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SOIL ORGANIC PHOSPHORUS - ITS MINERALISATION AND ITS IMPORTANCE IN THE NUTRITION OF WOODLAND PLANTS. A LITERATURE REVIEW

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Introduction

Phosphorus constitutes roughly 0.02-1% of the dry-weight of plants. Although only a small proportion, it is an essential element performing many varied and vital functions in their metabolism (42, 167, 175, 183, 276).

In woodland habitats, plants depend almost entirely on the soil for their supplies of phosphorus. Many soils have a poor capacity to supply the element. As a result of this the phosphorus status of the soil is one of the most important factors influencing the growth of woodlands or forests (140, 262). Recent soil-culture experiments using oak seedlings (198) have indicated that typical oak and oak/ash woodland soils on Silurian Slates and Carboniferous limestones in North Lancashire are deficient in available phosphorus (but have nearly enough available nitrogen). It was suggested that the currently poor increment growth, seedling production and regeneration in oak may therefore be due to this deficiency. This might well apply to most of the woods in the Lake District, the present centre of interest in Project 307. In addition, there are frequent references, direct or indirect, to P-deficient soils in forestry literature (17, 21, 76, 180, 186, 283). Also such soils are frequently associated with a number of different habitat types (51, 52, 168, 217, 245, 253, 272).

Distribution of the two oaks (Q. petraea (Matt.) Liebl. and Q. robur L.) are known to be different, though they do "overlap" in many areas (143). Because seedlings have different optimum available P requirements, the level of available P may have an influence on the distribution of the two species of oak, (198). Q. petraea tends to occur more widely in poor soils with lower available P levels.

Similarly, the distribution of many of the plants forming the herb layer in woodlands appear to be strongly influenced by the level of available phosphorus in the soil (45, 110, 111, 209,222). It is possible therefore that species composition of the herb layer in a woodland is a limited function of the available P. The diversity of herb species in a woodland may also be influenced by this soil characteristic.

The level of available phosphorus in soils is affected by a variety of soil and environmental characteristics. Perhaps one of the most important is the total quantity of the element in the soil. Thus the poor capacity of some soils to supply the element may result from the very small quantities of the element present. Another reason for poverty of available P in soil arises from the fact that a high proportion of the P in most soils is not readily available.

Much of this unavailable phosphorus is present in organic compounds. These compounds originate from a number of sources. A high proportion of the phosphorus added to soils in plant litters, decaying root systems, animal corpses and excreta is in organic compounds. The amount varies, depending on the type of organic matter, between 10 to about 95% (22, 109, 149, 150, 178, 239). Much of the phosphorus present as inorganic P may be converted to organic phosphate compounds during the initial phases of microbial decomposition of the organic matter (22, 40, 96, 149). Micro-organisms also convert available soil P to organic compounds (92, 100, 142). The same frequently applies to "fixation" of fertiliser P, where this is added to soils (57, 82, 132, 147, 261).

Plants, animals and micro-organisms thus draw on the "available" phosphorus supply and convert a large part of it to organic compounds which are eventually returned to the soil. The amount returned per year will vary with the woodland type and its productivity, but it could approach an amount approaching the total requirements by organisms in the year.

In view of the fact that soils generally contain only small quantities of phosphorus, the rate of breakdown of these organic compounds, with consequent release of inorganic phosphate, is of major importance in the long-term maintenance of "available" phosphorus supplies in soils.

Where soils conditions allow a fairly rapid breakdown, the phosphorus is made quickly available to the vegetation and the phosphorus status of the soil, given no losses due to erosion, leaching or cropping, is maintained. Where conditions are unfavourable, breakdown is slow and the organic P accumulates to the detriment of the available P supply.

A study of the relationships between rates of breakdown of organic phosphorus in soil and woodland soil conditions is therefore justified. This review has been produced as a background to research in Project 307.

Review

Quantity and distribution of organic phosphorus in soils

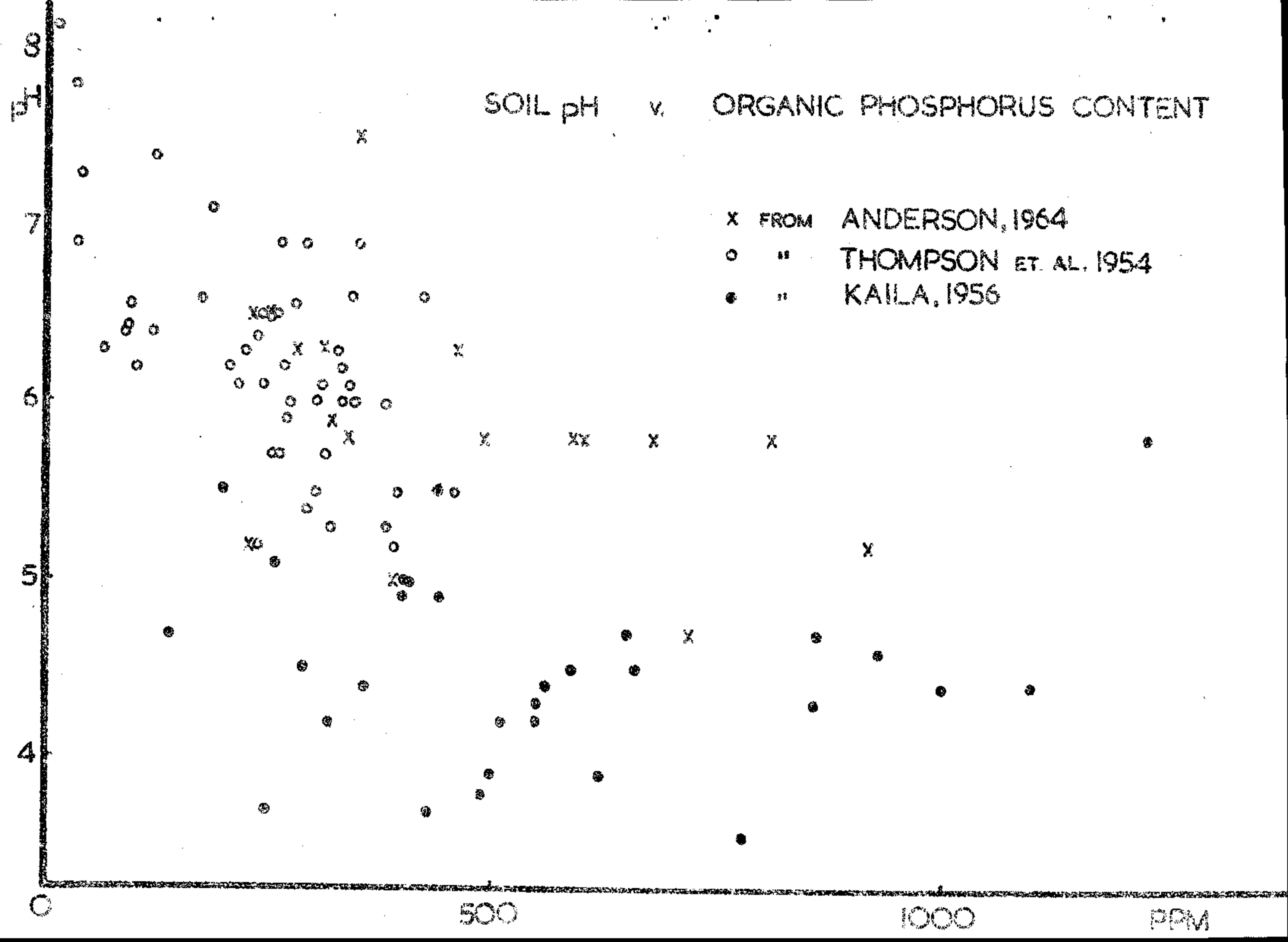
The quantity of organic phosphorus present in soils varies widely depending on the soil type, soil conditions and horizon. Many studies have been made of the organic phosphorus (OP) contents of soils, mainly of the surface horizons. (1, 30, 31, 56, 58, 62, 71, 80, 91, 93, 100, 132, 141, 145, 146, 148, 151, 154, 189, 192, 201, 202, 225, 226, 250, 251, 258, 266, 267, 279, 285.). Some of the available data have been included in Table 1.

A variety of determinations have been used in these determinations. Some of the methods for determination of the total organic phosphorus employ extraction procedures, which cause hydrolysis of some organic phosphorus compounds and therefore may give underestimates (7, 11, 27). Strictly speaking, therefore, no overall comparisons should be made. However, most soils contain between 50 and 500 ppm organic phosphorus, with extreme values of 18 ppm in an Orange-burg sandy loam from Mississippi and 1950 ppm for a peat in Finland (146, 204). In many cases, the data have been obtained from agricultural soils. Generally, cultivated soils have a lower organic phosphorus content than those which are virgin or undisturbed (85, 160, 204, 230, 251, 252, 254). This difference is particularly marked if liming to increase the soil pH has been part of the agricultural practice (54, 91, 151, 251).

The highest concentrations of organic phosphorus usually occur in the surface horizons. The concentration decreases down the profile, with relatively small quantities occurring below 30-40 cms. (5, 31, 80, 94, 141, 145, 191, 201, 205, 225, 258).

Some estimates have been made of the total organic phosphorus of whole soil profiles for chernosem, serozem and loess-derived soils. These are 0.5, 1.5 and 2.7 metric tonnes per hectare respectively (94, 159).

The total organic phosphorus content of a soil is probably directly related to the phosphorus content of the underlying parent rock and material from which the soil has been derived. Soils derived from parent materials rich in phosphorus tend to contain higher amounts of organic phosphorus than those derived from materials poor in phosphorus (258). Organic phosphorus is highest in soils derived from basic igneous materials and lowest in calcareous soils (264).



SOIL pH v. ORGANIC PHOSPHORUS CONTENT
x FROM ANDERSON, 1964
o " THOMPSON ET. AL. 1954
● " KAILA, 1956
pH
8
7
6
5
4
0
500
1000
PPM

Poorly drained soils usually have a smaller organic phosphorus content than those which are freely drained (12, 269, 271). This has been attributed to poorer plant growth, particularly root growth and penetration on those soils, with consequent poorer returns of organic matter to the soil. There may also be greater losses of the organic phosphorus from poorly drained soils (270).

The quantities of organic phosphorus and its distribution in soils are positively correlated with the amounts and distribution of organic matter, i.e. carbon and nitrogen (1, 4, 61, 80, 81, 85, 94, 151, 251, 252, 258, 270, 285). Soils with high organic matter content usually have a high organic phosphorus content. However, the organic phosphorus content of organic matter tends to increase with depth in the soil (81, 145, 201, 248, 258, 265).

The ratio of phosphorus to carbon and nitrogen tends to decrease with increase in soil pH (1, 250, 251, 264, 265). This relationship is consistent with the fact that acid soils tend to accumulate more organic phosphorus than do soils of alkaline pH's (1, 56, 250, 251). The accumulation of organic phosphorus in acid soils is thought to be due to its stabilisation by clays and sesqui-oxides. Considerable proportions of the organic phosphorus compliment in soils has been found to be associated with silt and clay particle fractions (131, 269, 270). Organic phosphates react with aluminium and iron hydroxides and the products become insoluble under acid conditions (9, 134).

A very much neglected aspect is the effect of natural vegetation on the quantities of organic phosphorus in soils. Many investigators have considered soil type characteristics and parent materials in conjunction with the concentrations of organic phosphorus, but hardly any mention vegetation. Some authors fail to mention whether or not the soils have been cultivated and are still under cultivation. In most cases, where no vegetation has been mentioned in the text, it is most probable that the soils are agricultural. There are a few reports in which a brief description of the vegetation has been given. There are a few indications that forest soils may contain higher levels of organic phosphorus than savannah or grassland soils (201, 258). Other results however show that some soils from open plots have higher OP contents than soils under forests (154). Peat soils have a wide range of OP contents (97, 144, 145, 146, 148). Whilst details of vegetation have been given, figures for any one type of habitat are so variable, that no between-habitat differences are readily apparent. The figures obtained for 4 Moor House sites are however amongst the lowest on record (97). Very small quantities of OP occur also in heathland soils (41). Though the quantities of OP are low in Moor House peats and heathland soils, the organic phosphorus is a very high proportion of the total phosphorus content.

TABLE 1

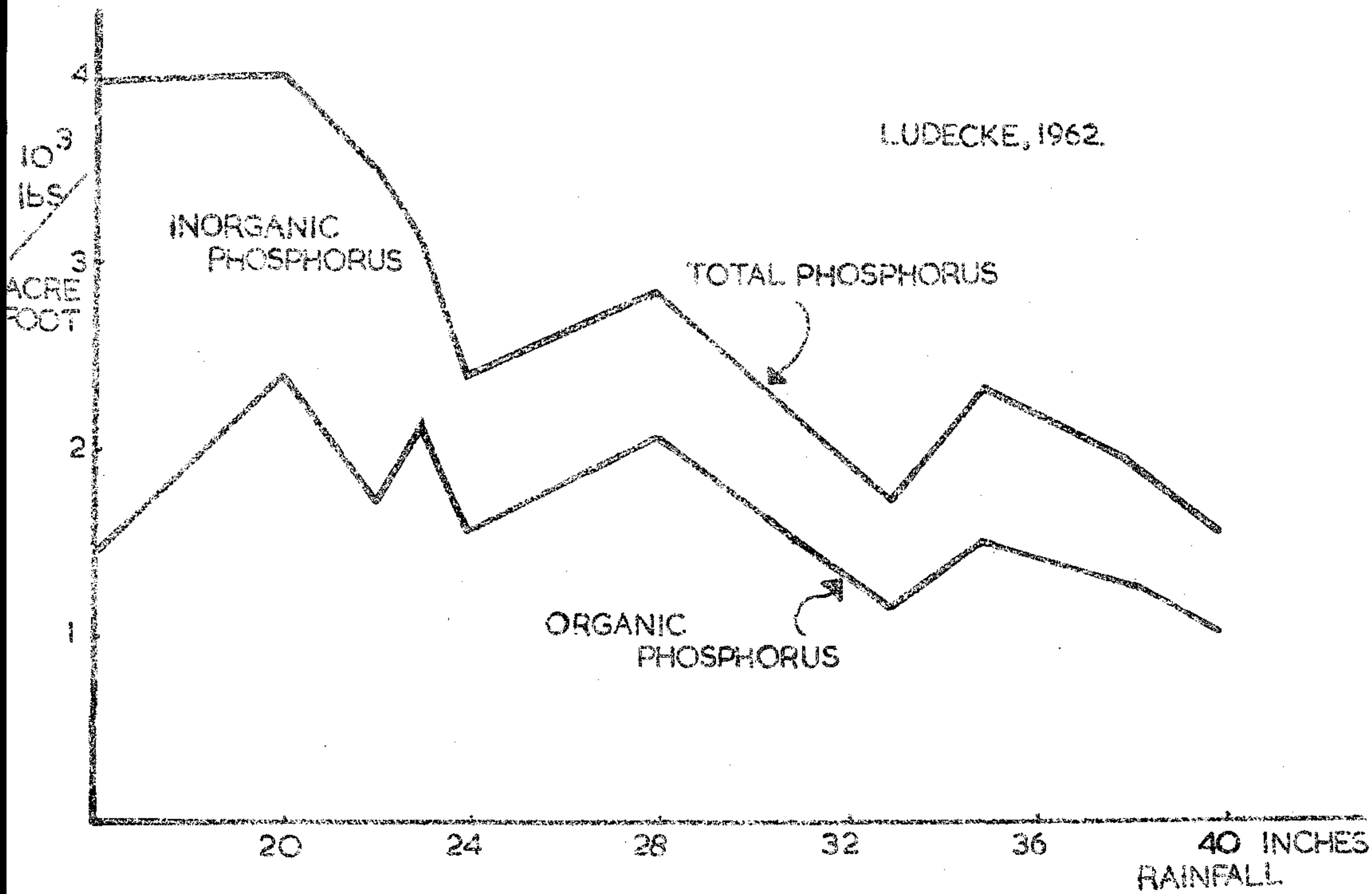
Soil type/parent material	Organic P content range (ppm)	% total P	Soil pH	Country	Reference
Podzols	75-150	-	-	Sweden	192
Podzols	346-386	49-57	-	Canada	279
Podzols (cultivated on slate)	179	56	5.3	Scotland	269
Podzols (cultivated on granite)	145	61	5.6	Scotland	269
Grey-brown Podzols (Old Red Sandstone)	162	58	5.5	Scotland	269
Grey-brown Podzols (limestone)	284-483	45-69.2	5.6-7.4	Ireland	117
Grey-brown Podzols (virgin)	240-277	37-40	6.5-6.6	U.S.A.	251
Grey-brown Podzols (cultivated)	87-183	30	6.4-7.1	U.S.A.	251
Brown-Podzols (basic igneous)	240	52	5.7	Scotland	269
Brown-Podzols (shale-sandstone)	523	61	5.3	Ireland	117
Brown-Podzols (granite)	402	52	5.1	Ireland	117
Brown Earths (cultivated)	-	24	6.3-6.9	Germany	226
Brown Earths (forest)	-	50	3.6-5.4	Germany	226
Brown Earths (limestone)	365-850	45-66.5	5.4-7.1	Ireland	117
Brown Earths (Old Red Sandstone)	343-492	56-69	5.5-5.8	Ireland	117
Brown Earths (shale drift)	510	60	6.3	Ireland	117
Brown Earths	117-141	-	-	Sweden	192
Brown Forest soils	318-430	30-41		Canada	279

Soil type/parent material	Organic P content range (ppm)	% total P	Soil pH	Country	Reference
Gley (mica-schist drift)	448	52.5	5.0	Ireland	117
Gley (limestone)	290-611	58-62.5	5.4-7.6	Ireland	117
Gley (Coal measure shales)	350-647	60.5-70	4.9-5.5	Ireland	117
Gley (Carboniferous shale)	289-367	59.5-67.5	5.3-5.4	Ireland	117
Peats	571-621	-	-	U.S.A.	60
Peats (Sphagnum-oligo-bog)	130-890	59-86	3.6-5.1	Finland	146
Peats (Carex-Sphagnum)	260-1570	57-89	4.1-5.3	Finland	146
Peats (Sphagnum-Carex)	340-1010	64-95	3.5-5.5	Finland	146
Peats (Sphagnum-Carex fen)	400-1910	74-93	4.3-5.8	Finland	146
Peats (Bryales-Carex fen)	200-980	59-90	3.9-5.8	Finland	146
Peats (Carex)	320-1950	55-91	4.1-6.1	Finland	146
Peats (Trichophorum-Eriophorum-Sphagnum papilosum bog)	31-43	95	3.4-3.8	England	97
Peats (Trichophorum-Eriophorum-losum Moor House)	21-24	95	3.1-3.3	England	97
Peats (Calluna-Eriophorum-Sphagnum-Acutifolium)	48-58	95	3.0-3.1	England	97
Peats (Eriophorum-Calluna-Vaccinium)	37-69	95	3.0-3.3	England	97
Rendzinas (virgin)	29-121	10-17	7.4-7.8	U.S.A.	251
Rendzinas (cultivated)	10-38	5-21	7.3-8.1	U.S.A.	251
Chestnut soils (virgin)	94-119	18-22	6.4	U.S.A.	251
Chestnut soils (cultivated)	93-101	18	6.2-6.6	U.S.A.	251
Prairie soils (virgin)	215-457	40-57	5.3-6.1	U.S.A.	251
Prairie soils (cultivated)	175-392	26-54	5.2-6.6	U.S.A.	251
Wiesenboden (virgin)	258-348	41-53	6.5-6.9	U.S.A.	251
Wiesenboden (cultivated)	205-257	39-50	6.2-6.7	U.S.A.	251
Planosol soils (virgin)	66-421	32-54	5.3-6.9	U.S.A.	251
Planosol soils (cultivated)	33-328	25-54	5.2-6.9	U.S.A.	251

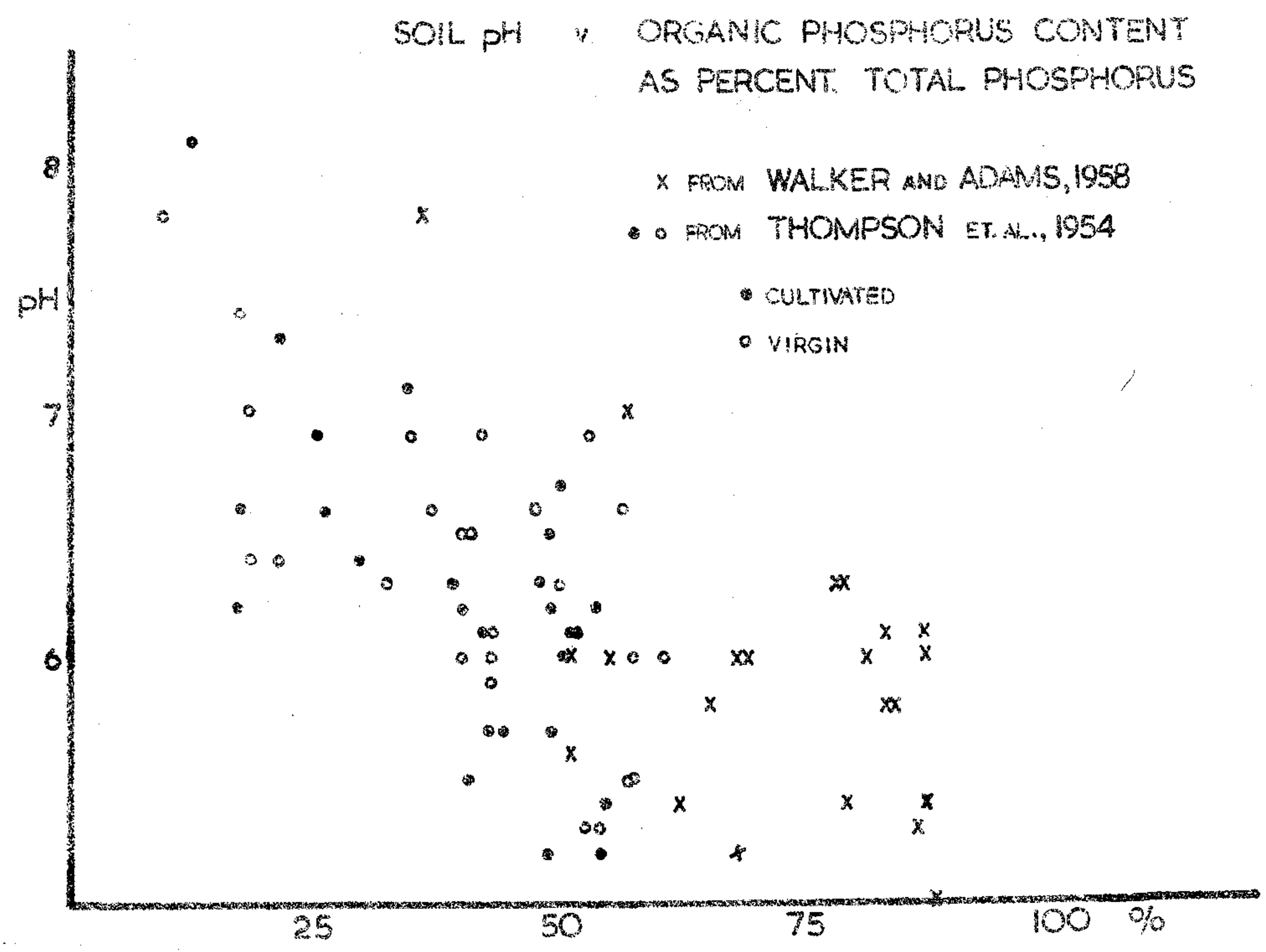
Soil type/parent material	Organic P content range (ppm)	% total P	Soil pH	Country	Reference
Granite (drift)	390-600		5.0-5.8	Scotland	8
Granite Gneiss or Schist (forest)	17-148		5.5-7.0	Ghana	201
Granite Gneiss (savannah)	7-26		6.0-7.0	Ghana	201
Granite (poorly drained)	90-105			Scotland	225
Granite (freely drained)	132-150			Scotland	225
Granite (drift)	402	52.0	5.1	Ireland	117
Granite (cultivated)	145	61	5.6	Scotland	269
Old Red Sandstone	340-490		5.8	Scotland	8
Old Red Sandstone (poorly drained)	84			Scotland	225
Old Red Sandstone (freely drained)	114-124			Scotland	225
Old Red Sandstone	343-492	59-69	5.5-5.8	Ireland	117
Sandstone (savannah)	10-55		5.6-6.7	Ghana	201
Sandstone (forest)	43-73		5.8-7.0	Ghana	201
Shale-Sandstone	523	61	5.3	Ireland	117
Shale (Coal measure)	350-647	60.5-70	4.9-5.5	Ireland	117
Shale (Silurian)	590		5.8	Scotland	8
Shale (Carboniferous)	289-367	59.5-67.5	5.3-5.4	Ireland	117
Slate (drift)	720		4.7	Scotland	8
Slate (cultivated)	179	56	5.3	Scotland	269
Graywacke	280		6.3	Scotland	8

Soil type/parent material	Organic P content range (ppm)	% total P	Soil pH	Country	Reference
Basic-igneous (drift)	680-810		5.8	Scotland	8
Basic-igneous (drift poorly drained)	310		6.3	Scotland	8
Basic-igneous	240	52	5.7	Scotland	269
Basic-igneous (poorly drained)	90-96		Scotland	225	
Basic-igneous (freely drained)	178-188			Scotland	225
Basic-igneous or Metamorphic (forest)	87-270		4.6-7.5	Ghana	201
Basic-igneous (savannah)	50-70		6.3-6.8	Ghana	201
Clay loams (poorly drained)	390		4.7	Scotland	8
Clay loams (lacustrine)	230		6.5	Scotland	8
Clay loams (slate drift)	720		4.7	Scotland	8
Clay loams (well drained)	288-850	38.4-57.5	5.2-6.0	Ireland	117
Clay loams (moderately well drained)	356-455	52-57	6.0-7.2	Ireland	117
Clay loams (poorly drained)	289-611	59.5-62.5	5.4	Ireland	117
Silt-Clay loams	407-417			U.S.A.	60
Silt-Clay loams	24-561		4.7-7.4	U.S.A.	100
Silt-loams	250-257			U.S.A.	60
Silt-loams	260-273			U.S.A.	60
Silt-loams	590		5.8	Scotland	8
Silt-loams (poorly drained)	448	51.5	5.0	Ireland	117
Loams (old Red Sandstone)	340-490		5.8	Scotland	8
Loams (well drained)	341-623	45-69	5.5-7.5	Ireland	117
Loams (moderately well drained)	431	69.2	6.3	Ireland	117
Loams (poorly drained)	350	70	5.5	Ireland	117
Loams	165-1239	21.1-54.7		Germany	29
Loams (basic igneous)	680-810		5.8	Scotland	8
Loams (poorly drained)	310		6.3	Scotland	8

Soil type/parent material	Organic P content range (ppm)	% total P	Soil pH	Country	Reference
Sand-Loams	210-365			Scotland	8
Sand-Loams	600		5.8	Scotland	8
Sand-Loams	220-920		5.2-6.3	Scotland	8
Sand-Loams	210-365	26.6-54.6		Germany	29
Sand-Loams	10-20	12-30		U.S.A.	154
Sand-Loams (well drained)	442-523	59.8-67	5.3-7.4	Ireland	117
Loamy-sands	115-550	14-54		Germany	29
Organic-loams	290-647	58-60.5	4.9-7.6	Ireland	117



LUDECKE, 1962.
10³ lbs / ACRE FOOT
4
3
2
1
INORGANIC PHOSPHORUS
TOTAL PHOSPHORUS
ORGANIC PHOSPHORUS
20
24
28
32
36
40 INCHES
RAINFALL


SOIL pH v. ORGANIC PHOSPHORUS CONTENT
AS PERCENT. TOTAL PHOSPHORUS
X FROM WALKER AND ADAMS, 1958
● ○ FROM THOMPSON ET. AL., 1954
● CULTIVATED
○ VIRGIN
pH
8
7
6
25
50
75
100 %

The proportion of total soil phosphorus present as organic phosphorus

In most soils, the organic phosphorus accounts for 10-70% of the total phosphorus compliment of the soil. There is considerable variation between soils of various types however (Table 1). Extreme values of 2.5% and 95% have been recorded (16, 97, 146). The world average is about 55% and more than 80% of world soils have more than 50%. With soils in the British Isles, the average proportion is about 70% and about 90% of soils have a proportion above 50%. From this evidence, it is clear that the organic phosphorus is a considerable proportion of the total present in soils.

Two factors appear to be important in conditioning the proportion that organic phosphorus makes of the total. These factors are soil pH (Fig. 2)and rainfall (Fig. 3).

The chemical nature of organic phosphorus in soils

The term 'organic phosphorus' has been used rather loosely by some authors to mean phosphorus associated with organic matter. Plant and animal tissues and excreta contain some inorganic phosphorus however (22, 40, 206, 239).

It is used here to mean phosphorus in chemical combination with carbon, oxygen, hydrogen, nitrogen, and perhaps other elements.

The chemical nature of much of the soil organic phosphorus is not yet known. Some of the organic compounds containing phosphorus are phytin, nucleic acids, muclectides, phospho-lipids and sugar phosphates (7, 27, 47,). It is uncertain whether any of these originates directly from plant and animal tissues or animal excreta (27). It is probable that most of the compounds in soils are of microbial origin; the majority of the phosphorus forms added in organic matter are probably transformed by the microbes in the process of organic matter decomposition. There is some doubt about this in the case of the phytins. These compounds occur widely in plant tissues and are the principle source of phosphorus in many grains (14) and have not been conclusively identified in micro-organisms (48).

Phytins are calcium-magnesium salts of inositol phosphate. The presence of these substances in soils has been detected by many workers (8, 12, 33, 37, 48, 62, 69, 187, 188, 237, 248, 278, 281).

Inositol, the parent cyclic polyol occurs in a number of stereo-isomeric forms. Of these myo-, scyllo-, neo-, and dl-inositol have all been isolated have been isolated in very small quantities (12).

The inositol phosphates are the phosphorus esters occurring in greatest quantity in soils. A range of quantities from 4 to 460 ppm have been found in a variety of soil types (8, 37, 48, 248). The proportion of organic phosphorus present as inositol phosphates varies from 2 to 58% (8, 37, 48, 62, 188, 248). The origin of these phosphates in soils is a subject of debate at the present time (8, 48). Of the various forms of inositol, only myo-inositol seems to be present as the hexaphosphate in plant and animal tissues (14, 121). Dl-inositol hexaphosphate has been found present in soil organic matter (50) but is not found in plant and animal tissues (14). It may thus be of microbial origin (50). The same argument applies to the presence of scyllo-inositol hexaphosphate in soils (38, 50) and may be also to neo-inositol hexaphosphate.

The nucleic acids occur in every living cell and are added to the soil in decomposing microbial, plant and animal remains probably in greater amount than most other phosphate esters. They are of two types RNA and DNA. The chemistry and biology of the nucleic acids are subjects of a number of reviews (42, 183). Relatively few investigations of the nucleic acid-nucleotide content of soils have been made. Some early work on this provided estimates, which are probably far too high. Figures given range from 19 to 65%* of the total organic phosphorus in soils (32, 238, 280). O

Other work has failed to reveal the presence of any nucleic acid in soils (2, 281). More recently estimates of 0.6-2.4%* of the organic phosphorus have been given (10). It seems unlikely that nucleic acids or nucleotides account for more than 5-10%* of the ester phosphate in soil (7).

A small proportion of soil phosphate is present in phosphatides or phospholipids, a biologically important class of phosphate esters soluble in ether, chloroform or benzene (175, 276). Among the most widely occurring are the glycerophosphatides which include phosphatidyl choline (lecithin) phosphatidyl ethanolamine and phosphatidyl serine. Lecithin may be one of the predominant soil phospholipids (116). The highest quantities of phospholipids found in soils are 18-34 ppm* (243). More recent work gives figures in the region of 3-7 ppm* (116, 238, 256).

* Some authors quote figures in per cent total phosphorus, others the proportion of the soil. These are distinguished more clearly by use of % and ppm respectively.

There is some evidence for the presence of glucose-1-phosphate (216) and glycerophosphate (188) in soils. These esters are very rapidly hydrolysed in acid and would not survive extraction procedures commonly used for the determination of organic phosphorus. Comparisons of different extraction procedures indicate that small amounts of acid-labile esters occur in some soils (63, 115, 120). A small amount of phospho-protein may also be present (10).

At present, the balance sheet for organic phosphorus in soils is far from complete. Low molecular weight organic compounds account at most for only 50-60% of the total organic phosphorus in soils. High-molecular- weight organic phosphorus compounds, in the order of 5×10^4 molecular weight have been extracted from some soils (249). Many yeasts of Hansenula and related yeast genera produce phosphorylated mannose polymers (98, 139, 236). The cell walls of many gram-positive bacteria contain techoic acids which are polymers of ribitol phosphate and glycerophosphate (28, 230, 277). It is possible therefore that this polymeric organic phosphate in soils is of microbial origin. Though this polymeric material has not yet been characterised or quantified, however, it may make up the remainder of the organic phosphate.

Mobility of organic phosphorus compounds in soils

The mobility of organic phosphorus (in contrast to the mobility of inorganic phosphate) in soils seems to have received hardly any attention at all. In general, very little organic phosphorus is found in soil solution (80, 82, 151, 208, 282). The insolubility of organic phosphate in soils is attributed to its formation of insoluble complexes with iron and aluminium, particularly under acid conditions, (9, 134, 278) and its adsorption on to clays (9, 101, 102, 103, 131, 201, 270, 271). It is not surprising therefore that inositol hexaphosphate is hardly mobile in soils (34). In this work, immobility was attributed to formation of insoluble ferric inositol phosphate. In contrast however, some early work demonstrated that 80 or more per cent of applied organic phosphate could be leached through some near neutral or neutral soils (124, 241).

On water-saturated calcareous soils, organic phosphorus can become mobile. The mobility is thought to be associated with microbial activity (118, 119, 286). In relation to this point, it is interesting to note that the so-called soluble soil organic phosphorus fraction has been considered to be in micro-organisms (44, 151).

Importance of organic phosphorus in plant nutrition

Evidence that the phosphorus combined in organic compounds in soils is of value in plant nutrition comes from a number of sources. Indirect evidence comes from the observation that on cultivation of soils the amount of organic phosphorus they contain decreases (85, 160, 204, 230, 251, 252, 254). Citric acid-soluble organic phosphorus in soils also decreases during the period of plant growth (73, 256). Phosphorus in various forms of organic matter, including sheep faeces, green manures and tree litter, is known to be available to plants (79, 83, 177, 178, 260). However, such materials are known to contain inorganic phosphorus so these results are inconclusive.

More direct evidence has come from experiments in which organic phosphorus compounds have been added to soils or culture solutions, containing actively growing plants. Such additions generally result in increased phosphorus uptake by the plants (6, 20, 89, [illegible], 215, 227, 228, 240). Though some reports have indicated that organic phosphorus may be taken up directly by plants under some conditions (75, 215, 221), it is generally considered that organic phosphorus is of little direct value in the phosphorus nutrition [illegible] (43, 58, 70, 208, 268). Since plants are able to use only soluble inorganic [illegible] a source of phosphate (20, 53, 77, 208, 231, 243, 259), the contribution [illegible] organic phosphorus makes to the plant available phosphorus pool in soils, is dependent on the rate at which it is mineralised. Consequently only in soils where much mineralisation occurs does a substantial part of phosphorus in plants come from soil organic matter (234).

Mineralisation of organic phosphorus in soils

Evidence that organic phosphorus undergoes mineralisation, i.e. decomposition into inorganic phosphate and organic radicals, occurs in soils, arises mainly from two types of observation. First, cultivation and liming of soils results in a decrease in the organic phosphorus content (54, 91, 113, 160, 201, 202, 204, 251, 254). Second, and more convincingly, in laboratory incubation experiments, the observed decrease in organic phosphorus content of soils incubated for various periods is usually accompanied by an increase in inorganic phosphate (32, 58, 91, 122, 144, 149, 151, 179, 215, 233, 251, 252, 261).

Much of the organic phosphorus in soils is particularly resistant to decomposition. In contrast, organic phosphorus added to soil in plant and animal residues is often mineralised more quickly. This difference may be due to the relatively insoluble state of the organic phosphorus in soils compared with that in the residues. The other most likely cause for this difference is that the overall compositions of the organic phosphates in soils and freshly decomposing organic matter are different and that the various components have intrinsically different decomposition rates. In support of the second point, the majority of the organic phosphorus components in plant and animal tissues and micro-organisms are compounds such as nucleic acids, nucleotides, phosphosugars, phospholipids (3, 78, 211, 223, 239) and comparatively little occurs as phytic acids (185, 247). Soils on the other hand contain mainly phytic acids and complex polymers and small amounts of nucleic acid, phospho-lipids and phosphosugars (see earlier).

The rates of mineralisation of various organic phosphorus compounds in soils have been studied by a number of workers (18, 19, 46, 65, 66, 68, 101, 133, 194, 203, 210, 219, 229). A survey of the results of these workers shows that glycerophosphate, nucleic acids, and phospho-lipids are all fairly rapidly mineralised. The rate of decomposition however varied with different soil types. These materials form the majority of the organic phosphorus components in organic matter. Phytic acid on the other hand is slowly mineralised in soils. This accounts for its occurrence in fairly large quantities in soils. The quantities of the various compounds found are roughly inversely related to their rate of decomposition in soils. This accounts for the relatively high resistance to decomposition of soil organic phosphorus as compared to that in plant and animal residues. It has also been found that the availability of phosphorus in various organic compounds to plants is directly related to the rate at which the organic compound is mineralised, namely in the order phosphoglycerate phosphosugars nucleic acids phospho-lipids phytins (20, 89, 215, 227, 228).

The organic phosphorus of bacteria and fungi is decomposed rapidly by soils (15, 203). This rapid rate of mineralisation is probably related to the relatively high proportion of phosphorus to carbon in these substrates. Addition to soils of materials low in phosphate results in the microbial fixation of the phosphorus (149, 150, 151, 184, 246). Whether mineralisation or microbial fixation of organic phosphorus occurs is partly due to the balance between energy sources and phosphorus content of the added material i.e. the C:P ratio. When organic material contains in the order of 0.2% or more phosphorus, initial net mineralisation of the organic phosphorus component occurs. If present in less than about 0.2% microbial immobilisation of the OP occurs (40, 79, 150, 151, 173, 203, 235). Mineralisation occurs in soils if the C:org. P ratio is below 200:1 and immobilisation occurs if it is above 300:1 (4, 27, 151). In the intermediate levels, the situations vary with organic matter and/or soil conditions. Thus it can be seen why high C:P and N:P ratios of soils may be indicative of regions where phosphorus deficiencies occur (1, 201, 268). During the mineralisation of organic phosphorus in soils there is concurrent mineralisation of carbon and nitrogen. Frequently the amounts of all three mineralised are positively correlated (1, 251, 284). In other cases, the amounts mineralised correspond to the proportions of the minerals in the organic matter. In general, the amount, form and characteristics of the soil humus and its relation with the mineral part of the soil, strongly determine the accumulation and stability or the decomposition of soil organic phosphorus (226).

The behaviour of organic phosphorus is however not completely analogous to those of carbon and nitrogen during mineralisation. The rate of mineralisation of organic phosphorus may be more dependent on temperature than the rates of mineralisation of other organic matter components (1, 263). The rate of mineralisation of organic phosphorus is low at low temperature, increases with increase in temperature and is particularly marked at 25-30°C and above (1, 32, 71, 122, 284).

Heating, drying and rewetting of soils appear to increase the rate at which organic phosphorus is mineralised (23, 122, 170, 174). These physical factors are known to lead to a general increase in the rate of decomposition of organic matter (23, 122, 170, 174, 242, 274). This probably results from the antagonistic effects of these factors on microbial populations (136, 170, 242) and, may be, from physical fragmentation of the organic matter (25).

Clays have been shown to markedly decrease the rate of mineralisation of organic phosphorus in soils (102, 103, 105, 135, 194). This probably results from the adsorption of the organic phosphorus on to the clay (9, 32, 46, 101, 102, 104, 124, 151, 210) or the adsorption of phosphatase enzymes (155, 194, 213). The adsorption of substrates by clays is pH dependent. The amount adsorbed is far greater at acid than at alkaline pH's (101, 102). The adsorption of organic phosphates preventing their mineralisation, may thus be more important in acid than alkaline soils. The inorganic phosphorus produced on mineralisation of organic phosphorus is also adsorbed by clays (55, 123). They may therefore also affect the availability of the product to plants.

The soil pH is a major factor in determining the rapidity of organic phosphorus mineralisation. The rate markedly increases with increase in soil pH (1, 65, 203, 219, 251). Liming to increase the pH of acid soils, generally leads to an increase in the rate at which the OP is mineralised (91, 113, 152, 182). The effect of pH on the rates of mineralisation of carbon and nitrogen is not so marked (251). This pH effect on mineralisation of organic phosphorus may operate in a number of ways. Firstly there is the adsorption of substrate or enzymes on to clays, mentioned above. Secondly the iron and aluminium complexes or organic phosphates vary in their solubility with pH. These complexes are much less soluble under acid than alkaline conditions (9, 134). Phosphatase enzyme activity is also influenced by pH (125, 212) but this is discussed below.

Though a very small part of the organic phosphate may be hydrolysed by soil acids, the vast majority of that mineralised is hydrolysed by the phosphatase enzymes. A large number of studies have been made of these enzymes in soils (65, 88, 90, 112, 125, 126, 129, 155, 161, 164, 165, 166, 181, 212, 213, 214, 219). Phosphatase enzyme activity has been found to vary with soil type (65, 88, 125, 153, 161). Phosphatase enzyme activity is lowest in calcareous podzolised and deep chernozems and greater in brown forest, and pale to dark gray podzols (88, 161). However other results show the activity in brown forest (beech-oak vegetation) to be relatively low compared with meadow and steppe renzina soils (65). Some investigators have observed an inverse relationship between soil phosphatase activity and the amount of plant-available phosphorus in soils (36, 138, 164, 165). Others have shown a direct relationship (126, 129). Some workers have therefore suggested that the determination of phosphatase might be a useful index of plant-available phosphorus in soils (126, 164, 165). As with the distribution of organic phosphorus, the phosphatase activity of soils decreases with depth down the soil profile (36, 126, 129, 153).

The activity of this enzyme on soil may also be correlated with organic matter content and distribution (112, 153). Many observations show that the optimum pH for phosphatases is near to neutral pH (65, 112, 212, 219). However there is good evidence that there are both "acid" and "alkaline" phosphatases in soils (112, 125, 126, 127, 129). There is also some evidence for the presence of acid, neutral and alkaline phosphatases in the same soils (67, 125). The optimum pH's for enzyme activity are not necessarily the natural pH's of the soils.

(65, 125, 133, 219). Phosphatase activity in soils has been shown to be reduced by drying (88, 133, 213). Phosphatase activity is also inhibited under some circumstances by clays (129, 155, 194, 213). It is also considered to be influenced by other factors such as soil genetic and physico-chemical properties (36), humus content (67), nitrogen and organic matter levels in soils (126, 129).

The origin of the phosphatases in soils is somewhat uncertain. Some authors consider that soil enzymes are mostly derived from soil micro-organisms (4, 47, 87, 88, 127, 128, 130, 152, 163, 190). In support of this, phosphatases have been found to be excreted by a wide variety of microbes (39, 64, 74, 95, 107, 138, 156, 157, 196, 207, 224, 244). These phosphatase-producing organisms are far more abundant in the rhizospheres of root systems than in soil some distance away (108, 224). Acid-phosphatases are however rarely produced by soil bacteria from alkaline soils (172) and not all species of micro-organisms are able to decompose organic phosphorus compounds (108, 156).

In support of the hypothesis that the enzymes mostly originate from micro-organisms, it has been shown in some studies that phosphatase activity of soils is closely related to microbial activity (65, 87, 88). Furthermore, the rate of mineralisation of organic phosphorus in soils is in many cases paralleled by micro-organism activity (73, 113, 251). On the other hand, no correlation between phosphatase and microbial activity or numbers has been shown in other investigations (90, 153, 164).

Enzymes may also come from other live or dead material present in soil (84, 158, 199, 200, 232) or from animals (162). Some investigations have demonstrated the release of phosphatases from plant root systems (72, 75, 215, 220). Some doubt has been expressed on the validity of these results in view of the difficulty of obtaining roots free from micro-organisms (106).

Conclusion

Apparently very little research on this topic has been directed to woodland and forest soils; by far the majority of it has been related to agricultural soils. Despite this, the fundamental relationships between soil organic phosphorus its mineralisation and soil conditions outlined in this review may be expected to apply to woodland and forest soils and thus provide a substantial background to the studies under project 307.

One aspect of this field of work has, however, hardly been touched upon. This is the relationship between vegetation and soil organic phosphorus and its mineralisation. In conclusion therefore it is very appropriate to suggest some generalised relationships.

The largest component of a woodland or forest is that of the trees. Trees are known to influence strongly the soil properties and different species to influence soil properties differently. It is probable that different tree species influence differently the rate of organic phosphorus mineralisation or accumulation in soils. There are three probable mechanisms:-

a) different tree species may merely alter, in different ways, the physical and biological properties of soil, which directly influence the mineralisation processes;

b) different tree species may add organic phosphorus to soils at different rates;

c) different tree species may add organic phosphorus of different chemical compositions; different substances have different 'intrinsic' rates of mineralisation in soil.

By causing differences in the rates of mineralisation or accumulation of organic phosphorus, trees will affect differently the availability of phosphorus in soils. The poorer the total phosphorus content of a soil, the greater will be the magnitude of the effect. The affects on the availability of phosphorus can have two important ecological consequences.
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First, some tree species may decrease over a period the availability of phosphorus in soil. In some cases, this may occur to such an extent that their own or other species may not regenerate. Local oak-oak/ash woodlands may be a case in point. Other tree species may have a favourable effect on the processes and thus may be regarded in this context as soil improvers.

Second, changes in the availability of phosphorus in soil probably have dynamic effects on the herb layer. It is possible therefore that different tree species, by their influence on the availability of phosphorus, partly condition the composition or changes in the composition of the herb layer below them.

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