Published July, 1998

Soil Warming: Consequences for Foliar Litter Decay in a Spruce–Fir Forest in Maine, USA

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ABSTRACT

Increased rates of litter decay due to projected global warming could substantially alter the balance between C assimilation and release in forest soils, with consequent feedbacks to climate change. This study was conducted to investigate the effects of soil warming on the decomposition of red spruce (*Picea rubens* Sarg.) and red maple (*Acer rubrum* L.) foliar litter at Howland, ME. Experimentally increased Oa horizon soil temperatures (increase of 4–5°C) were maintained during the snow-free season from 1993 through 1995 in replicated 15 by 15 m plots using heat-resistance cables. For red maple litter, significant treatment effects included greater loss of mass (27%) and C (33%), and greater accumulation of Zn (54%) during the first 6 mo of decay in the heated plots than the control plots. After 30 mo of decay, significant treatment effects were no longer evident for red maple litter. Few treatment effects were observed for red spruce litter during the initial 18 mo of decay. However, after 30 mo of decay, significant treatment effects included greater loss of mass (19%), C (19%), N (24%), Ca (27%), Mg (12%), K (4%), Zn (60%), and cellulose (40%) in red spruce litter in the heated plots than the control plots. We conclude that a modest increase in Oa horizon soil temperature (4–5°C) can significantly increase litter decay rates and alter litter decay dynamics in this coniferous forest stand, and that these changes exhibit variations in their temporal development as a function of species and litter quality attributes.

LITTER DECOMPOSITION plays a central role in regulating the balance between C assimilation and release in terrestrial ecosystems. Temperature is a well-established environmental factor governing litter decomposition rates, with litter decay rates generally increasing with increasing temperature in the range 5 to 30°C (Daubenmire and Prusson, 1963; Witkamp, 1966; Alexander, 1977; Meentemeyer, 1978; Swift et al., 1979; Jansson and Berg, 1985; Moore, 1986; Ruark, 1993). Greenhouse gas emissions are predicted to raise mean global temperature by 2 to 5°C in the next 50 to 100 yr, with greater warming occurring at higher latitudes than at the equator (Bolin et al., 1986; Hansen et al., 1988; Intergovernmental Panel on Climate Change, 1990). It is reasonable to hypothesize that warmer temperatures could provide a positive feedback to elevated atmospheric CO_2 concentrations by increasing net fluxes of C from the soil to the atmosphere through increased rates of decomposition.

A growing number of studies are using in situ soil temperature manipulations or "soil warming" experiments to test the response of key soil processes to altered thermal conditions (Van Cleve et al., 1990; Peterjohn et al., 1994; Harte et al., 1995; McHale et al., 1996; Lukewille and Wright, 1997). These in situ soil warming experiments are not intended to simulate global climate change, i.e., the gradual increase in both soil and air temperature on decadel time scales. Rather, they provide a uniquely powerful tool to evaluate temperature controls on soil processes under field conditions. For example, Van Cleve et al. (1990) demonstrated a significantly increased decomposition of the forest floor in a black spruce [*Picea mariana* (Miller) B.S.P.] stand in Alaska in response to an 8 to 10°C increase in soil temperature. Lukewille and Wright (1997) showed a significant increase in NO_3 and NH_4 concentrations in runoff, which they suggested was due to increased N mineralization in a boreal forest catchment in Norway in response to a 3 to 5°C increase in soil temperature. McHale et al. (1996) reported significant increases in decomposition of American beech (*Fagus grandifolia* Ehrh.) foliar litter in a northern hardwood stand in the Adirondack Mountains of New York in response to a 5 to 7.5°C increase in soil temperature.

In order to better understand the in situ effects of increased temperature on foliar litter decomposition, we evaluated the response of red spruce and red maple litter decay to a 4 to 5°C increase in Oa horizon soil temperature as a component of a soil warming experiment at the Howland Integrated Forest Study site in central Maine.

MATERIALS AND METHODS

Study Site

The study site is located in a low-elevation (60 m) commercial spruce–fir forest in east-central Maine (45°10′N, 68°40′W), adjacent to the Howland Integrated Forest Study (HIFS) site (Fernandez et al., 1993, 1995; Lawrence and Fernandez, 1991).

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Published in Soil Sci. Soc. Am. J. 62:1072–1080 (1998).

Vegetation is dominated by red spruce (≈50% of live basal area), with occasional codominant eastern white pine (*Pinus strobus* L., ≈22%) and eastern hemlock [*Tsuga canadensis* (L.) Carriére, 13%], and a minor component of red maple (≈10%). Few balsam fir [*Abies balsamea* (L.) Miller] >4 cm diameter at breast height remain from the last spruce budworm infestation. Stand age is uneven (45–130 yr), which reflects a logging history of single-tree selection. Basal area is 51 m^2 ha^{-1}. Little or no understory vegetation is present. Topography of the area is generally flat. Soils at the site are classified as primarily coarse-loamy, mixed, frigid Aquic Haplorthods from the moderately well-drained Skerry series, which have developed from the underlying dense basal till. The climate is humid, cool, and continental. During the last 10 yr, mean annual temperature was between 5 and 6°C, mean January and July temperatures were −9.9 and 20.1°C, respectively, and mean precipitation was 1063 mm (National Oceanic and Atmospheric Administration, 1981–1990). The growing season varies from 120 to 140 d. The forest site was chosen as representative of the low-elevation commercial spruce–fir resource that is prevalent across a large region in central Maine and extends northward into Canada.

Experimental Design

Three 15 by 15 m plots were established in each of two locations (separated by ≈300 m) at the study site in the spring and summer of 1992. One warming treatment (5°C above ambient) and two controls (an undisturbed "control", with no disturbance from cable installation, and a "cabled control", in which subsurface cables were installed but not heated) were assigned to one plot in each location in a randomized complete block design, with location as the blocking factor. Cable installation was completed by July 1992 and treatments were initiated in May 1993, providing a 10-mo equilibration period to minimize disturbance effects. Plots were heated from mid-May through early November (which represents roughly the snow-free period at this site and encompasses the entire growing season) for 1993, 1994, and 1995.

A buried cable method was used to experimentally increase soil temperatures in the heated plots. In this method, heat-resistance cables were installed 1 to 2 cm below the surface of the Oi horizon at 20-cm intervals in each of the heated plots. After cable installation, six intensive sampling stations were established systematically in each plot in an approximate H pattern. All sampling stations were located within an inner 12 by 12 m area within each 15 by 15 m plot to avoid edge effects. Temperature-control thermistors, connected directly to a Campbell CR-10 datalogger (Campbell Scientific, Logan, UT), were installed midway between cables at each of the six stations at either a depth of 7 cm in the O horizon (≈5 cm from the cables) or at the interface between the O and E horizons (mean O horizon depth 9.0 ± 2.1 cm). The datalogger read temperatures from all temperature-control thermistors and calculated mean plot temperatures at 10-min intervals. If the mean temperature in a heated plot was <5°C above the mean temperature in the adjacent control plot, then the datalogger would turn the heating cables on for that plot; conversely, if the mean temperature in the heated plot was ≥5°C higher than the mean temperature in the adjacent control plot, then the datalogger would turn off the heating cables. Cabled control plot temperatures were recorded for comparison.

Field and Laboratory Methods

In addition to the temperature-control thermistors, a second set of thermistors were located at each station in the Oa horizon and at depths of 10, 25, and 50 cm in the mineral soil to evaluate the efficacy of the treatment in warming the whole soil volume, and to provide temperature data for evaluation of soil response to warming. These soil temperatures were recorded at 4-h intervals throughout the field season (May–November) by the datalogger. Gravimetric soil moisture in the O horizon was determined at 6-wk intervals and was expressed on a dry-mass basis. These data were used to determine if treatment effects on soil moisture were evident in this study.

Litter decay was studied using a litter bag method (Bocock, 1964) as modified by Rustad and Cronan (1988) for use with red spruce needles. Red spruce and red maple litter were collected from the site in September 1992 by gently shaking senescent needles or leaves from branches onto clean plastic bags. Litter samples were air dried to a constant mass. Subsamples of the leaves from each species were oven dried at 85°C for 48 h to calculate a moisture correction factor and were then analyzed for initial nutrient concentrations. Approximately 5 g of air-dry litter of each species were placed into 10 by 15 cm mesh bags and initial mass was recorded. To avoid loss of spruce needles during transport to and placement in the field, a fine (0.3-mm) mesh was used on the bottom of the litter bag, while a larger (1-mm) mesh was used on the top. Reference bags to assess the input of exogenous debris (sensu Rustad, 1994) were also prepared by placing ≈3 g of polyester batting into similar mesh bags. Because the surface characteristics of the polyester batting are not identical to decomposing litter, these reference bags were used as a relative index of the amount of debris falling into the bags and not as a quantitative measure of exogenous inputs into the actual litter bags.

During installation in the field, surface litter was removed and litter bags were placed within the Oi horizon. Additional Oi material and surface litter were then replaced, providing an insulating effect. Results from a pilot study showed that Oi soil temperatures were only slightly lower than temperatures in the Oa horizon (8.8 vs. 9.4°C), despite the likely higher convective heat loss in the Oi. We believe that this is because of (i) the insulating quality of the dense matt of spruce, pine, and hemlock needles that made up the loose litter and Oi layer (as shown in our pilot study on cable design and placement) and (ii) the fact that the cables were buried in the Oi layer and thus provided a continuous source of heat to this layer. It is also noteworthy that our extensive testing of the distribution of the temperature effect showed that, although soil temperature in the immediate vicinity of the cables was more than 5°C above ambient (e.g., 7–9°C), this effect was extinguished within 1- to 2-cm distance from the cables and thus did not affect a large volume of soil or the decaying litter.

Five bags of each litter type were placed in each of five subplots located within each of the 15 by 15 m treatment plots (total of 25 bags per litter type per plot) in early May 1993. One bag of each litter type was collected from each subplot (total of five bags per litter type per plot) at 6 and 18 mo. Two bags of each litter type were collected from each subplot at 30 mo (total of 10 bags per litter type per plot). Litter was carefully removed from the bags, oven dried at 85°C for 48 h (or to constant mass), and the percentage of mass remaining was recorded. The two bags per subplot for the 30-mo collection were pooled by subplot for chemical analyses. A subsample from each litterbag (or pooled litterbags) was then ground to pass an 850-μm stainless steel mesh, digested with a dry-ash–HCl procedure (Munter and Grande, 1981), and analyzed for Ca, Mg, P, Al, Fe, Mn, Zn, Cu, and B by inductively coupled plasma spectroscopy (Jarrel Ash Plasma Atomcomp Model 975 ICP, Thermo Jarrell Ash, Franklin, MA) and for K by atomic absorption spectroscopy (Instrument Labs Model Video-12 AAS, Thermo Jarrell Ash, Franklin, MA). A second subsample was pulverized in a Spex 8000 ball mill (Spex Industries, Edison, NJ) and analyzed for C and N on a Carlo Erba NA1500 C/N analyzer (Carlo Erba Strumentazione, Milan, Italy). For red spruce only, cellulose, hemicellulose, and lignin were determined on a third subsample of the original litter and on the 30-mo litter by neutral-detergent and acid-detergent fiber and acid-detergent lignin procedures (Van Soest and Goering, 1970). Organic chemical analyses were not performed on the red maple litter due to insufficient sample size. Total element content was normalized to 1 g of original litter, and was determined by multiplying element concentration by mass percentage remaining (based on 1 g of original litter).

Statistical Analyses

Differences in dry mass, element concentrations, and total element contents between treatments within years and between species were determined using a paired *t*-test. Differences between collection periods within a treatment were investigated using analysis of variance followed by the Scheffe method for means separation (Berensen et al., 1983). The Scheffe method was chosen because it is robust to sample size differences and because it is compatible with the overall analysis of variance *F* test in that it rejects the null hypothesis at the same time as the *F* test (SAS Institute, 1985). Correlation analyses were used to investigate relationships among the elements. All statistical analyses were performed on the Statistical Analysis System at the 0.05 level of significance unless otherwise noted (SAS Institute, 1985).

RESULTS AND DISCUSSION

Evaluation of Treatment Methodology

The buried cable method used in this study was effective at maintaining Oa horizon soil temperatures at approximately 5°C above ambient during each of the three growing seasons of this study (Fig. 1). Departures from the 5°C temperature differential, particularly in the third year (as shown in Fig. 1), were largely a result of the ground fault interrupter protection system, which automatically interrupted power to the heating cables when it detected an electrical failure, particularly ground faults. These ground faults were more common in the third year of the study due to continued wear on the cables, which included rodent damage and degradation due to contact with the acidic environment of the forest floor. Based on results from a pilot study, Oa horizon temperature deltas of 5°C corresponded to Oi horizon (and litterbag) temperature deltas of approximately 4°C due to convective heat loss in the Oi horizon. No significant disturbance effects due to cable installation were observed, allowing us to pool the results from the control and cabled control plots for this discussion. Also, no block effect was observed based on plot location.

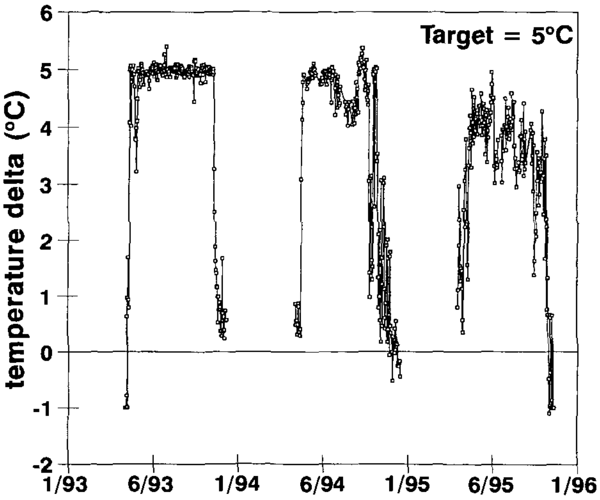

Fig. 1. Daily midnight (0:00 h) temperature deltas (calculated as the mean temperature in the Oa horizon of the heated plots minus the mean temperature in the Oa horizon of the control plots) for the Howland Integrated Forest Study site warming plots.

Soil Moisture

Mean summer precipitation was significantly lower ($P < 0.02$) during the three summers of this study (mean 183 ± 9 mm for the summers of 1993–1995) compared with the other seven summers of record at the HIFS (mean 264 ± 61 mm for the summers of 1987–1992, and the summer of 1996, Fernandez, unpublished data). This suggests that summer soil moisture may have been uncharacteristically low during this study. The 5°C increase in Oa horizon soil temperature resulted in a further reduction ($P < 0.0001$) in O horizon soil moisture from a mean of 2050 g kg^{-1} in the control plots to a mean of 1770 g kg^{-1} in the heated plots. Similar reductions in soil moisture in response to thermal manipulations have been reported by Peterjohn et al. (1994), Hantschel et al. (1995), Harte et al. (1995), and Pajari (1995). Since moisture availability has a well documented and direct effect on microbial decomposition (Alexander, 1977), it is possible that heating effects on decomposition during this study may have been partially offset by moisture limitations.

Initial Litter Chemistry

The two litter types used in this study were chosen to represent a contrast in litter quality between the typically more recalcitrant red spruce and the more easily decomposed red maple (Rustad and Cronan, 1988). Contrary to our expectations, initial N concentrations were significantly higher ($P < 0.05$) in the red spruce litter (9.8 g kg^{-1}) than the red maple litter (6.6 g kg^{-1}), and C/N ratios were significantly lower ($P < 0.05$) in the red spruce litter (52) than the red maple litter (75) (Table 1). Given that N concentrations in live foliage were not significantly different between the two species (1.1% N for red maple litter and 1.2% N for red spruce litter), we attribute the differences in litter N concentrations to a greater resorption of N in the red maple litter than the red spruce litter. Greater resorption in red maple is also evidenced by the significantly lower K and P (which tend to be relatively mobile during senescence) and the higher Ca and Mg (which tend to be less mobile) in the red maple than the red spruce litter (Table 1). Although we do not have initial C fraction chemistry for red maple litter on our plots, data for red maple litter from a nearby site collected concurrently with our study (Delaney et al., 1996) suggests that red spruce litter probably had higher initial concentrations of lignin and higher initial lignin/cellulose ratios than the red maple litter (Table 2). Initial lignin/N ratios, however, were similar because both lignin and N were proportion-

Table 1. Percentage of mass remaining and element concentration in decomposing red maple and red spruce litter from heated and control plots at Howland, ME.

Element	Initial value	6 mo		18 mo		30 mo	
		Control	Heated	Control	Heated	Control	Heated
				Red maple			
Mass, %	100A†	67Ba (16)‡	58Bb (9)	58C§ (13)	53BC§ (7)	49C (8)	47C (13)
C, g kg^{-1}	492.6A (1)	502.3B (1)	50.01 (1)	500.0B (1)	49.82 (2)	482.0ABa (4)	494.1b (1)
N, g kg^{-1}	6.6A (1)	9.8B (9)	9.9B (11)	14.1C (6)	14.7C (4)	15.7D§ (7)	16.7D§ (6)
C/N	75A (1)	52B (9)	50B (13)	36aC (6)	33Cb (4)	31D (6)	29C (6)
Ca, mg kg^{-1}	8451A (2)	9565A§ (10)	13562AB§ (40)	18494B§ (14)	16972B§ (7)	8278A (13)	7836C (7)
Mg, mg kg^{-1}	1927A (1)	1030B (13)	1168BC (38)	1332C (13)	1267CB (9)	864D (11)	856C (10)
K, mg kg^{-1}	2701A (2)	915B (12)	1201B (41)	1998C (11)	1868C (9)	1010B (13)	955B (8)
P, mg kg^{-1}	768A (4)	743A§ (9)	1054A§ (41)	1975B (7)	2020B (6)	1172C (9)	1170A (7)
Al, mg kg^{-1}	23A (20)	217A (44)	306B (50)	982B (32)	888C (13)	716C (22)	809C (18)
Fe, mg kg^{-1}	54A (20)	289A (36)	394B (58)	1209B (39)	1044C (8)	875B (20)	981C (15)
Mn, mg kg^{-1}	562A (3)	717A (13)	929AB (38)	1505B (35)	1504B (40)	874A (31)	879B (37)
Cu, mg kg^{-1}	10A (99)	9A (32)	14 (68)	17B (21)	20 (30)	12AB (29)	11 (7)
Zn, mg kg^{-1}	19A (3)	67aB (18)	103bB (30)	151C (24)	154C (17)	78B (26)	85B (9)
B, mg kg^{-1}	32A (5)	13B (14)	15B (42)	18C (15)	16B (8)	14B (26)	13B (22)
				Red spruce			
Mass, %	100A	71B (9)	69B (8)	59C (13)	55C (9)	48Da (10)	38Db (14)
C, g kg^{-1}	513.2A (1)	527.1B (1)	526.5B (1)	522.8AB (2)	520.0A (2)	520.8AB (2)	519.2A (1)
N, g kg^{-1}	9.8A (2)	11.0Ba (4)	11.3Bb (13)	13.2Ca (6)	14.3Cb (7)	15.2Da (7)	17.7Db (5)
C/N	52A (2)	48B§ (4)	46B§ (3)	39Ca (7)	36Cb (7)	34Da (7)	29Db (6)
Ca, mg kg^{-1}	6471A (3)	8244B (21)	8446AB (5)	8070AB§ (13)	8817B§ (11)	8333A (19)	8600B (23)
Mg, mg kg^{-1}	796A (2)	788A (11)	830 (16)	526B (24)	614 (28)	689A (30)	732 (46)
K, mg kg^{-1}	3563A (2)	1561B§ (21)	1327B (22)	821C (20)	833C (8)	952C (41)	881C (19)
P, mg kg^{-1}	805A (3)	941AB (6)	931A (7)	832ABa (11)	902Ab (6)	988Ba (12)	1137Bb (11)
Al, mg kg^{-1}	34A (11)	84A (29)	86AB (36)	163B (39)	150B (25)	272C (47)	316C (24)
Fe, mg kg^{-1}	40A (23)	97A (35)	93AB (29)	177A (42)	157B (24)	307B (51)	337C (27)
Mn, mg kg^{-1}	944A (5)	1834Ba (15)	2183Bb (15)	1965Ba (20)	2417Bb (19)	2439C (29)	2864B (36)
Cu, mg kg^{-1}	2A (17)	5 (36)	6B (45)	5 (156)	3A (19)	5 (45)	5B (27)
Zn, mg kg^{-1}	39A (1)	50A (10)	50AB (10)	54B (14)	64B (34)	61C (15)	60AB (23)
B, mg kg^{-1}	14A (3)	11B (11)	11AB (6)	9C (17)	9B (19)	11AB (21)	13AB (27)

† Lowercase letters indicate significant differences between the treatments within a collection period; uppercase letters indicate significant differences between the collection periods within a treatment at the $P = 0.05$ level.

‡ Coefficient of variation in parentheses.

§ Significant difference between treatments within a collection period at the $P = 0.10$ level.

ately lower in the red maple litter than the red spruce litter.

Mass Loss

General Trends in Decay

Both litter types showed a rapid loss of >30% of their initial mass during the first 6 mo of the study, which reflects, in part, the leaching of water-soluble organic materials from the fresh litter (Table 1, Fig. 2; Hovland et al., 1980; Berg and Staaf, 1981). By the end of 30 mo of decay, both red maple and red spruce litter in the control plots had lost ≈50% of their initial mass. No significant differences in mass loss were observed between the two species in the control plots at any time during this study, which may reflect similar initial lignin/N ratios (Table 2), as discussed by Aber et al. (1990). Reference bags with polyester batting showed a mean

Table 2. Cellulose, hemicellulose, and lignin C fractions in decomposing red spruce (this study) and red maple (Delaney et al., 1996) litter at Howland, ME.

	Initial values		30-mo red spruce	
	Red spruce	Red maple	Control	Heated
	Concentration, g kg^{-1}			
Cellulose	187.2A†	174.0	228.7Ba	205.1Bb
	(2)‡		(7)	(7)
Hemicellulose	90.4A	103.0	61.9Ba	84.4Ab
	(9)		(38)	(22)
Lignin	159.4A	106.0	380.9B	355.1B
	(2)		(13)	(12)
	Ratio			
Lignin/cellulose	0.85A	0.62	1.68B	1.73B
	(1)		(16)	(10)
Lignin/N	16.2	16.1	25.1	20.06
	(2)		(18)	(13)
	Content, kg kg^{-1} original litter			
Cellulose	0.187A		0.110Ba	0.079Bb
	(2)		(13)	(18)
Hemicellulose	0.090A		0.030B	0.033B
	(9)		(44)	(33)
Lignin	0.159A		0.183Ba	0.137Ab
	(2)		(16)	(24)

† Lowercase letters indicate significant differences between the treatments within a collection period; uppercase letters indicate significant differences between the collection periods within a treatment at the P = 0.05 level.

‡ Coefficient of variation in parentheses.

mass gain of 6% (≈0.18 g) during the study (with no significant differences between plots or treatments). This is consistent with the ≈10% mass gain in reference bags after 35 mo in the field for a red spruce stand at Tunk Mountain, Maine (Rustad, 1994). Visual examination of the reference bags indicated that the contaminant material was composed primarily of bud scales, needle fragments, and unidentifiable organic debris, with no obvious mineral material present. A decrease in ash content for red maple (mean loss 35%) and red spruce (mean loss 42%) litter during the 30-mo study supports the observation that no significant mineral contamination occurred. The true mass loss of litter at this site was, thus, slightly greater than the values reported in Table 1.

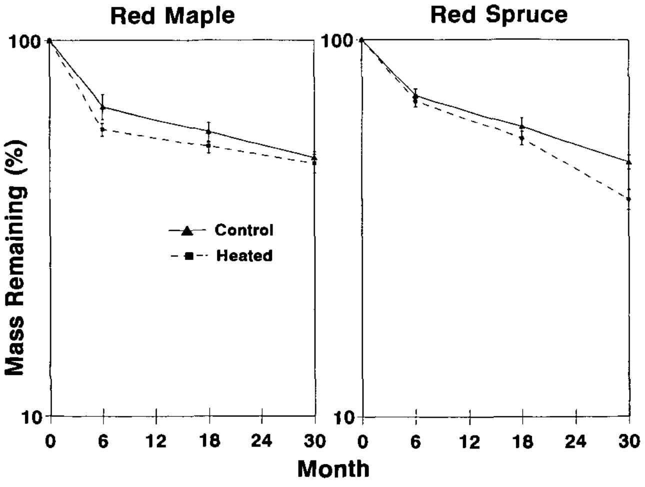

Fig. 2. Semilog plots of mass loss (±standard error) for red maple and red spruce litter at the Howland Integrated Forest Study site warming plots.

For comparison, first-year mass loss for control-plot red maple litter at this site (33%) was comparable to that reported by Delaney et al. (1996) for red maple litter at a gradient of sites in Maine (mean 40%), by McHale et al. (1996) for red maple litter in a northern hardwood forest in New York (37%), by Rustad and Cronan (1988) for red maple litter at a red spruce site at Tunk Mountain, Maine (32%), and by Melillo et al. (1982) for red maple litter in a northern hardwood forest in New Hampshire (≈34%). First-year mass loss for control-plot red spruce at this site (31%) was comparable to that reported for red spruce litter by Rustad and Cronan (1988) (26%) at Tunk Mountain, Maine.

Treatment Effects

The two litter types showed contrasting responses to the temperature manipulations (Table 1, Fig. 2). Red maple litter decayed significantly ($P < 0.05$) more rapidly in the heated plots (42% mass loss) than the control plots (33% mass loss) during the first 6 mo of decay. After this initial period, red maple litter decay rates in the heated plots were lower than in the control plots, resulting in no significant difference in mass loss by the end of the study (Table 1, Fig. 2). Red spruce litter, in contrast, decayed at the same rate in the heated and control plots during the first 6 mo of the study (31 and 29% mass loss, respectively). After this initial period, red spruce litter decay rates were greater in the heated plots than the control plots, resulting in a significantly ($P < 0.05$) greater red spruce mass loss in the heated plots (62% mass loss) than the control plots (52% mass loss) at the end of 30 mo of decay (Table 1, Fig. 2). We hypothesize that warming increased initial decay rates for the red maple litter, with a decline in treatment effects as a greater percentage of the more labile C components (i.e., simple sugars and starches) were decomposed. For red spruce litter, we hypothesize that the lag in response to the warming treatments may reflect the additional time required to break down the resistant cuticular boundary of the needles and to physically expose the more labile litter components to microbial decay. Once the initial physical barrier to decay was overcome in red spruce litter, warming appeared to have stimulated decay, resulting in greater mass loss in the heated plots relative to the control plots by the end of the study period. Eventually, we would expect that decay rates would again be limited by litter quality, with slower rates reflecting higher lignin/cellulose ratios.

Carbon, Nitrogen, and Carbon/Nitrogen Ratios

General Trends in Decay

Carbon loss was highly correlated with total mass loss in both red maple ($r^2 = 0.99$, $P < 0.0001$) and red spruce ($r^2 = 0.99$, $P < 0.0001$) litter. Thus, C concentration changed little during the study and C mass loss mirrored total mass loss, i.e., control-plot red maple litter had lost a mean of 51% of its original mass and 51% of its C, and control-plot red spruce litter had lost a mean of

52% of its original mass and 53% of its original C after 30 mo of decay (Tables 1 and 3).

Nitrogen concentrations increased significantly during the 30-mo study for both litter types, and C/N ratios decreased significantly (Table 1). For control-plot red maple litter, total N content increased significantly ($P < 0.05$) by 17% during the 30-mo study, reflecting biological immobilization of N (Table 3). For control-plot red spruce litter, which had significantly higher ($P < 0.05$) initial N concentrations than the initial red maple litter, 20% of the initial N was released during the first 6 mo of decay, after which the remaining N was immobilized for the duration of the study (Tables 1 and 3). The increase in red maple N content and decrease in red spruce N content resulted in a convergence of the N chemistry for the two litter types during the 30 mo of the study. A similar convergence of N chemistry during the initial 57 mo of litter decay was observed by Rustad (1994) for red spruce, red maple, and white pine litter at Tunk Mountain, Maine.

Treatment Effects

Treatment effects for C were similar to those described for mass. For red maple, a significantly greater ($P < 0.05$) loss of C was observed in the heated-plot litter than the control-plot litter during the first 6 mo of decay, followed by equivalent or slightly lower rates of C loss in the heated-plot litter than the control-plot litter thereafter (Table 3). For red spruce, initial rates

Table 3. Total element content in decomposing red maple and red spruce litter from heated control plots at Howland, ME. Content is normalized to 1 g of original litter.

		6 mo		18 mo		30 mo	
Element	**Initial values**	**Control**	**Heated**	**Control**	**Heated**	**Control**	**Heated**
				Red maple			
C, kg kg^{-1}	0.49A†	0.34Ba	0.29Bb	0.29Ca	0.26BCb	0.24D	0.23C
	(1)‡	(15)	(10)	(13)	(6)	(7)	(13)
N, g kg^{-1}	6.6A	6.6Aa	5.7Ab	8.2B	7.79B	7.69A	7.85B
	(1)	(17)	(8)	(9)	(8)	(8)	(10)
Ca, mg kg^{-1}	8451A	6430A	7862A	10 634Ba	8913Ab	4121C	3713C
	(2)	(20)	(40)	(19)	(10)	(14)	(15)
Mg, mg kg^{-1}	1927A	690B	679B	767B	683B	433C	403C
	(1)	(22)	(37)	(19)	(14)	(12)	(14)
K, mg kg^{-1}	2701A	610B	696B	1 151aC	994Cb	491B	451B
	(2)	(19)	(41)	(17)	(15)	(17)	(14)
P, mg kg^{-1}	768A	496B	608A	1 133C	1085B	569A	553A
	(4)	(17)	(39)	(12)	(11)	(10)	(12)
Al, mg kg^{-1}	23A	148A	175B	568B	478C	343C	380C
	(20)	(54)	(47)	(36)	(13)	(20)	(18)
Fe, mg kg^{-1}	54A	196A	223B	695B§	556C§	415C	462C
	(20)	(45)	(38)	(39)	(12)	(18)	(17)
Mn, mg kg^{-1}	562AB	478A	541AB	847B	808B	440A	423A
	(3)	(20)	(38)	(29)	(36)	(36)	(45)
Cu, mg kg^{-1}	10	6	8	10	11	6	5
	(99)	(34)	(66)	(23)	(30)	(24)	(16)
Zn, mg kg^{-1}	19A	45Ba	59Bb	86C	82C	39AB	41D
	(3)	(22)	(24)	(29)	(19)	(22)	(18)
B, mg kg^{-1}	32A	9BC	9B	11Ba	9Bb	7C	6B
	(5)	(23)	(41)	(19)	(11)	(31)	(20)
				Red spruce			
C, kg kg^{-1}	0.51A	0.37B	0.36B	0.31C	0.28C	0.24Da	0.19Db
	(1)	(10)	(9)	(14)	(10)	(9)	(15)
N, g kg^{-1}	9.8A	7.8B	7.8B	7.8B	7.9B	7.3Ba	6.7Cb
	(2)	(8)	(9)	(11)	(5)	(10)	(11)
Ca, mg kg^{-1}	6471A	5858A	5844A	4 808B	4884B	3950Ca	3269Cb
	(3)	(10)	(24)	(22)	(16)	(15)	(24)
Mg, mg kg^{-1}	796A	560B	579B	315C	342C	328C§	273C§
	(2)	(15)	(21)	(29)	(33)	(29)	(40)
K, mg kg^{-1}	3563A	1106B§	921B§	485C	462C	449Ca	339Cb
	(2)	(22)	(21)	(22)	(14)	(37)	(28)
P, mg kg^{-1}	805A	668B	645B	489C	497C	471C	436C
	(3)	(9)	(10)	(13)	(9)	(12)	(21)
Al, mg kg^{-1}	34A	59A	60AB	96AB	82B	130B	119C
	(11)	(29)	(35)	(42)	(17)	(48)	(31)
Fe, mg kg^{-1}	40A	69AB	66AB	105ABC	85B	147C	128C
	(23)	(34)	(35)	(45)	(20)	(54)	(31)
Mn, mg kg^{-1}	944A	1303a	1517Bb	1159	1340AB	1158	1052A
	(5)	(17)	(18)	(23)	(22)	(29)	(28)
Cu, mg kg^{-1}	2A	4	4B	3	2A	2	2A
	(17)	(40)	(50)	(164)	(16)	(42)	(21)
Zn, mg kg^{-1}	39A	36A	34A	32B	35A	29Ba	23Bb
	(1)	(14)	(8)	(16)	(32)	(19)	(23)
B, mg kg^{-1}	14A	8B	8B	5C	5C	6C	5C
	(3)	(15)	(11)	(24)	(26)	(21)	(34)

† Lowercase letters indicate significant differences between the treatments within a collection period; uppercase letters indicate significant differences between the collection periods within a treatment at the $P = 0.05$ level.

‡ Coefficient of variation in parentheses.

§ Significant difference between treatments within a collection period at the $P = 0.10$ level.

of C loss were similar in the heated and control plots, followed by a more rapid loss of C in the heated plots thereafter (Table 3).

Treatment effects for litter N dynamics were more dramatic for red spruce than red maple litter. For red spruce, warming resulted in significantly higher N concentrations and significantly lower C/N ratios in heated-plot litter than control-plot litter for all three collection periods (Table 1). At 6 and 18 mo, the increase in temperature had no significant effect on total N content of the red spruce litter because the higher heated-plot N concentrations were compensated for by slightly greater mass loss (Table 3). At 30 mo, however, a clear release of N was observed in the heated-plot red spruce litter, with no significant concurrent release of N in the control-plot red spruce litter (Table 3). It is noteworthy that C/N ratios had decreased to <30 in the heated-plot red spruce litter but not in the control-plot red spruce litter by 30 mo of decay. The critical C/N ratio has been defined as the ratio above which N is immobilized in decaying litter and below which it is mineralized at roughly the same rate as C (Berg and Staaf, 1981). Rustad (1994) reported critical C/N ratios of ≈30 for decomposing red spruce and red maple litter, which were attained between 18 and 24 mo of decay at Tunk Mountain, Maine. Based on C/N ratios, we would expect that N would be released from the control-plot red spruce litter within the next 12 to 24 mo.

For red maple litter, N concentrations tended to be higher and C/N ratios tended to be lower in the heated-plot litter than the control-plot litter (Table 1). However, with the exception of the 6-mo collection when there was a loss of 14% of the original N in the heated plots but not in the controls, no significant differences were observed between treatments in total N content of the red maple litter (Table 3). As with the red spruce litter, C/N ratios were at or near the critical values after 30 mo of decay and a significant release of N was either beginning to occur (control-plot red maple litter) or was probably imminent (heated-plot red maple litter).

The primary effect of warming on litter C and N chemistry was to increase the *rate* of decay — particularly the rate of C loss. For the red spruce litter, this resulted in significantly higher N concentrations, lower C/N ratios, and a more rapid release of N in the heated-plot litter relative to the control-plot litter. Warming had little effect on N dynamics in the red maple litter after 30 mo of decay.

Nutrient Elements and Aluminum

General Trends in Decay

After 30 mo, decaying litter in the control plots had lost significant amounts of Ca (51% loss for red maple and 39% loss for red spruce), Mg (78% loss for red maple and 59% loss for red spruce), P (26% loss for red maple and 42% for red spruce), K (82% loss for red maple and 87% loss for red spruce), and B (78% loss for red maple and 57% loss for red spruce) (Table 3). Red spruce litter also lost significant amounts of Zn (26%), whereas red maple litter accumulated significant amounts of Zn (105%). No significant changes in total content were observed in either litter type for Mn (because an initial increase in content was followed by a decline) or for Cu. Both litter types accumulated significant amounts of Fe (668% accumulation for red maple and 268% accumulation for red spruce) and Al (1391% accumulation for red maple and 282% accumulation for red spruce). These patterns of accumulation are consistent with those reported by Rustad (1994), who showed increases, after 35 mo of decay, for Fe of 793 and 341% for red maple and red spruce litter, respectively, and for Al of 2295 and 418% for red maple and red spruce litter, respectively. The accumulation of Fe and Al in decaying litter is hypothesized to reflect an increase in carboxylic acid exchange sites, which have a high affinity for Fe and Al, with time in decaying litter (Rustad, 1994).

Treatment Effects

Although there was a general tendency for litter in the heated plots to have lost more nutrient mass than litter in the control plots, this trend was only significant for K and B in 18-mo red maple litter, and Ca, Mg, K, and Zn in 30-mo red spruce litter (Table 3). The lack of a significant decline in nutrient mass for the other elements analyzed in this study is because element concentrations tended to be higher in heated-plot litter (for example, see Ca, Mg, K, P, Mn, Cu, and B in 6-mo red maple litter and P, Mn, and B in 30-mo red spruce litter in Table 1), compensating for the greater mass loss in the heated plots. This decline in litter mass but increase in element concentration indicates that C was being lost at a faster rate in the heated plots than the controls for these nutrient elements.

Red Spruce Organic Carbon Chemistry

After 30 mo of decay, decomposing red spruce litter had lost >40% of its initial cellulose and >60% of its initial hemicellulose (Table 2). The effect of warming was a significantly greater loss (40%) of cellulose in the heated-plot litter than the control-plot litter (Table 2). The loss of hemicellulose was nearly identical between the two treatments (Table 2). Total lignin content increased significantly ($P < 0.05$) by 15% compared with initial values in the control plots and decreased by 14% ($P < 0.06$) compared with initial values in the heated plots (Table 2), suggesting that the lignin in the heated plots was beginning to decompose. Lignin/cellulose ratios increased significantly during the study for both treatments, largely due to the >40% decline in total cellulose. No significant treatment effects were observed for this ratio because the significantly lower cellulose concentrations in the heated-plot litter were accompanied by slightly lower lignin concentrations as well. These data suggest that the decline in total C content of the decomposing red spruce litter was largely attributable to a significant loss of both cellulose and hemicellulose. The greater loss of C in the heated plots than the control plots (at 30 mo) was due primarily to the more rapid decomposition of cellulose, and secondarily due to the loss (vs. gain) in lignin content.

Ecosystem Budgets

Although we did not examine litter decay for all the tree species on the plots, we know the total litterfall for the site (2105 kg ha^{-1} yr^{-1} [Johnson and Lindberg, 1992]), and we can estimate the contribution of red spruce (the dominant species) and red maple litter to this total litterfall from regression equations of leaf mass (for all the major species) on diameter at breast height (Young et al., 1980). From this exercise, we estimate that red spruce foliage accounts for 34% or 716 kg ha^{-1} yr^{-1} of the litterfall and red maple accounts for 26% or 547 kg ha^{-1} yr^{-1}. Based on the results from the 30-mo litter bags, we can then estimate that this "cohort" of red spruce and red maple litter, which accounts for ≈60% of litterfall at the HIFS site, provided a net release of C, N, Ca, Mg, K, P, Cu, and B and a net uptake of Al, Fe, Mn, and Zn after 30 mo of decay (Fig. 3). The effect of warming was that litter released a greater mass of C (43.7 kg ha^{-1}), N (0.34 kg ha^{-1}), Ca (0.71 kg ha^{-1}), and Cu (0.35 g ha^{-1}), and accumulated less Mn (0.08 kg ha^{-1}) and Zn (3.2 g ha^{-1}) after 30 mo of decay. Although the increased rates of N and Ca release could eventually have a positive feedback on foliar nutrient levels, litter quality, and ultimately decay rates, the magnitude of these changes is relatively small. The increased release of litter N and Ca is <2 and 8% of the estimated total wet plus dry atmospheric deposition of N and Ca, respectively, during the same 30-mo period (atmospheric deposition estimates based on data from Johnson and Lindberg, 1992). The increased release of litter N is also small compared with the estimated additional 8 kg N ha^{-1} yr^{-1} mineralized due to the warming treatments during this same study and the increased release of litter C is small compared with the estimated additional 403 kg C ha^{-1} yr^{-1} released via soil respiration due to the warming treatments (Rustad and Fernandez, 1998).

Comparison with Other Studies

Two recent studies have also looked at in situ effects of temperature on litter decomposition. In a soil warming experiment similar to the one described here, McHale et al. (1996) reported no effect of temperature (up to and increase of 7.5°C) during the first 2 yr of red maple litter decay in a northern hardwood stand at the Huntington Forest, New York. American beech, on the other hand, did show subtle but significant responses to these warming treatments, with greater first-year decay rates in plots heated 5 and 7.5°C above ambient compared with both plots that were heated 2.5°C above ambient and control plots. Second-year decay rates were significantly greater only in plots heated 7.5°C above ambient compared with plots heated 2.5°C above ambient and with control plots.

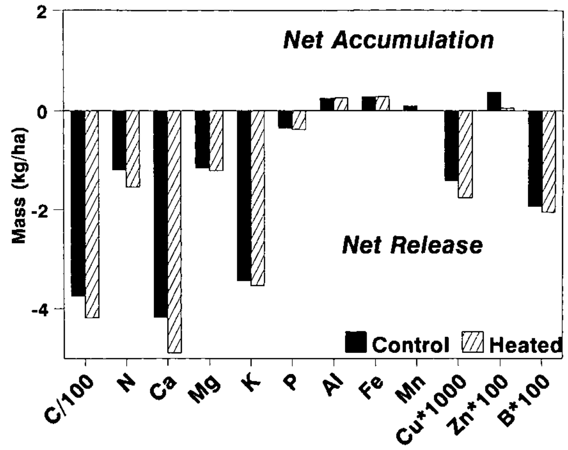

Fig. 3. Element budgets for an annual "cohort" of red spruce and red maple litter after 30 mo of decomposition in heated and control plots at the Howland Integrated Forest Study site.

Delaney et al. (1996) used a gradient approach to examine initial (6-mo) decay rates for red maple and white pine litter in 16 northern hardwood stands including the HIFS site, located in four major climatic regions in Maine. Results showed no significant differences in initial mass loss for the four regions for either species. They attribute this lack of response to (i) the short duration of the study, (ii) the high variability, and (iii) the relatively small magnitude of regional temperature differences along the gradient (i.e., mean May to October O horizon temperatures ranged from 10.3 to 13.4°C).

Both these studies suggest that initial litter decay rates are relatively insensitive to small (i.e., <3°C) increases in soil temperature. Even 3 to 5°C increases in soil temperature resulted in only modest increases in litter decay rates (this study; McHale et al., 1996). The lack of a more dramatic temperature effect at the HIFS study site may reflect factors that include a relatively low soil moisture condition that characterized the three summers of the study, a reduction in soil moisture due to treatments, or unexpected inefficiencies in the experimental warming of the litter bags themselves not captured by our temperature measurement regimes.

CONCLUSIONS

Experimentally increased Oa horizon soil temperature resulted in subtle but significant changes in litter decomposition at this coniferous forest site in central Maine. For red maple litter, the predominant effect of warming was a more rapid loss of mass and C during the first 6 mo of decay. After 30 mo of decay, significant treatment effects were no longer evident for red maple litter. In contrast, few treatment effects were observed for red spruce litter during the initial 18 mo of decay. However, after 30 mo of decay, red spruce litter had lost significantly greater amounts of total mass, C, N, Ca, Mg, K, and Zn in the heated plots than the controls. Further, analyses of red spruce C fractions showed a greater loss of cellulose in the heated plots than the control plots for red spruce litter, and a slight *decrease* in lignin in the heated plots compared with a significant *increase* in lignin in the control plots after 30 mo of decay.

Overall, our results are probably conservative because (i) the plots were not heated from mid-November through April thereby limiting treatment influences, (ii) due to repeated electrical failures, mean Oa horizon temperature deltas were closer to 4 than to 5°C in the third year of the study, and (iii) it is likely that temperature deltas in the Oi horizon where somewhat lower or more variable than in the Oa horizon due to convective heat loss.

The results of this soil warming experiment suggest that, at the ecosystem scale, a 3 to 4°C increase in soil temperature could increase the rate of release of C and N from decomposing litter, with some related changes in litter nutrient release, such as that shown for Ca and K. Species and the related litter quality characteristics play an important role in determining temperature effects on litter decomposition dynamics. Clearly, longer term studies involving litter types of diverse substrate quality should be performed utilizing a variety of temperature regimes to better elucidate temperature controls on litter decay dynamics.

ACKNOWLEDGMENTS

We would like to thank Dr. Frank Bowles for his help with the technical design of this project, and Holly Hikel, Stephanie Arnold, and Steve Scaturro for their invaluable assistance in the field. We also appreciate the site support provided by International Paper. This manuscript has not been subjected to agency or corporate review, and no endorsements should be inferred. Funding for this study was provided by the U.S. Forest Service Northern Stations Global Change Research Program (Cooperative Agreement no. 23-640) and the USDA-CSRS (92-37101-7978). This is Maine Agriculture and Forest Experiment Station Publication no. 2162.

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