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Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality

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Abstract. The purpose of this study was to relate regional variation in litter mass-loss rates (first year) in pine forests to climate across a large, continental-scale area. The variation in mass-loss rate was analyzed using 39 experimental sites spanning climatic regions from the subarctic to subtropical and Mediterranean; the latitudinal gradient ranged from 31 °N to 70 °N and may represent the the largest geographical area that has ever been sampled and observed for the purpose of studying biogeochemical processes. Because of unified site design and uniform laboratory procedures, data from all sites were directly comparable and permitted a determination of the relative influence of climate *versus* substrate quality viewed from the perspective of broad regional scales.

Simple correlation applied to the entire data set indicated that annual actual evapotranspiration (AET) should be the leading climatic constraint on mass-loss rates (R^2_{adj} =

0.496). The combination of AET, average July temp. and average annual temp. could explain about 70% of the sites' variability on litter mass-loss. In an analysis of 23 Scots pine sites north of the Alps and Carpatians AET alone could account for about 65% of the variation and the addition of a substrate-quality variable was sufficiently significant to be used in a model.

The influence of litter quality was introduced into a model, using data from 11 sites at which litter of different quality had been incubated. These sites are found in Germany, the Netherlands, Sweden and Finland. At any one site most (> 90%) of the variation in mass-loss rates could be explained by one of the litter-quality variables giving concentration of nitrogen, phosphorus or water solubles. However, even when these models included nitrogen or phosphorus even small changes in potential evapotranspiration resulted in large changes in early-phase decay rates.

Further regional subdivision of the data set, resulted in a range of strength in the relationship between loss rate and climatic variables, from very weak in Central Europe to strong for the Scandinavian and Atlantic coast sites (R^2_{adj} = 0.912; AET *versus* litter mass loss). Much of the variation in observed loss rates could be related to continental *versus* marine/Atlantic influences. Inland locations had mass-loss rates lower than should be expected on the basis of for example AET alone. Attempts to include seasonality variables were not successful. It is clear that either unknown errors and biases, or, unknown variables are causing these regional differences in response to climatic variables. Nevertheless these results show the powerful influence of climate as a control of the broad-scale geography of mass-loss rates and substrate quality at the stand level.

Some of these relationships between mass-loss rate and climatic variables are among the highest ever reported, probably because of the care taken to select uniform sites and experimental methods. This suggest that superior, base line maps of predicted mass-loss rates could be produced using climatic data. These models should be useful to predict the changing equilibrium litter dynamics resulting from climatic change.

Introduction

Tenney & Waksman (1929) postulated that decomposition rates of soil organic matter are controlled by four distinct factors: (1) the chemical composition of the substrate, (2) a sufficient supply of nitrogen for the decomposer organisms, (3) the nature of the microorganisms involved, and (4) environmental conditions, especially aeration, moisture supply, pH and temperature.

At a given site and climate, one should expect the mass-loss rates of litter to be related primarily to its chemical and physical properties. Indeed many studies have demonstrated such relationships (e.g. Upadhyay & Singh 1985; McClaugherty et al. 1985; Fogel & Cromack 1977; Aber & Melillo 1982; and Dyer 1986). As the decay of litter progresses through time, the constitutents that regulate the rate of mass loss can change. A schematic model of these litter decay stages was presented by Berg & Staaf (1980). The early stages are regulated primarily by nitrogen and phosphorus concentrations whereas lignin concentration exerts the dominant control in the latter stages.

Climate, especially the heat and moisture delivery to the litter, is no doubt a control of the rate at which the decay phases postulated by Berg & Staaf (1980) can proceed. Thus in one climatic regime the early, nutrient controlled phase could persist while in other regimes this phase could be quickly passed (Dyer et al. 1990).

Because analyses of decay dynamics have been conducted using widely different litter types, and at sites in different climatic regimes and in different forest types, control by climate *versus* litter quality is often confounded. At broad regional scales the observed spatial patterns of mass-loss 'appear' to be dominated by climatic variables, whereas litter properties appear to be relatively insenstive indicators of regional patterns (Meentemeyer 1984). When the analysis is confined, however, to one or a few sites with similar climates, the influence of litter quality becomes apparent. With the recent increasing emphasis on understanding the impact of climate changes, and the broad scale patterns of biological processes, the issues of model sensitivity and geographic scale become critical.

It is the primary purpose of this study to investigate for Western and Central Europe (and a few sites in eastern USA) the regional relationships between mass-loss rates and (i) climate, and (ii) initial litter concentrations of nitrogen, phosphorus and water-soluble substances. These relationships will be examined using data from 39 sites of which 34 sites were located in Europe and 5 in the eastern part of the United States. At all sites a unified (or standard) needle litter was incubated in pine forests of different species. Also a set of experimental litter types was used.

A secondary purpose involves the creation of regional subsets of data from the 39 sites to identify differences in mass loss dynamics that are not readily explained by the climatic and litter quality variables used in this study. The sites are to be divided into North-European, Central-European, 'Atlantic' climate and Mediterranean climate sites. Finally these sites will be compared to identify unique regional responses in decay processes.

In a similar approach, using part of this material Berg et al. (1993) could distinguish different responses for litter mass loss vs actual evapotranspiration (AET) depending on type of climate and also obtained very good r^2 values for the relationships.

Experimental sites

All experimental sites for the incubation of litter in litter bags were pine forests. Figure 1 gives the approximate location of the sites and Table 1 presents summarized information on the sites including geographic loca-

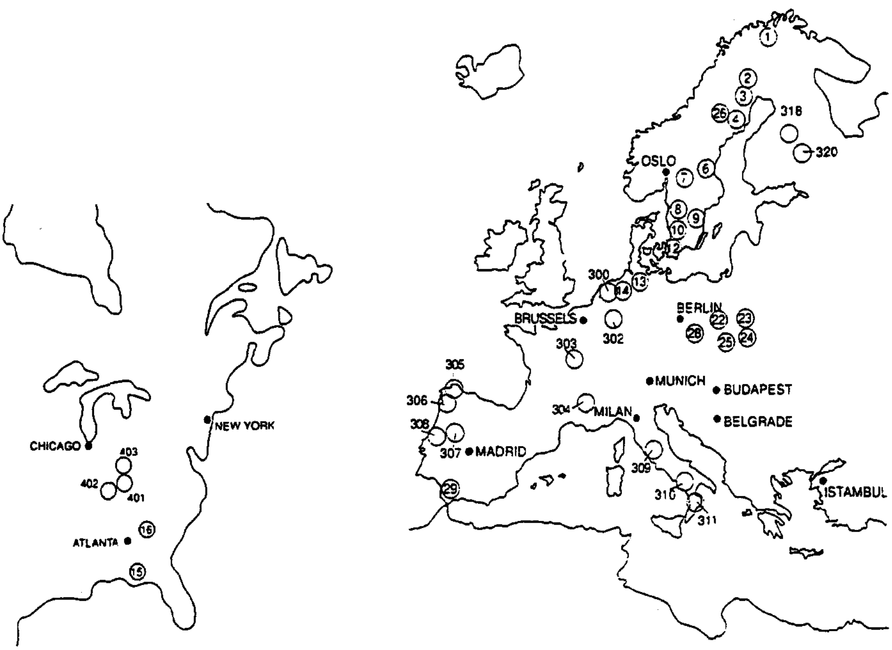


Fig. 1. Approximate locations of experimental sites. Identification of site numbers and summarized site information are provided in Table 1 and Appendix I provides additional, more complete site descriptions.

tion and elevation, mean temperature and precipitation and pine forest type. Most of the sites in our investigation were Scots pine monocultures. Exceptions include Stone pine (*Pinus pinea*), Maritime pine (*Pinus pinaster*), Radiata pine (*Pinus radiata*), Austrian pine (*Pinus nigra*) and Corsican pine (*Pinus nigra*), which were used in Europe and sites with Red pine (*Pinus resinosa*) and Loblolly pine (*Pinus taeda*) in North America, for a total of 8 different pine forest species. In all, 39 different sites spanning subartic to subtropical and Mediterranean climates are represented. This is perhaps the largest network of directly comparable experimental sites ever devised for the study of biogeochemical processes. Descriptions of each site are provided in Appendix I, as well as references for more complete site descriptions.

Some *a priori* restrictions were applied to the site characteristics before the start of the decomposition measurements to insure plots with as much uniformity as possible. All sites were located on sediments. Care was taken to select sites with either none or very low ground vegetation. The sizes of the experimental sites varied but all of them had a minimum size to account for local conditions, e.g. canopy covers. Thus site #6:51 had

Table 1. List of sites used in this investigation, their geographic location and some site data.

Site name	Site No	Lat/long	Altitude (m)	Ann mean precip (mm)	Ann mean temp. (°C)	Pine species	Lit ref
Kevo	1	69°45′N; 27°01′E	90	443	−1.7	Scots pine	(1)
Harads	2	66°08′N; 20°53′E	58	470	0.6	Scots pine	(1)
Manjärv	3:1	65°47′N; 20°37′E	135	516	0.2	Scots pine	(1)
Kajaani	318	64°23′N; 28°09′E	180	564	1.9	Scots pine	
Norrliden	4:23	64°21′N; 19°46′E	260	595	1.2	Scots pine	(1, 3)
Granö	26	64°19′N; 19°02′E	300	527	1.5	Scots pine	(2)
Ilomantsi	320	62°47′N; 30°58′E	145	600	2.0	Scots pine	
Jädraås	6:51	60°49′N; 16°01′E	185	609	3.8	Scots pine	(1, 4)
Brattforsheden	7	59°38′N; 14°02′E	178	850	5.2	Scots pine	(1)
Nennesmo	8	58°16′N; 13°35′E	155	930	6.2	Scots pine	(1)

Table 1 (Continued)

Site name	Site No	Lat/long	Altitude (m)	Ann mean precip (mm)	Ann mean temp. (°C)	Pine species	Lit ref
Målilla	9	57°25′N; 15°40′E	105	670	6.2	Scots pine	(1)
Mästocka	10:1	56°36′N; 13°15′E	135	1070	6.8	Scots pine	(1)
Vomb	12	55°39′N; 13°19′E	46	770	7.0	Scots pine	(1)
Roggebotzand	300	52°34′N; 05°47′E	−5	826	10.3	Austrian pine	
Ehrhorn	13	53°00′N; 09°57′E	81	730	9.0	Scots pine	
Czerlonka	23	52°41′N 23°47′E	165	594	5.7	Scots pine	
Mierzwice	24	52°20′N; 22°59′E	142	569	7.2	Scots pine	(1)
Pinchow	25	50°31′N; 20°38′E	191	689	7.6	Scots pine	(1)
Ede	14	52°02′N; 05°42′E	45	765	9.3	Scots pine	(1)
Olobok	28	52°22′N; 14°36′E	60	604	8.1	Scots pine	(1)

Table 1 (Continued)

Site name	Site No	Lat/long	Altitude (m)	Ann mean precip (mm)	Ann mean temp. (°C)	Pine species	Lit ref
Wilkow	22	52°24′N; 20°33′E	74	500	7.8	Scots pine	(1)
La Gileppe	302	50°34′N; 05°59′E	370	1200	6.9	Scots pine	
La Viale	304	44°11′N; 03°24′E	920	793	8.2	Scots pine	
Bois de la Commanderie	303	48°17′N 02°41′E	83	677	11.0	Scots pine	
Alberese	309	42°40′N; 11°10′E	4	650	15.0	Stone pine	
Capelada	305	43°40′N; 07°58′W	500	1062	12.9	Radiata pine	
Aguas Santas	306	42°44′N; 08°45′W	450	1500	12.5	Maritime pine	
El Raso	307:1	41°47′N; 05°26′W	760	402	12.4	Maritime pine	
El Raso	307:2	41°47′N; 05°26′W	760	402	12.4	Stone pine	
Terzigno	310	40°49′N; 14°28′E	250	960	13.2	Stone pine	(5)

Table 1 (Continued)

Site name	Site No	Lat/long	Altitude (m)	Ann mean precip (mm)	Ann mean temp. (°C)	Pine species	Lit ref
Golia Forest	311	39°24′N; 16°34′E	1210	1225	9.0	Corsican pine	(5)
Doñana	29	37°07′N; 06°12′W	2	557	16.6	Stone pine	(1)
Furadouro	308:1	43°58′N; 09°15′W	80	607	15.2	Maritime pine	
Furadouro	308:2	43°58′N; 09°15′W	80	607	15.2	Mixed pine forest*	
Athens	16	33°53′N; 83°22′W	207	1049	16.5	Loblolly pine	(1)
Mohican	401	40°36′N; 82°17′W	390	970	10.3	Red pine	
Blue Rock	402	39°36′N; 81°51′W	275	990	11.9	Red pine	
Ball's	403	40°41′N; 81°18′W	300	960	9.7	Red pine	
Tifton	15:2	31°28′N; 83°32′W	101	1540	19.3	Loblolly pine	(1)

(1) Berg et al. (1991)
(2) Berg (1990)
(3) Bååth et al. (1980)
(4) Axelsson and Bråkenhielm (1980)
(5) Virzo De Santo et al. (199X)

* 50% Radiata pine
50% Maritime pine

an area of 100 m × 300 m. The other sites measured at least 50 m × 50 m, or, if irregular in shape covering a corresponding area (2500 m^2).

There were some obvious differences in the sites' regional soils and landuse history. For the sites north of the Alps and the Carpatians the sites were on sandy sediments from the latest glaciation. The more northern sites had well developed litter and humus layers; however, some sites in the south had virtually no organic layer (e.g. El Raso and Terzigno). As a constrast, some sites (Capelada and Aguas Santas) had very thick organic layers (about 1 to 1.5 m).

Materials and methods

Experimental design

The experimental design was almost identical at all sites. Litter bag and litter sample preparation and handling procedures were standardized and conducted in one laboratory as well as all subsequent analyses. For each litter sample the initial concentrations of nitrogen, phosphorus, and water-soluble substances were measured. The concentrations of these nutrients and of water-soluble substances have been shown to be good indicators of decomposition rates in early *versus* latter stages of decay (Berg et al. 1987; McClaugherty & Berg 1987).

Several studies have attempted to evaluate litter mass-loss data from litterbags as compared to other methods (Witkamp & Olson 1968; Louiser & Parkinson 1976; Johansson 1986). Minderman (1968) and later Rogers (1986) have shown that fractional decay constants based on litter-bag observations overestimate the decay rates of the entire litter layer because this layer includes much material in advanced stages of decay. This over-estimation is, apparently, constant from one climatic regime to another. Measurements made by the litterbag method are most useful during relatively early stages of litter decomposition in which the mass-loss rates are higher than in the more recalcitrant humus layers. Extrapolation to late stages of decay may not be possible but the measurements are clearly useful in the search for a climatic signal in decay dynamics.

Two main kinds of litter have been used in the present investigation, namely a 'unified' Scots pine (*Pinus sylvestris*) needle litter and experimental needle litter. A set of experimental litter types of different substrate qualities was incubated at selected Scots pine sites in northern Europe. The experimental design was nearly identical with all sites.

The litter samples

Unified needle litter. The Scots needle litter was collected at the Jädraås site (the old site of the Swedish Coniferous Forest Project in east central Sweden) in early September from the branches of trees in a stand that was about 15 years old in 1973 when samples were first collected. The trees were samples at abscission and were located within an area of about 100 m × 100 m. Annual variation in the quality of this litter is shown in Table 2. Collections were made annually and the chemical composition varied somewhat among years (cf. Berg 1986). The chemical composition of the litter preparations used in this study are given in Table 2.

Experimental needle litter. The needle litter from fertilized Scots pine stands was collected at the site of an optimum nutrition experiment at Lisselbo (Tamm et al. 1974). Litter from this site have been described earlier by Berg & Staaf (1980). The natural brown and green needle litter

Table 2. Annual variation in organic and inorganic chemical composition of Scots pine (*P. silvestris*) needle litter. Needle litter was collected (at a stand about 15 years old in 1973) at the time of needle abscission in September of each year. Standard deviation within parenthesis. Part of the data are from Berg (1986).

Sampling (yr)	Concentration (mg g^{-1})										
	Solubles		Lignin	N	P	S	Ca	K	Mg	Mn	Ash
	water	ethanol									
1973[1]	92	120	223	3.8	0.19	0.42	6.5	0.73	0.38	1.55	23
1974	145	84	276	4.2	0.22	0.29	5.4	0.71	0.49	n.d.	24
1975	172	107	238	3.4	0.20	0.32	4.7	0.61	0.39	n.d.	19
1976	151	89	255	4.0	0.21	0.36	4.9	0.53	0.42	n.d.	n.d.
1977	202	102	224	4.1	0.19	0.38	6.0	0.87	0.42	1.02	n.d.
1978	164	96	257	3.8	0.21	0.33	5.5	0.62	0.55	1.00	20
1979	129	95	288	10.4	0.29	0.78	2.3	0.97	0.39	0.31	12
1980	180	102	246	3.8	0.18	0.50	6.1	1.72	0.53	0.77	17
1981	213	94	231	3.9	0.28	0.61	7.1	1.02	0.58	1.17	23
1982	164	113	231	4.8	0.33	0.55	4.4	1.07	0.49	0.79	19
1983	178	112	229	3.8	0.30	0.45	5.9	0.90	0.39	1.08	26
1984	82	116	288	3.7	0.21	0.47	6.3	0.82	0.44	1.12	22
1985	182	94	241	2.9	0.19	0.45	4.8	0.52	0.38	1.24	18
1986	170	89	257	4.0	0.23	0.44	5.6	0.58	0.57	1.13	20
1987	162	100	250	3.8	0.21	0.42	4.9	0.55	0.41	1.18	18
1988	165	94	247	3.8	0.21	0.39	5.0	0.67	0.38	1.18	19
1989	n.d.	n.d.	n.d.	3.6	0.17	0.38	4.0	0.59	0.42	0.92	n.d.

also was collected at the Jädraås site and brown Lodgepole pine needle litter was collected at a Lodgepole pine forest described by Berg & Lundmark (1987). The chemical composition of this litter is shown in Table 3.

Table 3. Chemical composition of four experimental Scots pine and Lodgepole pine needle litter incubated at sites numbered 1—14.

Litter type	water solubles	ethanol solubles	lignin	N	P	S	Mg	Ca	Mn	K
	Concentration ($mg\ g^{-1}$)									
Scots pine										
— brown, natural	164.2	112.6	231.4	4.8	0.33	0.55	0.49	4.42	0.79	1.07
— brown, fertilized	134.9	91.4	264.9	7.0	0.33	n.d.	0.37	2.5	0.70	1.02
— green, natural	198.6	63.3	284.2	13.4	1.47	0.98	0.85	2.82	0.41	4.90
Lodgepole pine										
— brown natural	102.5	41.7	380.5	3.9	0.34	0.62	0.95	6.35	0.95	0.56

Brown current needles to be shed, were abscissed from the trees by shaking their limbs. After collection the litter was dried at room temperature and stored until sample preparation. The experimental green Scots pine needles were picked from the branches and were selected to be third year needles (C + 2).

The dry mass of the litter to be placed into litterbags was determined on 25 samples, dried at 85 °C for 24 h. The largest difference in moisture content among samples was less than +/−0.5% of the average.

Litter-bags, (8 cm × 8 cm) were made of terylene net with a mesh size of about 1 mm. For each type of litter, 0.6—1.0 g of needles was placed in separate litter bags. At each site the bags were placed on the litter (L) layer in a measurement site (1 m × 1 m) in each of 25 'spots' in a randomized design within a larger site. Bags were fastened to the ground by 10—15 cm long metal pegs; a new placement of bags for incubation was made whenever retrieval of samples was made. Retrieval of litter bags took place between once to six times annually. At a given site on each occasion one litter bag of each litter type was collected from each of the 25 spots measuring 1 m × 1 m.

Laboratory analyses

Determination of mass loss

After collection and drying at a laboratory near each site, the 25 litter bag samples of each type were sent to one common laboratory and cleaned. Plant remains, such as mosses, grass and shrub materials were removed. The loss of dry mass was then determined by drying the samples to a constant mass at 85 °C. Mean values of mass loss were calculated for each sample set of 25 bags.

Chemical analyses

Chemical analyses were carried out on the fresh, initial litter samples only. The samples were ground in a laboratory mill equipped with a filter allowing particles of less than 1 mm to pass. The amounts of water-soluble and ethanol-soluble substances were determined by sonicating the milled samples three times in a sonicator bath and weighing the samples after filtration and drying. The analysis for sulfuric-acid lignin and soluble substances in the needle litter were carried out according to Bethge et al. (1971) (see also Berg et al. 1982). The milled samples were further analyzed for total concentrations of the elements nitrogen, phosphorus, sulfur, potassium, calcium, magnesium, manganese, and total ash.

Elemental nitrogen was determined by combustion (Elemental Analyzer NA 1500; Carlo Erba, Strumentazione, 20090 Rodano, Milan, Italy). For the analysis of phosphorus, sulfur, magnesium, potassium, calcium and manganese, samples were digested for 2 days in a 2.5:1 (v/v) mixture of nitric and perchloric acid. The analyses were performed by plasma atomic emission spectrometry ICP-AES (Jobin YVON JY-70 Plus 16—18, rue du Canal 91163, Longjumean, France). Ash concentration was determined by combustion at 550 °C for 2 h.

Climatic data

Site data were used whenever possible to assist in the calculation of a suite of climatic and water balance variables. For most of the sites the monthly temperature and precipitation had to be estimated on the basis of data from surrounding weather stations. For all of the sites long term, average climatic data were based on world climatic data records collected by Willmott et al. (1981a, b). In addition to interpolation among surrounding stations, adjustments were also made for the site's elevation.

The climatic data were in turn used to calculate the water balance variables of each site based on the procedures of Thornthwaite & Mather

(1957). A computer program (WATERBUD) designed by Sharpe & Prowse (1983) was used to calculate monthly and annual values of potential evapotranspiration (PET), actual evapotranspiration (AET), soil moisture deficit (DEF) and soil moisture surplus (SUR). For each site a soil moisture storage value of 300 mm was assumed for the root zone to make the results of the present study comparable with previous work (e.g. Meentemeyer 1978, 1984; Meentemeyer & Berg 1986; Dyer et al. 1990). The temperature, precipitation, and water budget and litter quality variables used in this study, as well as a short code used for each variable, are presented in Table 4.

Table 4. List of variables and their computer codes.

LOSS	Mass loss in the first-year of decomposition (%)
NITR	Initial nitrogen concentration (mg g^{-1})
PHOS	Initial phosphorus concentration (mg g^{-1})
WSOL	Initial water solubles concentration (mg g^{-1})
JULT	Average temperature for July (°C)
AVGT	Average annual temperature (°C)
RNG	Annual temperature range (°C)
PRECIP	Total annual precipitation (mm)
PRANGE	Annual precipitation range (mm)
PET	Potential evapotranspiration (mm)
AET	Actual evapotranspiration (mm)
SUR	Soil moisture surplus (mm)
DEF	Soil moisture deficit (mm)

Statistical analysis

To compare the coefficient of determination among sets with different numbers of samples we have used the adjusted R^2 (R^2_{adj}). It has been shown by Ekbohm & Rydin (1990) that mean square error and R^2_{adj} are equivalent as criteria of goodness of fit. The formula $R^2_{adj} = 1 - (1 - r^2)(n - 1)/(n - p)$ where p equals 2 for straight lines has been used.

Results and discussion

All needle litter samples were incubated in regions with AET ranging from more than 300 to less than 1000 mm and all sites had a first-year mass loss of less than 56 percent.

The sites representing the entire data set had differing numbers of observations, ranging from 19 first-year mass-loss values for site 6:51 (Jädraås) to just one value for ten sites. Some of the sites with only one observation have just recently started operation.

The *unified litter* was incubated either annually, twice or three times a year at the different sites. Although the litter originated from the same site there were some differences in chemical composition among years. The nitrogen concentration ranged from 4.8 to 2.9, phosphorus from 0.33 to 0.19. Sulfur varied from 0.78 to 0.29 and calcium from 7.1 to 4.4 mg g^{-1}. Ash concentrations were comparatively low going from about 26 to 20 mg g^{-1}. Also the more mobile ions, including potassium and manganese had a variation of the same magnitude as phosphorus; concentrations ranged from 1.02 to 0.52 and 1.55 to 0.79 mg g^{-1} respectively.

Of the *experimental litter*, one set of four different litter types was incubated at 11 sites in northern Europe (cf. Table 4). For the site 6:51 (Jädraås) additional data sets used in previous studies were also available. Thus for the Jädraås site 10 additional observations could be taken from a paper by Berg & Staaf (1980) and four values from Berg & Ekbohm (1991).

Analysis of the whole data set

In a first step to determine the degree of relationship among the climatic variables, litter quality variables and mass-loss rates, a correlation matrix was created using data from all 39 sites. Potential variables for use in a broad-scale climatic/litter quality model were selected based on degree of relationship and minimization of multicolinearity (cf. Appendix II). Because long-term climatic average values were used, the average for mass loss, and the substrate quality variables were used for the sites that had more than one year of observation.

Simple correlation and regression

All of the independent variables selected were individually plotted and regressed against annual mass-loss rates (LOSS) for the 39 sites to check for curvilinear relationships. None was found so the linear form was deemed adequate. Regression coefficients were then examined to narrow the list of potential explanatory variables.

Of the suite of climatic variables, the best positive correlations were obtained for the relationship between LOSS and actual evapotranspiration

(AET), the total annual precipitation (PRECIP), and average temperature (AVGT) with R^2 values of 0.509, 0.323 and 0.203 respectively, all statistically signficant at $p < 0.01$ (Table 5). Potential evapotranspiration (PET) gave a significant correlation at the $p < 0.05$ level. Water deficit (DEF) also gave a significant correlation even if barely so. This factor was considered of interest for regional comparisons since some sites clearly had high values for water deficit.

The best single variable (AET) was plotted against first-year mass loss and each site was located on the plot (Fig. 2). The progression in rates from the subartic (site #1) to the subtropical (site #15) is readily

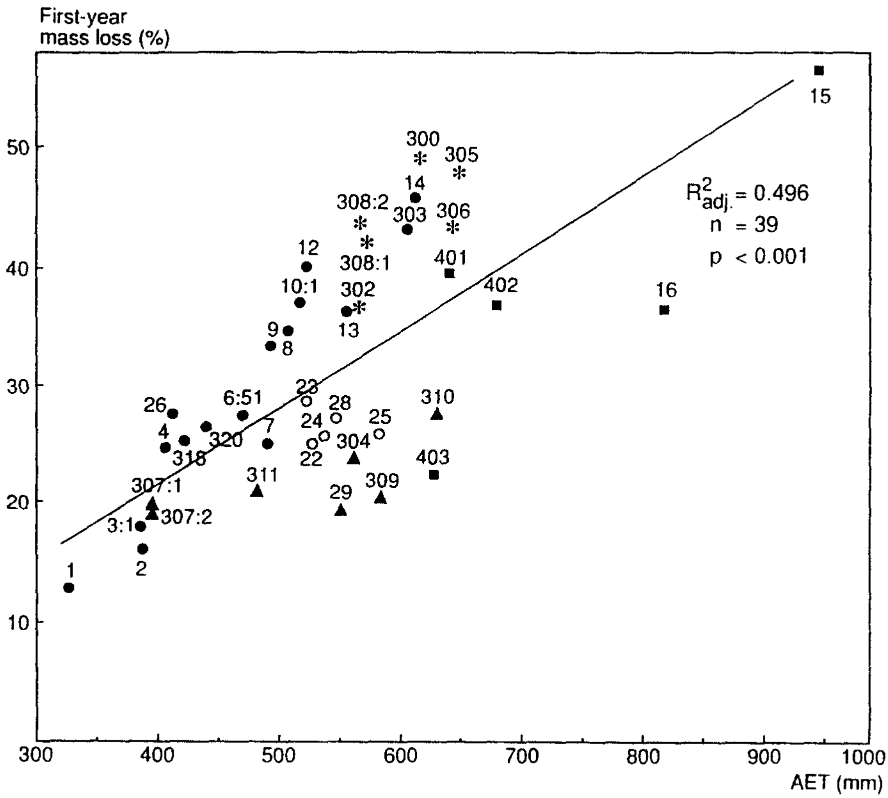


Fig. 2. Bivariate plot of average first-year litter mass loss *vs* actual annual evapotranspiration (AET). All sites used, (n = 39). (●) Scots pine sites in an intensively studied Scandinavian-NW-continental transect ranging from northern Finland to central Holland; (*) pine sites close to the European west coast or sites relatively exposed to Atlantic climate; (▲) pine sites around the Mediterranean; (O) Central European Scots pine sites (Poland) with characteristics of inland climate; (■) pine sites in the eastern inland of the United States.

apparent. Some of the scatter in Fig. 2 can be attributed to the use of long-term climatic normals rather than information about the weather during incubation. The Georgia sites (#15 and 16) should be expected, for example, to have higher rates of mass loss (than those shown) in normal years because incubation occurred in an extremely dry year. Some of the variation must also be caused by variations in litter quality and local site conditions. As will be seen later, stratification of the data sets can lead to much stronger relationships. The use of additional climatic variables can greatly improve the explained variance in some cases.

Multiple variable relationships

In a multiple linear regression procedure, it appeared that the climatic factors AET and JULT (temperature in July) gave the best regression equation using two climatic variables (Table 5). This equation can account for 68.1 percent of the variability in mass-loss rates, a clear improvement over the best single-variable relationships. Considering the differences among the sites and the different years of litter bag placement this is a good relationship with climate.

With three climatic factors (AET, JULT and AVGT) in the regression procedure an R^2_{adj} value of 0.708 was obtained (Table 5). Because of the high sample size (n = 39), we may rely on this relationship to hold. Even in this analysis using all of the sites, climatic factors were seleccted by the statistical routine rather than the litter quality variables.

Within the whole data set it was possible to distinguish regional differences. In a first approach to the study of different climatic situations, the sites with high summer temperatures (JULT > 20 °C) were excluded meaning that all North European sites were selected (29 sites) for analysis. As in the previous analyses the climatic factor AET was the leading variable with an R^2_{adj} value of 0.661. As a second factor, the program selected precipitation (PRECIP) resulting in an R^2_{adj} value of 0.661. In this analysis a substrate-quality factor was included by the program as a third variable *viz.* water-soluble substances (WSOL), resulting in a small increase in the R^2_{adj} value to 0.706.

For the 11 sites with JULT above 20 °C a separate analysis was run, and the best climatic variables was again AET with an R^2_{adj} value of 0.701. Water deficit (DEF) the next best variable gave a negative relationship with an R^2_{adj} of 0.358. JULT gave an R^2_{adj} of 0.352. This demonstrates again the power of AET as a predictor of mass loss rates. But it also shows that the mix of useful climatic variables can change with the region and its climatic regime. Because of the small sample size (n = 11) no further analyses using multiple variables was performed.

Table 5. Annual mass loss (LOSS) of litter at a broad regional scale as a function of some single climatic factors as well as multiple ones (n = 39).

Eq.	R^2	R^2_{adj}	p	Comments
Single linear regression				
LOSS = f (AET)	0.509	0.496	<0.001	
LOSS = f (PRECIP)	0.323	0.304	<0.001	
LOSS = f (AVGT)	0.203	0.181	<0.01	
LOSS = f (PET)	0.187	0.165	<0.05	
LOSS = f (DET)	0.097	0.073	<0.05	DEF gave a neg. rel.
Stepwise multiple linear regression				
All sites (n = 39)				
LOSS = f (AET)	0.509	0.496	<0.001	
LOSS = f (AET) + f (JULT)	0.689	0.681	<0.001	JULT gave a neg rel.
LOSS = f (AET) + f (JULT) + f (AVGT)	0.716	0.708	<0.001	
All sites with lower summer temperatures (n = 29)				
LOSS = f (AET)	0.670	0.661	<0.001	
LOSS = f (AET) + f (PRECIP)	0.670	0.661	<0.001	
LOSS = f (AET) + f (PRECIP) + f (WSOL)	0.714	0.706	<0.001	

Analysis of the Scots pine sites

A special set of sites with numerous observations was investigated — a set of 13 sites in Scandinavia and the northwestern part of the continent. These sites had mass-loss measurements over a period which varied between 6 and 19 years. Of the single factors, AET gave a highly significant relationship with an R^2_{adj} value of 0.867 (Table 6). It is likely that the multiple years of observations gave an average calculated mass-loss rate more representative of the climatic norms used in this study. The addition of substrate quality factors such as WSOL, NITR, and PHOS did not improve the fit, probably because the variation in this set of litter types was relatively small. At each of these sites, however, a special set of experimental litter was incubated (cf. Table 3) which permitted an attempt to model the unique influence of litter quality in early decomposition stages.

Table 6. Linear correlations and regressions between litter mass loss (LOSS) and selected climatic factors, as well as some substrate quality factors. Sites were grouped and labeled; groups were investigated separately as well as in combinations of groups.

Eq.	R^2	R^2_{adj}	p	Comments
Scots pine sites north of the Alps and the Carpatians ($n = 23$)				
LOSS = f (AET)	0.647	0.630	<0.001	
LOSS = f (AET) + f (WSOL)	0.748	0.736	<0.001	
Scandinavian-Northwest European sites ($n = 13$)				
LOSS = f (AET)	0.878	0.867	<0.001	
LOSS = f (AET) + f (NITR)	0.895	0.885	<0.001	
Scandinavian-NW-European plus Atlantic sites ($n = 22$)				
LOSS = f (AET)	0.916	0.912	<0.001	
LOSS = f (NITR)	0.066	0.019	n.s.	
LOSS = f (AET) + f (NITR)	0.917	0.913	<0.001	
Mediterranean sites plus Central European ones plus North American sites ($n = 17$)				
LOSS = f (AET)	0.753	0.736	<0.001	
LOSS = f (NITR)	0.063	0.000	n.s.	
LOSS = f (AET) + f (NITR)	0.757	0.739	<0.001	
LOSS = f (AET) + f (DEF)	0.766	0.750	<0.001	
LOSS = f (AET) + f (JULT)	0.761	0.745	<0.001	

The effect of substrate quality on mass-loss rates

At a given site it has been shown that litter materials decay at rates dictated mostly by their chemical and physical properties (e.g. Berg & Staaf 1980; Berg & Ekbohm 1991). These relationships appear to be unique to the site and its decomposer organisms and prevailing micro-climate. Predictions of decay rates for other sites cannot therefore be made with confidence. Nevertheless the decay dynamics at a site must include the combined effects of both climate and litter quality varibles. A separate analysis to produce models of this combined effect was performed. At 11 sites, at least four litter types of different properties were incubated. These sites occur in Germany, The Netherlands, Sweden and Finland (Table 1). For each site the litter quality variables (nitrogen, phosphorus and water-soluble constituents) were regressed against annual mass loss. Most of the regressions, even considering the small N-size at each site, were significant (at $p < 0.1$). Examination of the alpha and beta coefficients for each regression equation at each site suggested a consistent change in coefficients which is influenced by climate. This is in agreement with patterns in alpha and beta coefficients found by Dyer (1986). In earlier work Meentemeyer (1978) demonstrated a geographically and climatically varying influence by lignin concentration on mass-loss rate.

A new data set of alpha (intercept) and beta (slope) coefficients for the 11 sites was devised and a second order regression analysis performed using each of the climatic variables to determine the degree to which the coefficients vary with climate. For both nitrogen and phosphorus the alpha coefficients for the sites were strongly and positively related to annual potential evapotranspiration (PET) and the beta coefficients were related to the site's precipitation (PRECIP). Thus the intercepts appear to be driven mostly by climatic heat and the slopes of the relationship (mass loss *versus* quality) by the gross water supply (PRECIP). The relationships using coefficients for water solubles (WSOL) were very weak and deemed inadequate for modelling purposes.

The 'expanded' model for the influence of initial phosphorus concentration at any particular site may be written as:

$$\text{mass loss}_{\text{Phos}} = (-29.3 + 0.111(\text{PET})) + (0.749 + 0.013(\text{PRECIP}))(\text{PHOS}) \qquad (1)$$

where the first statement in parenthesis is in reality a new alpha coefficient determined by a site's PET (mm) and the second term is a new beta coefficient driven by annual precipitation (mm). The third term is the individual litter's phosphorus concentration.

For nitrogen control of mass loss the expanded model may be written as:

$$\text{mass loss}_{Nitr} = (127.3 + 0.100(PET)) + (-0.067 + 0.0022)(PRECIP))(NITR) \quad (2)$$

where the first statement is again determined by site PET, the second by precipitation and the third by the litter's nitrogen concentration.

Figure 3 is a nomogram constructed from equation 1 (phosphorus). Selected PET values are shown on the left vertical axis, annual precipitation (PRECIP) on the horizontal axis and predicted mass-loss rates on the right vertical axis. The figure provides predicted loss rates for PET values between 400 mm and 600 mm, variable precipitation (from 200–650 mm) and initial phosphorus concentration of 0.15(a), 0.30(b), 0.60(c)

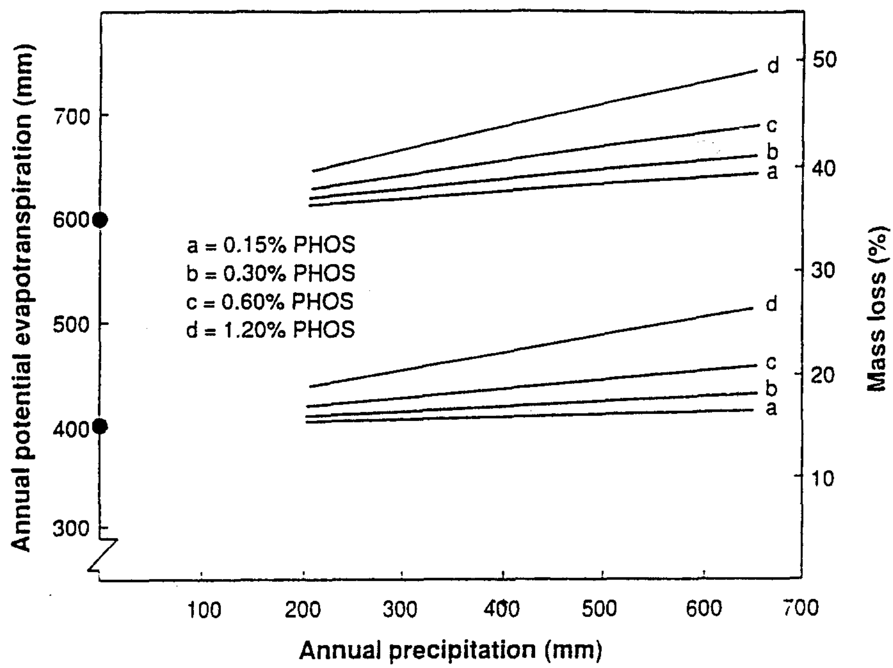


Fig. 3. Nomogram constructed from equation 1. Selected PET values are shown on the left vertical axis, annual precipitation (PRECIP) on the horizontal axis and predicted mass-loss rates on the right vertical axis. The figure provides predicted loss rates for PET values of 400 mm (lower set of graphs) and 600 mm (upper set of graphs) and four initial phosphorus concentrations (PHOS) of 0.15 mg g^{-1} (a), 0.30 mg g^{-1} (b), 0.60 mg g^{-1} (c), and 1.20 mg g^{-1} (d).

and 1.20(d). Thus PET selects the intercept, precipitation, the slope and initial phosphorus concentration and then predicts the loss rate for a given site's PET and precipitation.

These relationships also suggest that most of the regional variation in loss rates across northern European Scots pine forests is driven by temperature/ heat constraints. As precipitation increases the differences in loss rates for litter of differing phosphorus concentrations became larger.

This figure shows in a different way our conclusion regarding climate *versus* litter-quality influences drawn from analyses of observations of mass-loss rates covering large geographical areas. Even small changes in climate, can produce greater changes in early-stage decay rates than rather large differences in litter quality. Thus it should not be surprising that quality variables are important at local scales but their influences are 'apparently' less significant when viewed at broad spatial scales. Nevertheless the equations presented here should permit predictions of the influence of litter quality across a broad area of Northern European pine forests, especially Scots pine forests.

Regions and regional comparisons

Within the whole data set it was possible to distinguish differences in mass loss among regions, and data sets that tended to deviate from the general AET model. Based on climatic data and the results from the analysis of the whole data set (cf. Fig. 2) we made an attempt to distinguish groups of sites at which the decomposition followed certain patterns. The grouping was based on annual mass loss and climatic factors that could explain the rate. The terminology of the regions does not fully coincide with the traditional one for climatic regions but has been used in a looser sense. We also combined some regions that had some characteristics in common (cf. Table 6).

All Scots pine sites north of the Alps and the Carpatians

Special attention was given to the Scots pine sites because many of the sites in Europe represent this kind of ecosystem. The geographical range presented here covers almost the entire north-south range of this species in Europe; the northernmost site is in Northern Finland close to Barents Sea and the southernmost (La Viale) in Southern France. The sites also are relatively homogeneous with respect to thickness of the soil organic layer and ground vegetation.

In a special analysis for the Scots pine sites north of the Alps and the Carpatians (n = 23), AET as a single variable gave a highly significant relationship (R^2_{adj} = 0.630). The addition of WSOL as a substrate-quality index increased the R^2_{adj} value to 0.736, whereas the concentrations of N and P (NITR and PHOS) did not improve the fit. Within this group, the Polish sites could be seen to form a group with lower than expected mass-loss rates (Fig. 2; see the Central-European sites) possibly reflecting the inland climate.

Analysis of the Scandinavian-Northwest-European sites

An analysis was conducted using data from a transect in which studies had been carried out for at least about 10 years, thus giving good long-term average values for litter mass-loss. Using all 13 sites a regression using AET alone gave an R^2_{adj} value of 0.867 and $p < 0.001$. The addition of other climatic factors added very little to the explained variance. Substrate quality factors alone did not give any significant relationship but the inclusion of NITR or WSOL as a substrate-quality index improved the relation somewhat; for NITR an R^2_{adj} value of 0.885 was obtained.

Part of this transect was placed in Scots pine standardized forests on flat ground and sediment soils. Thus it appeared that the 'standard transect' of 10 Scots pine sites on sandy, nutrient-poor sites gave a fit to AET at nearly the same level as all the 13 sites (n = 10; R^2_{adj} = 0.866; $p <$ 0.001).

All Scandinavian-Northwest European sites plus those with Atlantic climate

The sites in the long-term Scandinavian transect (n = 13) and the sites with an Atlantic climate (n = 7) had similar responses between LOSS and AET (Fig. 2) as had data from two eastern Finnish sites (#318 and 320). They had low DEF with the exception of site #308 that is, however, located very close to the coast. As they seemed to have similar responses an attempt was made to combine them for an analysis. Using these 22 values and comparing AET and LOSS gave a very good fit with an R^2_{adj} value of 0.912 (Table 6; Fig. 4A). This relationship was not improved by the addition of other climatic factors or substrate quality.

Sites with dry and warm summer climate

The mass-loss values from the five North American sites fit well to the linear regression that was used for all data although all five of them were relatively low as compared to the other data. This may be due to the fact that these sites all had just one mass-loss value each and that long-term climatic data were used. For example at sites #15 and 16 the year for which mass loss was measured was extremely dry, thus giving very low values.

We had just a few values for each of the separate regions with typical Mediterranean climate and inland climate. However, also for such small sets AET was a useful predictor and a clearly significant relationship was seen using AET and DEF for the Mediterranean sites ($p < 0.05$).

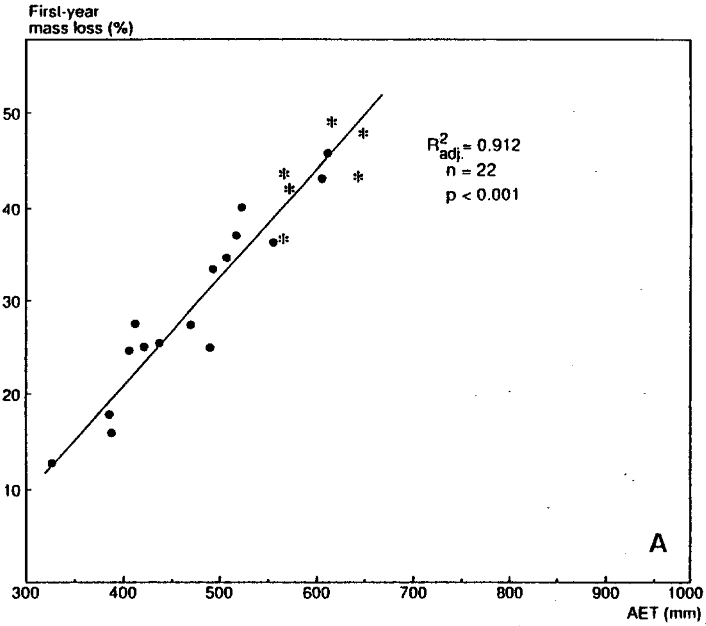
Mass-loss values for the sites characterized by dry and warm summers were combined into a linear regression encompassing sites called 'Mediterranean,' 'Central European', and 'North American' thus allowing us to investigate the effect of a main climate type on 17 sites on a broad geographical range.

A linear regression of LOSS *vs* AET gave a clearly significant relationship ($R^2_{adj} = 0.736$; $p < 0.001$) (Table 6; Fig. 4B). Attempts to include DEF or JULT, which indicate seasonality did not improve the relationship nor did substrate quality factors. It may be worth noting that upon a comparison to the relationship obtained for the combined Scandinavian and Atlantic sites it is evident that the two relationships were significantly different.

Regional comparisons

These results show that general broad-scale models of climatic control of loss rates of pine needle litter can be devised. As in previous work annual AET is a particularly useful variable, but the results also show that regions have differing responses. Although R^2 values can be similar, the slopes and intercepts of the relationship can vary. The question remains whether this is a truly differing response or due to unknown errors or biases. Perhaps the forest floor environments are indeed different under pine forests of different regions even though macroclimatic AET values are similar. We included climatic variables which respond to seasonality and continentality, but none of these variables could help explain lower rates in Mediterranean and Inland sites. The mix of years and sites used suggest this is not an experimental error. Furthermore, the results using the Fennoscandian and Atlantic sites are very similar to those found by Meentemeyer & Berg (1986) using earlier data sets for Fennoscandia and weather records for the actual incubation period. Regressions using AET versus LOSS had alpha and beta coefficients and R^2 values similar to those found here. Other variables must be in operation at more continental sites.

The difference observed between the combined NW-European-Atlantic sites and those with an inland climate and/or warm summers was highly significant ($p < 0.0001$; Fig. 4A, B). This indicates distinctive between 'decomposition climates' that apparently are dependent on the temporal distribution of precipitation events and temperature over the year.



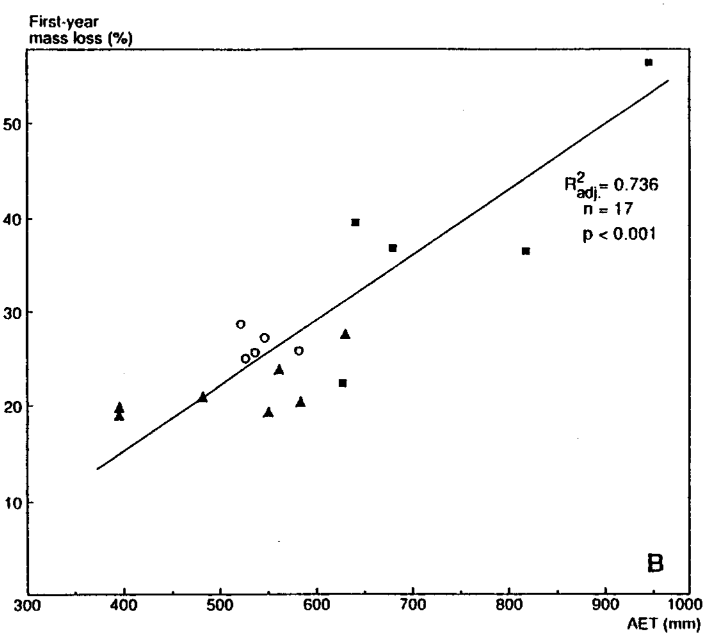


Fig. 4. Bivariate plot of average first-year litter mass loss *vs* actual evapotranspiration. Denominations as in Figure 2. A. Scots pine sites in a Scandinavian-NW-continental transect and pine sites close to the European west coast or sites relatively exposed to Atlantic climate ($n = 22$). B. Mediterranean sites, Central European ones and North American ones ($n = 17$).

Summary and conclusions

The purpose of this study is to understand regional variation in litter mass-loss rates (first year) across a large, continental scale area, dominated by pine forests. This variation could be analyzed using 39 experimental sites spanning climatic regions from the subartic to subtropical and Mediterranean: the latitudinal gradient ranged from 31°N to 70°N and may represent the largest geographical area that has ever been sampled and observed for the purpose of studying biogeochemical processes. Because of stratification procedures and uniform laboratory procedures, data from all sites are directly comparable. These procedures also permitted a determination of the relative influence of climate *versus* substrate quality viewed from the perspective of broad regional scales.

The observations of litter mass-loss, initial litter quality and a suite of climatic variables for each site permitted analyses of the entire data set as well as regional subsets. Tests of stratification procedures and litter quality permitted separate analyses. Simple correlation-regression procedures applied to the entire data set indicated that annual actual evapotranspiration (AET) should be the leading climatic constraint on mass-loss rates (R^2_{adj} = 0.496). The combination of AET, average July temperature (JULT) and average annual temperature (AVGT) could explain about 70 percent of the sites' variability on litter mass-loss. In an analysis of 23 Scots pine sites north of the Alps and Carpatians, AET alone could account for about 65 percent of the variation and the addition of a substrate-quality variable was sufficiently significant to be used in a model.

In an attempt to 'force' the influence of litter quality into a model, data from 11 sites at which litter of different quality had been incubated was selected. These sites are found in Germany, the Netherlands, Sweden and Finland. At any one site most ($\approx$ 90 percent) of the variation in mass-loss rates could be explained by one of the litter quality variables (NITR, PHOS, WSOL). However, even when these models include NITR or PHOS even small changes in PET (and to a lesser degree precipitation) can result in large changes in early-phase decay rates.

Further regional subdivision of the data set, resulted in a range of strength in the relationship between loss rates and climatic variables, from very weak in Central Europe to strong for the Scandinavian and Atlantic coast sites (R^2_{adj} = 0.912 AET *versus* LOSS). Much of the variation in observed loss rates could be related to continental *versus* marine/Atlantic influences. 'Inland' locations had mass-loss rates lower than should be expected on the basis of for example AET alone. Attempts to include seasonality variables were not successful. It is clear that either unknown errors and biases, or, unknown variables are causing these regional differences in response to climatic variables. Nevertheless these results show the powerful influence of climate as a control of the broad-scale geography of mass-loss rates and substrate quality at the stand level.

Some of these relationships between mass loss and climatic variables are among the highest ever reported, probably because of the care taken to select uniform sites and experimental methods. This suggests that superior, base line maps of predicted mass-loss rates could be produced using climatic data. These models should be useful to predict the changing equilibrium litter dynamics resulting from climatic change.

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Appendix I. Site descriptions, including summarized climatic data and references for more complete descriptions

Site *Kevo (No. 1)*, northernmost Finland in Kevo Natural Concervancy, about 120 km north of the town Ivalo, is located at 69°45′N; 27°01′E, at an altitude of 90 m. The average annual temperature is −1.7 °C and average annaul precipitation 420 mm. The stand has a Scots pine (*Pinus sylvestris*) monoculture and a very low and sparse ground vegetation composed mainly of lichens. The soil is nutrient poor sandy sediment and the humus form is a mor.

Site *Harads (No. 2)*, north Sweden, about 100 km north-west of the city Luleå is located at 66°08′N; 20°53′E at an altitude of 58 m. This site has a Scots pine monoculture and a ground vegetation composed primarily of cowberry (*V. vitis-idaea*) and lichens. The soil type is a podzol and the humus form is a mor. The soil class is nutrient-poor fine sand sediment. The Scots pine monoculture was 119 years old in 1980. Annual mean temperature is 1.3 °C and annual mean precipitation is 650 mm.

Site *Manjärv (No. 3:1)*, north Sweden, about 70 km west of the city Luleå located at 65°47′N; 20°37′E at an altitude of 135 m. The site has a Scots pine monoculture (46 years old in 1980) located on sediment soil. The ground vegetation is composed mainly of cowberry and lichens. The humus form is mor and the soil profile a podzol. The soil texture is fine sand. Annual mean temperature is 1.0 °C and annual mean precipitation is 700 mm.

Site *Kajaani (No. 318)*, in central Finland close to the city Kajaani, is located at 64°23′N;

28°09'E at an altitude of 180 m. The stand is a Scots pine monoculture (65 years old in 1989) located on sandy sediment. The humus form is mor and the soil type a podzol. The ground vegetation is composed mainly of heather, crowberry (*Empetrum nigrum*) and lichens. Annual mean tempertaure is 1.9 °C and the annual mean precipitation 564 mm.

Site *Norrliden (No. 4)*, in north-west Sweden about 100 km north-west of Umeå is located at 64°21'N; 19°46'E at an altitude of 260 m. The site has a Scots pine monoculture (33 years old in 1986) with a ground vegetation composed mainly of bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*), located on till. Annual mean temperature is 1.3 °C and annual mean precipitation is 595 mm.

Site *Ilomantsi (No. 320)*, in central east Finland close to the town Ilomantsi, located at 62°47'N; 30°58'E at an altitude of 145 m. The Scots pine monoculture (40 years old in 1988) is located on fine sand sediment. The humus type is mor and the soil type a podzol. The ground vegetation is dominated by cowberry, bilberry and heather. Annual mean temperature is 2.0 °C and the annual mean precipitation 600 mm.

Site *Granö (No. 26)*, in north Sweden about 100 km northwest of the city of Umeå is located at 64°19'N; 19°02'E at an altitude of 300 m. The site has a Scots pine monoculture (41 years old in 1990) with a ground vegetation composed mainly of bilberry.

Site *Jädraås (No. 6:51)* in Central Sweden, about 200 km north of Stockholm has a Scots pine monoculture. The plot (No. 6:51) is sometimes also called Ih 5. It has a forest about 130 years old (in 1980) located at 60°49'N; 16°30'E at an altitude of 185 m. The forest is situated on a very nutrient-poor sediment soil. The annual mean precipitation is 609 mm and the long-term average temperature is 3.8 °C. The ground vegetation is composed mainly of bilberry, cowberry, heather, mosses and lichens. The humus form is mor and the soil profile a podzol. The soil texture is fine sand. Additional information on this site was provided by Axelsson & Bråkenhielm (1980).

Site *Brattforsheden (No. 7)* in central west Sweden, is located at 59°38'N; 14°02'E at an altitude of 178 m. The site has a mature Scots pine monoculture on a sandy sediment soil with a low ground vegetation composed mainly of bilberry, heather and cowberry. Annual mean temperature is 5.2 °C and mean annual precipitation 850 mm.

Site *Nennesmo (No. 8)*, in south-west Sweden, is located at 57°12'N; 13°35'E at an altitude of 155 m. The site has a mature Scots pine monoculture with a low ground vegetation composed mainly of bilberry, heather and cowberry. Annual mean temperature is 6.2 °C and annual mean precipitation is 930 mm.

Site *Målilla (No. 9)*, in south-east Sweden, is located at 57°25'N; 15°40'E at an altitude of 105 m. The site has a mature Scots pine monoculture with a low ground vegetation composed mainly of bilberry, heather and cowberry. Annual mean temperature is 6.2 °C and annual mean precipitation is 670 mm.

Site *Mästocka (No. 10:1)* is located in south-west Sweden (56°36'N; 13°15'E and 135 m) has a Scots pine monoculture with a low ground vegetation of mainly bilberry. The soil texture is sandy till and the humus type is a mor. Annual mean temperature was 6.8 °C and annual mean precipitation is 1070 mm.

Site *Vomb (No. 12)*, located in south Sweden (55°39'N; 13°19'E and 46 m) has a Scots pine monoculture with a low ground vegetation of mainly low grasses. The soil is sand and the humus type is a mor. Annual mean temperature is 7.0 °C and annual mean precipitation is 770 mm.

Site *Roggebotzand (No. 300)* at 52°34'N; 05°47'E and at an altitude of 5 m below s.l. is located on Flevoland in northern Netherlands. Annual temperature was 10.3 °C and annual mean precipitation was 826 mm (average for 1988 and 1989). The site has a monoculture of Austrian pine (*Pinus nigra*) with a closed canopy and no ground vegetation. The organic layer is a podzol.

Site *Ehrhorn (No. 13)* about 50 km south of Hamburg is located at 53°00'N; 09°57'E at an altitude of 81 m. The site has a mature Scots pine monoculture with a ground vegetation composed mainly of bilberry, heather and low grasses. Annual mean temperature was 8.7 °C and annual mean precipitation was 644 mm.

Site *Czerlonka (No. 23)* in east Poland is located at 52°41'N; 23°47'E at an altitude of 165 m. The site has a Scots pine monoculture with a ground vegetation composed mainly of bilberry and grasses, and the humus type is mor. Annual mean temperature was 6.7 °C and annual mean precipitation was 594 mm.

Site *Mierczwice (No. 24)* in east Poland is located at 52°20'N; 22°59'E at an altitude of 142 m. The site has a mature Scots pine monoculture with a very sparse ground vegetation composed mainly of some grasses and some bilberry. Annual mean temperature was 7.2 °C and annual mean precipitation was 569 mm.

Site *Pinczow (No. 25)* in south Poland about 100 km north of Cracow is located at 50°31'N; 20°38'E at an altitude of 191 m. The site has a mature Scots pine monoculture with an uneven and sparse ground vegetation composed mainly of low grasses and some low herbs. The stand is located on nutrient poor sediment soil of granite origin. Annual mean temperature was 7.6 °C and annual mean precipitation was 689 mm.

Site *Ede (No. 14)* in central Netherlands is located at 52°02'N; 05°42'E at an altitude of 45 m. This site has a mature forest of Scots pine mixed with some oak with a ground vegetation composed mainly of low grasses and low herbs. Annual mean temperature was 9.3 °C and annual mean precipitation was 765 mm.

Site *La Gileppe (No. 302)* in the Ardennes in east Belgium is located at 50°34'N; 05°59'E at an altitude of 370 m. The site has a mature Scots pine monoculture with a ground vegetation composed mainly of grasses. Annual mean temperature was 6.9 °C and annual mean precipitation was 1200 mm.

Site *Wilkow (No. 22)* just north of Warsaw is located at 52°24'N; 20°33'E at an altitude of 74 m. The site has a mature Scots pine monoculture with a sparse ground vegetation composed mainly of bilberry. Annual mean temperature was 7.8 °C and annual mean precipitation was 500 mm.

Site *Olobok (No. 28)* in west Poland just south of the town Swiebodzin is located at 52°22'N; 14°36'E at an altitutde of 60 m. The site has a mature Scots pine monoculture with a ground vegetation composed mainly of bilberry and low grass. Annual mean temperature was 8.1 °C and annual mean precipitation was 604 mm.

Site *Bois de la Commenderie (No. 303)* is located in north-central France south-east of Paris at 48°17'N; 02°41'E at an altitude of 83 m. The site has a mature Scots pine monoculture (30 years old in 1984). Annual mean temperature was 11 °C and annual mean precipitation was 604 mm.

Site *La Viale (No. 304)* is located in south France (Massif central) at 44°11'N; 03°24'E at an altitude of 920 mm. The site has a Scots pine monoculture (20—25 years old in 1991) with a ground vegetation composed mainly of low sparse grass. Annual mean temperature was 8.2 °C and annual mean precipitation was 793 mm.

Site *Capelada (No. 305)* is located in north-west Spain (Galicia) at 43°40'N; 07°58'W at an altitude of 500 m. The site has a mature Radiata pine (*Pinus radiata*) monoculture with a ground vegetation composed mainly of grass. Annual mean temperature was 12.9 °C and annual mean precipitation was 1062 mm.

Site *Aguas Santas (No. 306)* is located in north-west Spain (Galicia) at 42°44'N; 08°45'W at an altitude of 450 m. The site has a Maritime pine (*Pinus pinaster*) monoculture with a ground vegetation composed mainly of grass. Annual mean temperature was 12.5 °C and annual mean precipitation was 1500 mm.

Site *El Raso (No. 307)* is located in west Spain about 120 km north of Salamanca at 41°47'N; 05°26'W at an altitude of 760 m. The site has two plots, one with a Maritime pine monoculture (No. 307:1) the other with a Stone pine monoculture (No. 307:2) (both of them about 30—40 years old in 1990) with a very sparse ground vegetation composed mainly of grasses such as *Agrostis castellana.* Other species are *Tolpis barbata, Thymus mastichina, Echium vulgare,* and *Lupinus angustifolium.* The soils are chromic luvisols. Annual mean temperature was 12.1 °C and annual mean precipitation was 402 mm.

Site *Furadouro (No. 308)* in west central Portugal is located at 43°58′N; 09°15′W and at an altitude of 80 m.a.s.l. The site has a Maritime pine monoculture (No. 308:1) and a mixed pine stand with Radiata pine and Maritime pine in proportions of about 1:1 (No. 308:2). The plot has a scattered ground vegetation of low bushes of *Ulex* spp. Annual mean temperature was 15.2 °C and annual mean precipitation was 607 mm.

The site *Alberese (No. 309)* is located on the west coast of central Italy, in Maremma Nature Park in Tuscany at 42°40′N; 11°10′E at an altitude of 4 m. The site has a mature Stone pine (*Pinus pinea*) monoculture with a ground vegetation composed mainly of grasses and herbs. Annual mean temperature was 15.0 °C and annual mean precipitation was 650 mm.

The *Terzigno site (No. 310)* (40°49′N; 14°28′E), located on the southeastern slope of Mount Vesuve, and 20 km southeast of Naples (Campania) has a forest of Stone pine, aged about 40 years (in 1990) planted on volcanic lapillus. The forest has a very sparse ground vegetation. At the latest eruption in 1944 the actual area was covered with a lapillus layer about 1 m thick which covers the soil of a former mixed forest. The altitude is 250 m.a.s.l., the annual mean temperature is 13.2 °C and the annual mean precipitation 960 mm. The climatic data refer to the nearest meteorological station 'Osservatorio Vesuviano' at an altitude of 612 m.a.s.l. (1926—1950).

The site *Golia Forest (No. 311)* with a 50—80-year-old Corsican pine (*Pinus nigra var laricio*) forest is almost completely dominated by this tree species. It is located in the Sila mountains (Calabria) at an altitude of 1210 m at 39°24′N; 16°34′E. The annual mean temperature is 9.0 °C and the annual mean precipitation is 1225 mm. The climate data refer to the meteorological station of Cecita at the same altitude but 3 km distant from the Golia forest (1921—1950). The plot is situated on a weak slope to the south and the forest has a ground vegetation of adderspit (*Pteridium aquilinum*), and herbs in a lower frequency. It has a shallow, sandy soil on granite as parent material. The humus type is moder.

Site *Doñana (No. 29)* in south-west Spain at 38°07′N; 06°12′W and an altitude of 2 m is located close to the coastline in the Doñana National Park. Annual mean temperature was 16.6 °C and annual mean precipitation was 557 mm. The site has a mature Stone pine monoculture and the ground is without vegetation.

The site *Mohican (No. 401)* is located in north-east Ohio, USA at 40°36′N; 82°17′W and an altitude of 390 m a.s.l. The site has a Red pine (*Pinus resinosa* Ait.) monoculture about 43 years old (in 1991). The number of stems ha^{-1} was 869 and the trees' basal area was 41 m^2 ha^{-1} (in 1991). The soil was a Lordstown series sandy glacial till. Average annual temperature was 10.3 °C and annual average precipitation 970 mm.

The site *Blue Rock (No. 402)* is located in north-east Ohio, USA at 39°36′N; 81°51′W, and an altitude of 275 m a.s.l. The site has a Red pine monoculture about 40 years old (in 1991). The number of stems ha^{-1} was 891 and the trees basal area was 42 m^2 ha^{-1} (in 1991). The soil was a Berks silt. Average annual temperature was 11.9 °C and annual average precipitation 990 mm.

The site *Balls (No. 403)* is located in north-east Ohio, USA at 40°41′N; 81°18′W and an altitude of 300 m a.s.l. The site has a Red pine monoculture about 33 years old (in 1991). The soil was a Muskingum silt loam. Average annual temperature was 9.7 °C and annual average precipitation 960 mm.

The site *Athens (No. 16)* is located just outside the town of Athens in northeast Georgia, USA at 33°53′N; 83°22′W and at an altitude of 207 m. The site has a Loblolly pine (*Pinus taeda*) monoculture about 19 years old (in 1986) and a ground vegetation of Sweet gum (*Liquidambar styraziflua*) and Flowering dogwood (*Cornus florida*). The soil was a cecil sandy clay loam. Average annual temperature was 16.5 °C and annual mean precipitation was 1049 mm.

The site *Tifton (No. 16:2)* is located just outside the town of Tifton in south Georgia, USA at 31°28′N; 83°32′W at an altitude of 101 m. The site has a Loblolly pine monoculture about 30 years old (in 1986) and a ground vegetation of some Southern Magnolia (*Magnolia grandiflora*). The soil was an Alapaha loamy sand with 90 percent sand. Average annual temperature was 19.3 °C and annual mean precipitation 1540 mm.

Appendix II. Correlation matrix based on all variables selected for use in regional analysis portion of this study (39 sites and subsets). Coefficients within parentheses are not significant on the $p < 0.05$ level.

	LOSS	PET	PRECIP	AET	DEF	SUR	JULT	RNG	AVGT	NITR	PHOS	WSOL
LOSS	*	0.43	0.57	0.71	−0.31	0.33	(0.13)	(0.08)	0.45	(−0.00)	(0.14)	(0.17)
PET		*	0.36	0.80	0.48	(0.00)	0.83	(0.20)	0.98	(0.11)	(0.01)	0.30
PRECIP			*	0.68	−0.41	0.91	(0.29)	0.44	0.36	(0.07)	(0.13)	(0.26)
AET				*	(−0.14)	0.31	0.78	(0.12)	0.75	(0.10)	(0.19)	(0.19)
DEF					*	−0.45	0.42	(0.14)	0.52	(0.03)	(−0.25)	(0.19)
SUR						*	(−0.00)	0.50)	(0.03)	(0.04)	(0.05)	(0.23)
JULT							*	(0.08)	0.78	(0.15)	(0.06)	(0.15)
RNG								*	(0.25)	(0.29)	(−0.04)	(0.01)
AVGT									*	(0.09)	(−0.09)	0.31
NITR										*	0.53	(−0.24)
PHOS											*	(−0.06)
WSOL												*

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