

PHOSPHORUS IN THE SOIL MICROBIAL BIOMASS

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Summary—Phosphorus in the soil microbial biomass (biomass P) and soil biomass carbon (biomass C) were linearly related in 15 soils (8 grassland, 6 arable, 1 deciduous woodland), with a mean P concentration of 3.3% in the soil biomass. The regression accounted for 82% of the variance in the data. The relationship was less close than that previously measured between soil biomass C and soil ATP content and indicates that biomass P measurements can only provide a rough estimate of biomass C content. Neither P concentration in the soil biomass, nor the amount of biomass P in soil, were correlated with soil NaHCO₃-extractable inorganic, organic or total P.

The calculated mean annual flux of P through the biomass (in a soil depth of 10 cm) in 8 grassland soils was large, 23 kg P ha⁻¹ yr⁻¹, and more than three times the mean annual P flux through 6 arable soils (7 kg P ha⁻¹ yr⁻¹), suggesting that biomass P could make a significant contribution to plant P nutrition in grassland.

About 3% of the total soil organic P in the arable soils was in microbial biomass and from 5 to 24% in the grassland soils. The decline in biomass P when an old grassland soil was put into an arable rotation for about 20 yr was sufficient to account for about 50% of the decline in total soil organic P during this period. When an old arable soil reverted to woodland, soil organic P doubled in 100 yr; biomass P increased 11-fold during the same period.

INTRODUCTION

Methods have been developed (Brookes *et al.*, 1982; Hedley and Stewart, 1982) to measure the amount of phosphorus held in the cells of the soil microbial biomass (biomass P). In both methods the microbial cells are lysed by CHCl₃ fumigation, followed by extraction of the CHCl₃-released P with 0.5 M NaHCO₃. In this work we investigated the relationship between soil biomass P and soil biomass C by measuring both in 15 soils of contrasting agricultural history. The method developed by Brookes *et al.* (1982) was used to measure soil biomass P and the fumigation method (Jenkinson and Powlson, 1976) to measure soil biomass C.

The soil microbial biomass is a relatively labile constituent of soil organic matter (Jenkinson and Ladd, 1981) and is a key site for mineralization of organic P in soils. Soil microorganisms produce a variety of phosphatases capable of mineralizing organic P (Cosgrove, 1977). Cole *et al.* (1978) have shown that bacterial grazers such as amoebae can excrete inorganic P derived from the bacteria they consume.

There have been large changes in soil organic P in certain of the Rothamsted and Woburn long-term field experiments (Chater and Mattingly, 1980; Jenkinson, 1971) as a result of changing agricultural practices. A subsidiary aim of our work was to examine the relationship between the changes in organic P and the corresponding changes in biomass P.

MATERIALS AND METHODS

Soils

The soils used are described in Table 1. Soils 7, 8, 11 and 12 were sampled from the 5–15 cm soil layer, the others were sampled from the 0–10 cm layer.

After sampling, the soils were hand-picked to remove large pieces of plant material, earthworms, etc., sieved (< 2 mm), and then stored moist under aerobic conditions in large drums containing beakers of soda-lime and water for 7–10 days to allow respiration to settle down after sieving. Soils 1–9 came from Rothamsted Experimental Farm, Hertfordshire, soils 10–12 from Woburn Experimental Farm, Bedfordshire, soil 13 from Saxmundham Experimental Station, Suffolk, and soils 14–15 from the Macaulay Institute, Aberdeenshire.

Total N in soils was measured by the Kjeldahl method (Bremner, 1965). Soil pH was measured with a glass electrode using a 1:2 soil:water ratio. Organic C was determined by digestion with potassium dichromate and back-titrating with 0.2 M ammonium ferrous sulphate (Kalembasa and Jenkinson, 1973). Soil organic P was measured as the mean of organic P estimated by extraction (Mehta *et al.*, 1954) and by ignition (Saunders and Williams, 1955); total P by Na₂CO₃-fusion (Mattingly, 1970).

Measurement of biomass carbon and phosphorus

Biomass C and biomass P were measured in the moist, sieved soils after aerobic incubation for 7–10 days. Biomass C was measured by the fumigation method (Jenkinson and Powlson, 1976) in portions of moist soil containing 25 g (high organic matter) or 50 g (low organic matter) oven-dry (O.D.) soil. Biomass P (Brookes *et al.*, 1982) was calculated from the amount of inorganic P (P_i) extracted by 0.5 M NaHCO₃ from portions of moist soil (containing 10 g O.D. soil) that had been fumigated with CHCl₃ for 24 h, less the amount extracted from non-fumigated soil. Phosphorus was measured in neutralized aliquots (10 or 5 ml) of the NaHCO₃ extracts by the ammonium molybdate-ascorbic acid method described by Murphy and Riley (1962). Total P (P_t) in

Table 1. Description of soils used

Soil No.	Site and cropping history	Reference giving details of experiment	Manuring	Soil series and texture	pH	Total N (%)	Organic C (%)	Total P (%)	P extracted by 0.5 M NaHCO ₃ from non-fumigated soil ($\mu\text{g P g}^{-1}$ soil)			
									P ₁	P ₀	P ₂	P ₃
1.	Broadbalk Plot 03 (Continuous wheat)	Johnston (1969)	None	Batcombe (silt loam)	7.41	0.108	0.77	0.053	4.3	1.6	5.9	
2.	Broadbalk Plot 08 (Continuous wheat)	Johnston (1969)	NPKNaMg	Batcombe (silt loam)	7.21	0.108	1.04	0.105	76.0	5.9	81.9	
3.	Broadbalk Plot 022 (Continuous wheat)	Johnston (1969)	FYM	Batcombe (silt loam)	7.85	0.250	2.69	0.130	84.8	0.5	85.3	
4.	Broadbalk Wilderness (Deciduous woodland)	Jenkinson (1971)	None	Batcombe (silt loam to silty clay loam)	7.54	0.371	4.13	0.081	10.8	6.3	17.1	
5.	Park Grass Plot 3a (Unmanured permanent grass)	Warren and Johnston (1964)	None	Batcombe (silt loam)	6.70	0.453	4.81	0.061	3.1	3.4	6.5	
6.	Park Grass Plot 4/1a (Permanent grass)	Warren and Johnston (1964)	P	Batcombe (silt loam)	6.89	0.423	4.55	0.192	38.3	2.5	140.8	
7.	Highfield Permanent Arable (Arable rotation)	Johnston (1973)	NPK	Batcombe (silt loam)	6.64	0.186	1.91	0.095	53.2	9.1	62.3	
8.	Highfield Permanent Grass (Permanent grass)	Johnston (1973)	N	Batcombe (silt loam)	6.82	0.322	3.32	0.078	10.0	14.9	24.9	
9.	Non-experimental Permanent Grassland (Highfield)	None	None	Batcombe (silt loam)	6.80	0.357	3.78	0.092	12.4	12.3	24.7	
10.	Woburn Long Term Phosphate (Nil Plot) (grass/clover ley)	Johnston <i>et al.</i> (1976)	KMg	Stackyard & Cottenham (sandy loam)	6.97	0.120	1.04	0.066	6.5	8.6	15.1	
11.	Woburn Permanent Arable (Arable rotation)	Johnston (1973)	NPK	Cottenham (sandy loam)	6.75	0.119	1.19	0.092	41.1	12.2	53.3	
12.	Woburn Permanent Grass (8 yr grass ley)	Johnston (1973)	NPK	Cottenham (sandy loam)	7.00	0.115	1.21	0.074	28.6	5.0	33.6	
13.	Saxmudham Rotation I (Bonemeal Plot) (grass ley)	Williams and Cooke (1971)	Bonemeal	Beccles (sandy clay)	7.63	0.194	1.76	0.082	6.5	3.1	9.6	
14.	Counteswells (Permanent grass)	None	None	Counteswells (sandy clay loam)	5.59	0.390	5.61	0.092	7.2	23.9	31.1	
15.	Tarves (Barley/grass-clover/roots rotation)	None	NPK	Tarves (sandy loam)	6.04	0.332	2.90	0.202	67.4	34.4	101.8	

the NaHCO₃ soil extracts was measured after HClO₄ digestion, MgCl₂ being added to the digestion mixture to prevent P losses by volatilization (Brookes and Powelson, 1981). Correction for P fixation during NaHCO₃-extraction was made by adding a known quantity of P_i (as KH₂PO₄) during the NaHCO₃ extraction stage and measuring the recovery of added P_i. Correction for incomplete conversion of soil biomass P to NaHCO₃-extractable P_i was made by assuming that 40% of the P in the biomass is rendered extractable to NaHCO₃ as P_i by CHCl₃ (Brookes *et al.*, 1982). All results are expressed on an oven-dry soil basis (105°C, 24 h) and are the means of three replicate determinations.

RESULTS AND DISCUSSION

Relationship between CHCl₃-released P_i and P_t

The method used to measure soil biomass P is based on the measurement of CHCl₃-released P_i in NaHCO₃-soil extracts, rather than CHCl₃-released total P (P_t). The justification for this (Brookes *et al.*, 1982) is that there was a high and reasonably constant percentage of P_i in the CHCl₃-released P_t (90.7 ± 9.5%) in seven out of eight soils. In Table 2, more soils are included and the results support this original decision, the mean percentage P_i in the CHCl₃-released P_t (90.2 ± 2.2%) being very similar to that originally reported (omitting soils 11 and 15).

Measurements of biomass P in soils containing little biomass or large amounts of NaHCO₃-extractable P_i are subject to large analytical errors. This is presumably why CHCl₃-released P_i in soil 11 appeared to be greater than CHCl₃-released P_t (Table 2). The amount of CHCl₃-released P_i was small (< 3 µg P_i g⁻¹ soil) compared with the amount of NaHCO₃-extractable P_i from unfumigated soil (41 µg P_i g⁻¹ soil). A similar explanation holds for soil 1 but probably not for soil 15 in which CHCl₃-released P_i was comparatively large. Of all the soils yet analysed, soil 15 is the only one in which

CHCl₃-released P_i is so appreciably less than 90% of P_t that the result cannot be attributed to analytical error.

Soil biomass P can therefore be measured with reasonable accuracy from the increase in NaHCO₃-extractable P_i due to CHCl₃ fumigation, rather than the increase in P_t. This avoids the need for HClO₄ digestion of soil extracts to convert organic P (P_o) to P_i and also makes it possible to correct for soil fixation of CHCl₃-released P by measuring the recovery of P_i (added as a spike of KH₂PO₄) at the extraction stage.

The phosphorus content of the soil microbial biomass

There was a linear relationship between soil biomass P and biomass C for the 15 soils. The regression equation was biomass P = (0.063 ± 0.008) biomass C + (2.19 ± 6.07). This regression accounted for 81% of the variance, and the intercept was not significantly different from zero. The corresponding regression through the origin (Fig. 1) was biomass P = (0.065 ± 0.005) biomass C, which accounted for 82% of the variance, biomass P and biomass C both expressed as µg g⁻¹ soil. From the slope of the regression line (Fig. 1), the mean P concentration of the soil microbial biomass for these 15 soils was 3.3%, assuming that dry cells contain 50% C.

Another regression was calculated, omitting soil 5 (encircled in Fig. 1), which did not fit the regression well. The regression equation through the origin was then biomass P = (0.074 ± 0.004) biomass C, accounting for 92% of the variance in the data, and giving a mean biomass P concentration of 3.7%. Since repeat analyses have confirmed the validity of the biomass C and P values obtained for soil 5, we believe that these measurements simply reflect the relatively wide fluctuations in the P concentrations of the soil biomass. It may be significant that soil 5 had the lowest NaHCO₃-extractable P of all the soils investigated (Table 1).

Table 2. Soil biomass carbon and soil biomass phosphorus, and the relationship between CHCl₃-released biomass P_i and P_t

Soil No.	Biomass C (µg g ⁻¹ soil)	Biomass P	% P in biomass ^a	Biomass C/P ratio	CHCl ₃ -released P _i as % P _t
1.	158	6.0	1.9	26.3	74.0
2.	190	5.3	1.4	35.9	86.5
3.	342	28.9	4.2	11.8	91.8
4.	715	67.2	4.7	10.6	99.6
5.	1627	72.3	2.2	22.5	96.7
6.	1379	106.0	3.8	13.0	84.3
7.	305	21.0	3.4	14.5	83.8
8.	847	61.7	3.6	13.7	87.8
9.	1112	87.6	3.9	12.7	95.3
10.	300	15.0	2.5	20.0	96.8
11.	99	7.0	3.5	14.1	(129.0) ^d
12.	148	12.0	4.1	12.3	89.3
13.	635	24.8	2.0	25.6	102.1
14.	569	48.6	4.3	11.7	84.7
15.	492	27.5	2.8	17.9	(65.5) ^d
Mean and standard error			—	—	90.2 ± 2.2
Slope of regression line			3.25 ^b ± 0.25 ^c	14.3 ^b ± 1.1 ^c	—

^aAssuming dry biomass contains 50% C.

^bSlope of regression line.

^cStandard error of slope of regression line.

^dOmitted from calculation of mean.

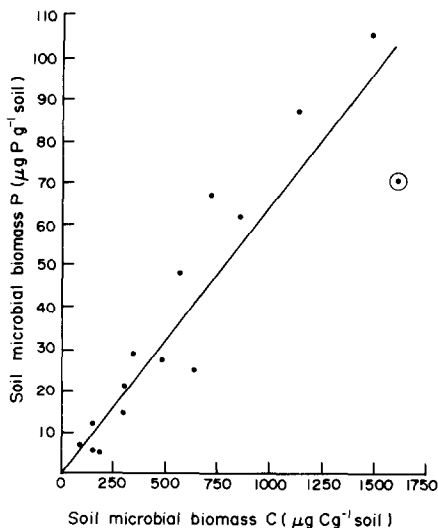


Fig. 1. Relationship between phosphorus and carbon in the soil microbial biomass. Encircled value—see text.

In the soils studied, % P in the biomass (Table 2) ranged from 1.4 to 4.7% (C/P ratios 10.6–35.9; mean 14.3). Similar variation in biomass C/P ratios were reported by Perrott and Sarathchandra (1982). They measured soil biomass C and P contents by the same methods that we used in 21 New Zealand pasture soils and also found them to be closely correlated ($r = 0.75$). They found that soil biomass C/P ratios ranged from 15–63 with a mean biomass C/P ratio of 27. Later, two of the biomass C/P ratios were thought unusual, and excluded (K. W. Perrott, personal communication, 1983), giving a range from 15–36 with a mean of 24.

Although there is no obvious reason why soil biomasses developed under different conditions should *not* show considerable variation in biomass C/P ratios, it is possible that the variation could, at least in part, be a reflection of differences in true k_p (the fraction of the total soil biomass P extracted as P_i after fumigation) values between soils. Obviously, the accuracy of soil biomass P and C measurements depend heavily on k_p and k_c (the fraction of the total soil biomass C evolved as CO_2 after fumigation). Because of the difficulties involved in extracting representative fractions of living microbial cells from soils, estimates of k_p and k_c have, so far, only been made using microorganisms grown *in vitro*. Brookes *et al.* (1982) suggested an average k_p of 0.4, based on recoveries of added microbial P from 8 lyophilized species of microorganisms added separately to three soils. Hedley and Stewart (1982) suggested an identical value based on recoveries of microbial P from two fresh fungi and two fresh bacteria grown *in vitro* and added to soil. These measurements were all made on soils of a relatively narrow pH range (5.6–7.4) and may not be applicable to soils that fall much outside this. Similarly, the k_c values normally used, 0.45 at 25°C, (Jenkinson and Ladd, 1981) or 0.41 at 22°C, (Anderson and Domsch, 1978) were again obtained from lyophilized (Jenkinson, 1976) or fresh microorganisms grown *in vitro* (Anderson and Domsch, 1978) and are also only applicable to soils above about pH 5.

Only when methods become available for extracting representative, uncontaminated microorganisms in quantity from soil can the accuracy of our method for measuring soil biomass P (or indeed soil biomass C) be satisfactorily evaluated. The best that can be done at present is to compare our values for P concentrations in the soil biomass with those for microorganisms grown *in vitro*.

Anderson and Domsch (1980) measured P in 14 representative species of soil fungi, grown on several concentrations of glucose, and 10 species of bacteria, all grown on 10 g glucose l^{-1} . In fungi, mean P concentrations ranged from 4.8% at 1.0 g glucose l^{-1} to 3.1% P at 10 g glucose l^{-1} . Bacteria (grown at 10 g glucose l^{-1}) contained a mean of 2.4% P (dry wt basis). Other workers, however, have measured P concentrations of soil microorganisms grown *in vitro* that are considerably lower than those obtained by Anderson and Domsch (1980). Kapoor and Haider (1982) reported P concentrations in fungal mycelia ranging from 0.65–0.85% P (dry wt basis), for five out of six fungal species (the other containing 1.8% P). The fungi were grown separately on a culture medium containing 20 g glucose l^{-1} (twice the maximum level used by Anderson and Domsch (1980) with most other nutrients at only about half their concentration). van Veen and Paul (1979) reported P concentrations of from 0.091 to 1.98% P (dry wt basis) in microorganisms isolated from soil and grown *in vitro* under various moisture stresses.

Our range of P concentrations in the soil biomass (1.4–4.7%; mean 3.3%) and the similar range found by Perrott and Sarathchandra (1982) are thus not inconsistent with Anderson and Domsch's (1980) values but are higher than those obtained by some other workers using microorganisms grown *in vitro*.

P concentration is a more variable characteristic of the microbial biomasses than ATP concentration. Oades and Jenkinson (1979) and Jenkinson *et al.* (1979) established a close linear relationship between soil biomass C and ATP for a wide range of cultivated and uncultivated soils that accounted for more than 90% of the variance. They suggested that biomass C could be estimated from soil ATP content with reasonable confidence. However, our results suggest that while biomass C and biomass P are correlated, the relationship is not sufficiently close to provide anything other than a rough estimate of soil biomass C content.

Relationships between soil agricultural history and the concentration of P in the biomass

The biomass tended to have a higher and narrower range of P concentrations in soils under permanent grass than in arable soils. Thus, %P in the biomass of the six old grassland soils ranged from 3.6 to 4.3%, except for soil 5 (2.2%). Soils 10 and 13 were under grass for 9 and 13 yr respectively and %P in the biomass of these soils was 2.5 and 2.0% respectively. The %P in the biomass in the arable soils (excluding soil 3 which received organic manure) was much more variable—ranging from 1.4 to 3.5%.

Soil 2, from the Broadbalk wheat experiment receives P fertilizer annually. It contained about 20 times more $NaHCO_3$ -extractable P than soil 1, from the unmanured plot of the same experiment. How

ever, %P in the biomass was similar in the two soils (1.9 and 1.4% respectively). Soil 3, from the same experiment, receives FYM every year and contained about the same amount of NaHCO_3 -extractable P as soil 2. However, %P in the biomass of soil 3 (4.2%) was more than twice that in soil 2. The other Broadbalk soil (soil 4, Broadbalk Wilderness), which has been under deciduous woodland for about 100 yr, contained much less NaHCO_3 -extractable P than soil 2, but the biomass P concentration (4.7%) was higher than in any of the other soils.

Soil NaHCO_3 -extractable P and the concentration of P in the soil biomass

There was no significant relationship between concentration of P in the biomass and NaHCO_3 -extractable P_i , P_o or P_t in these soils (Table 2). This is surprising. Many microorganisms grown *in vitro* accumulate P in excess of that required for growth either as polyphosphate (e.g. Harold, 1966) or as cell-P reserves (e.g. teichoic acid) that can be utilized under conditions of P deficiency (Grant, 1979). Why the soil biomasses developed under different systems have such different P concentrations is as yet unknown. There must be a theoretical limit below which %P in the microbial biomass cannot fall if the cell is to survive. However, the results in Table 2 suggest that, at least over the range of biomass P concentrations occurring in our soils, factors other than soil NaHCO_3 -extractable P concentrations determine the concentration of P in the soil microbial biomass.

Relationships between soil biomass P and total soil organic P

The soil microbial biomass, although only accounting for about 1–3% of the total organic matter in soil, is highly labile relative to most other soil fractions (Jenkinson and Ladd, 1981). This suggests that the P in the biomass is also more labile than most other soil organic P fractions, many of which, e.g. the inositol phosphates, are very stable in soil (Anderson, 1980; Williams and Anderson, 1968).

Table 3 shows the total soil organic P and soil biomass P in 12 soils. In 4 of the 5 arable soils biomass P comprised about 3% of the total soil organic P. In the grassland soils biomass P was a larger and considerably more variable fraction of the total soil organic P than in arable soils (14%, meaned

over 6 soils) and was 19.2% in the woodland soil. In soil 7, an arable soil ploughed from grass in 1948, biomass P was about 8% of total soil organic P, probably because the biomass has not yet had time to decline to the low level found in arable soils.

There are few field studies on the effects of changes in agricultural practice on the mineralization of organic P or on soil biomass content. Chater and Mattingly (1980) measured the changes in soil organic P in some long-term field experiments. Net P mineralization ranged from about 0.5 to 8.5 kg P $\text{ha}^{-1} \text{yr}^{-1}$. The largest amounts of P mineralized were from soils containing residues from recent large dressings of farmyard manure or ploughed out permanent pasture, and represented about half the annual P offtake by an average (5.0 t ha^{-1}) cereal crop.

Some of the results in Table 3 can be used to estimate the likely contribution of P derived from the biomass to soil P mineralization in a situation where soil organic matter is declining. Soils 7 and 8 were both taken from the Highfield Ley-Arable Experiment at Rothamsted. Soil 8 has been under permanent grass for more than 100 yr and soil 7 was ploughed out of this permanent grass in 1948 and put into an arable rotation. Assuming that our measurements made on soil 8 are representative of soil 7 before it was ploughed, total soil organic P fell by 2.4 $\mu\text{g P g}^{-1} \text{yr}^{-1}$ between 1948 and 1982 as a result of ploughing out the old grassland. Biomass P fell by 1.2 $\mu\text{g g}^{-1} \text{yr}^{-1}$ over the same period (Table 3). Thus the decline in biomass P accounted for half the decline in total organic P observed when permanent grass was ploughed.

Hawkes *et al.* (1984) used ^{31}P -NMR spectroscopy to compare the forms of organic P extracted by 0.5 M NaOH from two contrasting soils. One (soil 9 in this paper) was from old grassland on Rothamsted Experimental Farm and the other from an adjacent area that had been under grass until 1960 and thereafter under permanent fallow. The decrease in organic P in the fallow soil was mainly due to a decrease in the orthophosphate diester fraction, which contains nucleic acids and various phospholipids, rather than to a decrease in the other forms of organic P, notably the inositol phosphates. In the grassland soil the diester fraction was 40% of the NaOH-extractable organic P, but in the fallow soil it was only 8%. While this fraction will not reside exclusively in the biomass, it is likely that a large proportion of soil diester P will

Table 3. Soil biomass P expressed as a percentage of total soil organic P

Soil No.	Agricultural history	Total soil organic P		Biomass P as % of total soil organic P
		($\mu\text{g P g}^{-1}$ soil)	Biomass P	
1.	Arable	180	6.0	} $3.0^a \pm 0.2$
2.	Arable	210	5.3	
11.	Arable	242	7.0	
15.	Arable/grass	810	27.5	
7.	Arable out of grass	270	21.0	7.8
5.	Grassland	330	72.3	} $13.7^a \pm 3.5$
8.	Grassland	352	61.7	
10.	Grass/clover ley	190	15.0	
12.	Grassland	210	12.0	
13.	Grassland	500	24.8	
14.	Grassland	200	48.6	
4.	Deciduous woodland	350	67.2	19.2

^aMean and standard error.

either be present in the biomass or its associated metabolites. The calculated decrease in biomass P given above is thus consistent with the findings of the NMR study.

In an old arable soil reverting to woodland (soil 4), soil organic P nearly doubled in 100 yr, assuming that present measurements made on soil 1 can be taken as representative of soil 4 before reversion started in 1881 [see Jenkinson (1971) for a justification of this assumption]. On the same assumption, biomass P increased much more rapidly—more than 11-fold (Table 3).

Annual P flux through the soil microbial biomass

The annual flux of P through the biomass is given by: biomass P content (kg ha^{-1})/biomass P turnover time (yr). This was calculated for all the soils (Table 4) assuming that the biomass P turnover time, 2.5 yr, was the same as that calculated for biomass C by fitting a turnover model to data from field measurements made on Rothamsted soils (Jenkinson and Ladd, 1981). Turnover times may well vary from soil to soil and this single value of 2.5 yr is merely used to assign an order of magnitude to the P flux. The mean P flux for the eight grassland soils was $23 \text{ kg P ha}^{-1} \text{ yr}^{-1}$, more than three times the mean P flux in the six arable soils ($7 \text{ kg P ha}^{-1} \text{ yr}^{-1}$). These values are all calculated for a 10 cm soil depth so that the annual biomass P flux will be even greater if the total volume of soil explored by the plant roots is considered.

Annual crop P removals, where available, are also given in Table 4. In soils 10 and 13, P flux was about the same size as P offtake by grass, but in the other grassland soils the P flux was much greater than P offtake by grass. A biomass P flux of, say, $40.4 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (soil 6, Table 4) does not mean that this quantity of P is available for crop growth each year; some will be directly transferred to the next generation of organisms and some released to the soil solution, from which it can be taken up by plants, fixed by the soil colloids, or taken up again by soil

organisms. The relative importance of these different processes is, as yet, unknown. However the data in Table 4 suggest that the contribution of biomass P to plant nutrition is much more important in grassland than in arable soils. This is particularly so in the UK, when more than 40% of the permanent grassland is classified as below ADAS phosphate index 2 (i.e. contains less than $16 \mu\text{g NaHCO}_3$ -extractable $\text{P}_i \text{ g}^{-1}$ soil; C.A.S. Report 2, 1978), whereas more than 75% of arable soils are above index 2 (more than $25 \mu\text{g NaHCO}_3$ -extractable $\text{P}_i \text{ g}^{-1}$ soil). Thus, in UK grassland soils, the importance of the inorganic P supply tends to be less and the importance of biological cycling tends to be greater than in arable soils.

However, in areas of the world with less intensive agriculture, using smaller inputs of inorganic P fertilizer, P released from the biomass may make a significant contribution to the P nutrition of arable crops. The annual flux of biomass P in soil 1 (an unmanured soil growing continuous wheat for about 140 yr) was more than $6 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (to a depth of 23 cm), about 60% of the total P removed in the crop (Table 4).

Biomass P as a source of error in total soil organic P analyses

Total soil organic P (SOP) analyses are subject to large errors. Very different results can be obtained by the ignition (Saunders and Williams, 1955) and extraction (Mehta *et al.*, 1954) methods of measuring SOP [see Jenkinson (1971) for a discussion of this]. The work in this paper shows a further probable source of error.

SOP analyses are normally done on finely ground (<80 mesh: $180 \mu\text{m}$) air-dried soil, while biomass P measurements must be made on fresh, moist soil. Brookes *et al.* (1982) showed that NaHCO_3 -extractable P_i increased nearly three-fold when a moist soil was air-dried probably mainly because of P_i released from organisms killed by air-drying. Thus, particularly in grassland soils, where biomass P can be more than 20% of the total SOP (Table 3), some

Table 4. The soil biomass phosphorus contents and calculated annual P flux through the biomass in the 0–10 cm soil layer. Crop P removals given where available

Soil No.	Agricultural history	Soil weight ($\text{t ha}^{-1} < 6.24 \text{ mm}$ in a 10 cm soil depth) ^b	Biomass P (kg P ha^{-1})	Annual biomass P flux ($\text{kg P ha}^{-1} \text{ yr}^{-1}$) ^a	P removed in crop ($\text{kg P ha}^{-1} \text{ yr}^{-1}$)
1	Arable	1135	6.8	2.7	9.3
2	Arable	1048	5.6	2.2	22.8
3	Arable	948	27.4	11.0	28.8
7 ^c	Arable out of grass	1200	25.2	10.1	ND
11 ^c	Arable	1620	11.3	4.5	ND
15	Arable/grass	940	25.9	10.4	ND
5	Grassland	952	68.8	27.5	8.0
6	Grassland	952	100.9	40.4	12.0
8 ^c	Grassland	1050	64.8	25.9	ND
9	Grassland	1050	92.0	36.8	ND
10	Grassland	1500	22.5	9.0	9.0
12 ^c	Grassland	1500	18.0	7.2	ND
13	Grassland	1522	37.8	15.1	17.8
14	Grassland	1018	49.5	19.8	ND
4	Woodland	808	54.3	21.7	NA

ND = Not determined; NA = Not applicable.

^aAssuming a biomass P turnover time of 2.5 yr.

^bSoil weights calculated as described by Jenkinson and Powlson (1976).

^c5–15 cm soil layer.

^dMean and standard error.

SOP (i.e. P_0 held in the soil biomass) will probably be lost by conversion to P_1 when the soil is dried and ground prior to organic P analysis.

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REFERENCES

- Anderson G. (1980) Assessing organic phosphorus in soils. In *The Role of Phosphorus in Agriculture* (F. E. Khasawneh, E. C. Sample, E. J. Kamprath, Eds), pp. 411–431. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison.
- Anderson J. P. E. and Domsch K. H. (1980) Quantities of bacteria and fungi in chloroform-fumigated soils. *Soil Biology & Biochemistry* **10**, 207–213.
- Anderson J. P. E. and Domsch K. H. (1980) Quantities of plant nutrients in the microbial biomass of selected soils. *Soil Science* **130**, 211–216.
- Bremner J. M. (1965) Total nitrogen. In *Methods of Soil Analysis* Vol. 2, (C. A. Black, Ed.), pp. 1149–1178. American Society of Agronomy, Madison.
- Brookes P. C. and Powlson D. S. (1981) Preventing phosphorus losses during perchloric acid digestion of sodium bicarbonate soil extracts. *Journal of the Science of Food and Agriculture* **32**, 671–674.
- Brookes P. C., Powlson D. S. and Jenkinson D. S. (1982) Measurement of microbial biomass phosphorus in soil. *Soil Biology & Biochemistry* **14**, 319–329.
- C.A.S. Report 2 (1978) *Phosphorus: a Resource for U.K. Agriculture* Centre for Agricultural Strategy, Reading.
- Chater M. and Mattingly G. E. G. (1980) Changes in organic phosphorus contents in soils from long-continued experiments at Rothamsted and Saxmundham. *Rothamsted Experimental Station, Report for 1979 Part 2*, pp. 41–61.
- Cole C. V., Elliott E. T., Hunt H. W. and Coleman D. C. (1978) Trophic interactions in soils as they affect energy and nutrient dynamics. V. Phosphorus transformations. *Microbial Ecology* **4**, 381–387.
- Cosgrove D. J. (1977) Microbial transformations in the phosphorus cycle. In *Advances in Microbial Ecology* (M. Alexander, Ed.) Vol. 1, pp. 95–135. Plenum Press, New York.
- Grant W. D. (1979) Cell wall teichoic acid as a reserve phosphate source in *Bacillus subtilis*. *Journal of Bacteriology* **137**, 35–68.
- Harold F. M. (1966) Inorganic polyphosphates in biology: structure, metabolism and function. In *Bacteriological Reviews* (American Society for Microbiology) **30**, 772–794.
- Hawkes G. E., Powlson D. S., Randall E. W. and Tate K. R. (1984) A ^{31}P nuclear magnetic resonance study of the phosphorus species in soils from long-term field experiments. *Journal of Soil Science* In press.
- Hedley M. J. and Stewart J. W. B. (1982) Method to measure microbial biomass phosphorus in soils. *Soil Biology & Biochemistry* **14**, 377–385.
- Jenkinson D. S. (1971) The accumulation of organic matter in soil left uncultivated. *Rothamsted Experimental Station, Report for 1970 Part 2*, pp. 113–137.
- Jenkinson D. S. (1976) The effects of biocidal treatments on metabolism in soil. IV. The decomposition of fumigated organisms in soil. *Soil Biology & Biochemistry* **8**, 203–208.
- Jenkinson D. S. and Powlson D. S. (1976) The effects of biocidal treatments on metabolism in soil—V. A method for measuring soil biomass. *Soil Biology & Biochemistry* **8**, 209–213.
- Jenkinson D. S. and Ladd J. N. (1981) Microbial biomass in soil: measurement and turnover. In *Soil Biochemistry* (E. A. Paul and J. N. Ladd, Eds), Vol. 5, pp. 415–471. Marcel Dekker, New York.
- Jenkinson D. S., Davidson S. A. and Powlson D. S. (1979) Adenosine triphosphate and microbial biomass in soil. *Soil Biology & Biochemistry* **11**, 521–527.
- Johnston A. E. (1969) Plant nutrients in Broadbalk soils. *Rothamsted Experimental Station, Report for 1968 Part 2*, pp. 93–115.
- Johnston A. E. (1973) The effects of ley and arable cropping systems on the amounts of soil organic matter in the Rothamsted and Woburn ley-arable experiments. *Rothamsted Experimental Station, Report for 1972 Part 2*, pp. 131–159.
- Johnston A. E., Mattingly G. E. G. and Poulton P. R. (1976) Effect of phosphate residues on soil P values and crop yields. I. Experiments on barley, potatoes and sugar beet on sandy loam soils at Woburn. *Rothamsted Experimental Station, Report for 1975 Part 2*, pp. 5–36.
- Kapoor K. K. and Haider K. (1982) Mineralisation and plant availability of phosphorus from biomass of hyaline and melanin fungi. *Soil Science Society of America Journal* **46**, 953–957.
- Kalembasa S. J. and Jenkinson D. S. (1973) A comparative study of titrimetric and gravimetric methods for the determination of organic carbon in soil. *Journal of the Science of Food and Agriculture* **24**, 1085–1090.
- Mattingly G. E. G. (1970) Total phosphorus contents of soils by perchloric acid digestion and sodium carbonate fusion. *Journal of Agricultural Science, Cambridge* **74**, 79–82.
- Mehta N. C., Legg J. O., Goring C. A. I. and Black C. A. (1954) Determination of organic phosphorus in soil. I. Extraction method. *Soil Science Society of America Proceedings* **18**, 443–449.
- Murphy J. and Riley J. P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**, 31–36.
- Oades J. M. and Jenkinson D. S. (1979) Adenosine triphosphate content of the soil microbial biomass. *Soil Biology & Biochemistry* **11**, 201–204.
- Perrott K. W. and Sarathchandra S. U. (1982) Phosphorus in soil microbial biomass. *New Zealand Soil News* **30**, 153.
- Saunders W. M. H. and Williams E. G. (1955) Observations on the determination of total organic phosphorus in soils. *Journal of Soil Science* **6**, 254–267.
- van Veen J. A. and Paul E. A. (1979) Conversion of biovolume measurements of soil organisms, grown under various moisture tensions, to biomass and their nutrient content. *Applied and Environmental Microbiology* **37**, 686–692.
- Warren R. G. and Johnston A. E. (1964) The Park Grass Experiment. *Rothamsted Experimental Station, Report for 1963 Part 2*, pp. 240–262.
- Williams C. H. and Anderson G. (1968) Inositol phosphates in some Australian soils. *Australian Journal of Soil Research* **6**, 121–130.
- Williams R. J. B. and Cooke G. W. (1971) Results of the Rotation I Experiment at Saxmundham, 1964–69. *Rothamsted Experimental Station, Report for 1970 Part 2*, pp. 68–97.