allen, 1989) with a Technicon AutoAnalyzer for N and P,

and by atomic absorption spectrophotometry (Perkin-Elmer model 2380) for K, Ca and Mg. Variation in tree nutrient status was based on the means of concentrations of all trees sampled in the watershed for individual years.

Litterfall was collected within each plot using five 0.25 m² traps. Litter sampling was done on a monthly basis during spring and summer, and every two weeks in the fall from 1994 to 1997. Shortly after collection, litter samples were oven-dried for 48 h at 65 °C and then weighed for later determinations of annual litter mass production.

One mini-rhizotron was installed in June 1993 in each of the nine sampling sites. The rhizotrons were installed vertically to a depth of 30 cm from the soil surface and consisted of large 10-cm diameter PVC tubing in which thirty holes (1.25 cm dia.) had previously been drilled to allow roots to penetrate. A 30-cm length of small 5-cm diameter PVC tubing was then placed inside the 10-cm tubing, and the space between the two tubes was filled with washed silica sand (0.15 mm). Sampling consisted of removing the 5-cm tube while leaving the 10-cm tube undisturbed in the ground; this caused the silica sand to fall inside the 10-cm tube. Roots that had grown into the interspace were then collected and the remaining sand was removed. As such, the method used is equivalent to an ingrowth core method. The narrow tube was then placed inside the wide tube as before, the gap between the two tubes filled with new sand and the rhizotron was left until the next sampling date. The sampling was done twice a year in early May before leaf expansion and late in the fall when soil temperature was less than 1 °C. The harvested roots were brought to the laboratory where they were washed free of sand, dried at 65 °C for 48 h and weighed. To eliminate the bias caused when a coarse root occasionally penetrated a rhizotron, roots ≥ 1 mm dia. were removed before weighing. Rhizotrons were sampled in October 1993 to ensure that roots sampled in May 1994 would be roots produced in the weeks preceding that sampling.

Zero-tension lysimeters were installed in each plot in September of 1993 below the LFH forest floor (0 cm) according to the procedure described by Hendershot and Courchesne (1991). From 1994 to 1997, soil solutions were collected every 2 weeks from June to September and every 4 weeks in 1999. Soil solution samples were filtered through 0.4 μ m polycarbonate membranes within 24 h after collection and stored at 4 °C until analysis. Soil solution chemistry was determined with atomic absorption/emission spectro-

photometry for K^+ , Ca^{2+} , Mg^{2+} , and by ion chromatography (Waters) for NO_3^- and NH_4^+ . Mean annual concentrations were determined as arithmetic means of all concentrations for individual years.

Daily air temperature data were obtained from Environment Canada for the weather station of Saint-Hippolyte located in the Station de Biologie of Université de Montréal. This weather station is located about a kilometer away from the study site. Climatic variables were averages of different combinations of monthly averages of air temperature for the months of May through October (growing season) of the current and previous year's growth.

Biomass calculations and statistics

Large root and stem biomass of individual trees were determined with the allometric equations used in the forest growth model JABOWA II version 1.1 (Botkin, 1989). Large root and stem biomass per plot was determined by summing up the biomass of all trees greater than 9 cm in diameter and extrapolating to a hectare basis; mean annual production of large root and stem biomass was determined by calculating the average difference in biomass production of individual plots between consecutive years ($n = 9$). Because stem biomass determination was based on tree diameter of dormant trees after leaf fall, leaf biomass production was measured as litterfall biomass production. Litter production by plot was calculated as the mean of all 5 traps per plot and mean annual litter production was calculated as the average of the plots ($n = 9$). Annual variation in leaf litter production was small (about 5%) and litter collection was therefore discontinued in 1998.

The rate of small root (<1 mm in diameter) production measured in the rhizotrons was extrapolated to a hectare basis by assuming a stone-free soil to a depth of 30 cm, and a fine root production in the rhizotron proportional to the area of the holes relative to the total surface area of the 10-cm pipe. Mean annual small root production was calculated as the mean of all rhizotrons for each year of sampling ($n = 9$).

Relationships among air temperature variables, leaf chemistry, soil solution chemistry and growth of the different tree components were assessed with Pearson correlation coefficients. Annual precipitation and its distribution pattern were also considered but yielded non-significant relationships and, therefore, are not reported. Delayed responses of some growth parameters and leaf and soil chemistry were assessed with

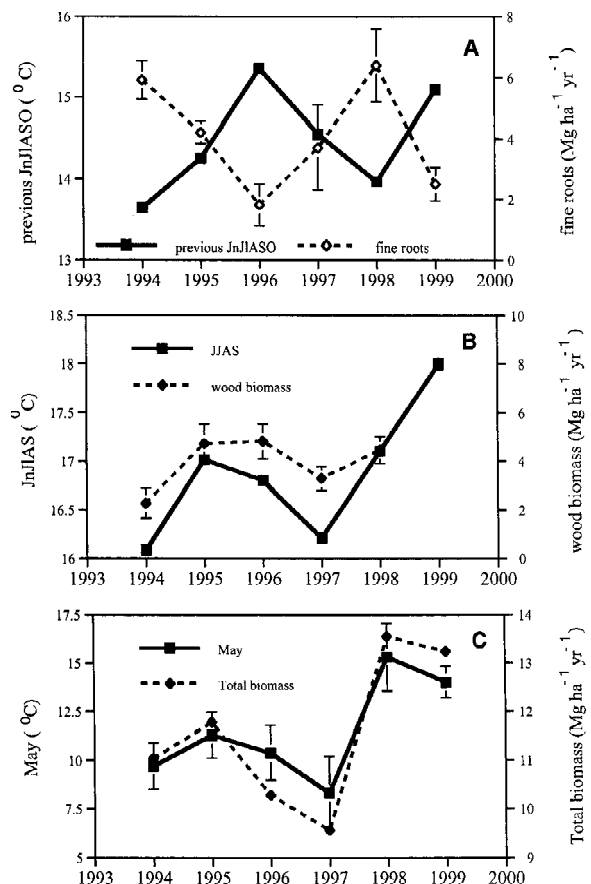


Figure 1. Annual variation for the period of 1994–1999 of: (A) mean of June, July, August, September and October (JnJIASO) temperature of the previous year and fine root production, (B) mean of June, July, August and September (JnJIAS) temperatures and wood biomass production, and (C) mean May temperature and total biomass production.

distributed lags analysis by computing polynomial distributed lags. Statistics were calculated with Statistica (StatSoft, 1994) for a probability level of 5% unless otherwise stated.

Results

Temporal variation of growth parameters

Fine root production was highest in 1994 and 1998, and lowest in 1996 and 1999 (Figure 1A). Woody biomass production was high in 1995 and 1996, highest in 1999, and lowest in 1994 and 1997 (Figure 1B). Total biomass production was high in 1998 and 1999 and lowest in 1997 (Fig 1C). Comparison of temporal variation of fine root and woody biomass production

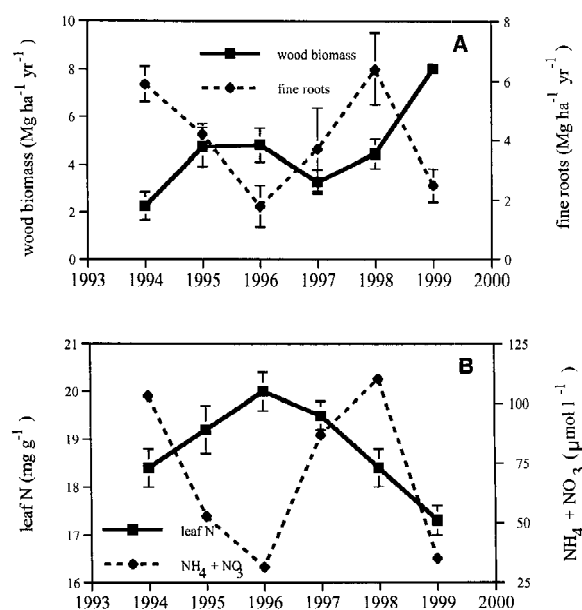


Figure 2. Annual variation for the period of 1994–1999 of: (a) woody biomass production and fine root production and b) leaf N concentration and soil solution $\text{NH}_4^+ + \text{NO}_3^-$.

Table 1. Summary of analysis of polynomial distribution lags between some combinations of fine root biomass production, woody biomass production, leaf N and soil solution N ($n = 6$)

Independent variable	Dependent variable	Lag (years)	Regression coefficients	<i>t</i> -value	Prob.
Fine root biomass	Woody biomass	0	0.21	1.0	0.38
		1	0.86	4.8	0.02
Fine root biomass	Leaf N conc.	0	2.2	1.7	0.19
		1	2.2	1.9	0.15
Soil $\text{NH}_4^+ + \text{NO}_3^-$	Fine root biomass	0	0.44	6.9	0.006
		1	0.13	2.5	0.09

shows that: (a) woody biomass peaked one year after fine root production or that fine root production peaked one year earlier than woody biomass production (Figure 2 and Table 1), and (b) years with high production of fine roots had low woody biomass production and vice versa (Figure 2).

Air temperature

Growing season temperature (June through September (JnJIAS)) showed small annual variation with low mean temperature being recorded in 1994 and 1997 and highest temperature in 1999 (Figure 1B). May

Table 2. Pearson correlation coefficients between mean monthly temperatures and annual production of total biomass (leaf+wood+fine roots), woody biomass (wood + bark) and fine roots (<1 mm)

Mean temperature (°C)	Total biomass		Woody biomass		Fine roots	
	<i>r</i>	Prob.	<i>r</i>	Prob.	<i>r</i>	Prob.
<i>Current year</i>						
May (M)	0.96	0.002	0.62	0.19	0.22	0.67
June (Jn)	0.03	0.95	0.51	0.30	0.45	0.37
July (Jl)	0.63	0.18	0.71	0.12	0.10	0.82
August (A)	0.45	0.37	0.52	0.29	0.22	0.67
September (S)	0.48	0.33	0.74	0.09	0.40	0.43
October (O)	0.30	0.57	0.35	0.50	0.65	0.17
MJn	0.94	0.005	0.75	0.08	0.08	0.89
MJnJl	0.92	0.009	0.79	0.06	0.03	0.95
MJnJlA	0.87	0.02	0.79	0.06	0.04	0.93
MJnJlAS	0.90	0.02	0.85	0.03	0.10	0.85
MJnJlASO	0.94	0.006	0.74	0.09	0.05	0.92
JnJl	0.40	0.43	0.68	0.14	0.30	0.57
JnJlA	0.50	0.32	0.74	0.09	0.33	0.52
JnJlAS	0.76	0.08	0.97	0.002	0.36	0.49
JnJlASO	0.83	0.04	0.75	0.09	0.05	0.92
<i>Previous year</i>						
May	0.12	0.82	0.81	0.15	-0.61	0.20
June	-0.02	0.97	0.26	0.62	-0.42	0.40
July	-0.28	0.58	-0.07	0.90	-0.37	0.47
August	-0.41	0.42	-0.01	0.98	-0.40	0.43
September	0.09	0.86	0.37	0.47	-0.15	0.78
October	-0.03	0.95	0.66	0.16	-0.85	0.03
MJnJlASO	-0.06	0.91	0.65	0.17	-0.92	0.009
JnJlAS	-0.22	0.68	0.10	0.84	-0.84	0.04
JnJlASO	-0.17	0.75	0.55	0.26	-0.96	0.003

temperature showed higher annual variation than any other month or combination of months with a maximum in 1998 and a minimum in 1997 (Figure 1C). All models that included May temperature in the calculation of the predicting/independent variables were significant predictors of total tree biomass production (Table 2); May temperature alone was however the model with the highest *r* values (Table 2, Figure 1C). Most combinations of other monthly temperatures did not yield significant models for total tree biomass production (Table 2). Two models were significant predictors of woody biomass production (Table 2): mean monthly temperatures of May through September and of June through September (Figure 1). Fine root production was only associated negatively with the previous year temperature of October or of the previous growing season (May through October, June through September and June through October) (Table 2, Figure 1A).

Table 3. Pearson correlation coefficients between annual production of total biomass (leaf+wood+fine roots), woody biomass (wood + bark) and fine roots (<1 mm), and leaf ($n = 6$) and soil variables ($n = 5$)

Leaf/soil solution chemistry	Total biomass		Woody biomass		Fine roots	
	r	Prob.	r	Prob.	r	Prob.
<i>Leaf</i>						
N	-0.55	0.26	-0.36	0.49	-0.26	0.63
P	-0.68	0.14	-0.04	0.94	-0.65	0.16
K	-0.24	0.64	-0.36	0.49	0.03	0.96
Ca	0.08	0.88	0.60	0.21	-0.38	0.46
Mg	0.27	0.60	0.26	0.62	0.16	0.76
Mn	0.18	0.73	0.56	0.25	-0.21	0.69
<i>Soil solution</i>						
NH ₄ ⁺	-0.50	0.39	-0.87	0.055	0.72	0.17
NO ₃ ⁻	-0.14	0.82	-0.84	0.07	0.89	0.04
NH ₄ ⁺ + NO ₃ ⁻	-0.32	0.60	-0.91	0.03	0.87	0.055

Table 4. Annual variation in leaf nutrient concentrations of sugar maple between 1994 and 1999 (mean \pm SE, $n = 27$)

Year	N	P	K (mg g ⁻¹)	Ca	Mg	Mn
1994	18.4 \pm 0.4	1.0 \pm 0.03	5.7 \pm 0.2	8.3 \pm 0.3	1.3 \pm 0.05	0.83 \pm 0.06
1995	19.2 \pm 0.5	1.1 \pm 0.03	6.6 \pm 0.2	7.5 \pm 0.4	1.2 \pm 0.06	0.84 \pm 0.07
1996	20.0 \pm 0.4	1.2 \pm 0.02	6.7 \pm 0.2	8.4 \pm 0.5	1.1 \pm 0.05	0.91 \pm 0.07
1997	19.5 \pm 0.3	1.1 \pm 0.01	6.6 \pm 0.2	8.3 \pm 0.3	1.2 \pm 0.05	1.03 \pm 0.07
1998	18.4 \pm 0.4	1.0 \pm 0.02	6.3 \pm 0.2	8.4 \pm 0.5	1.2 \pm 0.05	1.04 \pm 0.08
1999	17.3 \pm 0.3	1.0 \pm 0.02	4.9 \pm 0.2	10.2 \pm 0.4	1.3 \pm 0.06	1.12 \pm 0.09

Soil solution and leaf nutrients

Soil solution NO₃⁻, NH₄⁺ and NO₃⁻ + NH₄⁺ concentrations were highest in 1994 and 1998 and lowest in 1996 and 1999 (Figure 2B for NO₃⁻ + NH₄⁺ only). Soil solution NO₃⁻, NH₄⁺ and NO₃⁻ + NH₄⁺ concentrations were positively correlated with fine root production and negatively correlated with woody biomass production (Table 3, shown in Figure 2B for NO₃⁻ + NH₄⁺ only). Soil solution concentrations of Ca²⁺, Mg²⁺, K⁺ and H⁺ were not significantly related with any growth parameters (data not shown).

Leaf N (Figure 2B) and P were highest in 1996 and lowest in 1999. Both leaf N and P concentrations were negatively correlated ($r = -0.99$, $p < 0.002$ and $r = -0.98$, $p < 0.003$, respectively) with fine root production for the period of 1994–1998 but not for 1993–1999 (Table 3); leaf N was also negatively correlated with soil solution NO₃⁻ +

NH₄⁺ ($r = -0.86$, $p < 0.06$). Foliar K and Ca showed less gradual variation than N, P and Mg (Table 4), the former showing marked differences in 1999 with K being lowest and Ca being highest. No significant correlation was observed between leaf K, Ca and Mg, and growth parameters for the 1994–1999 period (Table 3).

Discussion

Total biomass production was high in 1998 and 1999 and was associated with high growing season temperatures, particularly high May temperatures. In the boreal forest of Canada, growth has been observed to be higher (Black et al., 2000) and the annual carbon balance to be positive (Frolking et al., 1996) in years with early spring that resulted in longer growing seasons. High rates of photosynthesis coupled with relatively low rates of respiration early in the growing season are thought to be responsible for these effects. Our results suggest that forest growth at the Hermine Watershed is also limited by low temperature particularly early in the growing season. Such a relationship may not have been observed if basal area or tree ring increments had been measured instead of total biomass production. Indeed, fine root production and woody biomass production contributed large but variable amounts to total annual biomass production and they usually peaked in different years. This resulted in temporal variation in total biomass production that differed from that of individual growth components.

Woody biomass production (stem+large roots) was less dependent on high May temperature than total biomass production. Woody biomass production is strongly dependent on radial growth. In a previous study, the rate of radial growth (mm day⁻¹) was found to be higher with higher growing season temperature (Côté et al., 1998). The monitoring of dendrometer bands at our site (data not shown) also revealed that diameter growth typically begins in late May to early June and becomes undetectable in August or September. These observations provide strong evidence for causal relationships between high overall summer/growing season temperatures (i.e. June through September; JnJIAS) and woody biomass production.

Fine root production was not related to any current-year climatic variable. This is in contrast with the common observation that roots of most species usually show increased rates of growth with temperature even at higher temperatures than normally observed in

the field (Kozłowski et al., 1991). Instead, fine root growth was correlated negatively with the mean temperature of the previous year growing season. Such a relationship suggests a rather indirect or delayed effect of temperature on fine root growth dynamics. Since fine root growth was positively associated with soil solution NO_3^- and NH_4^+ concentrations, it is likely that May temperature had a significant effect on soil processes controlling soil solution N. The combination of fine root production being negatively correlated with leaf N and with previous-year growing season temperature (JnJIASO), while being positively correlated with current-year soil solution NO_3^- , suggests that a cool growing season results in low nutrient uptake and, therefore, results in low leaf N and increased availability of NO_3^- and NH_4^+ in soil solution the following year. Both the increased availability of soil solution N and low tree N-status could then trigger increased production of fine roots through feedback mechanisms and, therefore, increase N uptake and leaf N of trees.

This proposed mechanism suggests that any environmental factors that would result in increased soil solution N and/or low leaf N could have the same effect as a cool growing season. Severe droughts and soil frost that result in increased mortality of easily decomposed fine roots but at the same time result in reduced nutrient uptake (Boutin and Robitaille, 1995), insect epidemics that reduce leaf area but at the same time accelerate nutrient cycling while reducing nutrient uptake through reduced transpiration are factors that could generate high soil solution N and, therefore, induce an increase in fine root production. Such a strategy would not only contribute to the survival of the trees/forest on the short term but would also contribute to the conservation of soil nutrients on the long term.

The concomitant monitoring of above- and below-ground tree components revealed a 1-year lag in woody biomass production relative to fine root production. This suggests that fine root growth is not only linked to soil solution N and potentially to leaf N but also to carbon partitioning within the plant. Consideration of this additional factor leads us to propose a feedback loop in which: (1) low leaf N and high soil solution N as observed in 1994 initially trigger increased production of fine roots; (2) more fine roots increase uptake of soil solution N; (3) more N uptake increases leaf N ($p = 0.15$ for lag of one year) but lowers soil solution N; (4) low soil solution N coupled with high leaf N trigger a decrease in fine root production and an increase in above-ground production; (5)

decreased fine root production lowers uptake of soil solution N; (6) low N uptake then leads to a decrease in leaf N (potentially deficient levels) and an increase in soil solution N; (7) such a condition again triggers higher fine root production and, therefore, completes the feedback loop. Close examination of the temporal variation in growth components and variables likely associated with them (Figures 1 and 2) suggests that this series of feedback mechanisms could result in more or less cyclic variation with a duration of 3 to 4 years based on the time elapsed between minimums and maximums of woody and fine root biomass production for the period examined at our site. Given the nature of this plant-soil system that is governed by deterministic growth processes which are in turn dependent on factors that are oscillating and chaotic in nature, such as air temperature (Lean and Rind, 1998) and possibly precipitation, the concept of deterministic chaos could be useful in getting a better understanding of the dynamics of tree growth, leaf and soil chemistry, and climate system (Stone and Ezrati, 1996). Such an upper scale approach would clearly have to be coupled with a better knowledge of the processes occurring at smaller scales if models are to be improved and used to improve the management of forest ecosystems.

Both leaf N (1994–1998) and soil solution N (1994–1999) appear to be driving growth and carbon partitioning. Burns et al. (1997) hypothesized that the form of the relationship between the relative growth rate and plant nutrient concentration could vary depending on whether a plant's external supplies or internal reserves of a particular nutrient are more limiting. In our study, both leaf N and soil solution N were significantly correlated with fine root production from 1994 to 1998 (Figure 2B). Unless large amounts of N uptake occurred after the mid-August leaf sampling of the very hot 1999 growing season, the low fine root production observed in 1999 when leaf N and soil solution N were low suggests that the effect of soil solution N dominated over the effect of plant N reserves and/or plant N status.

The fact that C (biomass) allocation in trees may be following a 'chaotic cycle' extending over a few years in the Hermine Watershed, and the fact that this C allocation appears to be dependent on climatic fluctuations and both soil and plant N status, provides a framework for the diagnostic of forest nutrition and interpretation of forest growth dynamics following manipulation of tree nutrition (e.g., fertilization) and growth (e.g., thinning). In terms of diagnostic, de-

termination of deficient nutrient levels in foliage in a particular year may not be indicative of a chronic deficiency but rather of a temporary reduction in uptake that results from the dynamics of nutrient cycling in the complex vegetation–soil–atmosphere system. Our results therefore, support the earlier recommendation for obtaining more than one year of leaf chemistry to diagnose tree/forest nutrition (Côté et al., 1994). Our results also suggest that precautionary measures be taken when interpreting forest growth and nutritional response to manipulation of soil fertility or to effects of natural and anthropogenic stresses. Indeed whether fertilization or stress provides a similar nutritional and growth response when performed or imposed at extremes of the spectrum of leaf chemistry, soil solution chemistry or fine root production remains unknown and will require further large-scale and long-term experimentation.

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References

- Abrams M D, Ruffine C M and Morgan T A 1998 Tree-ring responses to drought across species and contrasting sites in the ridge and valley of Central Pennsylvania. *For. Sci.* 44, 550–558.
- Allen S E 1989 Analysis of vegetation and other organic constituents. *In* Chemical Analysis of Ecological Materials. pp 160–200. Blackwell Scientific, Oxford.
- Axelsson E and Axelsson B 1986 Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Phys.* 2, 189–204.
- Bartsch N 1987 Response of root systems of young *Pinus sylvestris* and *Picea abies* plants to water deficits and soil acidity. *Can. J. For. Res.* 17, 805–812.
- Bernier B and Brazeau M 1988 Nutrient deficiency symptoms associated with sugar maple dieback and decline in the Québec Appalachians. *Can. J. For. Res.* 18, 762–767.
- Bevington K B and Castle W S 1985 Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature, and soil water content. *J. Am. Hort. Soc.* 110, 840–845.
- Black T A, Chen W J, Barr A G, Arain M A, Chen Z, Nesic Z, Hogg E H, Neumann H H and Yang P C 2000 Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Lett.* 27, 1271–1274.
- Botkin D B 1989 Manual for Jabowa-II, Version 1.1, Forest Growth Model, Santa Barbara Institute for Environmental Studies, Santa Barbara, CA. 90 pp.
- Brooks J R, Flanagan L B and Ehleringer F R 1998 Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Can. J. For. Res.* 28, 524–533.
- Burke M K, Raynal D J and Mitchell M J 1992 Soil nitrogen availability influences seasonal carbon allocation patterns in sugar maple (*Acer saccharum*). *Can. J. For. Res.* 22, 447–456.
- Burke M K and Raynal D J 1994 Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. *Plant and Soil* 162, 135–146.
- Burns I G, Walker R L and Moorby J 1997 How do nutrients drive growth? *Plant and Soil* 196, 321–325.
- Burton A J, Pregitzer K S and Hendrick R L 2000 Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. *Oecologia* 125, 389–399.
- Campagna M A and Margolis H A 1989 Influence of short-term atmospheric CO₂ enrichment on growth, allocation pattern, and biochemistry of black spruce seedlings at different stage of development. *Can. J. For. Res.* 19, 773–782.
- Comité d'experts sur la prospection pédologique d'Agriculture Canada. 1987 Le système canadien de classification des sols. Seconde édition, Direction de la recherche, Ministère de l'Agriculture du Canada, publ. 1646. 170 pp.
- Côté B, Hendershot W H, Fyles J W, Roy A G, Bradley R, Biron P M and Courchesne F 1998 The phenology of fine root growth in a maple-dominated ecosystem: relationships with some soil properties. *Plant and Soil* 201, 59–69.
- Expert Committee on Soil Survey of Agriculture Canada, 1987 The Canadian Soil Classification System, 2nd edn. Supply and Services, Canada, Pub. 1646.
- Fahey T J and Hughes J W 1994 Fine root dynamics in a northern hardwood forest ecosystem. Hubbard Brook Experimental Forest, NH. *Ecology* 82, 533–548.
- Frolking S, Goulden M L, Wofsy S C, Fan S M, Sutton D J, Munger J W, Bazzaz A M, Daube B C, Crill P M, Aber J D, Band L E, Wang X, Savage K, Moore T and Harriss R C 1996 Modeling temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biol.* 2, 343–366.
- Fyles J W, Côté B, Courchesne F, Hendershot W H and Savoie S 1994 Effects of base cation fertilization on soil and foliage nutrient concentrations, and litterfall and throughfall nutrient fluxes in a sugar maple forest. *Can. J. For. Res.* 24, 542–549.
- Hendershot W H and Courchesne F 1991 Comparison of soil solution chemistry in zero tension and ceramic-cup tension lysimeters. *J. Soil Sci.* 42, 577–583.
- Hendrick R L and Pregitzer K S 1992 The demography of fine roots in a northern hardwood forest. *Ecology* 73, 1094–1104.
- Hendrick R L and Pregitzer K S 1996 Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *Ecology* 84, 167–176.
- Horsley S B, Long R P, Bailey S W, Hallett R A and Hall T J 2000 Factors associated with the decline disease of sugar maple on the Allegheny Plateau. *Can. J. For. Res.* 30, 1365–1378.
- Kozlowski T T, Kramer P J and Pallardy S G 1991 The physiological ecology of woody plants. *In* Physiological Ecology, A series of monographs, texts and treatises. Ed. H A. Mooney, Academic Press.
- Krause H H, Weetman G F, Koller E and Veilleux J M 1987 Programme interprovincial de fertilisation des forêts 1968–1983. Inf. Rep. DPC-X-21, For. Can. Serv., Ottawa.

- Kuhns M R, Garrett H E, Teskey R O and Hinckley T M 1985 Root growth of black walnut trees related to soil temperature, soil water potential and leaf water potential. *For. Sci.* 31, 617–629.
- Lean J and Rind D 1998 Climate forcing by changing solar radiation. *J. Climate* 11, 3069–3094.
- Lebourgeois F 2000 Climatic signals in earlywood and total ring width of Corsican pine from western France. *Ann. For. Sci.* 57, 155–164.
- Lortie M 1979 Arbres, forêts et perturbations naturelles au Québec. Presses Univ. Laval, Québec, Canada, 173 pp.
- Lyr H and Hoffmann G 1967 Growth rates and growth periodicity of tree roots. *Internat. Rev. For. Res.* 2, 181–236.
- McClagherty C A, Aber J D and Melilo J M 1982 The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63, 1481–1490.
- Moore J D, Camiré C and Ouimet R 2000 Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Quebec, Canada. *Can. J. For. Res.* 30, 725–732.
- Morrow R R 1950 Periodicity and growth of sugar maple surface layer roots. *J. For.* 48, 875–881.
- Nadelhoffer K J 2000 The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* 147, 131–139.
- Rolland C, Desplanque C, Michalet R and Schweingruber F H 2000 Extreme tree rings in spruce (*Picea abies* [L.] Karst.) and fir (*Abies alba* Mill.) stands in relation to climate, site, and space in the southern French and Italian Alps. *Arct. Antarct. Alp. Res.* 32, 1–13.
- Rubino D L and McCarthy B C 2000 Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-growth forest of southeastern Ohio, USA. *J. Torrey Bot. Soc.* 127, 240–250.
- Ruffner C M and Abrams M D 1998 Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Can. J. For. Res.* 28, 347–358.
- Savage C 2001 Recolonisation forestière dans les Basses Laurentides au sud du domaine climatique de l'érablière à bouleau jaune. M.Sc., Univ. Montréal. 51 pp.
- Splechtna B E, Dobry J and Klinka K 2000 Tree-ring characteristics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in relation to elevation and climatic fluctuations. *Ann. For. Sci.* 57, 89–100.
- StatSoft. 1994 Statistica for the Macintosh. Statsoft Inc. Tulsa, Oklahoma, USA.
- Stone L and Ezrati S 1996 Chaos, cycles and spatiotemporal dynamics in plant ecology. *J. Ecol.* 84, 279–291.
- Taylor J S and Dumbroff E B 1975 Bud, root, and growth-regulator activity in *Acer saccharum* during the dormant season. *Can. J. Bot.* 53, 321–331.
- Teskey R O and Hinckley T M 1981 Influence of temperature and water potential on root growth of white oak. *Physiol. Plant.* 52, 362–369.
- Tisdale S L, Nelson W L and Beaton J D 1985 Soil Fertility and Fertilizers, 4th edn. Macmillan, New York.
- Zarnovican R 2000 Climate and volume growth of young yellow birch (*Betula alleghaniensis* Britton) at three sites in the sugar maple-yellow birch forest region of Quebec. *Ecoscience* 7, 222–227.

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