SELECTED ECOSYSTEM PROCESSES IN A PINUS RESINOSA AIT. FOREST IN RELATION TO OTHER FIRE-AFFECTED EASTERN NORTH AMERICAN FOREST ECOSYSTEMS

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Abstract

Litterfall, decomposition, organic matter turnover, and forest soil respiration (CO_2 evolution) in a mature (75 yrs) eastern Ontario red pine (*Pinus resinosa* Ait.) ecosystem were compared with similar eastern North American fire-affected forest types. Litterfall patterns were shown to be variable seasonably as well as from year to year. Annual littermass inputs varied from a high of 5300 kg·ha^{-1} to a low of 2400 kg·ha^{-1} during the three-year observation period. Nutrient inputs through litterfall followed mass input patterns. Understorey litter decomposed more readily than overstorey litter (needles) probably because of the higher nutrient content in understorey material, pointing to the importance of the understorey in overall nutrient cycling processes.

Organic matter turnover rates, or residence time, were between 19 and 16 years for the three red pine stands studied. This represents intermediate values between rapid rates such as 2 to 3 years for south central Wisconsin forests and relatively slow rates such as 43 years for jack pine (*Pinus banksiana* Lamb.) ecosystems in northern New Brunswick. Strong climatic control over ecosystem processes, as well as substrate quality, is implicated in the observed variability among forest types. It is apparent that climatic controls will assume added importance in studies of ecosystem structure and function in light of anticipated global greenhouse warming.

Soil respiration was measured *in situ* with soda lime and shown to be very similar to levels observed in adjacent jack pine forests. Seasonal respiration means in red and jack pine forests with various fire histories were around 4300 mg of CO_2·m^{-2}·d^{-1}. In comparison, local fire-origin aspen stands had soil respiration rates in excess of 5000 mg CO_2·m^{-2}·d^{-1}, reflecting better nutritional status of the aspen site. Temperature appeared to be the overriding controlling factor in determining substrate respiration patterns. Soil moisture content and rainfall proved to be poor predictors of respiration activities in this study.

Introduction

Red pine (*Pinus resinosa* Ait.)[1] is an important commercial tree species in eastern Canada and the northeastern United States. Its north-south range is delineated roughly by the 50° and 40° parallels and its western limit from the Atlantic coast is the 97th meridian (Fowells 1965).

In the province of Ontario it is harvested from old growth, naturally-regenerated stands as well as from plantations. The annual volume cut (203 800 m^3) is only in sixth place compared to other commercial softwood species, but its stumpage cost per cubic meter ($Can 3.99) is the second highest after white pine

1. Nomenclature follows Scoggan 1978.

(*Pinus* strobus L.) ($Can 4.38), emphasizing its economic importance (Anonymous 1986).

Continued use of red pine as a plantation or old growth product requires a thorough understanding of the processes controlling ecosystem development under natural conditions. One of the major controlling factors is fire. Fire is recognized as a necessary agent for the establishment of red pine in any quantity in the natural forest (Van Wagner 1970) and most old growth stands have been established following fire, presumably in combination with a good seed year (Fowells 1965). Red pine's dependence on fire is almost solely related to the regeneration requirements of the species. Optimum conditions are characterized by fires which (a) expose a mineral soil seedbed or at least substantially reduce the forest floor organic layers, (b) reduce understorey competition temporarily, and (c) open up the overhead canopy (Van Wagner and Methven 1978).

Once the regeneration step has been completed successfully, ecosystem development is subject to local constraints such as climate and site quality. Ecosystem processes, and the rate at which they proceed, can be expected to reflect local conditions. Monitoring of key processes allows us to rank forest stands along a productivity continuum and to follow the rate of recovery to pre-disturbance conditions.

This paper quantifies litterfall, decomposition, organic matter turnover, and soil respiration rates in a mature eastern Ontario red pine ecosystem and compares the estimates with other studies reported in the literature. The objective is to place this red pine forest in perspective with regard to other fire affected forest ecosystems in eastern North America and to compare ecosystem processes in fire dependent forests.

Location

The study area is located at latitude 46°00′N and longitude 77°33′ within the Research Forest of the Petawawa National Forestry Institute in eastern Ontario. Rowe (1972) places the local forests into the Middle Ottawa Forest Section (L.4c) of the Great Lakes – St. Lawrence Forest Region. The underlying bedrock of Precambrian granites, gneisses, and schists is covered with glacial deposits. Typical glacial till is sandy, non-calcareous, and grey, comprising materials from silt to boulder size in a heterogeneous mixture (Gadd 1962). Soils are podzolic with poor profile development (Gillespie *et al.* 1964).

The climate is continental and locally moist-humid (Hills 1959). Total annual precipitation is 820 mm of which 610 mm falls as rain, the remainder as snow. Mean annual daily temperature is 4.3 °C. Mean daily maximum and minimum temperatures are 25.4 °C (July) and – 18.4 °C (January), respectively. Temperature extremes of 38.9 and – 40.6 °C have been recorded during these respective months. Freezing temperatures can be expected during all months except July (Anonymous 1982) and there are generally 112 frostfree days during a growing season of approximately 180 days (Hills 1959).

Within this setting a 70-year-old red pine forest of fire origin was selected for study. The forest is even-aged within a 5-year timeframe which represents the establishment phase. Tree density is approximately 1000 stems·ha^{-1} with a minor

admixture of white pine which originated from the same fire. Average tree height and diameter (dbh) are 24 m and 29 cm, respectively.

Dominant understory vegetation consists of patchy, dense thickets of *Corylus cornuta* Marsh., *Pteridium aquilinum* (L.). Kuhn, and smaller perrenials such as *Maianthemum canadense* Desf., *Linnaea borealis* L., *Trientalis borealis* Raf., *Cornus canadensis* L., *Cyprepedium acaule* Ait., *Vaccinium myrtilloides* Michx., and *Gaultheria procumbens* L.

Materials and methods

Field methods

Three 200 m transects were randomly located within the forest. These lines served as markers along which litterfall, decomposition, soil respiration, and forest floor sampling, as well as stand description, was carried out at random locations. Field methods for determination of these ecosystem attributes have previously been described by Weber (1985, 1987). Briefly, litter was collected in wooden traps with 1 mm mesh size fiberglass bottoms and 12 cm high sides. Traps were emptied three times a year after key litterfall episodes in April (*i.e.* after winter litterfall), June (after abscission of male and female flowers, pollen sheeding, etc.), and November (after autumn leaf fall).

Decomposition was determined using the litterbag technique. The reader is referred to Lousier and Parkinson (1978), Suffling and Smith (1974), Witkamp and Olson (1963), and Woods and Raison (1982) for discussions of the relative merit of the techniques and the precautions that have to be taken in the execution of the technique and interpretation of results.

In this study 1-mm mesh size, 10 × 10 cm fiber-glass bags were used. Litter material consisting of red and white pine needles and proportionately representative deciduous foliage was collected separately from overstorey and understorey plants prior to autumnal leaf abscision. Individual litterbags were filled with c. 10 g of ovendried (65 °C) material and the weight recorded to the nearest 0.01 g. A numbered aluminum tag was placed inside each bag for identification and the bag was stapled shut. Twenty-one bags of each of the two litter types were prepared for each of the three transects. This permitted seven retrievals in replicates of three over a 27-month period. Litterbags were placed on the forest floor surface (top of the litter layer) and secured with two metal pins.

Forest soil respiration (CO_2 evolution) was estimated *in situ* using the soda lime technique of Edwards (1982). Gordon *et al.* (1987), Schlentner and Van Cleve (1985), and Weber (1985) have discussed the usefulness of the technique for comparative purposes as well as its limitations. Carbon dioxide evolution was measured once every week at random locations along each transect in replicates of ten for a 24-hour period. Measurements were started as soon as the continuous snow cover disappeared in the spring and they were terminated with freezing of the ground in the fall. Forest floor sampling was carried out randomly in replicates of six along each transect as in Weber *et al.* (1985). Rainfall and soil surface temperatures were measured along each transect as described by Weber (1985). Soil moisture was determined gravimetrically in replicates of six after the 24 hr exposure period.

Laboratory methods

Drying and weighing of material prior to chemical analyses was carried out according to standard operating procedures (*e.g.* Weber 1987), and Black *et al.* (1965) served as the technical reference for N, P, K, Ca, Mg, and Fe analyses. Carbon dioxide evolution estimates by drying and weighing the soda lime followed Edwards (1982) and Monteith *et al.* (1964). As soon as the weight of CO_2 absorbed in the field had reached approximately 7% of the initial weight of soda lime it was discarded; fresh soda lime was used to maintain alkali absorption efficiency. Results were multiplied by a factor of 1.4 to correct for chemical water lost during the drying process (Edwards 1982).

Results and discussion

Litterbag mass loss

Weight losses from over- and understorey litter types are shown in Fig. 1. Decomposition patterns of individual litter types along the three transects was essentially identical. However, overstorey litter had a greater proportion of original weight remaining (44% – 53%) than understorey litter (25% – 32%) at the end of the study. This is a reflection of the more recalcitrant nature of conifer needle litter compared to deciduous leaf litter. Litter decomposition is more rapid when lignin content is low and nutrient contents are high (Aber and Melillo 1982; Melillo *et al.* 1982). Although lignin content was not determined in this study, initial nutrient contents of understorey litter were certainly noticeably higher than overstorey litter (Table 1). This demonstrates the principle of rapid decomposition in the presence of increased substrate nutrient supply relative to microbial energy needs. Conversely, low substrate nutrient supplying power, as observed in overstorey litter, will result in reduced decay rates because scarce resources are sequestered in microbial tissue (Binkley 1986).

Higher initial understorey nutrient concentration and resultant greater weight loss after the 2-year exposure period, compared to overstorey litter, is consistent with studies that investigated the relative contributions of these two input types to overall nutrient cycling. Thus, Foster (1974), MacLean and Wein (1977a, b), Scott (1955), Tappeiner and John (1973), and Yarie (1980), working in different forest ecosystems, all concluded that subordinate vegetation exerts a greater influence over nutrient cycling than its proportional biomass would indicate. For example, Tappeiner and John (1973) investigated biomass and nutrient content of *Corylus cornuta* in red and jack pine stands of Minnesota and showed that up to 50% of the annual litterfall mass originated from the hazel understorey, contributing even larger proportions of the total nutrients returned annually to the forest floor.

It should be pointed out that final weight loss in both litter types would be expected to be greater had the litter material not been confined in nylon mesh bags. As noted by Lousier and Parkinson (1976), Witkamp and Crossley (1966), and Witkamp and Olson (1963) nylon mesh of the size used in this study represents an effective barrier to soil arthropod movement, preventing litter fragmentation and
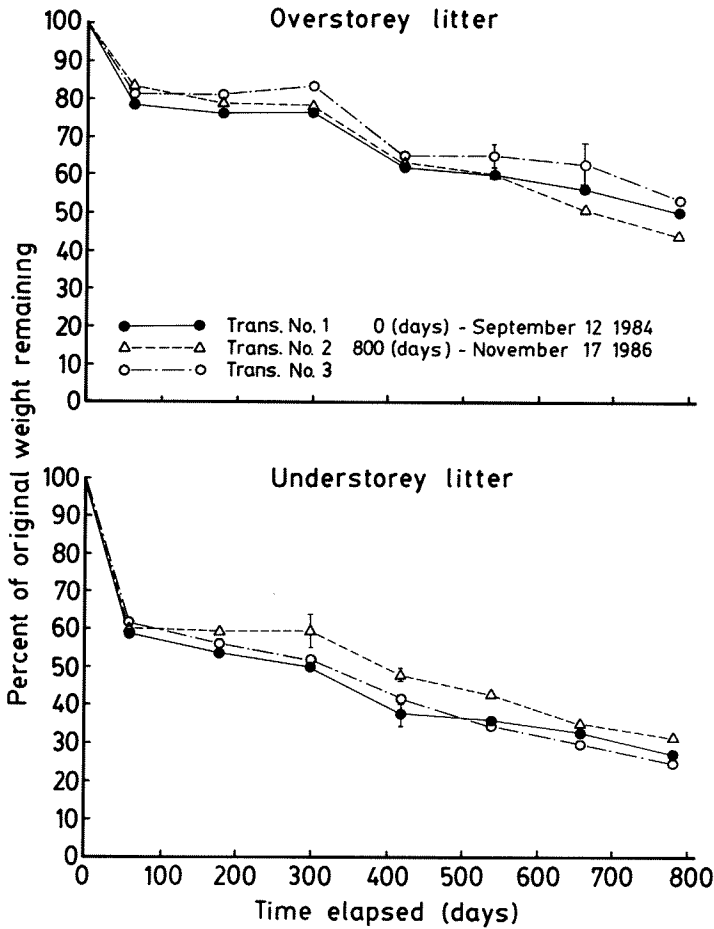
Fig. 1. Percentage of original overstorey and understorey littermass remaining over a period of two years. Representative standard error bars are indicated. Each point represents the mean of three litter-bag weights.

Table 1. Per cent initial nutrient concentration (time zero) in overstorey (O) and understorey (U) litter along three transects.

Trans. No	N		P		K		Ca		Mg		Fe[1]	
	O	U	O	U	O	U	O	U	O	U	O	U
1	0.85	1.55	0.11	0.21	0.49	1.82	0.36	1.01	0.11	0.26	33	86
2	0.95	1.70	0.13	0.20	0.52	1.77	0.34	0.59	0.11	0.22	153	44
3	1.00	1.65	0.13	0.21	0.57	2.09	0.37	0.78	0.11	0.24	32	74

[1] ppm

Overstorey litter   Understorey litter

Trans. No. 1
Trans. No. 2
Trans. No. 3

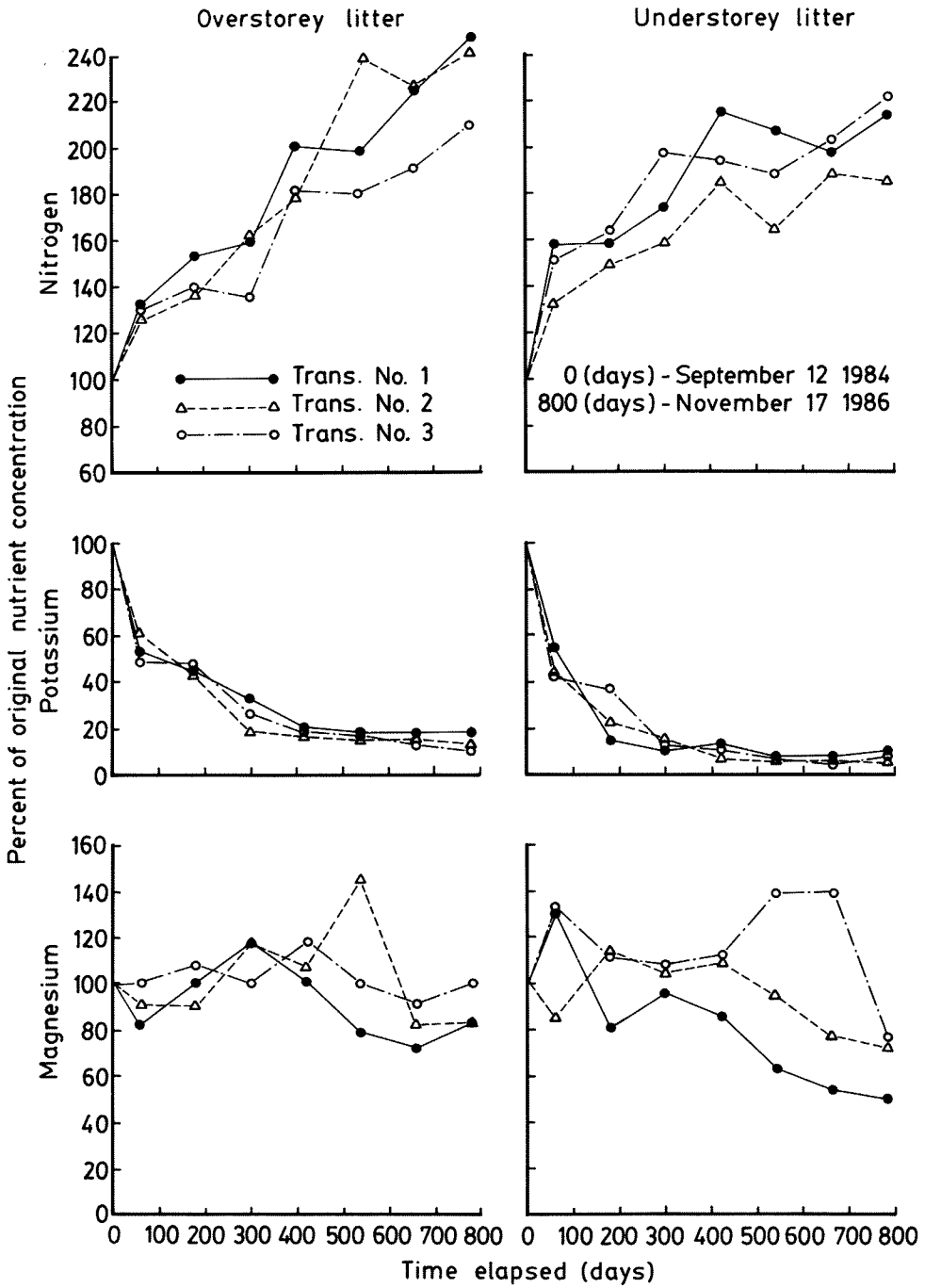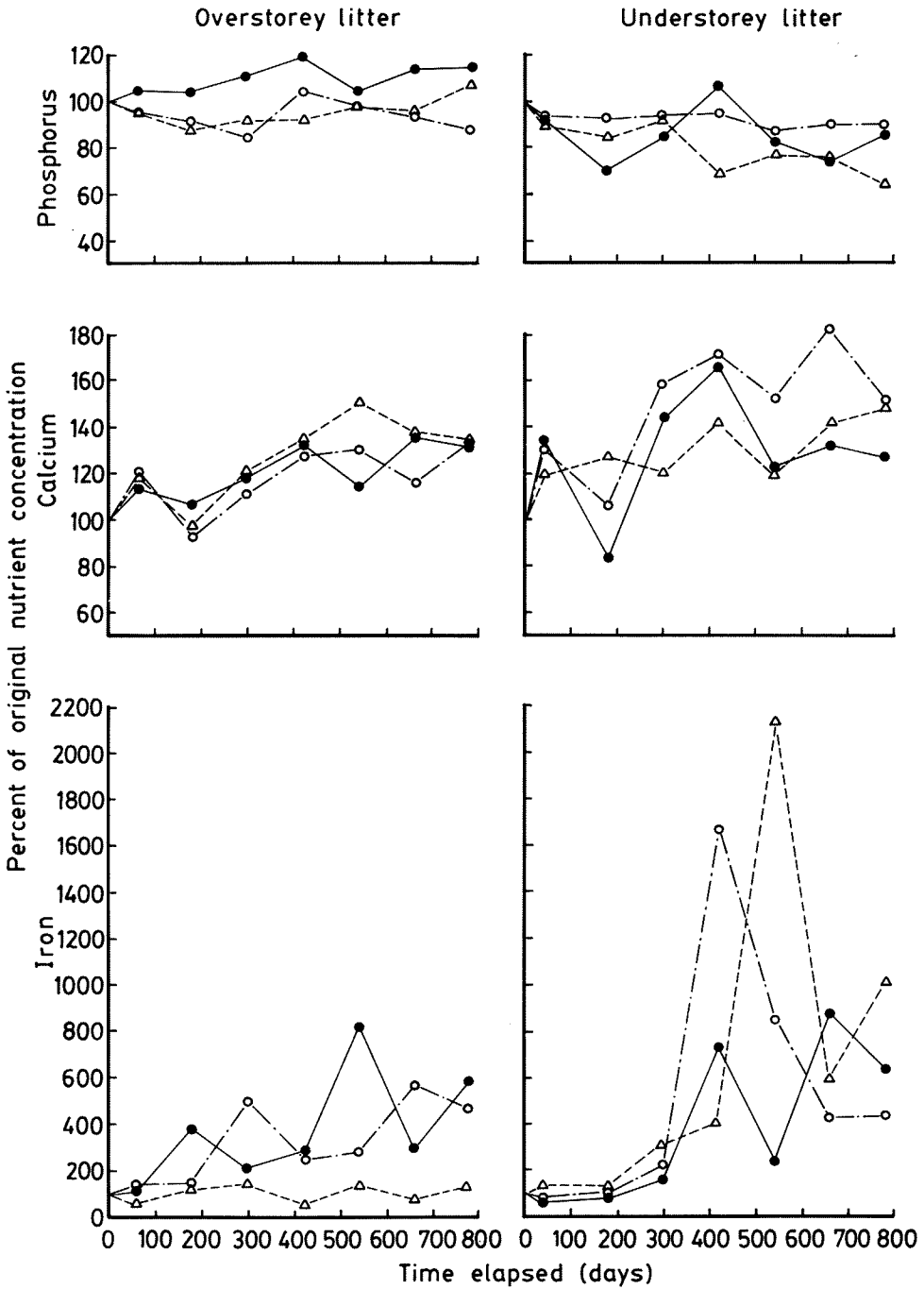0 (days) - September 12 1984
800 (days) - November 17 1986

Fig. 2. Percentage of original overstorey and understorey litter nutrient concentration remaining over a period of two years. (Also opposite page)

Overstorey litter   Understorey litter

Percent of original nutrient concentration

Phosphorus

Calcium

Iron

Time elapsed (days)

reducing the potential surface area available for microbial attack and leaching. St. John (1980) further advised that litter confinement restricts access by vegetative fungal structures, resulting in decompositionn underestimates. The litterbag technique has continued to enjoy widespread popularity, however, due to the longer time during which decomposition processes can be monitored, ease of retrieval, and avoidance of physical loss of undecomposed material.

Litterbag nutrient dynamics

Nutrient changes in over- and understorey litter over the two-year observation period is shown in Fig. 2. Nitrogen concentration increased in both litter types until the end of the exposure period, a commonly observed phenomenon (see Weber 1987 for additional references). Total weight of N per litterbag increased from 90 to 100 mg in overstorey material compared to a steady decrease from 170 to 90 mg in understorey bags. This indicates that overstorey litter accumulated N for the duration of the exposure period while understorey litter released N. The accumulation phase, the duration and magnitude of which is a function of substrate quality, is followed by a period of net N release (Bosatta and Berendse 1984). Staaf (1980), working in Swedish beech forests, made the generally applicable observation that the onset of the N release phase of litter decomposition is dependent on the initial litter nutrient content; the lower the initial concentrations, the longer the delay. The start of the release phase has been reported to have been delayed for as long as four years in particularly recalcitrant litter (Berg and Theander 1984).

The N dynamics in over- and understorey litter are virtually identical to those observed for pure jack pine stands on deep outwash sands only a few km away (Weber 1987). In the jack pine study three fire origin age classes were examined (ages 8, 21, and 65) as well as two non-lethal surface fires. This emphasizes the similarity that exists in N dynamics of fire dependent ecosystems (at least in this particular geographic area) regardless of age class, type of fire, cover type, or substrate.

The differences in P dynamics between litter types can also be traced to differences in initial nutrient content, being almost twice as large in understorey compared to overstorey litter (Table 1). The effect was that needle litter retained between 90% and 115% of original concentrations whereas the deciduous understorey material lost 60 to 90%. With respect to change in total amounts of P in litterbags, needle litter decreased by 4 mg at the end of the study whereas understorey litter had released 17 mg of P. Again, the importance of the understorey to nutrient dynamics becomes apparent.

Potassium dynamics followed classical patterns: rapid initial loss due to the mobility of this cation, a function of its water solubility and ease of leaching, and subsequent stabilization. During the first exposure year about 80% of the original amounts were lost. Needle litter stabilized then, while leaf litter continued to lose another 10% until the end of the experiment (Fig. 2). Potassium behavior also exhibited a two-phase pattern. The rapid early loss was possibly regulated by initial nutrient content of the litter while subsequent loss was dependent on lignin levels in the decomposing material (Rosswall 1982). Potassium mass loss tracked the concentration changes.

Calcium concentration increased erratically over the 2-year period by both litter types, more so in understorey litter. Calcium dynamics has been described as highly site specific depending on such parameters as latitude, altitude, invertebrate population type and structure, and parent material and its weathering rate (Lousier and Parkinson 1978). Addition of calcium to the substrate is due to precipitation and foliar leaching, with most of the Ca being retained in the litter layer rather than being further transported into the soil profile (Olson *et al.* 1981; Parker 1983; Thomas 1969). In terms of total amounts of Ca lost, this nutrient behaved similarly to P, with understorey litterbags showing much greater release (70 mg) than overstorey material (20 mg).

Magnesium dynamics were variable, but the trend in both litter types was one of initial increase followed by gradual release. Understorey litter Mg levels after 800 days were lower than in needle litter, again pointing to the recalcitrant nature of overstorey litter on the one hand and greater nutrient dynamics in deciduous litter on the other. Absolute changes in litterbag Mg content reflect these trends. Overstorey litter lost approximately 50% of the original Mg mass compared to about 90% for understorey litter.

Iron dynamics are complex and the element is a difficult one to study (see Gosz *et al.* 1973; Weber 1987). In the present study Fe was accumulated in both litter types of all three sands. Accumulation levels were as low as 120% and as high as over 2000% of original amounts (Fig. 2). Extreme accumulations were also observed by Weber (1987) in a 65-year-old jack pine stand near the red pine stands considered here. The difficulty in studying iron dynamics is related to the microbial activity that is primarily responsible for the rate at whch Fe accumulates in decomposing litter. Microbial activity, in turn, is locally variable and dependent on such environmental factors as organic matter quality, source and pH of litter, substrate temperature and moisture, to name a few. This makes comparisons between ecosystem types difficult, but allows the general observation that more easily decomposable material accumulates more Fe than decay-resistant litter (Gosz *et al.* 1973; Lousier and Parkinson 1978).

Litterfall

Three-year litterfall averages (Table 2) are comparable to inputs reported by Foster and Gessel (1972) and Weber (1987) in jack pine forests of central and eastern Ontario, respectively. Annual totals in the present study, however, indicate that there can be substantial variation in littermass input from year to year. For example, litterfall during the last year of the study was about half the amount estimated for the preceding year. Seasonal patterns of litter input also become evident from Table 2. The greatest amount was consistently deposited in the fall after abscission and the smallest quantities were collected in the summer after shedding of reproductive parts (male and female flowers, budscales, etc.). The spring collectionn, representing plant material which fell during the winter months, occupied an intermediate position with respect to littermass deposited.

Amounts of nutrients returned with litterfall are shown in Table 3. The pattern of nutrient return follows that of mass input, *i.e.* the second year of the study showed greatest amounts, followed in decreasing order by the first and third

Table 2. Annual litter mass input (kg·ha^{-1}) for three years.

Trans. No	1984–1985				1985–1986				1986–1987				3-year average (± S$\bar{x}$)
	Fall	Spring	Summer	Annual total	Fall	Spring	Summer	Annual total	Fall	Spring	Summer	Annual total	
1	2390	816	337	3543	3392	1569	300	5261	1573	576	263	2412	3739 ± 828
2	2426	853	568	3847	2693	1610	572	4875	1486	583	576	2645	3789 ± 644
3	2449	873	766	4088	2968	1838	536	5342	1524	1030	307	2861	4097 ± 716

Table 3. Annual litterfall nutrient input (kg·ha⁻¹ for three years.

Year	Transect No	N	P	K	Ca	Mg	FE
1984–1985	1	22.9	2.1	4.4	19.5	3.8	0.2
	2	23.8	2.3	4.9	19.6	3.6	0.3
	3	24.9	2.3	4.8	21.0	3.7	1.2
	x̄	23.9 (0.6)[1]	2.2 (0.1)	4.7 (0.2)	20.0 (0.5)	3.7 (0.1)	0.6 (0.3)
1985–1986	1	34.9	2.6	6.5	29.1	5.9	0.3
	2	25.4	2.5	5.8	22.7	4.5	0.2
	3	26.3	2.7	7.2	24.0	4.8	0.2
	x̄	28.9 (3.0)	2.6 (0.1)	6.5 (0.4)	25.3 (2.0)	5.1 (0.4)	0.2 (0.03)
1986–1987	1	18.1	1.7	3.3	14.2	2.7	0.1
	2	16.4	1.6	3.6	12.5	2.2	0.1
	3	18.8	1.7	3.7	13.5	2.7	0.2
	x̄	17.8 (0.7)	1.7 (0.03)	3.5 (0.1)	13.4 (0.5)	2.5 (0.2)	0.1 (0.03)
3-year average		23.5 (3.2)	2.2 (0.3)	4.9 (0.9)	19.6 (3.0)	3.8 (0.8)	0.1 (0.03)

[1] s x̄

Table 4. Organic matter dynamics in a red pine forest in eastern Ontario.

Trans. No	Forest floor wt. (kg·ha⁻¹	Annual[1] litterfall (kg.⁻¹)	Residence[2] time (yrs.)	Fractional[3] annual turnover (%)
1	58 366	3739	15.6	6.4
2	68 357	3789	18.0	5.6
3	77 439	4097	18.9	5.3

1: 3-year average

2: Residence time (RT) $RT = \dfrac{\text{forest floor wt.}}{\text{annual litterfall}}$

3: Fractional annual turnover (k) $k = \dfrac{1}{RT}$

years. Nutrient quantity along the three transects was similar for a given year, indicating that net production, of which litterfall is a convenient index (Bray and Gorham 1964), was fairly uniform in the forest as a whole.

Organic matter dynamics and process comparisons

Forest floor residence times and fractional annual turnover are shown in Table 4. Residence time is calculated by dividing the forest floor mass by annual litterfall (*e.g.* Reiners and Reiners 1970). Thus, a residence time of 1 would indicate that complete incorporation of litter into forest floor layers takes place within one year. The reciprocal of residence time is commonly called fractional annual turnover and is expressed as a percentage. From a fire ecological perspective residence time provides two important pieces of information. Firstly, it gives an indication of organic matter accumulation and, hence, the type of fire required to expose a mineral soil seedbed for fire-adapted species such as red pine and jack pine.

Table 5. Comparison of selected ecosystem processes in various eastern North American fire-affected forest types.

Stand type and origin	Age	Location	Decomp. time (months)	Mass remaining (%)[1]						Forest floor mass (kg·ha⁻¹)	Litterfall (kg·ha⁻¹·yr⁻¹)	Forest floor[2] turnover (yrs)	Authority
				Organic matter	N	P	K	Ca	Mg				
Pinus banksiana (fire)	29	Northern New Brunswick	12	76–70	85	148	22	47	43	104 500	1600	43	MacLean and Wein 1978a;b
Pinus banksiana (fire)	57	Northern New Brunswick	24	63–57	102	185	17	50	68	74 100	2000	24	
Populus tremuloides (fire)	29	Northern New Brunswick	24	53	77	41	3	62	27	50 200	2000	20	
Populus grandidentata (old field invasion)	?	Southcentral Wisconsin	24	38						5 300	3400	1.6	McClaugherty et al. 1985
Pinus strobus (?)	?	Southecentral	24	33						10 000	3100	3.2	
Pinus resinosa (fire, planting)	41	Northcentral Minnesota								26 000	5468	5	Perala and Alban 1982; Alban 1982
Pinus banksiana (fire, planting)	41	Northcentral Minnesota								25 000	5322	5	
Populus tremuloides (fire)	49	Northcentral Minnesota								20 000	3675	6	
Pinus resinosa *Pinus strobus* *Pinus banksiana* (plantation)	34	Central Wisconsin	12	80	91	85	25	96	64	27 822	3900	7	Bockheim and Leide 1986

Table 5. Continued.

Stand type and origin	Age	Location	Decomp. time (months)	Mass remaining (%)[1]						Forest floor mass (kg·ha⁻¹)	Litterfall (kg·ha⁻¹·yr⁻¹)	Forest floor[2] turnover (yrs)	Authority
				Organic matter	N	P	K	Ca	Mg				
Pinus resinosa (fire)	60	Northern Minnesota								15 810	3290	5	Tappeiner and Alm 1975
Pinus resinosa (fire)	75	Eastern Ontario	26	50	122	60	8	67	50	58 366	3739	15.6	Present study
Pinus resinosa (fire)	75	Eastern Ontario	26	44	121	57	7	68	50	68 357	3789	18.0	
Pinus resinosa (fire)	75	Eastern Ontario	26	53	109	52	6	69	60	77 439	4097	19.0	
Pinus banksiana (fire)	30									20 000	4000	5	Foster and Morrison 1976
Pinus banksiana (fire)	65	Eastern Ontario	26	42						40 739	3986	10.2	Weber 1987
Pinus banksiana	21	Eastern Ontario	26	50						24 065	2400	10.0	

[1] Based on overstorey litter enclosed in fine mesh litterbags.
[2] Does not consider the contribution of fine roots.

Secondly, it is a rough measure of fuel accumulation because the rate at which fuels accumulate equals the difference between their rates of production and decomposition (Sousa 1984).

Organic matter residence times in the present study were between 16 and 19 years. These estimates exactly bracket the mean residence time of 17 years reported by Cole and Rapp (1981) for a large number of circumpolar temperate coniferous forest floors. This represents an intermediate timeframe between rapid turnover rates of 2 to 3 years observed by McClaugherty *et al.* (1985) and slower rates of more than 43 years in MacLean and Wein's study (1978a, b) (Table 5). Table 5 shows that forest floor turnover rates can be quite variable even when fire affected ecosystems are considered by themselves. If mean residence times of such geographically and ecologically widely separated forest types as tropical vs. boreal, for example, were to be compared, the differences would be even more striking (see Vogt *et al.* 1986).

Comparison of other ecosystem processes, such as decomposition patterns and litterfall (Table 5) similarly reveals the variability encountered in natural or plantation ecosystems of fire-adapted species. The rapid turnover rates observed by McClaugherty *et al.* (1985) for largetooth aspen and eastern white pine in south central Wisconsin are associated with rapid decay rates and low forest floor mass. In contrast, MacLean and Wein (1978a; b) encountered slow mass loss from their litterbags and high forest floor mass. Obviously local site conditions, including climatic differences, are responsible for the observed variability. Vogt *et al.* (1986), working with large data sets, concluded that greater forest floor accumulation occurred at latitudes above 40°, while lower average accumulations were observed at latitudes less than 40°.

The strong influence of climate on litter production and decomposition was demonstrated by Meentemeyer (1978) and Meentemeyer *et al.* (1982). Using actual evapotranspiration (AET) as an index of the climatic (energy and moisture) forcing function they concluded that AET is a more important predictor of decay rates and litter production than is litter quality (lignin content). Climate controls of ecosystem structure and function will probably assume greater importance and receive more intense attention in light of anticipated climate change in the northern hemisphere due to the accumulation of greenhouse gases (Harrington 1987).

It should be pointed out that the residence time calculations of Table 5 do not include estimates of the contribution of root turnover, throughfall, or stemflow. Vogt *et al.* (1983; 1986) and Fahey (1983) have cautioned that in some cold temperate and boreal ecosystems residence times may be underestimated by as much as 80% when root and throughfall inputs are ignored. Nevertheless, comparison of data from the literature provides useful indices of decomposition rates as long as it is understood that the information represents comparative rather than absolute values.

Soil respiration

Forest soil respiration for three growing seasons, expressed as amount of CO_2 evolved, is shown in Fig. 3. Midsummer respiration peaks, also reported for various other coniferous forest ecosystems (Gordon *et al.* 1987; Schlenter and
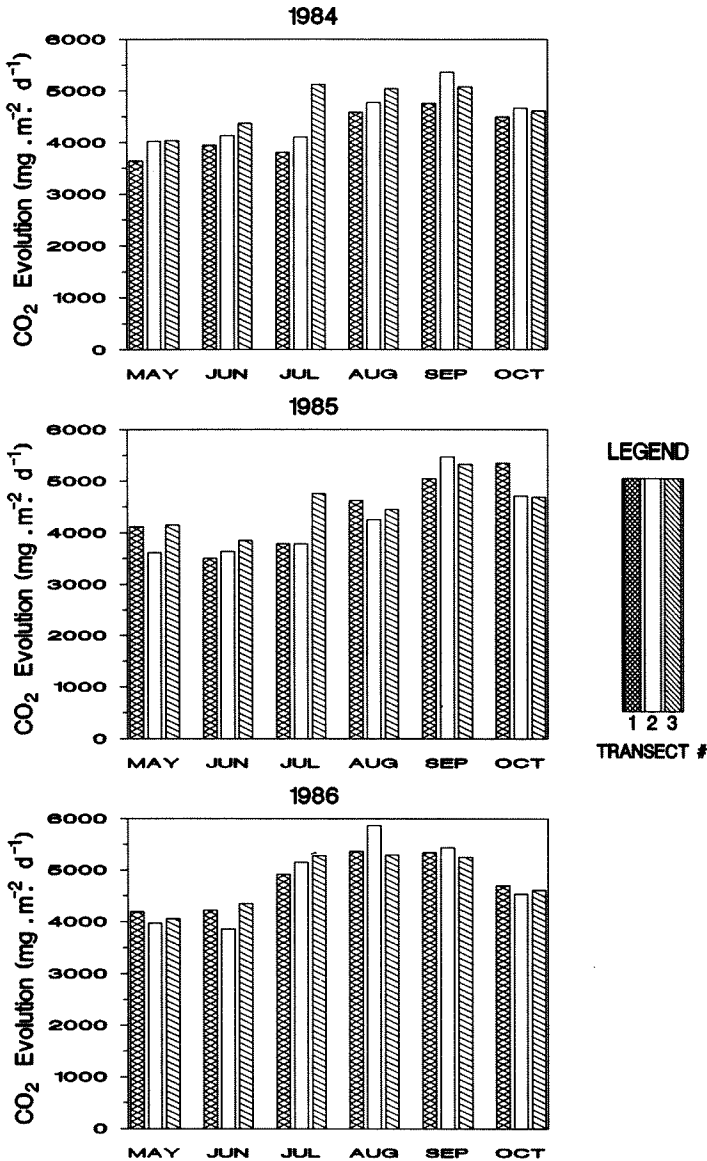
Fig. 3. Seasonal respiration pattern for three consecutive growing seasons. Monthly values were derived by averaging weekly readings.

Van Cleve 1985; Weber 1985, 1989) were pronounced only in 1986. Presumably, soil moisture and temperature regimes were not conducive to peak respiratory activity in the other two observation years (Orchard and Cook 1983; Salonius 1983). Monthly respiration rates are very similar to those of adjacent jack pine forests (Weber 1985), but lower than in neighbouring aspen stands (Weber 1989) (Table 6). Nutrient return in aspen litter was approximately 50% higher than in the red

Table 6. Comparison of seasonal forest soil respiration means in three fire-affected eastern Canadian forest ecosystems.

Forest type	Age since last fire (yrs7	Type of fire	Respiration rate (mg $CO_2 \cdot m^{-2} \cdot {}^{-1} \pm$ SE)
Pinus banksiana	65	Stand replacing wildfire	4504 ± 104[1]
	21	Stand replacing wildfire	4315 ± 134
	22	Non-stand replacing surface fire	4571 ± 123
	23	Non-stand replacing surface fire	4244 ± 114
Populus tremuloides	21	Stand replacing wildfire	5020 ± 161[2,3]
	3	Experimental, stand replacing surface fire	5033 ± 213
Pinus resinosa	75	Stand replacing wildfire	4274 ± 34[2,4]
	75	Stand replacing wildfire	4325 ± 95[2]
	75	Stand replacing wildfire	4486 ± 114[2]

[1] *Pinus banksiana* data from Weber 1985
[2] Three-year average
[3] *Populus tremuloides* data from Weber 1989
[4] Present study

pine forest of this study. The poorer nutritional status of the red pine and jack pine forests is reflected in reduced soil respiration rates compared to aspen. Soil respiration measurements, therefore, appear to be useful if forest stands are to be ranked along a productivity scale. Furthermore, it can be seen that coniferous fire-affected ecosystems (at least in this geographical area) show soil metabolic activities that are remarkably similar, regardless of age or type of fire. This would confirm the observation, previously made by Weber (1988, 1989), that fire-affected ecosystems have adapted to periodic exposure to fire by quickly resuming ecosystem processes at a rate comparable to pre-disturbance levels (Holling 1973).

Most workers studying soil respiration have related CO_2 evolution to temperature and moisture through regression analysis or other types of modelling (*e.g.* Cowling and MacLean 1981; Gordon *et al.* 1987; Schlenter and Van Cleve 1985; Weber 1989). For the present study simple regression techniques were used to investigate the relation of temperature and moisture to soil respiration (Table 7). The only environmental parameter that acted as a reasonably accurate predictor of soil respiration was maximum soil surface temperature sum and this was consistently so only for the last year of observation.

It would have been expected that soil moisture would provide some degree of predictability for soil respiration because higher soil moisture has generally been described as being conducive to accelerated respiration patterns (Singh and Gupta 1977). However, Cowling and MacLean (1981) point out that soil moisture, deter-

Table 7. Interaction between monthly respiration and selected environmental parameters.

Parameter	Trans. No 1	Trans. No 2	Trans. No 3
		r^2	
		1984–1985	
Rain sum[1]	– 0.36	– 0.28	0.11
Min. temp. sum[2]	0.32	0.15	0.58
Max. temp. sum[3]	0.31	0.17	0.64
Mean M.C.[4]	– 0.37	– 0.41	– 0.43
		1985–1986	
Rain sum	0.60	0.70	0.48
Min. temp. sum	0.41	0.52	0.68
Max. temp. sum	0.54	0.58	0.75*
Mean M.C.	0.10	– 0.15	– 0.41
		1986–1987	
Rain sum	0.43	0.46	0.46
Min. temp. sum	0.72	0.70	0.73
Max. temp. sum	0.89**	0.87***	0.91*
Mean M.C.	0.80*	0.45	0.50

[1]   Total monthly rainfall
[2]   Soil surface heat sum of monthly temperature minima above $0°C$
[3]   Soil surface heat sum of monthly temperature maxima
[4]   Average monthly per cent soil moisture
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

mined as gravimetric water content, is an imperfect descriptor of the physical state of water in soil because it does not differentiate between its physical and biotic components. As well, Douglas and Tedrow (1959) have shown that CO_2 flux is negativly affected above and below an optimum range.

Rainfall, being logically related to soil moisture, similarly proved to be a poor predictor for soil respiration. Nakane *et al.* (1983), Schlentner and Van Cleve (1985), and Weber (1989) also reported that rainfall events were not reflected in uniformly higher forest floor water contents or altered soil respiration rates. The forest canopy architecture is obviously important in determining throughfall and interception during a given rainfall episode and the subsequent respiratory response of the substrate.

Two issues emerge from the above discussion. Firstly, the necessity for multi-year observations as compared to single season measurements. Studying basic ecosystem processes for only one year is inadequate because that particular year may represent an extreme along a range of possible conditions. Secondly, temperature control appears to be an important environmental parameter affecting respiratory rates. Cowling and MacLean (1981) in Alaska and Weber (1985, 1989) in Ontario found similar strong temperature influences while precipitation acted as a secondary modifier, setting substrate moisture content at levels above or below the optimum for respiratory activity.

Acknowledgements

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