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Some effects of changing soil chemistry on decomposition of plant litters and cellulose on a Scottish moor

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Summary. Nitrogen (N), phosphorus (P), calcium (Ca) and soluble carbohydrates (CHO) were each added at three levels to a moorland podzol, and the decomposition of three contrasting untreated substrates (*Calluna vulgaris* stems, *Molinia caerulea* leaves, and cotton strips) compared between treated and untreated plots. All soil treatments increased decay rates of all three substrates, except for the highest levels of P and CHO, which appeared to inhibit decomposition of cotton and *Molinia*. The results generally indicated use by the decomposers of nutrients or energy sources from the soil to aid decomposition of untreated substrates. With all additives (N, P, Ca, CHO) maximum degree of change was inversely related to substrate quality. All responses were nonlinear. Optimal levels of N and Ca were in the same order as substrate quality, i.e. optimum for *Calluna* < cotton < *Molinia*, but this was not so with P and CHO. The patterns of change in decomposition rates with soil treatments could not be explained entirely by edaphic and substrate quality effects; it was also necessary to consider selection of decomposer organisms, both by substrate and by treatment. More generally, there were no simple 'limiting factors'. Rather, decay rates were controlled by the combined 'availability' of a number of resources (including availability of suitable decomposer organisms). The consequences of this, especially the importance of indirect and interactive effects, are discussed.

Key words: Decomposition – Litter – Cellulose – Soil chemistry

In podzols and acid peats, the rate of decomposition of dead organic matter can be a critical regulator of the whole ecosystem (Heal et al. 1981). Decomposition processes are in turn affected by soil chemical and physical conditions, and the associated decomposer populations.

Surveys of decomposition in moors, bogs and tundras, using both natural litters and standard cellulose substrates, have shown correlations of decomposition rates with: (1) general indices of soil nutrient status, derived from several physical and chemical variables by multivariate analyses (Heal and French 1974; Heal et al. 1974), (2) soil calcium, phosphorus and nitrogen (Kong and Dommergues 1970; Berg et al. 1975; Rosswall et al. 1975; Heal et al. 1981), and (3) soluble carbohydrates (Heal et al. 1978).

Heal and French (1974) also concluded that litter decomposition rates were better correlated with soil nutrients as litter quality decreased, and that this might imply transport of nutrients from soil (e.g. by fungi or soil animals) to make up any deficiences in the litter. With standard cellulose substrates, all mineral nutrients must be obtained from the soil, though over distances where they could be transported by abiotic processes.

Several experimental studies also show effects of one or more of N, P, Ca or soluble carbohydrates on decomposition rates (e.g. Moore 1981). But these studies have usually tested effects of amending a single substrate on the decay of the same substrate. Test of inter-substrate effects (e.g. of soil on decay of fresh incoming litter) are far rarer, and almost none have been done under field conditions. Also, very few studies consider how changes in the size and, especially composition of decomposer populations might affect decomposition rates. Yet numbers and types of soil and litter microflora vary with soil nutrients and availability of energy sources, in a very similar way to decomposition rates (Holding 1981; French and Smith 1986).

From the foregoing, therefore, I derived the following hypotheses:

In nutrient-poor soils with organic-rich surface horizons (e.g. podzols or acid peats) increasing nutrients or energy-sources should have a considerable effect on decomposition rates and processes, in both soil and litter, so that:

(1) Addition of soluble nitrogen (N), phosphorus (P), calcium (Ca) or soluble carbohydrates (CHO) to such soils, at the surface, will increase decay rates of unamended substrates subsequently introduced either into or onto those soils.

(2) All responses of decay rates to the additives will be nonlinear, with optimal levels of each additive above which the response will be zero or negative.

(3) The degree of change in decay rates will be inversely related to substrate quality (e.g. woody litters should show greater proportional increase than leaves, or substrates low in nutrients or sugars than substrates high in either or both).

(4) The optimal level of each additive will be in the same rank order as substrate quality. Decay of low-quality substrates will be increased more by low than by high levels of any additive; conversely decay of higher-quality substrates will be increased more by high than by low levels of any additive.

(5) Chemical additives will alter decomposition rates by selection of decomposer organisms, as well as by changing the activity of the original (pre-treatment) decomposer populations.

Table 1. Quantities of additives (g m^{-2}) applied to the soil on each of three occaisions during September and October 1979, prior to insertion of cotton strips and litter bags

Additive		Level 1	Level 2	Level 3
N:	ammonium nitrate (anhydrous granules)	4	16	40
P:	potassium dihydrogen orthophosphate (crystals)	6	24	60
Ca:	calcium carbonate (powder)	10	40	100
CHO:	glucose + potato starch (powder)	4	16	40

To test these hypotheses, I added N, P, Ca and CHO, separately, at three different levels, to the surface of a podzol. I then placed two contrasting (unamended) litters on, and cotton strips in, the amended soils, and compared their decay rates with decay rates of the same substrates on or in unamended control plots.

Study site

The site, 0.5 ha of uniform northeast-facing more dominated by *Calluna vulgaris* (L.) at Glen Dye, Kincardineshire, was described by Miles (1973). The soil is a humus-iron podzol over granitic till. The surface (sub-litter) horizon is a variable O/H/Ah/Ahe (horizon nomenclature according to Hodgson 1974).

The experimental area (ca. 200 m^2) was mown in April 1979 and the mowings removed. This removed most *Calluna* foliage. Grasses, particularly *Deschampsia flexuosa* (L.) Trin., increased in cover during the summer but on most plots *Calluna* had begun to regenerate within a year. The upper soil horizons and old litter were not visibly altered during the period of the experiment. Any changes due to the mowing were probably small compared to the fertilizer treatments and affected all plots equally.

Methods and materials

Some definitions

To avoid confusion, in subsequent parts of this paper, the following definitions apply:
(1) an *additive* is N, P, Ca or CHO. The term is used indiscriminately for an element (e.g. nitrogen), corresponding ion (e.g. nitrate), or the whole substance added to the soil (e.g. ammonium nitrate).
(2) a *level* is the quantity of any additive applied, specified as level 1, 2 or 3 as in Table 1.
(3) a *treatment* is a particular level of a particular additive (e.g. N1, P2, CHO3).
(4) a *substrate* is a plant litter or cellulose standard; soil is not a substrate in this paper.

Soil treatments

The additives used were 'Analar' ammonium nitrate and potassium dihydrogen orthophosphate, precipitated calcium carbonate and a 1:1 mixture of 'Analar' glucose and reagent-quality potato starch.

Each additive was applied at three levels (Table 1), the lowest chosen to be non-toxic to the native microflora and the highest to be within the range for agricultural or forestry applications on a moderately deficient soil. The actual amounts used give approximately 4, 16, and 40 g m^{-2}, at each application, of the 'functional part' of each additive, i.e. NO3− and NH4+, PO4−−−, Ca++, and CHO.

All additives were evenly broadcast, as crystals, powder or granules, onto the plot surface (i.e. the old litter layer) on three occasions during September and October 1979. The second and third applications were given after all visible traces of the previous one had disappeared. After these three applications, the plots received no further treatment.

Table 2. Initial chemical composition of decomposition substrates. Organic constituents: percent of dry weight. Nutrients: percent × 1000

	Calluna	Cotton	*Molinia*
N	300	<100	850
P	36		45
K	80		150
Na	10	<170[a]	10
Ca	230		290
Mg	38		110
Soluble carbohydrates	3.6	n.d.	2.0
Holocellulose	71	97	70
Soluble tannins	1.9	neg.	0.8
Lignin	25	neg.	16

[a] Total ash, i.e. total nutrients other than N probably <100
n.d. = not determined; neg. = "negligible" (not detectable)

Substrates for decomposition, their placement and retrieval

Three contrasting substrates were used:
(1) Cotton strips – strips (30 × 10 cm) of uniformly woven, sterile, cotton cloth (Walton and Allsopp 1977). These were rich in carbon, but with almost no mineral nutrients and no readily-leached constituents. They also did not contain extremely resistant fractions such as lignins, nor microbial inhibitors e.g. some tannins (Table 2).
(2) Severed *Calluna vulgaris* stems collected from the site a little over six months after mowing. During this time, all stems had completely died, and acquired a resident microflora typical of dead, rather than live stems. Pieces 2–4 mm in diameter and ca. 10 cm long were used, avoiding both young stems with shoot remains and very old stems which might contain heartwood or be already rotten. All stems used were therefore of approximately identical physical and chemical composition, and all at the same stage of decay. This substrate contained some mineral nutrients and sugars, had a moderate cellulose content, but was especially high in lignins and other polyphenols (Table 2). It was also physically harder and more structurally resistant to invasion by decomposers than the other two substrates.
(3) Freshly dead leaves of *Molinia caerulea* (L.). All the leaves collected had fallen within a week, so all were of approximately identical composition and uniform age.

These leaves contrasted with both cotton and *Calluna*. They were higher in mineral nutrients than either, and lower in lignins and other resistant fractions than *Calluna* (Table 2).

Substrate quality was assessed using similar criteria to Heal and French (1974). High-quality substrates have a high content of mineral nutrients and soluble carbohydrates, and low content of lignins, tannins and other resistant or inhibitory constituents, are physically soft, and have a high surface area to volume ratio. Moving towards the opposite of any or all of these conditions lowers the substrate quality. The order of increasing quality of my substrates is therefore *Calluna* < cotton < *Molinia*.

Placement and retrieval. Cotton strips were wrapped around turves 18 cm × 12 cm × 4–8 cm thick, cut in the upper soil horizon following French and Howson (1982). This gave, from each strip, two 'top' segments, lying horizontally at or near the L/F boundary, a single 'side' segment vertically through the O/H/Ah/Ahe horizon, and two 'bottom' segments horizontally near the boundary between the organic-rich horizon(s) and the E/Ea horizon (see French and Howson (1982) Fig. 1, for a detailed illustration).

Three batches of strips (130 per batch) were inserted and removed at three consecutive periods: 0–19 weeks (period 1), 19–34 weeks (period 2) and 34–45 weeks (period 3). Strips inserted in periods 2 and 3 were wrapped around the turves used in period 1, i.e. all three batches were inserted at the same locations.

Each time strips were removed, the main site litter (*Calluna*, moss, lichen, grass or mixed) at the sample locations was recorded, and soil moisture ranked as wet, mesic or dry.

The plant litters were air-dried, and samples of about 5 g (range 4.6–5.4) loosely wrapped in nylon hairnets (giving an effective mesh size of 2–7 mm). The litter pieces used were too large to fall through the mesh even when partly decomposed and the large mesh did not exclude soil fauna. The nets also allowed maximum contact between the confined litter and the underlying old litter or soil. The samples were placed on the site litter surface, and retrieved after 45 weeks. Soil moisture and composition of surrounding site litter were noted in the same way as for cotton strips.

Measurement of decay rates, and estimation of selection of decomposer populations

Cotton strips were prepared for testing following Latter and Howson (1977) and Harrison et al. (1988). The degree of cementation of test segments (French 1984) was assessed. The test segments were frayed to 3 cm width and torn on a Monsanto type 'W' tensometer with modified pneumatic jaws to determine their tensile strength (TS) and hence the loss in TS from that of the cloth originally inserted.

Litter samples were hand-sorted to remove extraneous debris and fauna, but not invertebrate faeces. The samples were then air-dried and weighed, to obtain the weight loss from each sample.

Selection of microflora on cotton strips was estimated indirectly, by noting the coloured stains on the strips on retrieval. These stains are often caused by particular species or groups of microflora (Walton and Allsopp (1977) and, while the same organism may produce different stains under different conditions, or several distinct organisms share staining patterns that are visually indistinguishable, it is not likely that two very different combinations of stains would be produced by the same population, nor that two very different populations would stain strips identically.

In this experiment, stains on cotton strips varied markedly in colour, texture and other characteristics, and mostly fell into three size classes: 'spots' (<4 mm width), 'blobs' (5–15 mm) and 'patches' (>25 mm). Using these criteria, twelve distinctive stains could be defined. The relative proportions of these, scored as present or absent within each test segment containing at least one recognizable stain, provided a simple index of selection by treatments. A second index was the percentage of segments without any distinctive stain.

Selection of litter fauna was estimated simply by noting presence or absence of the main groups of fauna in each sample on retrieval. These scores were then examined for any broad differences between treatments.

I did not try to assess selection of microflora in litters, nor of soil fauna associated with cotton strips.

Corrections for ground contact (cotton and litters) and cementation (cotton only)

The more complete the contact of a sample with the site litter or soil, the easier it is for decomposers to colonize the sample, and for nutrients and energy sources to be transported. Cementation of cotton strips can increase their TS, giving a biased estimate of their decay. I therefore corrected all data for ground contact, and cotton strips TS for cementation, before analysing for treatment effects.

Ground contact (cotton). Microscopic examination of test segments confirmed that cotton unstained on retrieval was almost uninfected by soil microflora. Where this was obviously because of bad contact between strip and soil (the normal cause of this was faulty insertion, which was easily recognizable) that segment was rejected. A substitute segment was taken from the same part (top, side or bottom) of the strip, if there was sufficient spare cloth in that part. If not, a weighted average TS (by treatment, strip and segment, by simple proportion) was used in place of the uninfected segment.

Ground contact (litters). The most important causes of bad ground contact in litters were disturbance by wind and movement of *Calluna* branches, lifting by growth of site vegetation under the samples, and some disturbance by birds and small mammals. Each time cotton strips were inserted, degree of ground contact of litters was scored as follows:

Good contact along full length of sample, partly buried	score 0
Good contact along full length of sample, not buried	score 1
Contact over about 2/3 to 3/4 of sample	score 2
Contact over about half length of sample	score 3
Contact over about 1/4 to 1/3 of sample	score 4
No, or almost no, ground contact	score 5

The contact scores for each sample were summed over the three sample periods, and the median total for each litter determined. Linear regressions of percent weight loss on total contact score were then calculated, separately for each treatment and litter to allow for any interactive effects of treatment × contact. All weight losses were corrected to the median score for the litter (*Calluna* = 7, *Molinia* = 6) by ap-

Table 3. Linear regressions ($y = a + bx$) of percent weight loss of litters (y) on total ground contact score (x)

Treatment	*Calluna*			*Molinia*		
	a	b	r	a	b	r
Control	4.1	−0.21	−0.40	37.3	−1.1	−0.66*
N1	6.7	−0.28	−0.69*	35.0	−0.6	−0.49*
N2	5.9	−0.26	−0.68*	40.8	−1.4	−0.64*
N3	8.4	−0.55	−0.53*	39.7	−1.2	−0.71*
P1	8.8	−0.16	−0.28	58.2	−2.4	−0.64*
P2	8.2	−0.17	−0.36	37.7	−1.3	−0.22
P3	11.0	−0.39	−0.66*	40.4	−1.4	−0.51*
Ca1	6.5	−0.21	−0.33	41.4	−1.2	−0.67*
Ca2	5.3	−0.26	−0.83*	42.4	−1.3	−0.32
Ca3	4.8	−0.24	−0.71*	43.8	−1.1	−0.67*
CHO1	7.3	−0.18	−0.27	42.1	−1.0	−0.55*
CHO2	6.2	−0.23	−0.62*	40.2	−0.9	−0.79*
CHO3	7.0	−0.31	−0.45	32.3	−0.4	−0.36

r is the correlation coefficient. * $P < 0.05$
Treatments as specified in Table 1

plying the appropriate regression coefficient (Table 3). Use of a midpoint score such as the median minimises the effects of any errors in the estimation of the regression line. The main effect of the correction is then to reduce that part of the sample variance due to factors other than experimental treatments. The sample mean was appreciably altered only when the contact scores were heavily skewed towards either low or high values, and in these cases uncorrected losses would have given a biased estimate of treatment effects.

(Analysis of ground contact and treatment effects could not be explicitly combined, e.g. by analysis of covariance, because of limits on possible comparisons imposed by the experimental design (see below) and considerations of site homogeneity).

Cementation of cotton strips. Two distinct kinds of cementation could occur (French 1984):
(1) 'Concretion' or physical binding by fine solids, and
(2) 'Biotic cementation' involving the production of binding agents (mainly polysaccharides and resins) by microflora or roots.
Where both occurred, I only corrected for concretion. Corrections were as follows:
(1) All strips in plots with added Ca or CHO were subject to concretion. The effect of this is measurable on unrotted strips, and the difference in TS between cemented and uncemented strips was added to the measured TS of all strips from Ca or CHO plots in period 1. I did not correct for concretion in later periods, because I could not be sure that sufficient of either additive remained in the soil to cement the strips. Observations of cemented strips from other experiments suggest that concretion effects may be more persistent than this, so it is a conservative correction. The corrections applied were:

Treatment:	Ca1	Ca2	Ca3	CHO1	CHO2	CHO3
Correction (kg):	+3	+5	+6	+1	+2	+2

(2) Biotic cementation was detected in about ten percent of test segments. The correction factors were derived from two observations. Firstly, if cumulative percentage frequency curves are drawn for TS of biotically cemented and uncemented strips, over all treatments and periods together (French 1988a) the difference between the two curves corresponds to an average difference of 1.8 kg and a maximum of 4.0 kg. Secondly, completely "rotted" strips, if highly cemented, typically had a TS of about 2 kg but, if uncemented, had no measurable TS. These observations suggest that moderate to high cementation is likely to increase the TS of a test segment by at least 1–2 kg. I therefore used the following (probably conservative) additions to measured TS to correct for biotic cementation:

Estimated cementation:	light	moderate	high	very high
Correction (kg):	0	+1	+2	+3

(With very high cementation, individual threads were not distinguishable and the whole segment appeared as if felted rather than woven; for further details of cementation estimation, see French 1988a).

Experimental design

The area available was very limited, so that a fully randomised design was not practicable. The design used was therefore a compromise between statistics and logistics, as follows:

Twelve plots, each 3 × 3 m, were laid out, one for each treatment. Ten cotton strips, 20 bags of *Calluna*, and 18 bags of *Molinia* were placed randomly within each treated plot. Untreated control plots, containing between them a total of ten cotton strips and 38 litter bags (as for treated plots) were arranged among the treated plots so as to give a systematic sample of the ground over the whole experimental area.

In treated plots, though not in controls, this arrangement is a pseudoreplicated design (Hurlbert 1984). Any test of treatment effects therefore assumes initial homogeneity of the ground over all plots.

A preliminary trial, using only cotton strips, placed in proposed plot areas, with ten strips per plot as for the main experiment, and including control plots, showed no significant plot effect, especially in top segments (analysis of variance, Table 4a). Plot-to-plot variation was examined further by pairwise comparisons using least significant difference, to maximise the chance of finding differences between plots (Table 4b). No treated plots were different from controls, so comparisons between treatments and controls are probably valid. The order of means varied between depths (top, side, bottom) so any treatment effects that were consistent over all depths were not likely to be merely coincidental. Similarly, while an increase in cotton decay rates with N in the order N1 < N2 < N3 might be spurious, other response patterns would not. However, direct quantitative comparisons among treatments N1 and CHO3, or between N3 and CHO1 or P3, might, in some cases, be suspect.

I did not test for homogeneity with litters, but the results for top segments of cotton strips suggest (1) that any apparent treatment effects on litter decay rates were unlikely to be spurious and (2) that, except possibly for direct comparison of N1 with CHO3, any comparison involving litters, including between levels of N, was probably valid.

Table 4. Tests of initial site homogeneity using cotton strips

(a) Analyses of variance, between-plots

Segment	F	d.f.		P
Top	0.64	12,	247	0.80
Side	1.75	12,	117	0.07
Bottom	1.62	12,	247	0.09
All	1.62	12,	637	0.08

(b) LSD tests for differences between individual pairs of plots

Segment	Plots (treatments) and mean TS losses (kg)												
Top	N1	N3	N2	CHO2	P1	P2	P3	CTRL	Ca1	CHO1	Ca3	Ca2	CHO3
	36	37	37	37	38	38	38	38	38	38	39	39	39
Side	CHO1	CHO2	CHO3	Ca1	N1	CTRL	Ca2	Ca3	P1	N2	P2	N3	P3
	38	40	40	40	41	41	42	42	42	42	43	44	44
Bottom	CHO1	N1	CHO2	Ca1	CHO3	CTRL	Ca3	P1	Ca2	N2	P2	N3	P3
	35	36	37	37	37	38	38	38	38	39	39	40	40
All	CHO1	N1	CHO2	Ca1	CTRL	CHO3	P1	N2	Ca3	Ca2	P2	N3	P3
	37	37	38	38	38	39	39	39	39	39	39	39	40

CTRL = Controls (lumped as a single 'treatment' for these tests). Bracketed plots are not significantly different from each other ($P < 0.05$)

Further evidence that site homogeneity continued throughout the experiment, and that treatment effects were not due to plot-to-plot variation, is given later in the paper (see Results).

In summary, the design puts some restrictions on interpretation of results, and is not suitable for more general use. But the arrangement of controls minimises the chances of obtaining spurious treatment effects because of the plot layout, and the evidence for site homogeneity is strong.

Statistical analyses

In all statistical tests, individual samples were used as replicates, i.e. site homogeneity was assumed to be 'proven'. Because of the partly pseudoreplicated design, statistical probabilities may not always be exact. However, they are likely to be a good guide to the actual significance of the results, provided the evidence for site homogeneity is accepted.

Hypothesis (1), that all four additives would each increase decomposition rates, was tested by comparing decay rates in each treated plot with those in control plots, by Mann-Whitney *U*-tests.

Hypothesis (2), that all responses to any one additive would be nonlinear, was tested by comparing linear and nonlinear response patterns against the null (no response) using a test of ordered alternatives (Jonckheere 1954).

Hypothesis (4), that optimal levels of each additive would be in the same rank order as substrate quality, concerns the shapes rather than the sizes of responses. To compare these, differences in decay rates in treated plots from those in control plots were expressed as a percentage of the maximum difference in each combination of substrate and additive. For example, if the highest increase in weight loss from *Calluna* with N was in treatment N1, then all increases in *Calluna* losses with N were expressed as a percentage of the mean increase with N1. This was done for all substrates and additives, and probable response patterns estimated by Jonckheere's test.

Hypothesis (3), relating degree of change in decay rates to substrate quality, and hypothesis (5), concerning selection of decomposer organisms, were not tested statistically. Data are, however, presented in support of both hypotheses.

Results

Tensile strength losses from cotton strips

Losses over the year. The tensile strength (TS) losses in each of the three sample periods were summed to give an index of potential annual cellulose decomposition when cellulose supply is not itself limiting. For example, in control plots, 36 kg in period 1 + 36 kg in period 2 + 44 kg in period 3 = 116 kg. The linearized 'cotton rotting rate' (CRR) of Hill et al. (1985) was not used, since TS losses were frequently outside the range where CRR can validly be calculated.

All treatments, except P3 and CHO3, increased TS losses over losses in control plots. The increases were present at all depths (Table 5) and most were significant at $P < 0.05$ (Mann-Whitney *U*-test). This result supports hy-

Table 5. Mean total TS losses (kg) over one year, from cotton strips in treated and untreated plots. Treatments as specified in Table 1

Treatment	Test segments		
	Top	Side	Bottom
Controls	116	128	116
N1	134[a]	143[a]	138[a]
N2	129[a]	137[a]	133[a]
N3	130[a]	137	136[a]
P1	128[a]	139[a]	129[a]
P2	135[a]	142[a]	131[a]
P3	121	126	121
Ca1	131[a]	134	123
Ca2	145[a]	149[a]	140[a]
Ca3	142[a]	149[a]	144[a]
CHO1	134[a]	142[a]	137[a]
CHO2	134[a]	138[a]	134[a]
CHO3	121	115[b]	118

[a] Significant difference from controls ($P<0.05$, Mann-Whitney U-test, n1 = n2 = 20 top or bottom, n1 = n2 = 10 side)
[b] Significant decrease

pothesis (1), that all four additives would each increase decomposition rates.

The shapes of the responses to increasing levels of additives were not the same with all additives. (All response patterns described are significant ($p<0.05$) deviations from the null (no difference from controls); they are also more probable than the simple linear pattern, which was generally not a significant alternative to the null). With N, the lowest level produced the greatest overall increase in TS loss. P showed a hump-shaped curve, rising to a maximum at P2 then falling, till at P3 there was no significant increase in TS loss over the year. The response to Ca reached its maximum at Ca2, with no further increase at the highest level. Levels 1 and 2 of CHO increased TS looses, but the highest level reduced them. This reduction was accompanied by visible inhibition of biotic activity on the plot (slow regrowth of *Calluna*, very little invasion by grasses, poor growth of mosses and lichens, and an apparent reduction in both numbers and activity of soil organisms).

All these responses are nonlinear, as predicted by hypothesis (2). The shapes of the TS loss profiles (trends with depth) were very similar with P and with CHO, especially at the highest levels.

Changes within the year. When TS losses were examined within sample periods, several additional patterns were discernible.

Firstly, differences between depths varied between sample periods. In period 1, the greatest positive effect of every treatment was in bottom segments. These were the segments having lowest TS losses in control plots. Similarly, in period 2, lowest losses in control plots, and greatest increases in treated plots, were in top segments (Fig. 1). In period 3, there were no strong differences between depths in control plots, and no general order to the magnitude of responses to treatments between depths.

Secondly, the size of the effects of individual treatments changed with time. This partly reflects the relative solubility of the additives used. With N1 (very soluble) the response

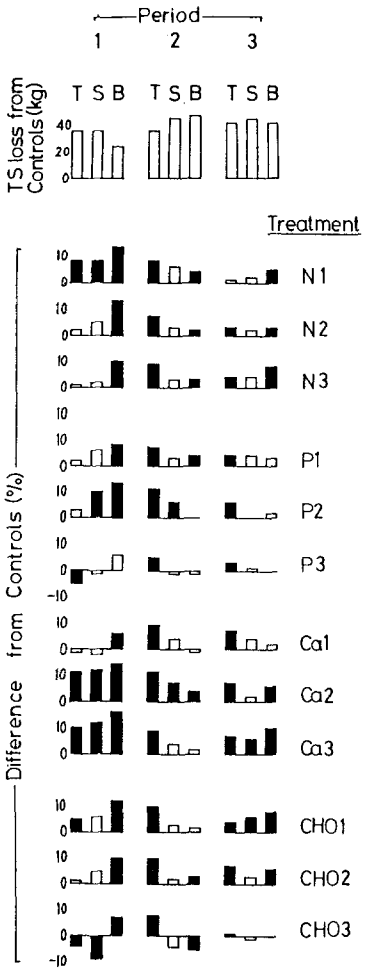

Fig. 1. TS losses (kg) from cotton strips in control plots, and mean differences (%) from controls of strips in treated plots, by treatment (see Table 1), segment (T = top, S = side, B = bottom), and sample period (Period 1 = 0–19 weeks, Period 2 = 19–34 weeks, Period 3 = 34–45 weeks). *Solid bars* represent differences significant at $P<0.05$ (Mann-Whitney U-test, n1 = n2 = 20 top and bottom, n1 = n2 = 10 side)

was initially high, declining progressively thereafter, but Ca1 (only slowly soluble) showed an opposite trend, with little effect in period 1 but more in the other two periods. Other trends over time were not related to solubilities, e.g. the increasing response to N3. Effects of treatments did not generally decrease with time, except with the two lowest levels of the two most soluble additives.

Thirdly, the similarity in responses to P and to CHO over the year (Table 5) also holds within each sample period (Fig. 1). Especially, the shapes of the TS loss profiles were similar, and in level 3, both additives reduced decay at corresponding depths.

Fourthly, the shapes of the responses to P, Ca and CHO were essentially the same in all three sample periods (P3 < P1 < P2, Ca1 < Ca2 = Ca3, CHO1 = CHO2 > CHO3). But with N the order of responses gradually reversed from N1 > N2 > N3 in period 1 to N1 < = N2 < N3 in period 3.

Weight losses from plant litters

Frequency distributions of weight losses in both control plots and treated plots showed two very distinct patterns in *Calluna* and *Molinia* (Fig. 2 gives some examples). In control

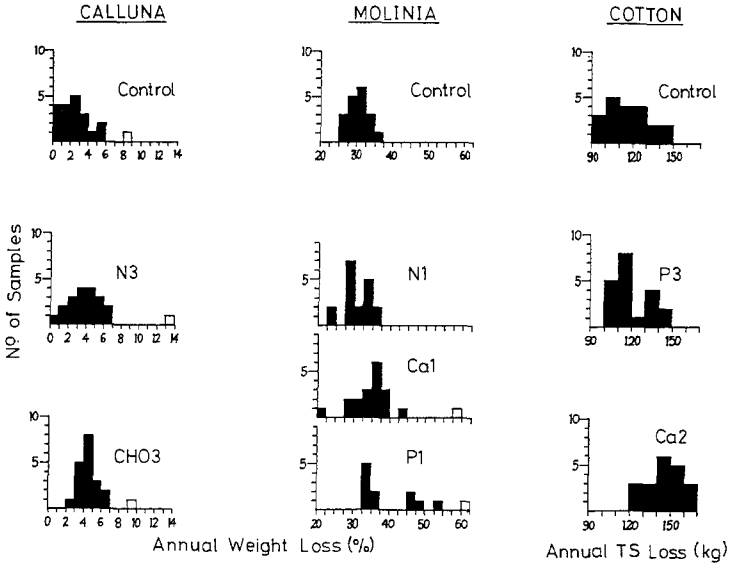

Fig. 2. Examples of frequency distributions of weight losses or TS losses in control plots and treated plots. 'Outliers' (single samples with decay rates more than one-sixth of the range from their nearest neighbour – see text) are unshaded

plots, losses from both litters had a fairly smooth, coherent distribution, but in treated plots *Molinia* losses had a very broken (multi-peaked) distribution. Only four *Molinia* distributions were unimodal, five were bimodal and the other three trimodal. All *Calluna* distributions, in both control and treated plots, were unimodal, but six also had one or more clear "outliers" (defined as losses more than one-sixth of the range from their nearest neighbour) including one outlier in control plots. There were possible outliers in a few of the *Molinia* distributions (e.g. Ca1, Fig. 2) but because of the multiple peaks there was not always a clear difference between outliers and the tail of the main distribution (the most extreme case was P1, illustrated in Fig. 2).

Outliers were considered to indicate peculiar combinations of site conditions and treatments, and/or presence of particular decomposer organisms not necessarily related to the presence or absence of an experimental treatment. I therefore discarded all outliers before analyzing the results from litter samples.

Differences from controls. Weight losses from *Calluna* stems were higher in all treatments than in controls (Table 6). The pattern of responses was essentially the same with N, Ca or CHO; the greatest increase in weight loss was at the lowest level of each additive, with a smaller increase at both higher levels. With P, the pattern was slightly different; a decreased response at level 2 was followed by a further increase at level 3.

Losses from *Molinia* showed no significant increases over controls with some treatments. Increases in decay rates, expressed as a percentage of control losses, were generally smaller than in *Calluna* and the pattern of responses was more complex (Table 6).

All additives increased decay rates at at least one level, as predicted by hypothesis (1). The response patterns were all nonlinear as predicted by hypothesis (2). But the related prediction, that all curves would rise to an optimum above which the response would be nil or negative, is not verified, within the range of treatments used, for *Molinia*. This is particularly so in Ca treatments, but possibly also with P and N. However, the response to N may be interpreted as approaching its optimum at level 3.

Table 6. Percent weight losses from plant litters after one year, ignoring 'outliers' (for definition see text). Treatments as specified in Table 1)

Litter	Treatment	*n*	Mean	SE	Mean difference from controls
Calluna stems	Controls	19	2.4	0.37	
	N1	20	4.5	0.27	2.14***
	N2	20	3.9	0.28	1.51***
	N3	19	3.7	0.36	1.39**
	P1	19	7.7	0.25	5.34***
	P2	19	6.8	0.17	4.43***
	P3	19	8.0	0.18	5.68***
	Ca1	18	4.2	0.36	1.88***
	Ca2	20	3.3	0.15	0.99**
	Ca3	20	3.4	0.23	1.01**
	CHO1	20	6.0	0.33	3.66***
	CHO2	20	4.6	0.18	2.26***
	CHO3	19	4.6	0.23	2.23***
Molinia leaves	Controls	18	30.4	0.65	
	N1	18	30.7	0.78	0.28
	N2	18	32.3	0.84	1.96*
	N3	18	32.6	0.49	2.18**
	P1	10	40.2	1.52	9.82***
	P2	18	30.1	1.45	−0.28
	P3	18	31.8	1.06	1.42
	Ca1	17	33.8	1.27	3.47**
	Ca2	17	33.0	1.45	2.58
	Ca3	17	36.6	0.71	6.23***
	CHO1	18	35.8	0.56	5.47***
	CHO2	18	34.2	0.58	3.79***
	CHO3	18	29.1	0.76	−1.30

* $P<0.05$, ** $P<0.01$, *** $P<0.001$ (Mann-Whitney U-test)

Comparison of all three substrates

Side and bottom segments of cotton strips were in a very different environment from litters, so only top segments were compared with the two plants litters.

If hypothesis (3), that degree of change is inversely related to substrate quality, is true, then the order of proportional increases in loss rates should be *Calluna* ≫ cotton > *Molinia*. The order is exactly that, with means and ranges as follows:

Calluna:	110%	(range 40 to 240)
Cotton:	14%	(range 3 to 25)
Molinia:	8%	(range < 0 to 20)

(The range for *Molinia* excludes losses with P1, because of the possibility that some losses may be spuriously high due to removal of material by voles. Including P1, the mean is 10% and maximum 35%).

Unlike degree of change, optimum levels of each additive were expected to be in the same order as substrate

Table 7. Ordering of responses of litter and cotton decomposition to soil additives, by Jonckheere's test

Change from controls, scaled as percent of largest change				Jonckheere ordering of responses[a]
	Treatment			
Substrate	N1	N2	N3	
Calluna	100	72	61	$0<(2, 3)<1$
Cotton[b]	100	69	75	$0<(2, 3)<1$
Molinia	14	86	100	$(0, 1)<(2, 3)$
	P1	P2	P3	
Calluna	95	79	100	$0<2<(1, 3)$
Cotton	63	100	25	$0<3<1<2$
Molinia	100	−3	16	$(0, 2, 3)<1$
	Ca1	Ca2	Ca3	
Calluna	100	51	56	$0<2, 3)<1$
Cotton	52	100	88	$0<1<(2, 3)$
Molinia	55	45	100	$0<(1, 2)<3$
	CHO1	CHO2	CHO3	
Calluna	100	61	61	$0<(2, 3)<1$
Cotton	100	100	25	$(0, 3)<(1, 2)$
Molinia	100	72	−22	$3<0<2<1$

[a] 0, 1, 2, 3 refer to controls and additive levels respectively. Bracketed levels have equal ranking
[b] Top segments only

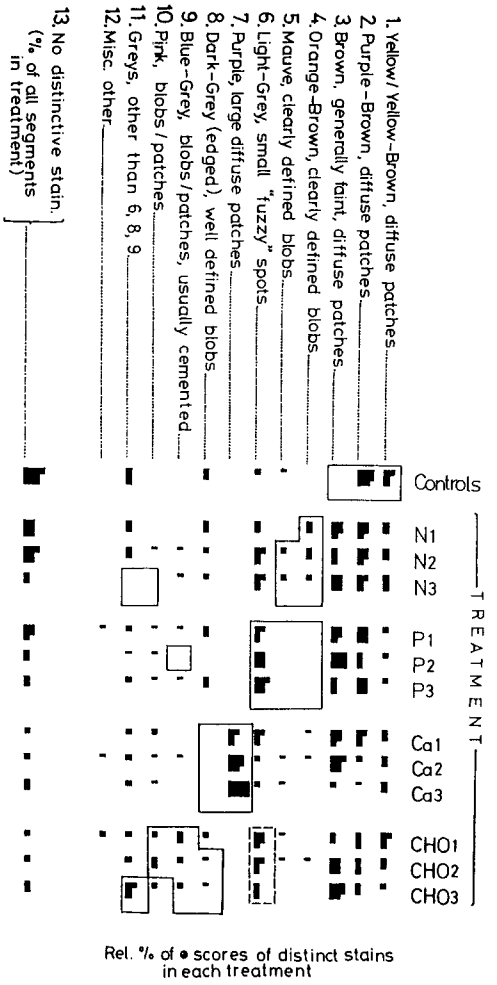

Fig. 3. Selection of microflora by treatments, indicated by relative percentages of the total positive scores of recognizably distinct stains in each treatment, and by the percentage of test segments showing no distinctive stain. ▪ 1–2%, ▪▪ 3–7%, ▪▪▪ 8–12%, etc. in steps of 5%. Characteristic stain combinations with each additive or treatment are outlined

quality. Optimal levels for *Calluna* should be lower than for cotton which, in turn, should be lower than for *Molinia*. This is the pattern found with N and with Ca (Table 7). With P, *Calluna* and cotton are in the expected order, though the shapes of the responses differ, but the response of *Molinia* decay is not as expected. The optimal level of CHO is approximately the same for all three substrates, and their responses to high levels are in exactly the opposite order to the expected one.

Selection of decomposer populations

The occurrence of different groups of soil and litter fauna showed no obvious treatment-related pattern except that earthworms were only found in Ca-treated plots.

Selection of microflora, however, was clearly indicated by the scores for staining patterns on cotton strips (Fig. 3). All four additives produced very different staining patterns, both from controls and from each other. Controls, for example, had higher scores for yellow or purple-brown diffuse patches (stains 1 and 2, Fig. 3) and for no distinctive stain (13) than all treated plots, and faint brown diffuse patches (stain 3) were absent. Strips from Ca-treated plots showed exactly opposite combinations of these stains (1, 2, 13 low, 3 high) and also were the only strips both with purple patches (stain 7), which they had in abundance, and without dark-grey blobs (8). Similar features characteristic of each additive (or in some cases treatment) are outlined in Fig. 3. Generally, strongest apparent selection was in P and Ca plots, then N3 and CHO1 and 2, with least in the lower levels of N.

These results tend to support the hypothesis (5) that changes in decay rates are through selection of decomposers as well as by overall changes in activity, at least in the case of cotton strips.

Effects of non-treatment factors (soil moisture, site litter and sample position)

The purpose of these analyses was to test further the assumption of site homogeneity.

Effects of soil moisture, and of the main litter type surrounding the sample, were tested by analysis of variance. Moisture and litter classes were not distributed in a balanced way among treated plots, and some combinations were not present at all, so effects were tested over all treatments together, including controls. A significance level of $p<0.1$ was used, to give ample chance of detecting any effect that might be present. Analyses using cotton were calculated separately for each sample period.

With cotton ($n=130$), there were no significant effects of moisture or site litter, and nearly half of all F-ratios were less than 1.

With *Calluna* ($n=252$) there was a significant effect of litter but only when fitted together with moisture and the

Table 8. Chemical constituents of the O/H/Ah horizon of soils from treated plots (bulked samples) and some individual control plots. Loss on ignition (LOI), total N, and soluble carbohydrates (CHO) are % of dry weight. "Extractable" nutrients (in acetic acid, or NaCl for NH_4-N) are ppm dry weight. Figures in parentheses are per dry weight of organic matter (i.e. corrected to constant LOI)

Treatment	pH	LOI	Total		Extractable			
			N	CHO	NH4-N	P	K	Ca
Control mean	4.4	71	1.5 (2.2)	3.4 (4.9)	37 (52)	18 (24)	67 (95)	77 (112)
±SE ($n=6$)		4	0.6 (0.1)	0.3 (0.5)	2 (4)	3 (3)	6 (9)	6 (13)
N1	4.3	72	1.7 (2.4)	3.7 (5.1)	36 (50)	14 (19)	51 (71)	62 (86)
N2	4.4	75	1.7 (2.3)	3.5 (4.7)	36 (48)	15 (20)	57 (76)	71 (95)
N3	4.3	80	1.8 (2.3)	3.5 (4.4)	41 (51)	13 (16)	65 (81)	70 (88)
P1	4.4	75	1.7 (2.3)	3.6 (4.8)	32 (43)	32 (43)	120 (160)	73 (97)
P2	4.4	83	1.8 (2.2)	4.2 (5.1)	32 (39)	46 (55)	120 (145)	83 (100)
P3	4.3	78	1.7 (2.2)	4.1 (5.3)	36 (46)	47 (60)	160 (205)	68 (87)
Ca1	4.5	76	1.8 (2.4)	2.9 (3.8)	40 (53)	24 (32)	60 (79)	180 (237)
Ca2	4.5	66	1.5 (2.3)	3.1 (4.7)	33 (50)	15 (23)	55 (83)	190 (288)
Ca3	4.8	75	1.6 (2.1)	3.6 (4.8)	33 (44)	11 (15)	64 (85)	350 (467)
CHO1	4.2	77	1.7 (2.2)	4.1 (5.3)	32 (42)	16 (21)	56 (73)	76 (99)
CHO2	4.1	61	1.3 (2.1)	2.7 (4.4)	30 (49)	13 (21)	54 (89)	65 (107)
CHO3	4.3	56	1.4 (2.5)	4.7 (8.4)	29 (52)	13 (23)	57 (102)	74 (132)

interaction (moisture × litter). However, this was entirely due to only four samples, all of which had the same moisture × litter combination. They were all in one treated plot (P1), but were not responsible for the observed treatment effect, since three of the four had losses well below the mean for the treatment, and the fourth was only slightly above the mean. Without them, therefore, the observed treatment effect would be even greater. After removing these samples from the analyses, there were no significant effects of moisture or site litter, and over half of all F were less than 1.

With *Molinia* ($n=223$) there were no significant effects at all and nearly all F were less than 1.

These results therefore support the assumption of site homogeneity and of treatment effects not being coincidental effects of plot-to-plot variation.

Trends in decomposition rates due to the layout of samples on the site were also assessed by correlating mean decomposition rates in treated plots with the rates in the adjacent control plots. In no case was the correlation greater than ± 0.3 ($n=12$, NS) and removal of even one point from any analysis could change the sign of the correlation.

These results suggest that spurious treatment effects are highly unlikely. They also imply that the site remained essentially homogenous throughout the experiment.

Chemical analyses of soils

At the end of the experiment, several chemical variables were measured on the O/H/Ah/Ahe horizons from a sample of control plots and on a bulked sample from each treated plot. All analyses were of air-dried, sieved (2 mm) samples with all except very fine (< 0.2 mm) roots removed. Analytical methods were as in Allen et al. (1974). Although no data were available from the start of the experiment from which to estimate retention or loss of additives in the initial stages, the final states of the soils (Table 8) indicate the following:

(1) Assuming that the variation in treated plots was equal to that in control plots, significant differences from controls (t-test, $p<0.05$) were confined to constituents corresponding to the additives in each treatment, further supporting the assumption of site homogeneity.

(2) Ammonium-N showed no significant retention in N-treated plots. Nitrate-N was almost undetectable in all plots, so all added N must have been either lost from the upper horizons or converted to non-extractable forms, e.g. incorporated into microbial biomass.

(3) In P-treated plots, K, as well as P, was retained.

(4) Ca was retained in all Ca-treated plots, but only Ca3 had a markedly higher pH than control plots. The effect of Ca could not, therefore, be entirely due to pH change (cf Tables 7 and 8).

(5) CHO was significantly higher than controls only in CHO3.

(6) If all additives had been retained in the top 10 cm of soil then, assuming an average bulk density (estimated from LOI) of 0.25, differences from controls would have been: N1 160 ppm, P1 170 ppm, Ca1 240 ppm, and CHO1 0.05%, with differences at levels 2 and 3 each 4 and 10 times these values. Measured differences in all treatments (except CHO3) were much lower than these, implying considerable losses from the upper soil horizons or, as with N, conversion to non-extractable forms.

Discussion

Possible sources of error in interpreting the results

There are five of these: two are common to all treatments, one affects only results from P-treated plots, and two are peculiar to a single substrate in P1.

Firstly, the experimental design assumes site homogeneity. But evidence has been provided to support that assumption, and the arrangement of control plots minimizes the risk of error. Statistical probabilities may not be exact, but are almost certainly a good guide to the actual significance of any result, especially when rank-order tests were used.

Secondly, in comparisons between all three substrates, I have assumed that top segments of cotton strips are equivalent to a cellulose-rich, nutrient-poor litter sample. This is probably true in relation to edaphic conditions and substrate quality, but for part of the year the cotton may have been in a different microclimate to the litter samples. Any such difference should not be large enough to affect rank-order comparisons, but quantitative differences should be treated with caution (see French 1988b for more detailed discussion of comparability of cotton and litters).

Thirdly, it was not possible to apply P without an accompanying ion which might itself affect decomposition rates, so any effect attributed to P might really be due to K, or to P and K together.

Finally, effects of P1 may be slightly underestimated with *Calluna* (because of moisture and site litter combinations) and overestimated with *Molinia* (because of undetected removal of material by voles).

Selection of decomposers and its effects on decomposition rates

Many models of decomposition assume that the substrate and its associated microflora can be treated as a single entity with a single aggregate response to changing conditions (e.g. Bunnell et al. 1977). But any environment or substrate will tend to select organisms adapted to, or tolerant of, those conditions. The stains on cotton strips show strong selection by most of my treatments. What effect might that selection have on decomposition rates?

Selection by a substrate or treatment is likely to favour only a part of the total array of decomposers present on the site. If both substrate and treatment select decomposers, their combined effects may be complementary or antagonistic, so might increase or decrease decomposition rates. Widden et al. (1986) sampled microfungi from cotton strips placed in some of my plots, and from soils in control plots. They found significant selection both by cotton and by treatments; they also showed correlations between some of the fungi selected for and TS loss rates. In this case, selection by substrate and treatment seems to be complementary, but that might not be so with other combinations of substrate and treatment.

If the possible effects of selection are taken into account, nearly all the responses observed in this experiment are explicable as combined effects of substrate and treatment on activity or composition of decomposer populations.

Calluna wood (a low-nutrient, high-lignin substrate) selects for ligninolytic organisms tolerant of low nutrient levels. High levels of additives select for organisms requiring higher nutrient levels or simpler carbon-sources, and these organisms may not be efficient lignin decomposers. Selection by substrate and treatment therefore tends to be slightly antagonistic, so that low levels of all additives consistently produce a big increase in decay rates, but higher levels induce less response.

Cotton has almost no mineral nutrients but also no inhibitory constituents. It is a simple substrate and its decomposers respond simply to the treatments. Antagonistic selection is less likely than with *Calluna*, except possibly with CHO3. So why is cotton decay reduced by both CHO3 and P3? Levels of additive retained in the soil should not be high enough to be toxic (Table 8) and selection of microflora did not vary much between levels of P (Fig. 3).

The similar TS loss profiles in P3 and CHO3 suggest a common factor. Initial acceleration of decomposition (by added P or CHO) may have exhausted some other resource, e.g. nitrogen (Smith 1980). Alternatively, rapid decomposition could lead to anoxia in wet soil (e.g. in the autumn), which would also account for the general inertness of the CHO3 plot.

The response of cotton decay to N may not at first seem simple. However, within N1, the within-year trends, and the staining patterns on the strips, show that there was little or no selection but only increased activity of the cellulolytic microflora. But with N3 there was considerable selection, probably for nitrogen-greedy microflora. Many of these are not efficient cellulose decomposers (Garrett 1976) but some are. The combined selection by substrate and treatment would gradually increase the proportion of cellulolytic organisms that could also utilize the extra nitrogen. So, with N1 activity immediately increased, then declined again as the added N was used up or immobilized. But with N3 an initial nil or negative response gradually changed to a positive response as the high-N cellulolytic microflora increased. This positive response should continue for some time after low-N samples have stopped showing any treatment effect.

Molinia has the most balanced composition, so there is least chance of antagonistic selection. Hence, as N and Ca increase, so do *Molinia*'s decay rates. With CHO the mechanism is probably similar to that suggested for cotton, but *Molinia* has a higher intrinsic decay rate so the system is exhausted sooner, and the reduction in annual loss rate is correspondingly greater. For the response to P, however, I have no explanation.

Limiting factors and resource availability

Seasonal changes in cellulose decay rates in cool-temperate and subarctic areas have been related to climatic changes (Heal et al. 1981; Berg et al. 1975) and a similar pattern seems to apply in control plots in this experiment (French 1988c). But in treated plots, the positive effects of all treatments were most marked in those segments with greatest apparent climatic limitation. This implies that, below the litter surface, nutrients 'limited' decomposition more than climate.

The apparent overcoming of detrimental climatic effects by added nutrients is surprising, since most microbial activity virtually ceases under extremes of temperature and moisture, irrespective of nutrient supply (Heal et al. 1981). But, as well as improving the ability of the decomposers to decay the test substrate, a treatment might also help them to grow and colonize new substrate. If so, they would then be more able to exploit short periods of better weather within an otherwise unfavourable climatic regime.

More generally, decomposition of dead organic matter in moorlands and similar ecosystems is rarely limited by any single factor, or even by simple combinations, but rather by the combined 'availability' of many resources.

Initial 'limits' may be set by availability of nutrients or carbon (as opposed to quantities in total pools), both in a substrate and in its environment. Soluble N, for example, is quickly converted to 'non-extractable' forms (Moore 1981; Chatterjee and Nandi 1981).

Physical availability of decayable surfaces may impose a second set of 'limits'. The response of cotton decay to

added Ca seems to be partly limited by lack of colonizable cotton surfaces. Soil and litter-dwelling animals often stimulate decomposition by comminution of the substrate.

A third series of 'limits' is set by the 'availability' of suitable decomposer organisms, as discussed in relation to seasonal variation. This is likely to be especially important where there is also selection for a restricted microflora, by climate, soil or substrate.

But, because so many of this formidable array of 'limits' are dependent on their interactions for their very existence, apparent limits may frequently be overcome by amelioration of some other factor. The reduction of adverse climatic effects by improving nutrient or carbon supply is one example.

This has two particular consequences. Firstly, it suggests that questions about decomposition expressed in terms of simple limiting factors (e.g. "is decomposition of poor-quality substrates carbon- or nutrient-limited?") are ultimately meaningless. Secondly, it casts doubt on the assumption that decomposition affects ecosystem productivity only through nutrient release. Instead, the system may benefit from increased availability of energy sources, if that in turn increases the chemical quality of plant litters, or the size or activity of decomposer populations. If maintained for long enough, such a change should eventually become self-sustaining.

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