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SOME MINERAL RELATIONS
OF PLANTS AND SOILS

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I. ABSTRACT

The following papers record an investigation of some relations between vegetation and the soil in three major types of habitat - (1) Lake District woodland on non-calcareous glacial drift, (2) aquatic and waterlogged sites in the same region, and (3) an upland granitic area in Scotland. An attempt has been made to relate certain properties of the soil exchange complex to processes of soil development, and to vegetational differentiation and nutrient status. The major conclusions drawn may be summarized as follows:

(1) In the woodlands studied, topography appears to be the main factor in determining whether a flushed brown earth with a <u>mull</u> humus layer and an ash-sycamore-oak-hazel tree community will develop, or a leached podzolic brown earth with a <u>mor</u> humus layer and oak, birch and rowan as the characteristic trees.

(2) In passing from relatively inorganic underwater soils - through marsh, fen and lacustrine bog soils - to highly organic raised bog peats; both the amount and strength of soil acids increase, <u>C/N</u> ratio rises, and base saturation falls. This is reflected in the nutrient status of the plants; those from underwater habitats being highest in minerals and nitrogen, and those from raised bogs being low in both these constituents.

(3) It appears that the first addition of organic matter to the Scottish granitic soils brings about a sharp increase in

acidity and a marked fall in base saturation. The presence of comparatively strong acids in the humus produced by the colonizing plants is suggested as a possible advantage, in view of the difficulty of obtaining mineral nutrients from the granite substratum.

A study has also been made of some elements and chemical properties figuring in the exchange complex of a peat profile (Journal of Ecology, 1949). Some of the variations may well be related to those in the vegetational composition of the peats, for a sequence of plant communities of very different character has occupied the site as distance from the mineral soil has increased.

Conjointly with A.M. Mayer an investigation of iron and manganese in natural vegetation of the Lake District has been carried out (Annals of Botany, 1951). The content of both elements is higher in natural vegetation than is usual in crop plants, probably because of the greater acidity and organic content of the natural soils. The amounts absorbed are shown to vary with the species, the plant group, and the habitat.

II. SOME CHEMICAL CHARACTERISTICS OF WOODLAND SOILS IN THE ENGLISH LAKE DISTRICT

In the study of soil formation, increasing attention is being given to the influence of relief on the processes by which mature soils are developed; and the concept of the catena (Milne, 1935) or hydrologic soil series (Mattson & Lönnemark, 1939) is proving of great value in attacking ecological as well as pedological problems. The aim of the present paper, which deals chiefly with the characteristics of the soil exchange complex, is to illustrate this role of topography as a soil-forming factor - with reference to a series of hillside woodlands along the shores of Windermere, in the English Lake District. In these communities there are two clearly recognizable trends in soil and floristic development, the nature of the relief appearing as the main factor responsible for their differentiation.

DESCRIPTION OF THE AREA

The Lake District is located in north-western England, longitude 3°, latitude 54-55°; and includes parts of Westmorland, Lancashire and Cumberland Counties. It is an area well-known for scenery and striking relief, with eight mountains of about 1,000 m and 15 lakes of considerable size within a circle of about 50 km diameter. In the southern part where the present work was carried out, the rocks are chiefly non-calcareous Silurian slates and grits;

and are overlain by glacial drifts. Rainfall is high, ranging from about 125 to 375 cm per year.

As might be expected, there is a wide range of plant communities in the district. Some of their wider ecological relations have been described by Pearsall and Pennington (1947) and Pearsall (1950). On the uplands (beneath the true montane zone) *Festuca-Agrostis* grassland predominates on the better soils, and in recent years has been much invaded by bracken (*Pteridium aquilinum*). In wetter and more heavily leached areas *Nardus* grassland may be present on rather peaty soils, often as a result of overgrazing. On the most poorly drained soils are found moorland and bog communities, dominated by such species as *Calluna vulgaris*, *Eriophorum vaginatum*, *Scirpus caespitosus*, *Molinia caerulea*, *Myrica gale* and *Sphagnum*.

The woodlands are usually found on the lower slopes, and through centuries of exploitation are now much reduced - though amenity planting has compensated to some extent for the ravages of the past. Much of what is now grassland and moorland has been derived originally from woodland; and parts of these lands are now being restored to forest (albeit of an unnatural type) through the activities of the Forestry Commission. The native woodlands in the district are generally dominated by oak (*Quercus petraea*) with hazel (*Corylus avellana*) often abundant in the understory. Along the lines of drainage, streaks of ash (Fraxinus excelsior) are common. This species is also plentiful both at the lowest levels along the lake shores, and at higher levels on unstable screes. On the valley bottoms alder woods were formerly common, but have largely been cleared for agriculture. On the most poorly drained of these alluvial lands are found fens and lacustrine bogs; and in a few cases true raised bogs have developed.

The sites investigated in the present study are mostly from rather fragmentary oak woodlands along the slopes beside the western shore of Windermere, in the southern part of the Lake District. While partly planted, they have been allowed to develop relatively undisturbed; and since oak has been the tree generally planted, these sites may be classed as semi-natural. A few samples have also been collected from coniferous plantations in the vicinity. Rainfall in this area is probably of the order of 175 cm per year. The soils are of the brown earth type, but are much modified in many places by severe leaching; so that two main subdivisions may be distinguished.

Flushed brown earths - on the gentle slopes and flatter lands near the lake shore, and extending upward along the lines of drainage; appearing in seepage zones. These soils show little or no surface humus accumulation, due to the activities of the soil fauna (especially the larger earthworms) in mixing fallen litter with the mineral soil. The upper layers are brown to dark brown in color, with a mull* type of humus layer and a pronounced crumb structure. Under-

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* For a clear and detailed description of the nature and differences of mull and mor see Romell and Heiberg (1931) and Romell (1932, 1935).

neath the soil becomes rather more plastic and yellowish brown (sometimes with a faint reddish brown tinge) and grades into greyish and rather clayey soil below.

These sites support woods characterised by ash (Fraxinus excelsior) and sycamore (Acer pseudoplatanus), with oak (Quercus petraea) frequent and hazel (Corylus avellana) abundant in the understory. The ground flora is rather open and rich in herbs. Mercurialis perennis is the most characteristic species, with Allium ursinum, Scilla nonscripta, Brachypodium sylvaticum, Melica uniflora, and Deschampsia caespitosa locally plentiful in addition to the wide variety of herbs.

Leached brown earths - on the upper slopes, extending down on to knolls near the lake shore. The most extreme examples of this group develop a strongly podzolic character. The surface consists of a mor* layer of matted or amorphous organic matter, brown to blackish in color and covering a greyish-mottled and heavily leached mineral horizon. Beneath this leached layer there is a zone of humus and sesquioxide accumulation, usually rusty colored with iron compounds, but loose and showing no tendency to hardpan formation. However, while surface humus accumulation is common, the profile development on these sites is usually not sufficiently extreme to develop a true "bleached layer"; and a direct transition from the unincorporated organic matter to reddish brown mineral soil is much more common (compare Lunt, 1948). The thickness of the organic surface layer varies considerably, but

* see footnote on previous page.

is seldom more than 5 cm, and in some of the leached soils may be entirely absent. These latter generally differ from the mulls in color, and always lack a crumb structure. They are also distinguished by quite different chemical properties, and in this respect resemble the mineral soils beneath the unincorporated organic matter of the extreme mor forms. The larger earthworms are not common on these soils, and are almost entirely absent where there is much humus accumulation.

On these sites birches (Betula pubescens and B. verrucosa) and rowan (Sorbus aucuparia) accompany the dominant oak, especially in the more open locations. The ground flora is largely a close carpet of mosses and grasses except in the more shaded places, and contains a much smaller proportion of herbs. Though Galium saxatile, Solidago virgaurea, Scabiosa succisa or Oxalis acetosella are generally to be seen on these soils, the only herbaceous species found on the highly organic leached surfaces in real abundance is Melampyrum pratense, which may grow in association with the roots of other plants. The dominant species in the ground cover of these organic and extreme mor surfaces are Deschampsia flexuosa, Vaccinium myrtillus and Dicranum majus while Pteridium aquilinum, Holcus mollis, Agrostis, Anthoxanthum odoratum and Mnium hornum often predominate on the less organic soils.

This leached soil type is the usual one under conifer plantations in the vicinity. These have a rather sparse ground flora, similar in species to that of the leached soils under oak.

The two soil classes described above are connected by intermediate types, usually with a surface of low organic content. The "average" soil in these woodlands would probably be defined as moderately leached, and bears oak-hazel wood with a rather variable ground flora. However, in the present study only the two clearly distinguishable series have been selected for study - characteristic flushed soils with a mull humus layer, good crumb structure, and little profile differentiation; and typical leached soils, usually with a well-defined fibrous or amorphous mor humus layer, and a clearly marked podzolic profile development.

Pearsall (1938) has also described woodland soils from this general area - in terms of their surface properties of acidity, redox potential and nitrification; and in relation to the plant communities they support. The extremely leached soils with a raw organic surface fall in Pearsall's group A, while the flushed soils correspond to group C. The less organic leached soils and the intermediate types in general belong to group B.

METHODS

The surface soils have been given most attention in this study, for they have undergone the greatest changes since the original glacial drift was laid down. However, the limits of the sub-surface differentiation have been roughly indicated by examination of three profiles illustrating (1) good flushed conditions and (2) extreme degrees of leaching, under both oakwood and a coniferous plantation.

For comparative purposes, and in order to obtain some idea of the nature of the original glacial drift, a series of samples has also been collected at depths between 2 and 4.5 m beneath the soil surface. At these levels there is very little organic matter present, and leaching appears to have had little effect on the soil material.

The data for the surface samples and the deep drifts have been examined chiefly in relation to the amount and type of organic matter present. In this way we may obtain a picture suggestive of a developmental trend, from the purely mineral soils of the immediate postglacial period to the often highly organic woodland soils of today. Such an interpretation must of course be applied with caution, since it is not certain that present-day organic soils once had entirely the same properties as present-day inorganic soils. In other words, variation in the amount of organic matter now present may reflect some other differences in the sites beside quantitative differences in rate of humus accumulation. Nevertheless, since organic and inorganic soils generally appear to form an intermixed mosaic of relatively small patches in these woodlands, and since extreme conditions of moisture were avoided, it is believed that such a method of treatment may be of some value.

The collections of soil were made in 1948 and 1949, during the months of June, July and August.

Sampling

Surface soils. Samples were taken at various depths within the top 10 cm of the soil, care being taken to avoid any mixing of different horizons. Certain of the less organic samples from leached soils represent the absolute surface layer, while others have been collected from just beneath a thin surface mor layer. These two types are not distinguishable in their chemical characteristics. Certain of the flushed soils received drainage from calcareous rocks, these are marked in the tables and figures. Specimen tubes 2.5 x 10 cm were filled, corked, and stored without drying. The period elapsing between collection and analysis varied from a few days to some months, in the latter case samples were stored during the winter in a refrigerator.

Deep drifts. These soils were collected from recent road workings and local clay quarries in the southern part of the Lake District. A fresh face was always exposed before sampling. The analyses were carried out within a fortnight, and usually within a few days.

Profiles. In order to ensure that the profiles obtained would be representative of brown earths under both typical flushed and extremely leached conditions, a number of shallow pits were dug in various places and their profiles compared. When the most suitable examples were selected, deeper pits were dug (in late August). Samples were then taken in vertical sequence down one side of the pit, from the centre of each morphologically distinguishable horizon, with additional samples in the case of the thicker horizons. The soils were stored in specimen tubes and the analyses carried out about two months later.

The first of the profiles was taken from a flushed brown earth about 1 m in depth, resting on an old sand beach of Windermere; under sycamore, ash and oak with Mercurialis and Brachypodium the chief species in the ground flora. The second was about 60 cm in depth, from a heavily leached knoll above the lake shore; under partly thinned oakwood growing up to birch and rowan, with Deschampsia flexuosa and Vaccinium myrtillus abundant. The third was 45 cm deep, from a plantation of spruce (about 10-25 cm diameter at breast height) at Nor Moss, which is somewhat over one km from the lake shore and roughly one hundred and fifty m above it. Here the soil is mostly less than 25 cm deep and very much podzolized. The samples were taken from a hollow on a slope, where enough soil had accumulated for a profile to develop. The sparse ground flora of Deschampsia flexuosa, Galium saxatile, Agrostis tenuis and Dryopteris spinulosa was not represented where the profile was taken.

Effects of Storage

Determinations of pH on a series of surface samples within ten days after collection (usually much less) and again just before analysis some months later, revealed that changes on storage in the sealed tubes were within the limits of pH fluctuation reported by Clapham & Baker (1939), and also well within the range of variability in different samples taken a few centimetres apart. Nor did the fluctuations transgress the natural boundary between the pH ranges of typical mull and characteristic mor soils, which is discussed farther on.

The results of these tests are of some interest, and are given in Table I. It appears that on long storage there has been a decrease in acidity. This contrasts with results obtained on the soil profiles. The pH of these samples was measured within 48 hours, and again after two months. Both soil types had become more acid, the flushed samples to the extent of about -0.3 pH and the leached samples to about -0.1 pH. In the writer's experience the initial reaction to sampling is on both soil types generally an increase in acidity. This is probably due to the disturbance caused by sieving, which may bring about oxidative acid production, perhaps in the nitrification process. Presumably on sealing the samples the pH change is gradually reversed once more anaerobic conditions set in.

We observe that the changes on storage are much greater in the flushed mulls than in the leached mors. This is true both for the profile series which became more acid, and for the surface samples which became less acid after a longer period of storage. The flushed mull changes are of the order 0.3 pH, while the leached mor changes are of the order 0.1 pH or less. This may perhaps indicate that mull represents a delicate and easily disturbed equilibrium, while mor tends to be a self-stable to a very great degree.

The pH values used in this paper are those made just before the other analyses, in order that the results for both shall be comparable.

Analytical

Before analysis the soils were pressed through a sieve (20 meshes per inch). This was necessary, not only to remove stones, but also to provide a more homogeneous mixture; differences of up to 0.5 pH units being not uncommon in different parts of the sample before sieving. The following values were determined:

pH. Glass electrode on undried sample, without the addition of water except in a few cases of extremely dry samples where steady and reproducible readings could not be secured. In this way the extra variable of dilution effects is avoided.

Water content. Soils dried to constant weight at 100-110°C, results as per cent dry weight of soil.

Ignition loss. Soils ashed in muffle furnace at 525-550°C, results expressed as per cent dry weight of soil. In these samples, with a negligible carbonate content, the ignition loss is chiefly due to the organic matter, except in the deeper soils where the combined water of the inorganic fraction becomes important.

Coefficient of humidity. Defined as the ratio of water content to ignition loss (Crump, 1913). This probably gives a more satisfactory expression of the water content in terms of its biological significance.

Total exchangeable bases. Estimated by the pH change of N acetic acid to which a measured fraction of soil is added (Brown 1943), the pH of the mixture being read off on a curve obtained by titrating N acetic acid with N/10 sodium hydroxide. Results expressed as milli-equivalents per 100 grams dry soil. While the acetic acid probably extracts more bases than N ammonium acetate, it would seem no more empirical to extract at pH 2.3 than at pH 7.0, since the pH values of these soils fall between the two extremes. And acetic acid may give a better picture of what is exchangeable in the unsaturated soils.

Exchangeable hydrogen. Estimated by the pH change of N ammonium acetate to which a measured fraction of soil is added (Brown, 1943), the pH of the mixture being read off on a curve obtained by titrating N ammonium acetate with N/10 hydrochloric acid. Results expressed as milli-equivalents per 100 grams dry soil.

Exchange capacity. Calculated as the sum of total exchangeable bases and exchangeable hydrogen, and expressed similarly.

% base saturation. An expression of total exchangeable bases as percentage of the exchange capacity.

Apparent pK. (pH at half base saturation). Calculated by means of the equation

$$pK = pH - \log \frac{(\text{salt})}{(\text{acid})}$$

using exchangeable bases as (salt) and exchangeable hydrogen as (acid). This is a rather empirical expression, since the soil contains a mixed group of acids in a very heterogeneous medium. However, it gives a rough approximation of their overall strength (low pK values denoting more strongly dissociated acids), and Chandler (1939) states that results obtained in this way correlate well with the values determined experimentally.

Nitrogen. By the micro-Kjeldahl method, on duplicate samples. Results expressed as per cent dry weight of soils.

Volume/weight ratio

The results as given in the tables and figures are expressed on the basis of soil dry weight, since it is the chemical properties of the soil with which we are primarily concerned. It may be of some biological value to compare the results on the basis of equal volumes of soil, though little is known about the extent of root development in soils of different organic content (and therefore different texture), and it cannot be said that plants exploit equal volumes of soils with very different types and amounts of humus. As a means for so calculating the data, some rough measurements have been made of the volume/weight ratios for surface soils in the area. These were obtained by gradually rotating a wide mouthed cylinder into the soil. The weight and volume of stones has been deducted. The results, giving the dry weight and fresh volume of the soil, are presented in Figures Ia and Ib. They indicate that on a volume basis the least organic are about four times as heavy as the most organic soils, and that the lightening effect of humus addition is greatest in the more inorganic soils. It also appears that the crumb structure of the flushed soils does not differentiate them in this respect from the leached soils with similar organic content.

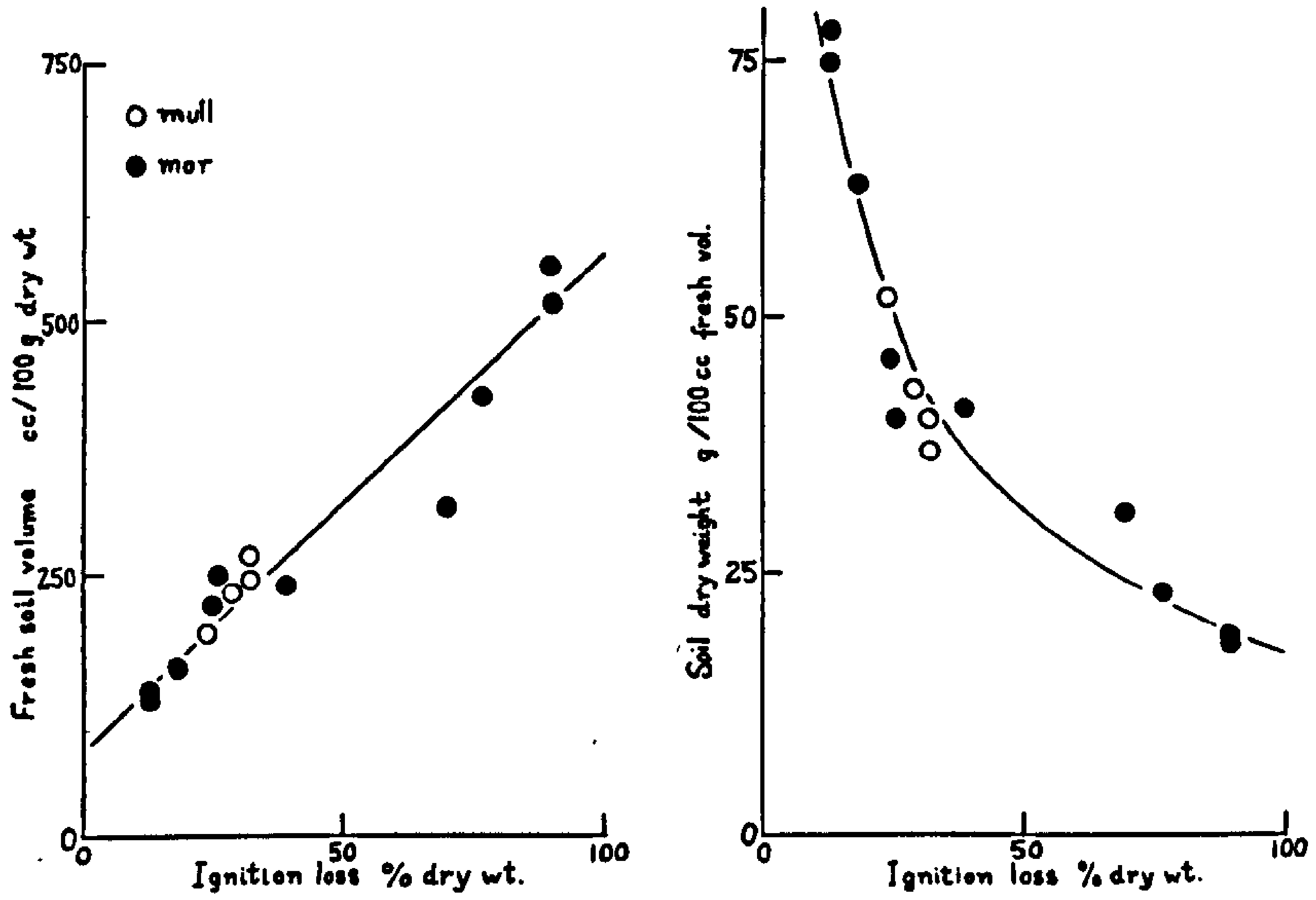

FIGURE I (a). Volume/weight of soil in relation to humus content.

(b). Weight/volume of soil in relation to humus content.

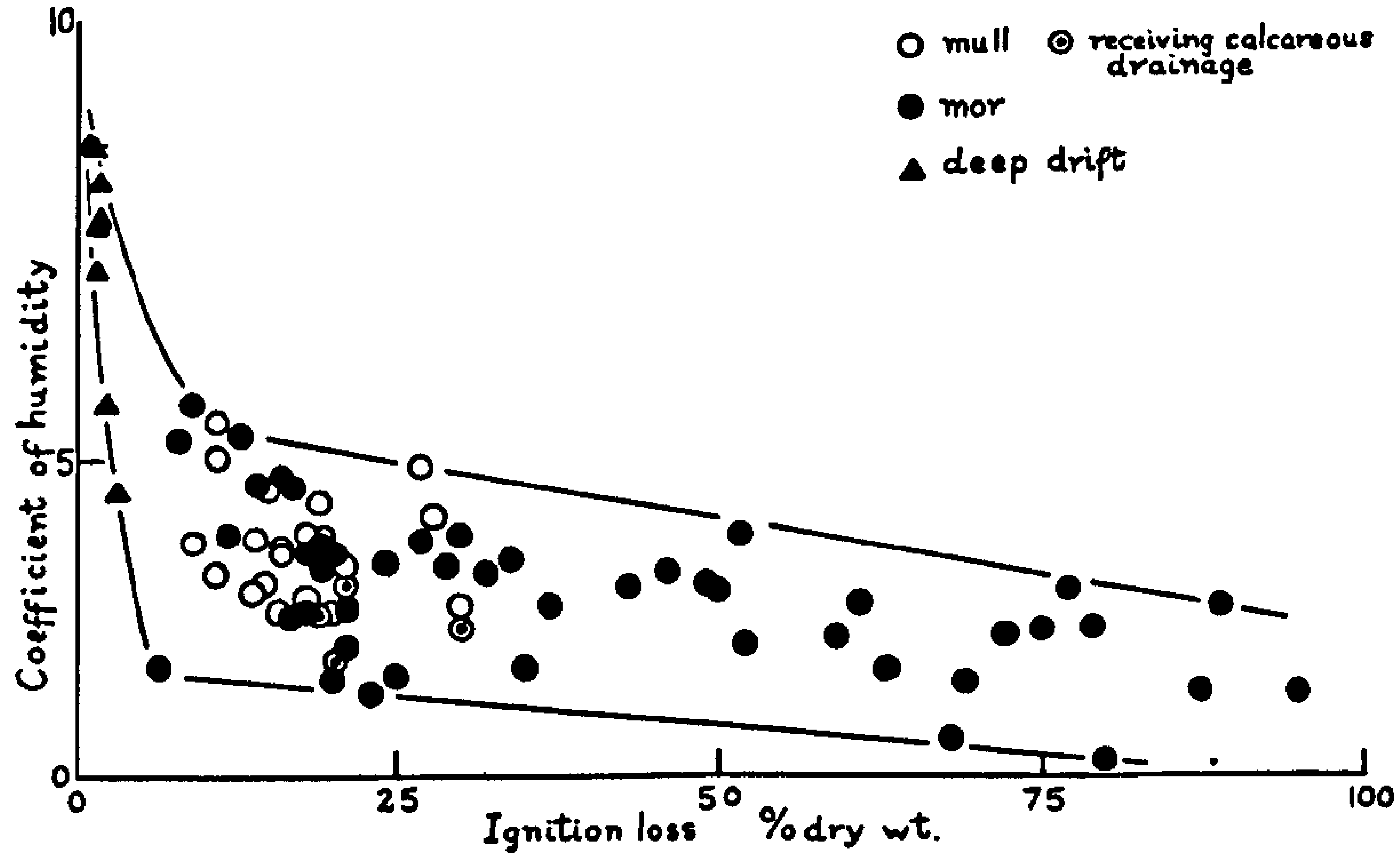

FIGURE II. The coefficient of humidity in relation to humus content.

RESULTS

Deep drifts and surface soils

The data for the deep glacial drifts are given in Table II, for the flushed brown earths in Table III, and for the leached brown earths in Table IV. The surface soils are arranged in order of increasing ignition loss, as a measure of humus accumulation. The drifts are presented in order of increasing depth.

Water and ignition loss. (Figure II). It is clear from the tables that as the organic matter increases in the soil the upper limit of water content also increases greatly, from about 16 per cent in the glacial drifts to as much as 240 per cent in the purely organic *mor* humus. However, these organic soils are not at all wet; and Figure II shows that the amount of water per unit of humus (coefficient of humidity, Crump, 1913) tends to fall as organic matter increases. In the deep drifts the coefficient ranges from 4.5 to 10, in mineral soils with less than 25 per cent ignition loss from 1.3 to 6.0, and in organic soils with more than 75 per cent ignition loss from 0.5 to 3.0. The change in water content is not very great if considered on a volume basis.

It may also be noticed that the flushed *mull* series never reaches a very high level of ignition loss, the highest found being 30 per cent. This is undoubtedly due to the activities of the soil fauna, the large numbers of earthworms being especially effective in mixing the plant residues into the mineral soil. Earthworms tend to be scarce or absent in the leached soils, particularly those with

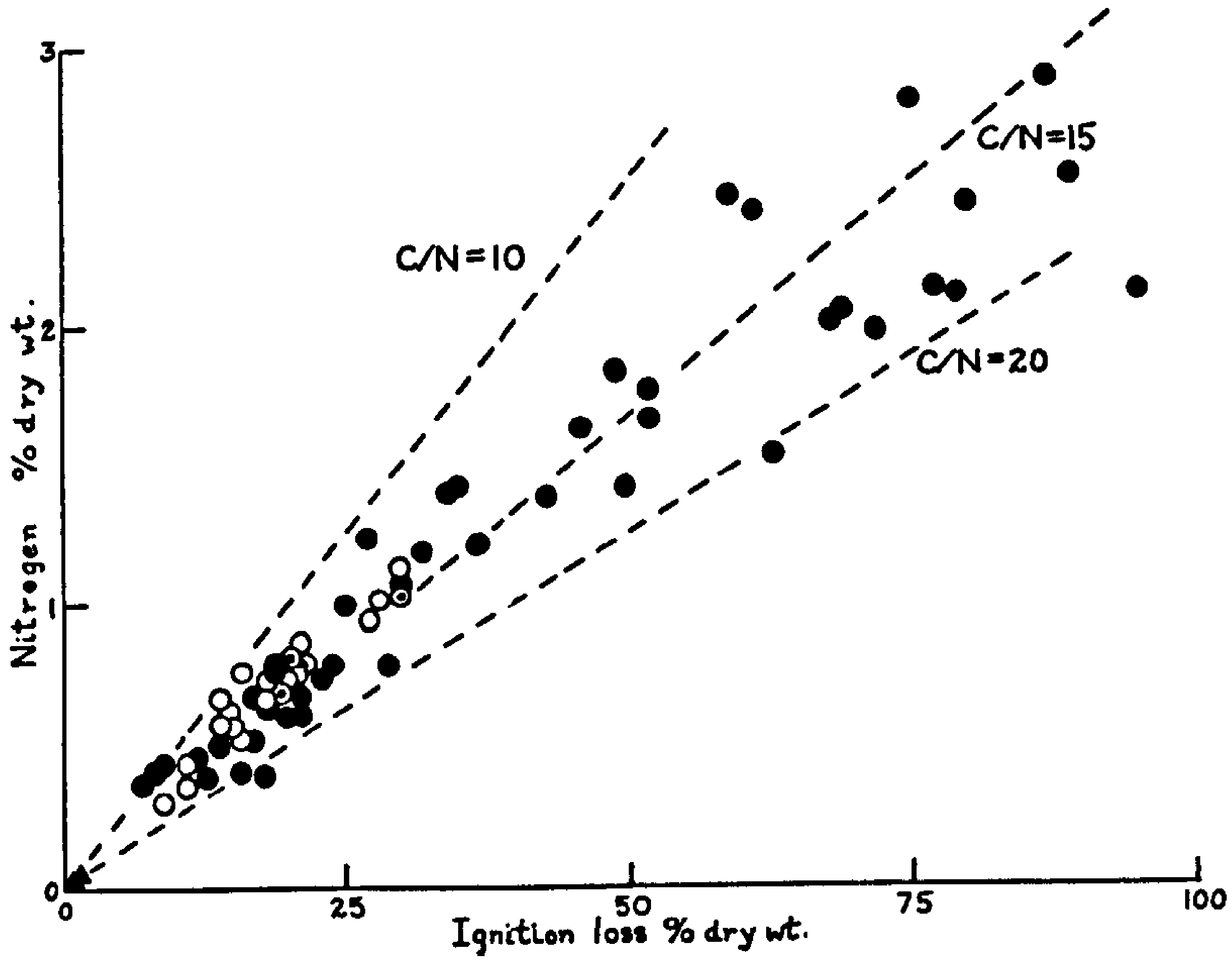

FIGURE III. Nitrogen in relation to humus content.

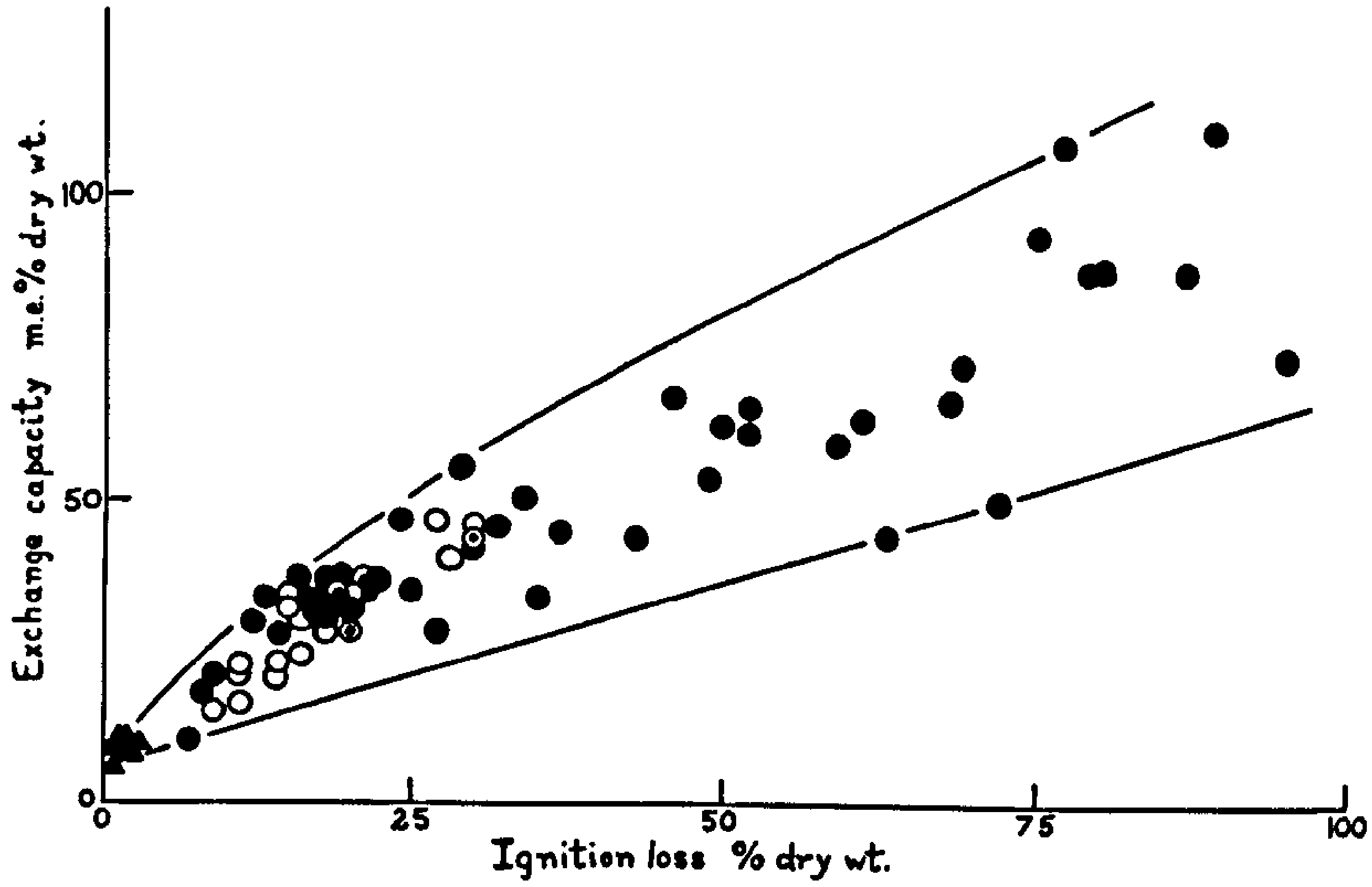

FIGURE IV. Exchange capacity in relation to humus content.

thick mor layers of unincorporated organic matter (Pearsall, 1938). This may be due to differences in palatability of the leaves on the two soil types (see Fenton, 1948) and possibly also to the acidity or to different moisture conditions in the soils.

An interesting example of the importance of earthworms for the maintenance of the mull equilibrium may be seen in the north of Sweden, near Abisko. Here only a very few of the smaller earthworms can be found in the soil, possibly due to the shortness of the frost-free period. It is presumably because of this that, even in the flushed birchwoods which receive calcareous drainage and have species such as Geranium sylvaticum, Lactuca alpina and Trollius europaeus dominating the ground flora, circum-neutral humus is accumulating in thick layers on the surface of the soil (Du Rietz, 1945).

Nitrogen (Figure III). The amount of this element is of course highly correlated with humus content, rising from about 0.05 per cent dry weight in the deep drift samples to between 2 and 3 per cent in the highly organic mor surfaces. If we calculate the ratio of carbon to nitrogen rather crudely, by assuming carbon to be half the ignition loss, we find it to range between 10 and 23. In Figure III the broken lines represent constant C/N ratios of 10 and 20, and can be seen to include all but three values. The values for mull lie between 11 and 16, averaging 13; while the mors range from 10 to 23 and average 15. There appears to be little difference between flushed and leached soils of similar organic content, but there is some tendency for C/N to rise as the soils become more organic. Eleven of the fifteen soils with more

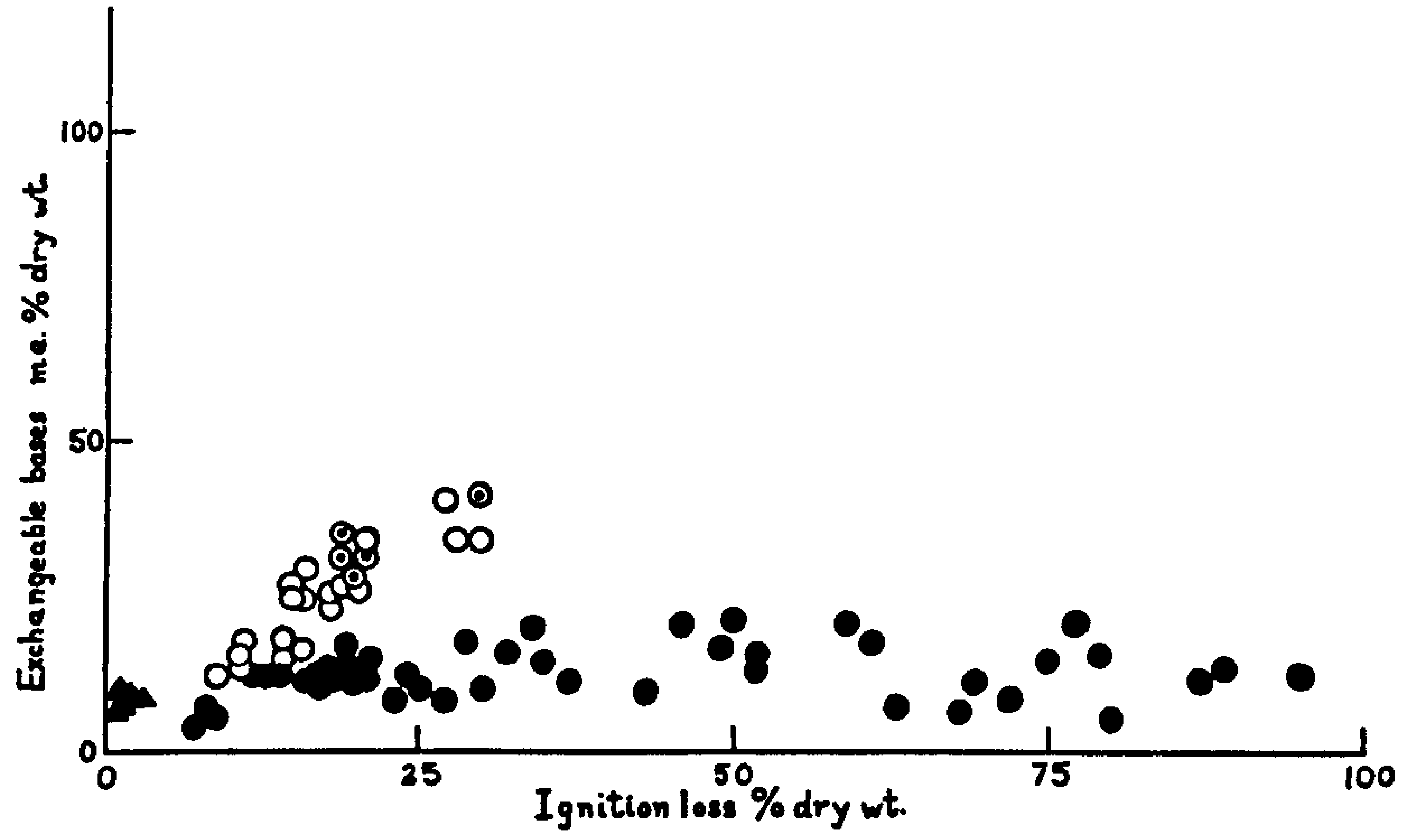

FIGURE V. Exchangeable bases in relation to humus content.

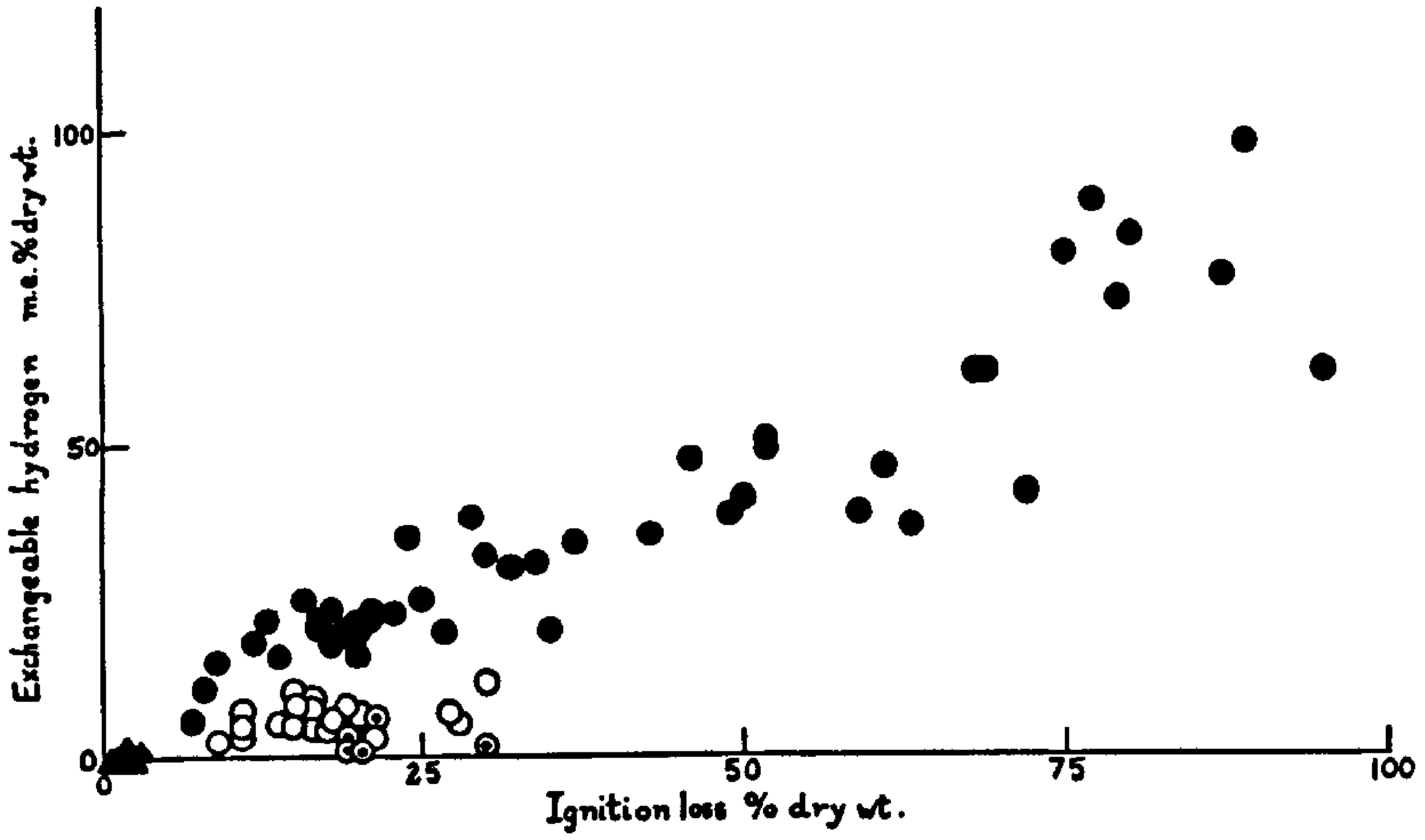

FIGURE VI. Exchangeable hydrogen in relation to humus content.

than 50% ignition loss show C/N ratios above 15. This tendency would presumably show more clearly if a correction could be made for the ignition loss due to the combined water of the mineral soil.

It must of course be recognized that the two soil series may differ considerably in "available" nitrogen. Pearsall (1938), in field tests during late summer, found nitrates most plentiful in mulls, and absent in extreme mors below pH 3.8.

Exchange capacity (Figure IV). The exchange capacity is seen to increase greatly in proceeding from the deep glacial drifts, with 6 to 11 m.e. per cent dry weight, to the highly organic mor layers with from about 50 to 110 m.e. In the latter the highest values are associated with a high degree of decomposition and a greasy amorphous type of organic matter, the lowest values with a more fibrous humus probably containing much living hyphal or root tissue. In this connection Mattson & Koutler-Andersson (1941a) have demonstrated a marked increase in colloidal acidoids during aerobic litter decomposition, which must be largely responsible for the increased exchange capacity. There is no observable difference in the exchange capacities of flushed and leached soils with similar amounts of humus.

Total exchangeable bases and exchangeable hydrogen (Figures V & VI). The results of these analyses are most instructive. The inorganic glacial drifts are low in both constituents, with less than 10 m.e. per cent dry weight of exchangeable bases and less than 2 m.e. of exchangeable hydrogen. The exchangeable bases in the leached soils are fairly constant over the whole range of humus content, the values

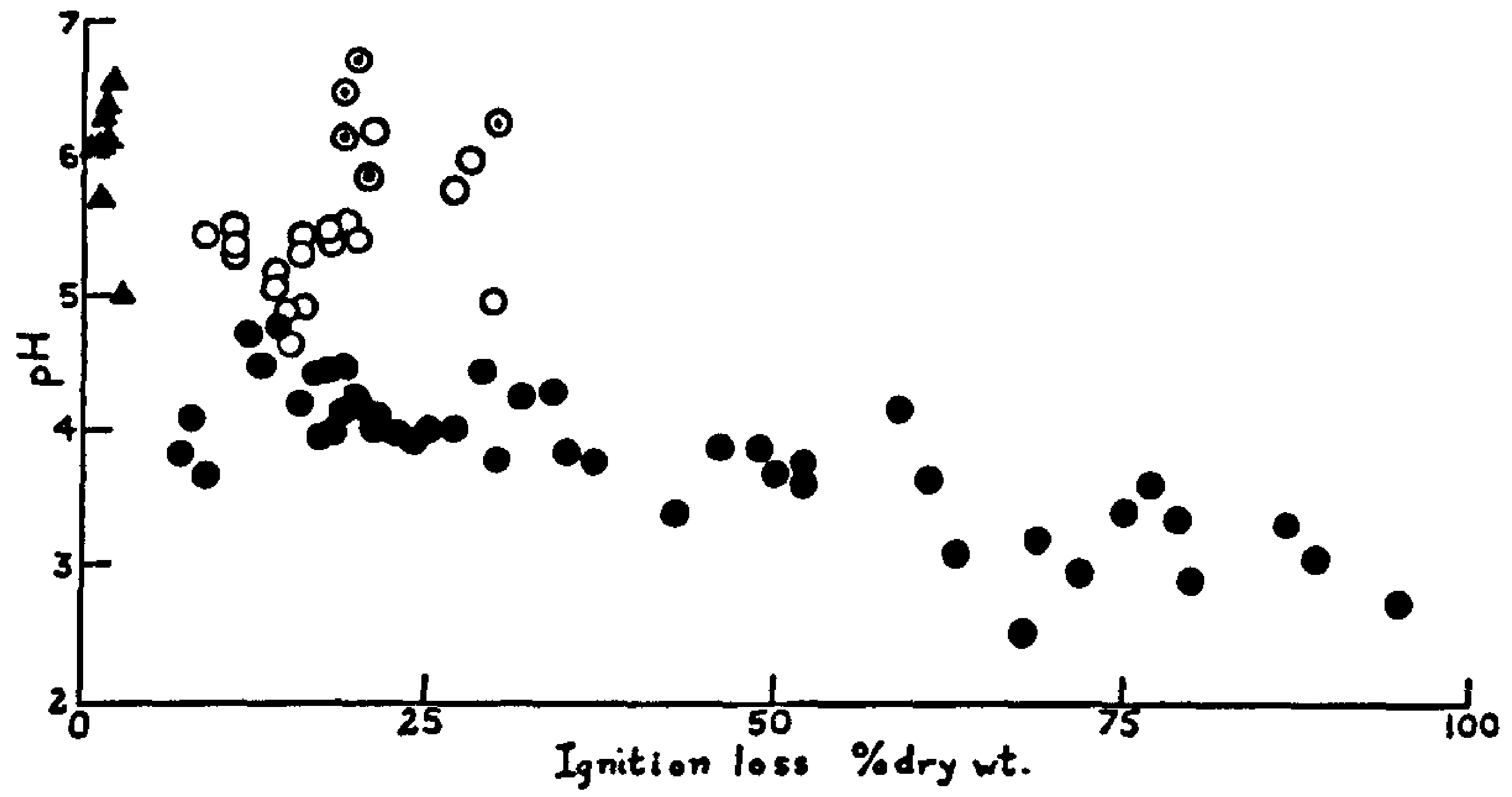

FIGURE VII. pH in relation to humus content.

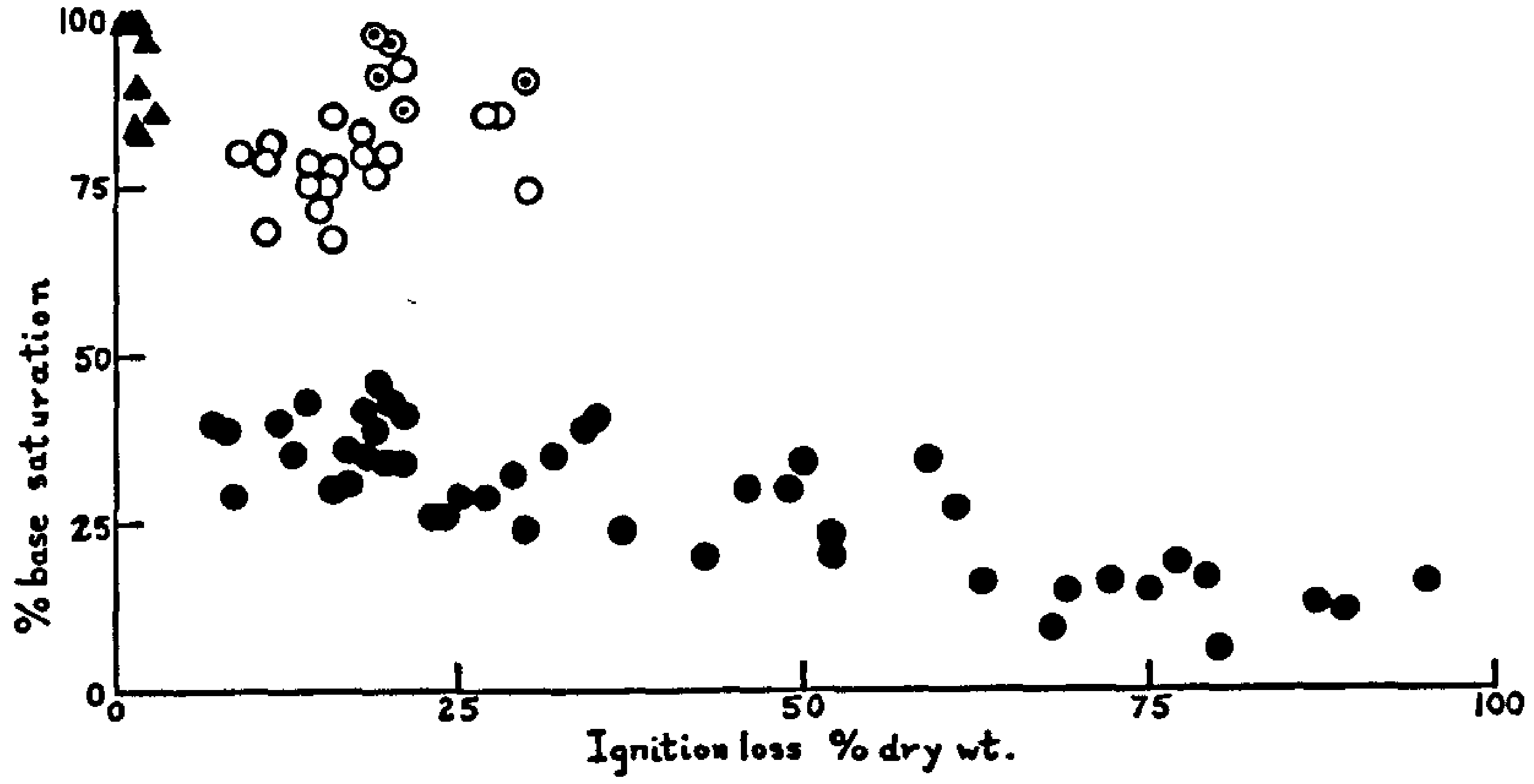

FIGURE VIII. Base saturation in relation to humus content.

falling between 4 and 21 m.e. per cent dry weight. A similar picture is given by the amounts of exchangeable hydrogen in the flushed soils, which increase only very slightly in the more organic soils, and are always less than 12 m.e. (Those soils receiving calcareous drainage show especially low figures.) On the other hand, in the leached series exchangeable hydrogen increases from about 10 m.e. per cent dry weight in the least organic samples to between 60 and 100 m.e. in the raw humus. And in the flushed soils exchangeable bases increase from an initial value of 12 m.e. to a maximum of 41 m.e. in the most organic sample. Thus the increase in exchange capacity with rising humus content leads chiefly to an increase in base adsorption on the flushed brown earths; while on the leached surfaces the increased adsorptive capacity becomes saturated by hydrogen ions.

Acidity and base saturation (Figures VII, VIII, IX, X and XI). The deep drift samples as might be expected, are only slightly acid; pH ranges from 6.58 down to 5.02 in the shallowest sample. This latter soil also shows the highest ignition loss and the only low pK among the drifts. Base saturation is high and never falls below 83 per cent. The apparent pK lies between 5.13 and 5.47, with the exception of the sample mentioned above which has a pK of 4.24 and is probably affected by the acid grassland vegetation above it (containing species such as *Nardus*, *Pteridium*, *Galium saxatile*, *Polytrichum formosum* and *Hylocomium squarrosum*).

The two surface soil series are clearly distinguishable on the basis of these three characteristics; the differences being very

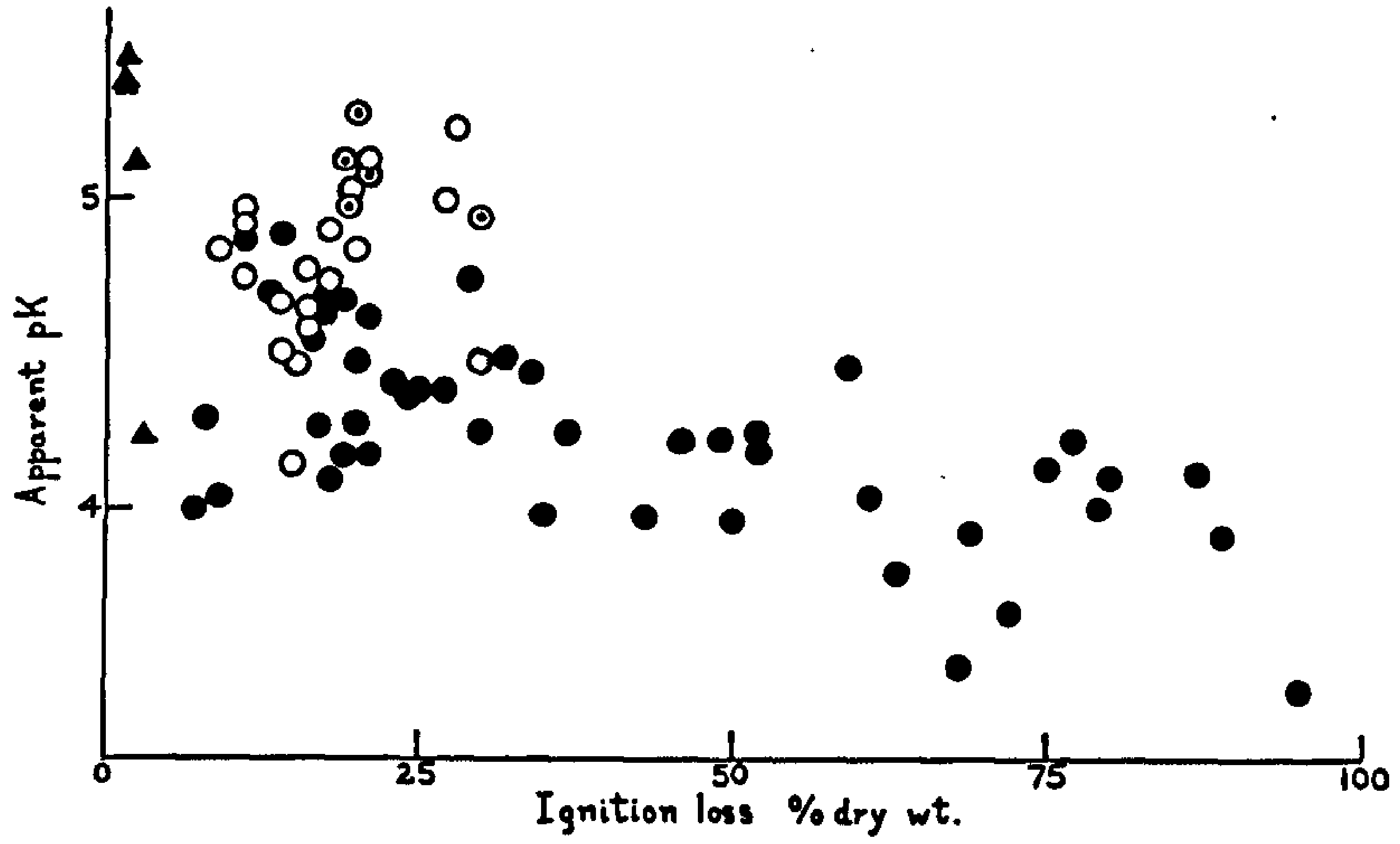

FIGURE IX. Apparent pK in relation to humus content.

marked in the case of base saturation, and least clear as regards the apparent pK.

The flushed soils with mull humus layers do not show any discernible trend of pH, base saturation or apparent pK with increasing organic matter. pH ranges from 4.62 to 6.70. The soils receiving calcareous drainage are all above pH 5.8; while in the other samples the values lie roughly about pH 5.4, toward the lower end of the range for the glacial drifts. Base saturation gives a similar picture. The figures here lie between 67 and 97 per cent, with the soils receiving calcareous drainage all above 86 per cent and the others lying mostly just below the lower limit for the drifts. The apparent pK values are very variable, as may be expected since the errors of three separate analyses are accumulated here. The range is from 4.47 to 5.27, with the exception of a single value of 4.14. Again, the values are mostly lower than those for the inorganic drifts, indicating that the acids produced from organic matter are in general stronger than those of the inorganic soil system. The soils receiving a flush from limestone apparently have weak acids, as shown by pK values above 4.93.

In contrast to the flushed mulls, the leached soils with mor humus layers show a definite decrease in pH, base saturation and apparent pK as the organic content increases. In the mineral soils with less than 25 per cent ignition loss pH ranges from 3.64 to 4.76, base saturation from 26 to 46 per cent, and pK from 4.00 to 4.88. In organic mors with over 75 per cent ignition loss the corresponding ranges are 2.73 to 3.58, 6 to 19 per cent, and 3.41 to 4.22. Thus as the surfaces

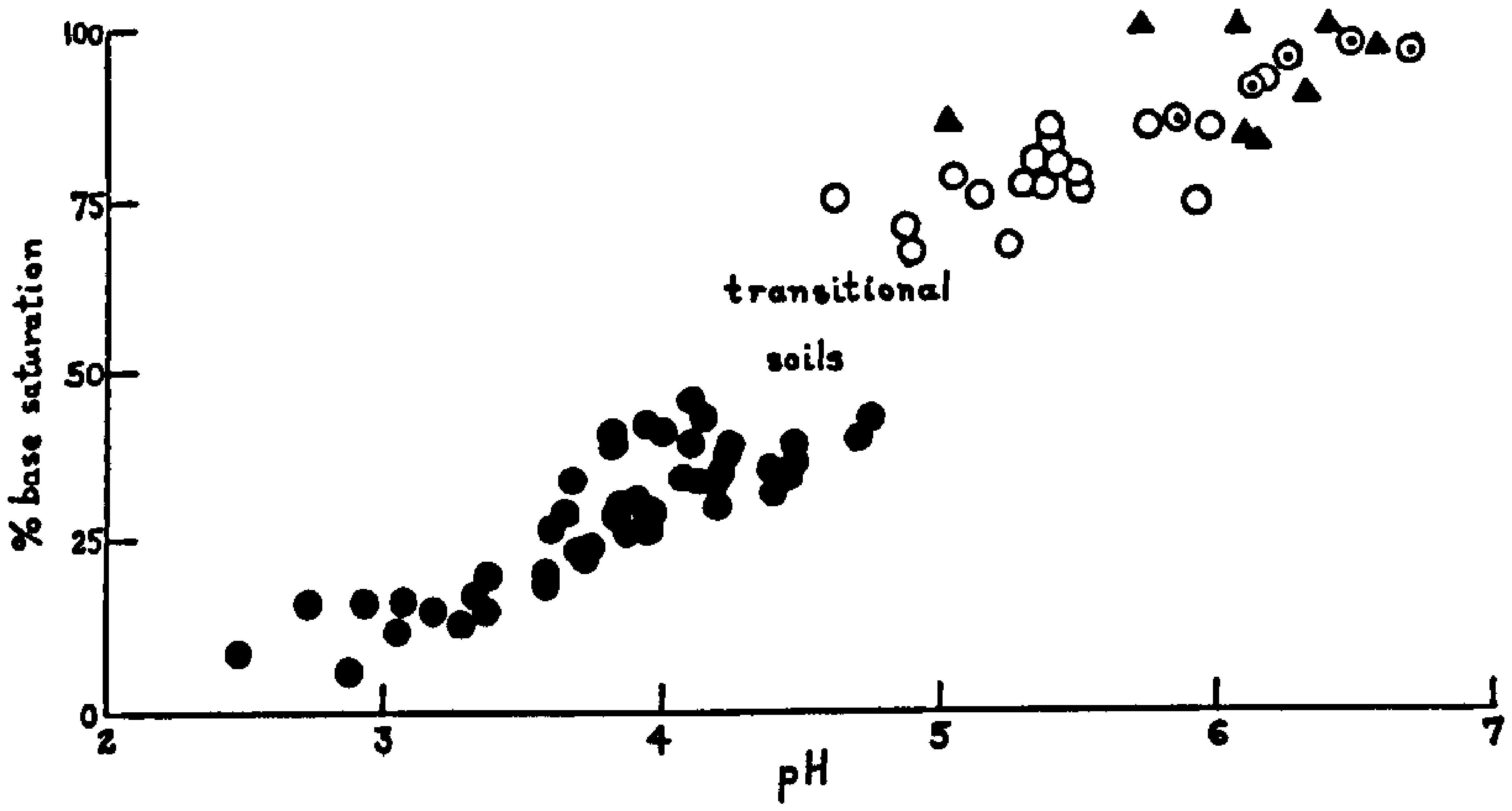

FIGURE X. Base saturation in relation to pH.

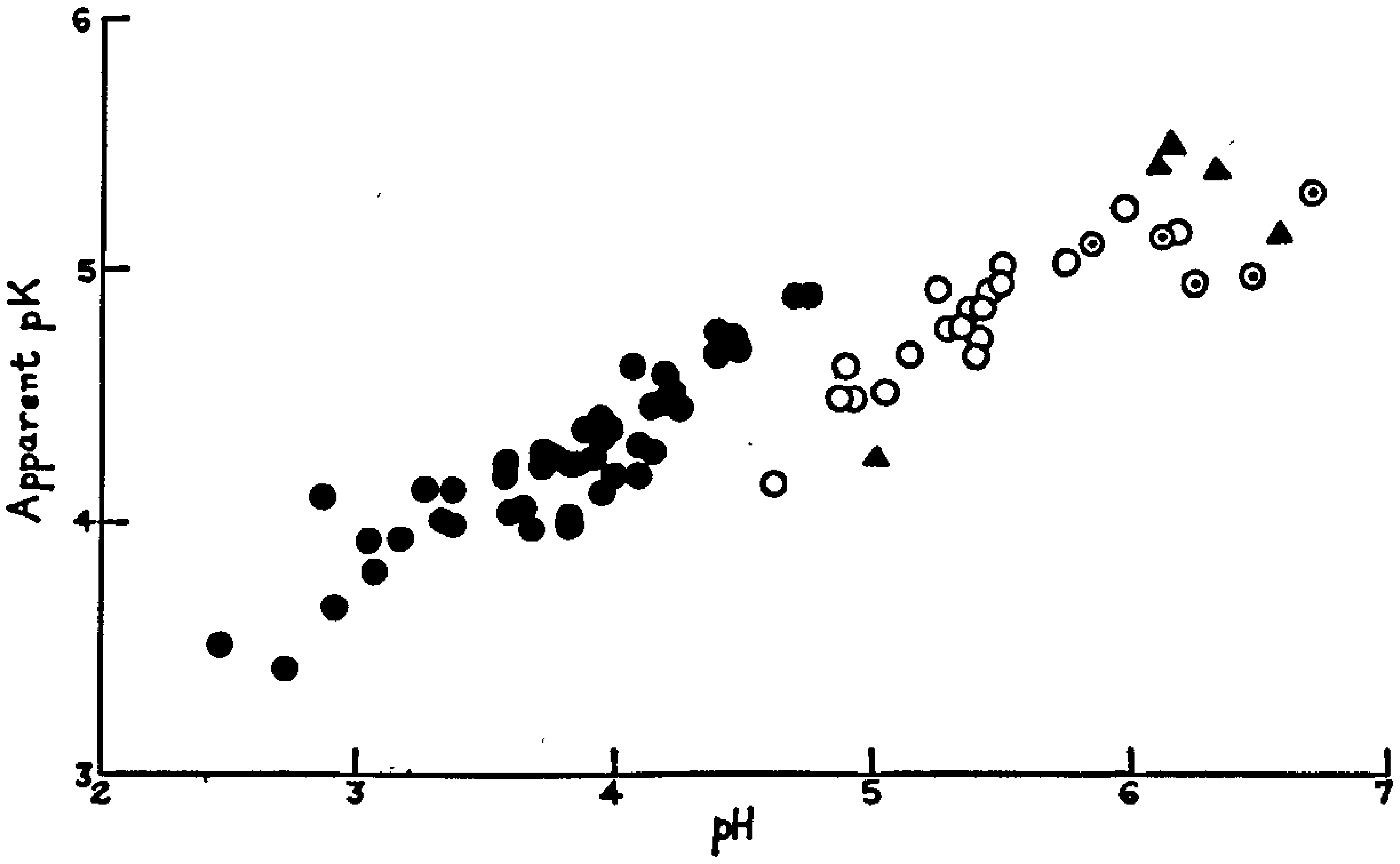

FIGURE XI. Apparent pK in relation to pH.

of the leached soils become more organic, both the amount and strength of the soil acids increase, and the base saturation in consequence declines.

The differences in base saturation of the two soil series are very great, the flushed brown earths being above 67 per cent and the leached podzolic soils below 46 per cent. There is a slight overlap of acidity values in the region of pH 4.75. The apparent pK values overlap very much; but it is clear that on the average the <u>mor</u> soils possess stronger acids. This conclusion has also been reached by Mattson & Karlsson (1944), using different chemical methods.

The relation of pH to base saturation is shown in Figure X. It takes the form of a sigmoid curve between the pH values of the two extracting solutions (N acetic acid at pH 2.3 and N ammonium acetate at pH 7.0). The gap in the centre is in nature filled by transitional soils, carrying plants of both soil series. It will be noticed that where the pH levels tend to overlap, the brown earths are more base saturated than the podzolic soils. This is connected with the values of pK, which have also been plotted versus pH in Figure XI. We see that as the soils become more acid pK drops, indicating that not only are more free hydrogen ions present but the acid groups are stronger and more dissociated as well. We may note, however, that where the pH levels overlap at about pH 4.75 the brown earths are seen to possess stronger acids than the podzolic soils. It is for this reason that the former are more base saturated at this pH level, as mentioned above. Much of the acid present in the soil is probably colloidal, and the stronger the acid the greater will be its base-binding power.

Nitrogen and exchange constituents per unit of soil volume (Table V). It may be of some interest to compare briefly the two soil series on a volume basis. In Table V are given both weight and volume data on nitrogen, total exchangeable bases and exchangeable hydrogen - for levels of 10, 30 and 95 per cent ignition loss. The average values used in these calculations have been selected by inspection of the figures, and are thus only approximate.

Table V shows that as the percentage of organic matter and nitrogen in the soil increases, so also does nitrogen on the volume basis. The most organic mors appear to contain slightly more nitrogen per unit of soil volume than do the most organic mulls, 0.5 g as compared with 0.4 g per 100 cc. Exchangeable bases in the flushed mulls rise slightly with increasing organic content, from 11 to 15 m.e. per 100 cc. In the leached soils there is a decrease, the most organic mors containing only 2 m.e. per 100 cc in contrast to 8 m.e. in the least organic samples. Exchangeable hydrogen in the flushed soils is fairly constant at 3 m.e. per 100 cc, in the leached soils it increases from 10 m.e. per 100 cc at 10 per cent ignition loss to 17 m.e. in the most organic mors.

Profiles

The general morphology of the profiles is presented in Figure XIII and Table VI, the familiar A, B and C horizon terminology being employed (see, for example, Lutz & Chandler, 1946). The data for the flushed brown soil are given in Table VII, for the leached podzolic soil under oak in Table VIII and for the leached soil under spruce in Table IX.

Water (Figure XII). The water content of the flushed soil profile drops from 45 per cent dry weight at the surface to 25 per cent in the lowest clayey layer of the C horizon.

The leached profile under oak shows a fall from about 120 per cent dry weight in the organic mor surface to about 60 per cent in the B_2 horizon and about 40 per cent in the clayey B_3 subsoil zone. In the profile under conifers the surface water content is similar to that under the oakwood, falling to 65 per cent dry weight in the upper mineral soil and 39 per cent in the bleached A_2 horizon. There follows a sharp rise to between 55 and 69 per cent in the organic B_2 layer.

Using the data on volume/weight ratio of the surface samples (Figures Ia and Ib), it would seem that on a volume basis the flushed mull surface contains much more moisture than the leached organic mors. And if one calculates the coefficient of humidity (water/ignition loss) for the surface soils, the values in the mors are about one as compared with three in the mull. The coefficient increases with depth in all three profiles.

Ignition loss (Figure XII). The ignition loss of the flushed brown earth is seen to drop from 15 per cent dry weight at the surface (there being no litter layer) to 2 per cent at the bottom level. There is no observable accumulation of leached humus substances in an illuviated B horizon, though some degree of sesquioxide mobilization is suggested by the slightly reddish brown tinge in the soil of the B layer and of the soil ash in both the A and B horizons.

The leached soils present a very different picture. Ignition loss is about 95 per cent dry weight at the surface. Under oak there is then a drop to 11 per cent at 14 cm depth, followed by a rise to 15 per cent at 26 cm. In the B_3 subsoil the values range from 7 to 9 per cent dry weight. Under the conifers the minimum of 9 per cent ignition loss comes in the bleached A_2 horizon at 19 cm depth. The B_2 layer exhibits an increase to between 19 and 23 per cent dry weight, due to the accumulation of colloidal complexes leached from above.

A peculiar feature of the oakwood results is that the horizon of minimum humus content (excluding the B_3 subsoil) is not the bleached layer. The latter, which is much mottled with organic matter in patches, lies at about 5-7 cm depth, above a thin layer of purplish-stained but less organic soil. The humus minimumof 11 per cent ignition loss comes just beneath this purplish horizon, in a rusty orange zone at about 10-17 cm. However, iron sesquioxide deposition appears to start in the purplish stained layer at 7-10 cm, as evidenced by the red color of the soil ash there. Thus it seems that the upper boundaries for the deposition of humus and sesquioxide do not coincide. The former begins at about 17 cm, from both the ignition loss and nitrogen data; and the latter starts at about 7 cm, judging from the evidence of soil bleaching and ash color. This is in contrast to the results from the conifer wood where both humus and sesquioxide

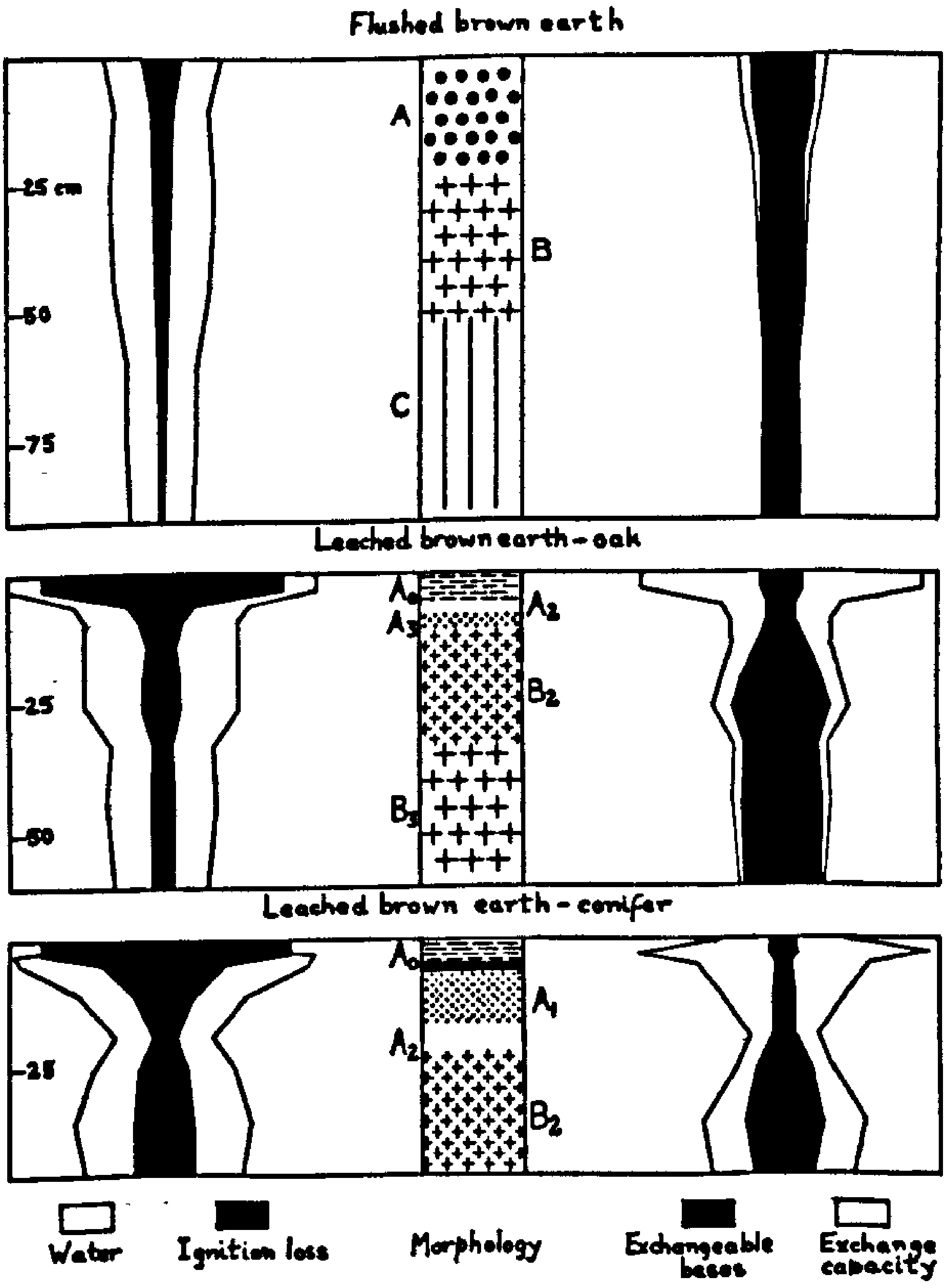

FIGURE XII. Morphology and chemical characteristics of some woodland soil profiles deposition appear to begin at about 22 cm depth; and to the results generally obtained in podzol soils (e.g. Lunt, 1932; Weiss, 1932; Mattson & Lönnemark, 1939; Bengtsson, Karlsson & Mattson, 1943; Lutz & Chandler, 1946).

If considered on a volume basis the differences in organic content between mull and mor are much less. The surface 5 cm of the flushed profile contains roughly half as much humus per unit volume as the surface 5 cm of the leached podzolic profile under oak.

Nitrogen. As might be expected, nitrogen follows much the same trend as does humus content. The flushed profile values fall from 0.61 per cent dry weight at the surface to 0.11 per cent in the lowest level. In the mor surfaces the values are 2.00 to 2.17 per cent. In the profile under oak there is a fall to 0.28 per cent at 14 cm, followed by a rise to 0.39 per cent at 26 cm depth. In the B_3 subsoil the values range from 0.16 to 0.21 per cent. Under spruce the minumum of 0.18 per cent comes in the bleached horizon at 19 cm, below which there is a rise to 0.54 per cent in the lowest B_2 sample.

However, there is not an exact correspondence between the humus and nitrogen results. Thus while the mull surface 5 cm contains only about half as much humus per unit volume as the surface 5 cm of the mors, nitrogen per unit volume is much the same in both. This may be seen by comparing the carbon/nitrogen ratios, assuming again that carbon constitutes half the ignition loss. The C/N of the mull is 12; while in the mors it is nearly twice as much, at 22 - 24. This difference is continued throughout the profiles; C/N in the flushed brown earth ranging from 6 to 16, and in the leached podzolic soils from 17 to 25. In the flushed soil there is a tendency for the C/N values to decrease with depth, which would be emphasized if the ignition loss could be corrected for the contribution of the inorganic colloids.

Exchange capacity(Figure XII). As in the previous case, there is a general correspondence in the trend of exchange capacity per unit dry weight and that of humus content. In the flushed brown earth we find 35 m.e. per cent dry weight at the surface, and 13 m.e. at the lowest level. In the leached profile under oak values range from 109 m.e. at the surface to a minimum of 37 m.e. in the B_3 subsoil; and under conifers from 112 m.e. in the decaying needles to as low as 27 m.e. in the bleached A_2 horizon. In the profile under conifers we find a very low exchange capacity of about 65 m.e. per 100 g organic matter in the dry needle mat. In the decayed needles immediately below, the exchange capacity rises to the same value as that of the oakwood mor layer.

Total exchangeable bases and exchangeable hydrogen (Figure XII). These analyses show clearly a major difference between the flushed brown earth and the leached podzolic soils. The former contains most base in the surface layers, the values ranging from 25 m.e. per 100 g dry weight of surface mull to 12 m.e. per 100 g of the subsoil C horizon. However, in the leached soils bases are very low in the surface, 16 m.e. per 100 g dry weight in the oakwood mor and 11 m.e. in the decayed needle mor. And on the volume basis, there is in the brown earth ranging from 6 to 16, and in the leached podzolic soils from 17 to 25. In the flushed soil there is a tendency for the C/N values to decrease with depth, which would be emphasized if the ignition loss could be corrected for the contribution of the inorganic colloids.

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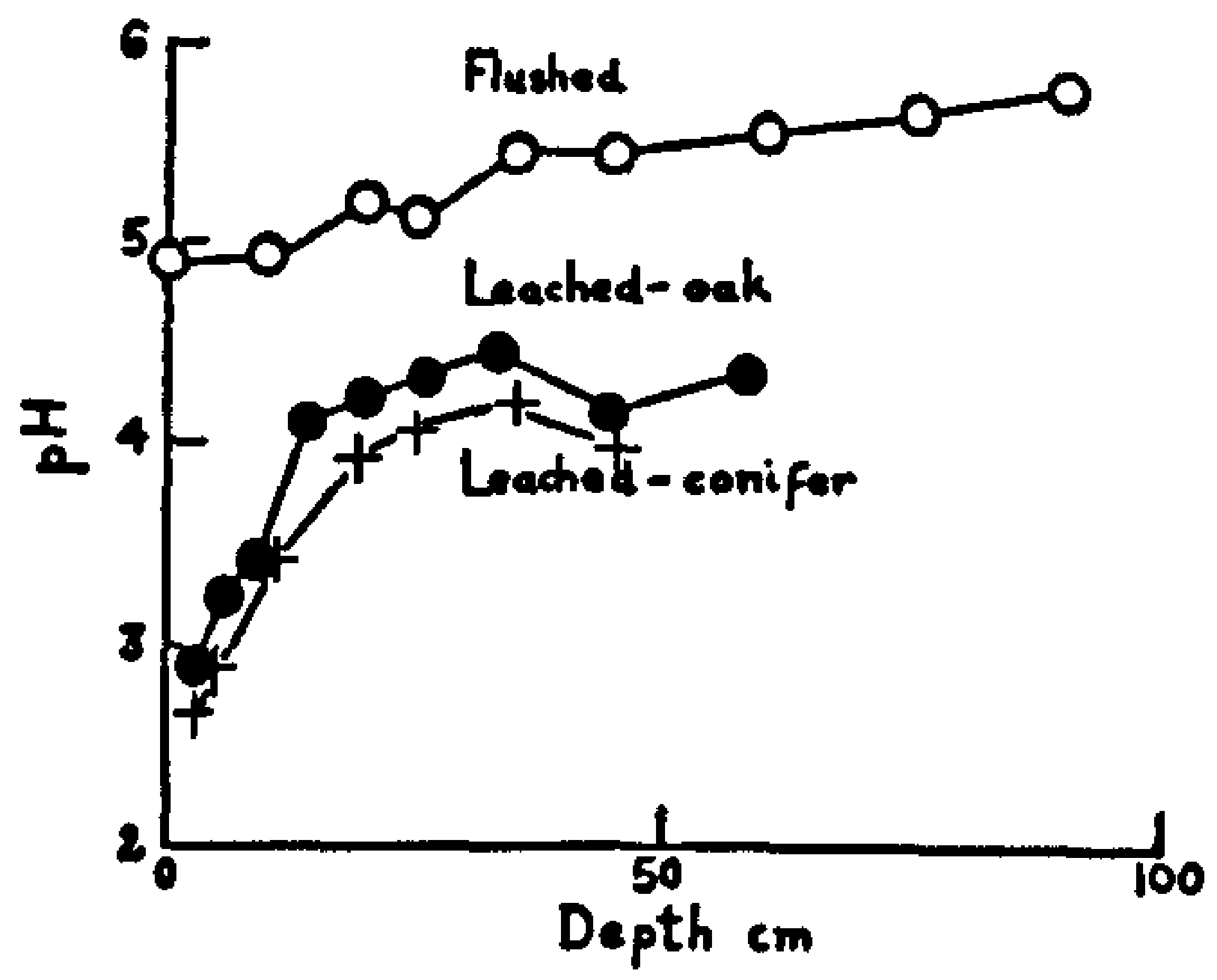
On the other hand, in the lower levels of the leached profiles there is a very marked accumulation of bases, as shown most clearly in Figure XII. The maximum levels are 39 m.e. per 100 g dry soil in the oakwood and 31 m.e. under the conifers, both being higher than the flushed soil values. These bases are presumably leached from above and adsorbed on the colloids of the B_2 accumulation horizons below. On a volume basis also, the accumulated bases in the B_2 horizons of the leached soils are probably greater in amount than in the bases in the mull surface.

As to exchangeable hydrogen, the leached profiles contain far greater amounts than the flushed profile. In both the flushed brown earth and the leached oakwood profile there is a steady decline downward; from 10 m.e. per 100 g dry weight to 1 m.e. in the former, and from 93 m.e. to 8 m.e. in the latter. The profile from the conifer plantation shows a surface maximum of 101 m.e., a minimum of 17 m.e. in the uppermost B_2 layer, and a secondary maximum of 33 in the middle B_2.

Acidity and base saturation (Figures XIII and XIV). All profiles are most acid at the surface. However, the acidity of the flushed soils is not great, pH ranging from 4.8 at the top to 5.8 at the bottom. In the leached series the surface pH is about 2.8

FIGURE XIII. pH of soil profiles from flushed and leached habitats.



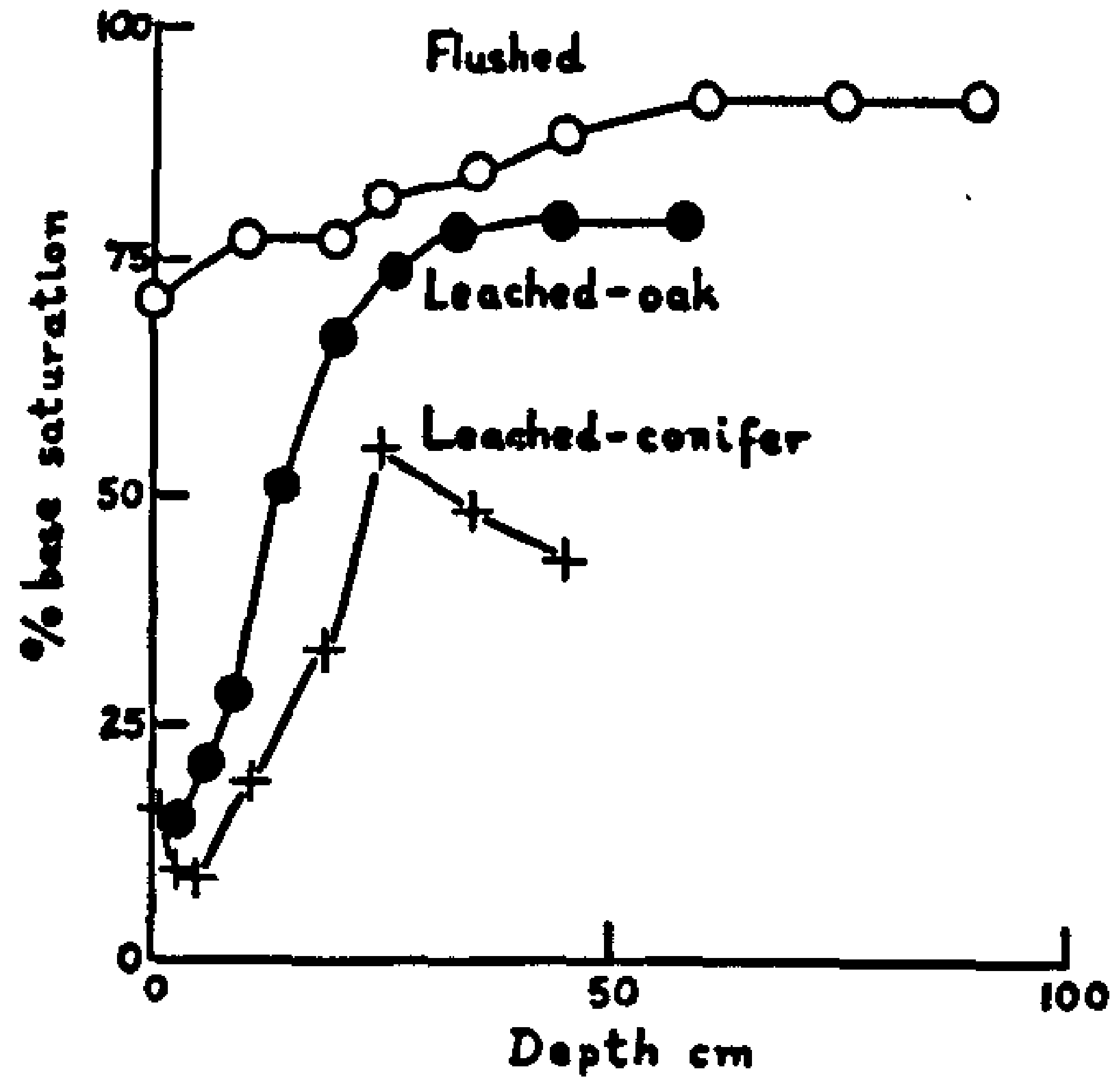


FIGURE XIV. Base saturation of soil profiles from flushed and leached habitats.

and there is a rapid increase of about 1.3 units in the upper 20 cm. There follows a slight drop, and in the case of the oakwood series another small rise. The conifer profile is 0.1 to 0.3 pH units more acid than that under oak.

Base saturation shows a generally similar picture. The flushed soil is 71 per cent saturated at the surface, and rises to 92 per cent in the C horizon. The oakwood profile increases from 15 per cent in the humus mat to over 50 per cent in the B_2 horizon and almost 80 per cent in the B_3. The conifer series increases from a low value of 10 per cent to a maximum value of 55 per cent in the upper B_2. There is a drop in the per cent saturation of the lower levels in the conifer profile.

It may be noted that the oakwood leached profile is slightly more base saturated at a given pH than is that under the conifers. This may be taken to indicate that the acids produced from the humus of the oakwood plants are stronger than those from the spruce needles.

pK for the flushed profile is above 4.25 throughout, the acids being much weaker than those of the leached profiles. As noted previously, a similar result has been obtained for surface soils in thisarea. pK in the flushed profile also increases slightly with depth, indicating that the acids are strongest near the surface.

In the leached profiles pK is low and the acids are relatively strong. From 3.64 at the surface pK increases in both profiles downward to the zone of low loss on ignition. Under oak it reaches 4.08 and then decreases markedly, indicating the presence of strong acids in the lower B horizon, and rises slightly again at the bottom. In the spruce profile this is not so clear, but after reaching 4.23 there is some indication of a fall in the upper B_2 horizon with a subsequent rise. The pK values confirm that the acids under oak are stronger than those beneath the spruce. The variation of pK with depth suggests that different acids accumulate at different levels.

DISCUSSION

A major point of interest in this study is of course the clearness with which these two soil series, separated on the basis of appearance and morphological characters in the field, can be distinguished by their chemical properties of acidity and base status. Figures V and VI show most distinctly that as the surface soils become more organic, and consequently more adsorptive, the increase in exchange capacity is largely saturated by bases in the flushed soils and hydrogen ions in the leached soils. The profile differentiation is equally clear, as illustrated by Figure XII.

Storage probably increases the differentiation slightly, but has not affected the boundary of pH 4.5 to 5.0. In the writer's experience, in this area surface soils below pH 4.5 are never wholly typical crumb <u>mulls</u>, or soils above pH 5.0 characteristic <u>mors</u>. The average incr ase in base saturation on storage (calculated from Table I and Figure X) should be less than 10 per cent in the <u>mulls</u> and 5 per cent in the <u>mors</u>.

In spite of the clear differentiation of mull and mor pH levels shown in this study, corresponding levels should not be used as indicators of mull or mor conditions elsewhere without careful investigation. As an illustration we may consider some data from woodlands near London, given in Table X. These woods are dominated by oak, with some sycamore, ash and beech; the major element in the ground cover being the well known Pteridium aquilinum Holcus mollis-Scilla nonscripta community. Five of these soils had the appearance of mull, though with a rather fine crumb structure; and the last was classed as incipient mor, under a beech tree. While highly base saturated their pH is relatively rather low, so that pK is extremely low in comparison to Lake District mulls. These samples also appear to contain less organic matter than the Lake District soils.

An even more extreme example has been furnished to me through the courtesy of Professor L.-G. Romell. He has determined pH values on a series of mull samples (with earthworms plentiful) from coniferous plantations at Frijsenborg in Denmark which are subjected to severe thinnings. The results ranged from 3.6 to 4.8. In comparison, a typical beechwood mor, above a leached A_2 horizon more than 20 cm in depth, gave a pH of 4.1 (F layer) and 3.8 (H layer); and a characteristic beechwood mull had a pH of 5.1. Evidently this acid mull condition is maintained by the silvicultural treatment, perhaps through activation effects like those described by Romell (1935).

As regards the differentiation of the two woodland soil types in the Lake District, the fundamental factor determining which will develop in a given situation appears to be the nature of the relief.

On the hillsides and knolls bases are continually being leached away both vertically and down the slopes, as hydrogen ions produced by organic decay replace them on the soil colloids. Some of these bases percolate down the hillsides and provide a flush effect along the drainage channels and the flatter land along the shore - that is, in just those sites where we find the brown earths with *mull* humus layers. Here the additional bases received probably tend to neutralise the acids produced by litter decay, so that a high degree of base saturation is maintained. It may be noted that even if the percolating water is not very high in bases, a constantly moving stream of low concentration may be just as beneficial as a higher but static soil reserve, since it counteracts local base depletion in the immediate vicinity of the plant roots (cf. Olsen 1950). On the hillsides and knolls the surface becomes more and more deficient in bases as leaching continues, and the soil develops a podzolic type of profile in the most extreme cases. There are probably two main factors which allow such a marked podzolization of clayey parent material. One is the high rainfall in the district, which greatly accentuates the leaching process. The other is the highly irregular topography, which allows free drainage and thus prevents the formation of *glei* soils and peats. The latter are common on the flatter uplands above the woodland zone (Pearsall 1950).

The influence of topography on soil base status (through its effects on leaching and flushing) has long been recognized by forest ecologists. It has been specifically pointed out by Hesselman (1917), Tamm (1920) and Glømme (1928) in Scandinavia; and by

Salisbury (1922) in England. Pearsall (1950) has recently emphasized its importance for mountain and moorland vegetation. It is also interesting that in 1923 a correlation of both flora and soil acidity with relief was shown in New England by Wherry, who was able to draw acidity contours which coincided fairly closely with altitudinal contours. Data on the amounts of nutrients involved are, however, scanty; and quantitative studies are much needed.

Chandler (1939) has explained a similar relation of vegetation and soil status to topography in the north-eastern United States as probably being due to differences in water relations. There a hardwood forest type is present on little-podzolized soil with a <u>mull</u> humus layer at the bottoms of the slopes. In these sites the severity of summer drought is probably less than on the uplands, where podzol soils with <u>mor</u> layers are dominated by spruce-hardwood and spruce forest types. In the Lake District, however, the abundant rainfall would seem to preclude an explanation on the basis of drought; and the concept of base-flushing may provide an equally possible alternative in the American areas.

There is probably also a flush of nitrogenous as well as mineral nutrients to the lower ground. However, if the competition for nitrogen in <u>mors</u> is as severe as claimed by Romell (1935), the losses by leaching should be relatively low, especially in view of the extensive mycorrhizal interpenetration of the rooting layers.

It is here necessary to point out a biological factor of much importance in maintaining or increasing the above-mentioned differences in base status, although it probably has little influence in originating them. On the flushed soils the dominant plants are often species with a high requirement of mineral nutrients (Gorham, unpublished). During the growing season they lock up in their tissues large amounts of bases which are thus removed from the action of the leaching process for part of the year. And the trees, which root in the deeper layers of the soil, bring up a good deal of bases from below which returns to the surface in the leaf fall. The leached soils on the other hand are dominated by species of low requirement, and the data of Mattson & Koutler-Andersson (1941a, 1941b, 1944) suggests that these plants also produce the most acidic residues. That mull plant litter tends to reduce soil acidity has been demonstrated by Bornebusch (1925). Moreover, many other workers have suggested that different trees may have very different effects on the same soil; species with a high nutrient requirement reducing acidity and favouring mull formation (cf. references in Lutz & Chandler, 1946).

In connection with biological factors, it is also most desirable to know something of the way in which the litter contributes to the soil acidity. A series of very valuable studies of "the acid-base condition in vegetation, litter and humus" have recently been carried out in Sweden by Mattson & Koutler-Andersson (1941-44), and bear directly on this question. The major points of interest with reference to the present work are summarized below.

These workers have studied the aerobic decay of plant litter (chiefly tree leaves) from both brown earth and podzol soils. As might be expected, the brown earth litter is much richer in bases and nitrogen. It is also much richer in acidoids (colloidal acids), and these acidoids are comparatively strong. Such results would appear to be in direct contrast to the soil conditions as measured in the present investigation and by Mattson & Karlsson (1944), for the latter studies suggest that both the amount and strength of the soil acids are greater on the more leached sites.

The factors responsible for this reversal of conditions are not at all clear, and may be varied. While the acidoid content of the brown earth plants is high, so also is their base content; thus much of the acidoid is neutralized and the acid/base ratio is lower than in the podzol vegetation. This high base status of the former may well favour a more rapid transformation of acidoids by the micro-organisms in the unleached soils. Another factor is probably the higher sesquioxide content to be expected in the unleached surfaces. Some earlier work by Mattson (1931) suggests that these combine with the acidoids to form iso-electric precipitates, thus destroying a part of the soil acidity. Lastly, much of the acidoid of the brown earth litter appears to consist of polyuronides of the hemicellulose fraction, while the part due to lignin is low (Mattson & Koutler-Andersson, 1944). In podzol vegetation on the other hand the hydrolyzable polyuronides are low, while lignin is high. Although the lignin acids are originally weak and probably made up of phenol hydroxyl groups, autoxidation produces large quantities of relatively strong acids. It is this oxidized lignin which is probably responsible for the larger part of the soil acidity once decay has proceeded for some time, as the strong polyuronide acids will be more easily broken down by the microflora. Transformations of lignin in mull and mor may well be of central importance in the question of soil acidity (cf. Romell, 1935; Mattson & Koutler-Andersson, 1944).

The effect of soil base status on the rate of litter decay has been the subject of some controversy. Laboratory studies (Broadfoot & Pierre, 1939; Matsson & Koutler-Andersson, 1941a, 1941c) suggest that high base status increases the rate of decay; and lend support to the old idea that the chief difference between mull and mor is in rate of litter decomposition (cf. references given by Romell, 1932, 1935). However, Romell (loc. cit.) presents evidence that the major distinction must lie rather in the type of decay - a fungal soil flora predominating in the mors, while in the mulls the activities of the soil fauna keep down the fungi and promote the development of a bacterial flora. Nevertheless, Romell "does not intend to deny the possibility of a certain average difference between mull and duff (= mor) in amount of accumulated organic matter" (1932, p.170). He merely points out that a good crumb mull may contain just as much organic matter per unit of soil area as a pronounced mor - in which case (granted that the annual litter production is similar) it would appear that the rate of decay is much the same in both. The field data available do not enable us to say at present whether there are real overall differences in this respect between mull and mor, or to determine their importance if present.

As regards nitrogen content, another most important biological soil characteristic, in this area there is little difference between the mull and mor surfaces if N is calculated as per cent of humus (represented by ignition loss). The C/N ratio of mull averages 13, and that of mor 15. However, there are probably greater differences in the ratios of the plants growing on these soils. While exact data are wanting, 18 plant samples from soils above pH 5 showed a C/N range (C calculated as half ignition loss) of 9 to 22, averaging 16 (S.D. ± 3.3). In contrast, a series of 40 plant samples from soils below pH 4.5 gave a range of 11 to 41 and an average value of 24 (S.D. ± 7.1). Thus it appears that in this area the differences in plant nitrogen on the two soil types tend to be equalized during the decomposition process in the soil, so that nitrogen conservation (or carbon loss) is relatively greater in the mors than in the mulls. Once again, however, it is necessary to keep in mind the greater differences between extreme mor and mull, as represented by the profile data.

We may now consider the probable course of events which has led to the extreme topographical differentiation of soils and floras recorded here. Starting as a relatively uniform inorganic glacial drift, the soil gradually becomes more and more organic under the influence of the developing plant cover. The increasing production of hydrogen ions by organic decay leads to their replacement of bases on the soil colloids, and the bases set free in the soil solution are then leached by the rainfall into the deeper soil layers or down the slopes. This leaching effect will be greatest on the uplands or knolls, since the percolation of bases from above tends to neutralise acid production in the flushed sites along the drainage channels and on the flatter lands below. In this way it appears that the flushed soils maintain their high base status as a dynamic equilibrium - between acid production and leaching on the one hand, and base-flushing from above on the other. The leached soils, however, become continually more and more base-deficient, especially at the surface. This appears very clearly if we consider Figure VIII as representing the trend of development. We see that, except where receiving calcareous drainage, the flushed brown earth surfaces with mull are maintaining themselves at a level of base saturation just slightly below that of the deep drifts. But as organic matter accumulates in the leached soils the base saturation of the surface layer falls steadily, until a final level of about 10 per cent is reached in the wholly organic mor surfaces.

As regards the flora, and also the type of humus layer, presumably in the beginning there is little or no differentiation due to base supply, species of high requirement and favouring mull formation being able to grow everywhere. However, as leaching proceeds such species will find it more and more difficult to compete over the whole area, and will become restricted in distribution. Even trees, which can pump up bases from the deeper accumulation horizons, will be subject to this limitation in their seedling stages. Gradually a flora of low base requirement will establish dominance on the uplands and knolls, leaving the species of high requirement in the flushed lowlands where they are able to compete more successfully. The development of characteristic mor and mull humus layers will go hand in hand with floristic differentiation, since the soil fauna necessary for mixing plant litter thoroughly into the mineral soil and for keeping down fungi is more generally found under a plant cover whose litter is rich in nutrients and poor in indigestible fibre (see references in Fenton, 1947).

The changes in biological characteristics initiated in this way will then tend to maintain and even enhance the soil differentiation. The brown earths with a mull humus layer and a flora of high base requirement, originally present over a wide area, will become restricted to unstable habitats such as scree slopes (Pearsall, 1950), and to those areas where flushing can maintain the soil equilibrium at a high base status. The leaching process, however, is to some extent autocatalytic in its action. By establishing a flora of low base requirement, mineral storage and replenishment by plants is minimized; and the leaching is even increased owing to the high acid/base ratio of the plant litter and the acid properties of the humus produced (i.e. of the decay-resistant lignin fraction, not of the more easily metabolized polyuronide fraction; cf. Mattson & Koutler

Andersson, 1944). Thus the leached surface will become more and more base-deficient, and more and more extensive; presumably until a balance is reached between the loss of nutrients by leaching and their supply by weathering, by a low degree of plant "pumping" from the lower horizons, by rainfall, and perhaps to some extent by absorption from the air (Liebig, see Ingham, 1950). When an equilibrium is reached, the two phases of leaching and flushing will be distinguished as the end points of a catena, or topographical soil series, from the leached and base-deficient uplands to the areas of lowland flushed by their collected drainage. The relative expanses of the leached and flushed areas, and the rate of their differentiation, will depend on the varying intensities of the factors affecting base supply, conservation and loss. In the Lake District the leached soils may be expected to predominate, owing to the high rainfall and marked relief.

At this point it would seem desirable to state clearly five independent soil-forming factors (cf. Jenny, 1941), all of which determine in varying degree the distribution of brown earths and podzolic soils, or mulls and mors; and any of which may exert the decisive influence in their differentiation. On the broad geographic basis climate appears to influence the two types (Romell, 1930, 1935), brown earths and mulls being commonest in the deciduous forests of the mild temperate climates and podzols and mors predominating in the colder northern coniferous forests.* The climate may act directly, through the effects

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* While mulls are generally correlated to a brown earth profile and mors to podzols, this is not always the case. Tamm (1930) has described a mull-podzol type of soil development, and Du Rietz (1945) records the accumulation of circum-neutral raw humus in flushed habitats near the northern border of Sweden.

of rainfall and temperature on the leaching process; or indirectly, by conditioning the distribution of organisms more or less favourable to mull or mor formation. In the transition zone between the two climatic extremes the nature of the soil parent material becomes very important, with brown earths and mulls occurring on the softer rocks richer in nutrients, podzols and mors on the harder sand-forming rocks which are poor in nutrients. If both climate and parent material are not too extreme, topography assumes a leading role, podzols and mors occupying the leached uplands, and brown earths and mulls the flushed lowlands. This is the case in the present study. Where none of these physical and chemical factors is limiting, organisms may play an independent part in the differentiation. In most cases where this is true on a large scale the primary factor is disturbance (either constructive or destructive) by man; but obstacles to migration may, through their effects on organism distribution, seriously influence the course of soil development (Beadle, 1950). Finally we come to the fifth primary factor, time, the importance of which is self-evident. In connection with time, we may expect that in general brown earths and mulls will precede podzols and mors, the latter being largely an expression of continued soil leaching. On soils originally poor in nutrients, however, mulls may never develop, or be found only in the earliest stages of colonization. In the latter case, successional development may be chiefly due to the increasing aggregate demand of the plant cover for nutrients, which may in turn force a reduction in the demands of the individual organisms.

The soil type thus expresses the integration of all these independent variables; and the absolute value of any one of them is of little significance unless considered in relation to the rest. For example, in regions of low rainfall podzols develop only on very sandy soils; but where the rainfall is high (as in the Lake District) even rather clayey soils may become podzolic, especially where the topographic situation favours leaching. It must be emphasized that purely local studies, without reference to a wide range of all environmental conditions, may often give a misleading impression if extrapolated or generalized. The results of the present investigation must be considered with this reservation in mind.

SUMMARY

A study of the exchange complex in some soils from Lake District woodlands reveals two very different trends in both surface and profile development, on similar parent material. Under the prevailing high rainfall, topography appears to be the major factor determining whether a flushed brown earth with a mull humus layer and an ash-sycamore-oak-hazel tree community will develop; or a leached podzolic brown earth with a mor humus layer and oak, birch and rowan as the characteristic trees.

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TABLE I. Effects of storage on pH of flushed and leached soils.

Soil type	Number of samples	Plus	Minus	Average sample deviation	Mean group deviation
Flushed	15	10	4	0.44	+0.28
Leached, less than 50 per cent ignition loss	20	12	8	0.26	+0.03
Leached, more than 50 per cent ignition loss	12	8	4	0.17	+0.04

TABLE II. Chemical characteristics of samples of deep glacial drifts.

Depth cm.	Color	Water % dry weight	Ignition loss % dry weight	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation	Nitrogen % dry weight
210	red	13	2.9	4.5	5.02	4.24	8.4	1.4	9.8	86	-
240	grey	16	1.7	9.4	6.16	5.47	9.3	1.9	11.2	83	-
240	brown	13	1.5	8.7	6.10	5.39	7.6	1.5	9.1	84	-
360	brown	12	1.5	8.0	6.32	5.37	9.7	1.1	10.8	90	-
360	grey	15	1.7	8.8	6.40	-	8.5	-	8.5	100	-
420	red	13	2.2	5.9	6.58	5.13	8.4	0.3	8.7	97	-
450	grey	8	0.8	10.0	6.07	-	6.2	-	6.2	100	0.04
450	red	12	1.2	10.0	5.72	-	9.5	-	9.5	100	0.06

TABLE III. Chemical characteristics of flushed soils with <u>mull</u> humus layers.

Water % dry weight	Ignition loss %dry weight	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e.%dry wt.	Exchange capacity m.e. % dry weight.	% base saturation	Nitrogen % dry weight
33	9	3.7	5.43	4.83	12	3	15	80	0.30
63	11	5.6	5.49	4.93	18	5	23	78	0.43
35	11	3.2	5.34	4.74	13	3	16	81	0.40
55	11	5.0	5.24	4.91	15	7	22	68	0.34
40	14	2.9	5.06	4.50	18	5	23	78	0.57
52	14	3.7	5.14	4.66	15	5	20	75	0.66
67	15	4.5	4.62	4.14	24	8	32	75	0.56
45	15	3.0	4.87	4.47	25	10	35	71	0.61
54	16	3.4	5.29	4.76	24	7	31	77	-
57	16	3.6	5.40	4.64	29	5	34	85	0.75
42	16	2.6	4.90	4.60	16	8	24	67	0.52
49	18	2.7	5.45	4.89	22	6	28	79	0.65
68	18	3.8	5.41	4.73	24	5	29	83	0.73
81	19	4.3	5.51	5.00	26	8	34	76	0.70
*47	19	2.5	6.12	5.11	31	3	34	91	0.68
*70	19	3.7	6.48	4.94	35	1	36	97	0.75
*36	20	1.8	6.70	5.27	27	1	28	96	0.81
51	20	2.6	5.40	4.83	26	7	33	79	0.74
70	21	3.3	6.12	5.13	34	3	37	92	0.85

* receiving drainage from limestone.

Table III (contd.) Chemical characteristics of flushed soils with *mull* humus layers.

Water % dry weight	Ignition loss % dry weight	$\frac{\text{Water}}{\text{Ignition loss}}$	pH	Apparent pK	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation	Nitrogen % dry weight
*60	21	2.9	5.86	5.07	31	5	36	86	0.77
132	27	4.9	5.75	4.99	40	7	47	85	0.94
115	28	4.1	5.97	5.22	34	6	40	85	1.02
*69	30	2.3	6.24	4.93	41	2	43	95	1.03
81	30	2.7	4.92	4.47	34	12	46	74	1.13

* receiving drainage from limestone.

TABLE IV: Chemical characteristics of leached soils with mor humus layers.

Water % dry wt.	Ignition loss % dry wt.	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
12	7	1.7	3.82	4.00	4	6	10	40	0.36
42	8	5.3	4.09	4.29	7	11	18	39	0.40
53	9	5.9	3.64	4.04	6	15	21	29	0.44
44	12	3.8	4.69	4.87	12	18	30	40	0.45
70	13	5.4	4.44	4.70	12	22	34	35	0.38
64	14	4.6	4.76	4.88	12	16	28	43	0.50
75	16	4.7	4.20	4.57	11	26	37	30	0.41
43	17	2.5	4.40	4.64	12	21	33	36	0.52
78	17	4.6	3.92	4.26	10	22	32	31	0.67
63	18	3.5	3.95	4.09	13	18	31	42	0.64
46	18	2.6	4.42	4.69	13	24	37	35	0.39
60	19	3.2	4.48	4.67	13	20	33	39	0.75
68	19	3.6	4.10	4.17	17	20	37	46	0.76
31	20	1.6	4.19	4.47	11	21	32	34	0.60
69	20	3.5	4.15	4.27	12	16	28	43	0.70
54	21	2.6	4.00	4.17	15	22	37	41	0.66
41	21	2.0	4.08	4.61	12	23	35	34	0.61
30	23	1.3	3.94	4.40	8	23	31	26	0.73
81	24	3.4	3.90	4.36	12	35	47	26	0.78
39	25	1.6	3.98	4.38	10	25	35	29	0.99
101	27	3.7	3.98	4.38	8	20	28	29	1.24
95	29	3.3	4.40	4.73	18	38	56	32	0.86

TABLE IV. Chemical characteristics of leached soils with <u>mor</u> humus layers (contd.).

Water % dry wt.	Ignition loss % dry wt.	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
115	30	3.8	3.74	4.24	10	32	42	24	1.07
103	32	3.2	4.22	4.49	16	30	46	35	1.18
115	34	3.4	4.25	4.44	20	31	51	39	1.39
60	35	1.7	3.82	3.97	14	20	34	41	1.41
101	37	2.7	3.76	4.25	11	34	45	24	1.21
130	43	3.0	3.38	3.97	9	35	44	20	1.38
149	46	3.2	3.85	4.22	20	47	67	30	1.63
146	49	3.0	3.84	4.22	16	38	54	30	1.83
147	50	2.9	3.67	3.96	21	41	62	34	1.42
195	52	3.8	3.72	4.24	15	50	65	23	1.76
107	52	2.1	3.57	4.18	12	49	61	20	1.66
131	59	2.2	4.16	4.45	20	39	59	34	2.46
162	61	2.7	3.60	4.03	17	46	63	27	2.40
110	63	1.7	3.07	3.79	7	37	44	16	1.53
43	68	0.6	2.48*	3.49	6	61	66	9	2.00
103	69	1.5	3.18	3.92	11	61	72	15	2.04
158	72	2.2	2.93	3.66	8	42	50	16	1.96
174	75	2.3	3.38	4.13	14	79	93	15	2.79
227	77	2.9	3.58	4.22	20	88	108	19	2.12
180	79	2.3	3.32	4.00	15	72	87	17	2.09
20	81	0.3	2.88*	4.10	5	82	87	6	2.42
111	87	1.3	3.28	4.12	11	76	87	13	2.87
244	89	2.7	3.04	3.91	13	97	110	12	2.52
126	95	1.3	2.73	3.41	12	61	73	16	2.10

* moistened for pH measurement.

TABLE V. Nitrogen and exchange constituents of the soil compared on the dry weight and volume basis.

Soil type	Ignition loss % dry wt.	Soil wt. g/cc	Exch. bases m.e.		Exch. hydrogen m.e.		Nitrogen g	
			100 g	100 cc	100 g	100 cc	100 g	100 cc
Flushed	10	0.8	14	11	4	3	0.4	0.3
"	30	0.4	38	15	7	3	1.1	0.4
Leached	10	0.8	10	8	13	10	0.4	0.3
"	30	0.4	14	6	30	12	1.1	0.4
"	95	0.2	12	2	85	17	2.6	0.5

TABLE VI. Morphology of soil profiles from flushed and leached habitats.

Flushed soil

A - 22 cm dark brown soil, upper part with coarse crumb structure

B - 28 cm yellowish grey soil, somewhat mottled with rusty brown

C - 50 cm grey and rather clayey subsoil, resting on old sand beach

Leached soils

Oakwood

A_0 - 5 cm fibrous brown organic matter

A_2 - 2 cm greyish soil, much mottled with brown and blackish patches, lumpy and compact

A_3 - 3 cm purplish compacted soil

B_2 - 20 cm looser brown loamy soil, orange iron staining in upper part, darker rusty color below

B_3 - 30 cm yellowish grey, lumpy and rather clayey soil, bedrock beneath

Conifers

L - 2 cm loose needle mat

F - 2 cm decaying needles

H - 2 cm black amorphous organic matter mixed with mineral soil

A_1 - 10 cm purplish brown soil

A_2 - 6 cm compact grey soil

B_2 - 23 cm looser soil, dark rusty brown, bedrock beneath

TABLE VII. Chemical characteristics of a flushed soil profile.

Depth cm	pH	pK	Water % dry weight	Ignition loss % dry weight	Nitrogen % dry weight	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation
0	4.87	4.47	45	15	0.61	25	10	35	71
10	4.93	4.38	37	9	0.30	24	7	31	77
20	5.18	4.61	39	8	0.26	17	5	22	77
25	5.13	4.49	40	7	0.29	17	4	21	81
35	5.44	4.68	39	6	0.19	16	3	19	84
45	5.43	4.63	37	5	0.23	15	2	17	88
60	5.56	4.66	27	3	0.15	11	1	12	92
75	5.62	4.69	27	2	0.16	12	1	13	92
90	5.76	4.83	25	2	0.11	12	1	13	92

TABLE VIII. Chemical characteristics of a leached soil profile under oakwood.

Depth cm	pH	pK	Water % dry weight	Ignition loss % dry weight	Nitrogen % dry weight	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation
3	2.88	3.64	120	94	2.17	16	93	109	15
6	3.25	3.82	68	26	0.78	10	37	47	21
9	3.39	3.82	59	17	0.50	11	29	40	28
14	4.11	4.08	60	11	0.28	20	19	39	51
20	4.22	3.90	60	14	0.37	31	15	46	67
26	4.36	3.92	59	15	0.39	39	14	53	74
33	4.44	3.88	40	7	0.17	29	8	37	78
44	4.15	3.56	42	9	0.21	31	8	39	79
58	4.36	3.79	37	8	0.16	30	8	38	79

TABLE IX. Chemical characteristics of a leached soil profile under conifers.

Depth cm	pH	pK	Water % dry weight	Ignition loss % dry weight	Nitrogen % dry weight	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation
1	-	-	25	96	2.00	10	53	63	16
3	2.67	3.64	117	95	2.11	11	101	112	10
5	2.87	3.88	112	49	1.41	6	61	67	9
11	3.41	4.05	65	23	0.56	9	39	48	19
19	3.93	4.23	39	9	0.18	9	18	27	33
25	4.05	3.96	55	19	0.40	21	17	38	55
35	4.20	4.23	69	23	0.53	31	33	64	48
45	3.97	4.10	62	23	0.54	24	32	56	43

TABLE X. Chemical characteristics of some woodland soils from the south of England.

Water % dry weight	Ignition loss % dry weight	$\frac{\text{Water}}{\text{Ignition loss}}$	pH	Apparent pK	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight.	% base saturation
12	6	2.0	4.68	4.38	8	4	12	67
23	7	3.3	4.58	4.18	10	4	14	71
22	5	4.4	4.30	3.87	8	3	11	73
23	5	4.6	4.53	4.13	10	4	14	71
23	5	4.6	5.22	4.43	12	2	14	86
27	7	3.9	4.18	4.18	7	7	14	50

III. THE NUTRIENT STATUS OF SOME WATERLOGGED SOILS AND THEIR PLANTS IN THE ENGLISH LAKE DISTRICT

It is generally accepted that the nutrient status of the soil is of the utmost importance to the establishment and development of vegetation. Yet surprisingly little is known of the nutrient status of waterlogged soils or of the vegetation which they support. It was with the hope of gaining some information on this point that in 1948 a survey was begun of soils and plants in some semi-aquatic and under-water habitats in the English Lake District, where wet soils are common. The investigation has been largely exploratory, for in view of the variability of habitats encountered it was deemed necessary to use relatively simple techniques on a large number of samples, rather than to concentrate on minute analyses of a few. The results obtained, however, appear to shed some light on the development of wet soils in the district, and on the relation of plant nutrient status to that of the soil.

DESCRIPTION OF THE AREA

The Lake District is well known as a region of high rainfall and marked relief. In the southern part investigated in this study the rocks are chiefly Silurian slates and grits, which are non-calcareous but weather more rapidly than the harder rocks in the north. They are overlain generally by glacial clays and clay loams.

Much ecological work has been carried out here, mainly by Professor W.H. Pearsall and members of the Freshwater Biological

Laboratory at Wray Castle. It deals chiefly with aspects of lake development, such as soil and water chemistry, shore vegetation, bottom fauna, plankton, fish populations, and also historical factors. Many references may be found in recent papers by Pearsall & Pennington (1947) and Lund (1950).

The sites studied by the writer fall into the following categories, which also roughly approximate to a developmental series common in the district:-

Underwater soils. Along the shores of lakes, in shallow water within the zone of plant growth.

Marshes and fens. Inorganic and peaty waterlogged soils along lake margins, with a vegetation dominated by reeds, grasses, sedges or alder-willow carr.

Lacustrine bogs. (Pearsall, 1938). Developed around small lakes and pools, with a vegetation in which Sphagnum has become one of the dominant plants, often with Molinia coerulea and Myrica gale; usually containing relics of a poor fen stage.

Raised bogs. Formed by the growth of Sphagnum above the influence of mineral ground water, and in this area developed above fen and carr (see Rankin, in Tansley, 1911). These bogs have all suffered to some extent from cutting and burning, so that the vegetation is generally dominated by Calluna vulgaris and Eriophorum vaginatum rather than Sphagnum species. Drainage has also resulted in some oxidation of the surface peats (Pearsall, 1938b).

It should be emphasized that the divisions imposed above are arbitrary and for purposes of convenience. In nature the whole group of soils form a complex showing varying degrees of relationship, but with a complete series of transitional stages generally to be found on searching for them. The marked separation of stages found in some areas are not found in others; and a system of classification ignoring the latter presents a convenient but sometimes misleading picture of vegetational and soil development (see Sjörs, 1950).

The localities from which most of the samples were collected are as follows:-

Underwater, marsh and fen - Windermere, Esthwaite Water, Blelham Tarn and Elterwater.

Lacustrine bogs - Blelham Tarn and Nor Moss.

Raised bogs - Rusland Moss and Striber's Moss.

Esthwaite Water shows an especially good marsh and fen vegetation, with well developed reedswamp, grass and sedge meadow, and alder-willow carr successions (Pearsall, 1918). In some places one can find a further stage of transition to *Sphagnum* bog with *Molinia* and *Myrica*, such as is characteristic of the lacustrine bog beside Blelham Tarn. This latter bog also shows remnants of a previous fen stage, being fronted by reeds and sedges, with much *Phragmites* at the margins. Nor Moss is a small lacustrine bog with many traces of a previous poor fen vegetation, e.g. *Carex inflata*, *Equisetum limosum* and *Menyanthes trifoliata*. Unfortunately there are no good examples of undisturbed raised bog in the Lake District today, so that it is difficult to determine what the conditions were before partial drainage led to oxidation of the surface peat and to floristic changes. However, the samples from these bogs have been selected with a view to obtaining specimens both from little altered areas dominated by Sphagnum, and from parts of the bogs showing the maximum drying and aeration. Furthermore, using pH data collected by Pearsall (1938b) from relatively undisturbed English and Irish bogs, we can obtain an idea of what must have been the conditions in such bogs in the Lake District.

The data on lacustrine bog peats have been separated into three groups. First there are the typical peats from the centre of the bog. A second group consists of some peats of relatively high base status, which are found at Nor Moss and Blelham bog along the margins where at times there is some water movement. The third group, of two samples, is from a dryer hillock of probably upturned peat at Blelham, now covered by Molinia and Myrica without Sphagnum and strongly resembling the raised bog peats in chemical properties. These latter peats have also been separated into three groups. One consists of two samples beneath growing Sphagnum, another of those sites dominated by Calluna and Eriophorum, and a third of areas obviously among those most affected by drainage, including the edge of a pathway and three samples from mature pinewood which is invading the mosses.

The results of this study will be presented in relation to increasing soil ignition loss, in order to follow one of the major natural trends in the development of these waterlogged soils; that is, from an original inorganic mineral soil to a highly organic peat. The observations of W.M. Rankin (Tansley, 1911) and of Professor Pearsall

(1918, 1938), as well as the writer's own examination of both vertical stratigraphy and horizontal zonation in waterlogged areas, suggest that wet inorganic soils in the district develop typically through the following stages, though of course there are many variations.

1. **Subaqueous stage** (if present), organic matter giving a somewhat gelatinous structure to the soil.
2. **Reedswamp**, with such plants as *Phragmites*, *Scirpus lacustris*, *Typha* and *Equisetum limosum*.
3. **Sedge meadow**, with various *Carices*; or grass meadow in more silted areas, with *Phalaris arundinacea* and *Calamagrostis lanceolata*.
4. **Alder-willow carr**, usually dominated by *Salix atrocinerea*.
5. **Lacustrine bog**, with genefally a *Sphagnum*, *Molinia*, *Myrica* community.
6. **Raised bog**, dominated by *Sphagnum* species.
7. **Raised bog**, dominated by *Calluna* and *Eriophorum vaginatum*, usually invaded by pine.

This sequence is characterized in general by an increasing accumulation of humus in the soil, though local silting causes a great deal of variability and may be responsible for lateral humus gradients in addition to those parallel to the main lines of succession (Pearsall, 1918). The last stage seems in England to be usually associated with human interference, either cutting or burning.

It is the purpose of this paper to show something of the changes in nutrient status of the soils and plants as the above succession proceeds. It may be noted that, as soil development cpntinues, the influence of the mineral soil (and of groundwater from it) tends to diminish; until in the raised Sphagnum bog there are probably no nutrients reaching the upper layers of peat from the mineral soil.

METHODS

Soils

Samples were collected during the summers of 1948, 1949 and 1950; from the surface of the underwater soils and from approximately 10 cm depth in other soils. Specimen tubes 10 X 2.5 cm were filled, corked and stored until analyses could be carried out, usually within one or two months. Some samples, however, had to be kept for analysis during the winter, in the intervening months they were stored at a low temperature. Occasional determinations of pH immediately after sampling and later on indicated that the changes on storage were similar to those in woodland soils (Gorham, in prep.) and probably did not go beyond the range of pH for each of the major categories listed above. The following determinations were carried out:

pH - glass electrode on fresh sample.

Water - soils dried at 105-110°C.

Ignition loss - soils ashed at 525 - 550°C.

Coefficient of humidity - water/ignition loss (Crump, 1913).

Total exchangeable bases - on the undried soil by the method of Brown (1943).

Exchangeable hydrogen - on the undried soil by the method of Brown (1943).

Exchange capacity - sum of exchangeable bases and exchangeable hydrogen.

% base saturation - total exchangeable bases X 100/ exchange capacity.

Apparent pK - (= pH at half base saturation) - calculated from the equation

$$pK = pH - \log \frac{(salt)}{(acid)}$$

using exchangeable bases as salt and exchangeable hydrogen as acid. This is of course only a rough approximation, since there are many acids present in a heterogeneous medium; but Chandler (1939) states that for woodland soils the values correlate highly with those obtained experimentally. A low pK is evidence of a high degree of dissociation and therefore of a strong acid.

Nitrogen - by the micro-Kjeldahl technique, on duplicate samples.

Water, ignition loss and nitrogen are expressed as % dry weight, the exchange constituents as milli-equivalents per 100 grams of dry soil (referred to in the text simply as m.e.).

Plants

Samples were collected of the green tops of mosses and monocotyledons (except pondweeds, *Phragmites* and *Phalaris*), and of the leaves of other plants. The analyses thus represent the major photosynthetic organs. All plants were collected from abundant growths in what appeared to be their natural habitats and each matches a soil sample. An attempt was made to gather members of the same plant group at the same time. The fresh samples were carefully water-washed, air-dried and stored. During the winter the following determinations were carried out, after drying the plants at 105-110 °C.

Ash - ignition in muffle furnace at 525-550 °C.

Excess base - back titration of the acidified ash, using mixed bromocresol green and methyl red.

Nitrogen - by the micro-Kjeldahl technique, on duplicate samples.

Ash and nitrogen are expressed as % dry weight, excess base as milli-equivalents per 100 grams of dry plant material (referred to in the text as m.e.).

It is not known how far the time of sampling and stage of development has affected the values obtained.

RESULTS

Soils

The results for underwater soils are given in Table I, for marsh and fen soils in Table II, for lacustrine bog peats in Table III and for raised bog peats in Table IV. They are also shown graphically in Figures I to X.

Water and humus (Figure I).

It is clear from the tables that the water content usually accounts for the greater part of the weight of the fresh soil. And as humus increases, so does water content. However, the amount of water per unit of humus tends to fall. Using the coefficient of humidity (*water/humus* ratio) as a measure, we find that the underwater soils are generally above 10, and range up to 33; while the marsh and fen soils lie between 4 and 19; the undisturbed lacustrine bog peats between 4 and 14; and the raised bog peats generally between 2 and 12 (except for

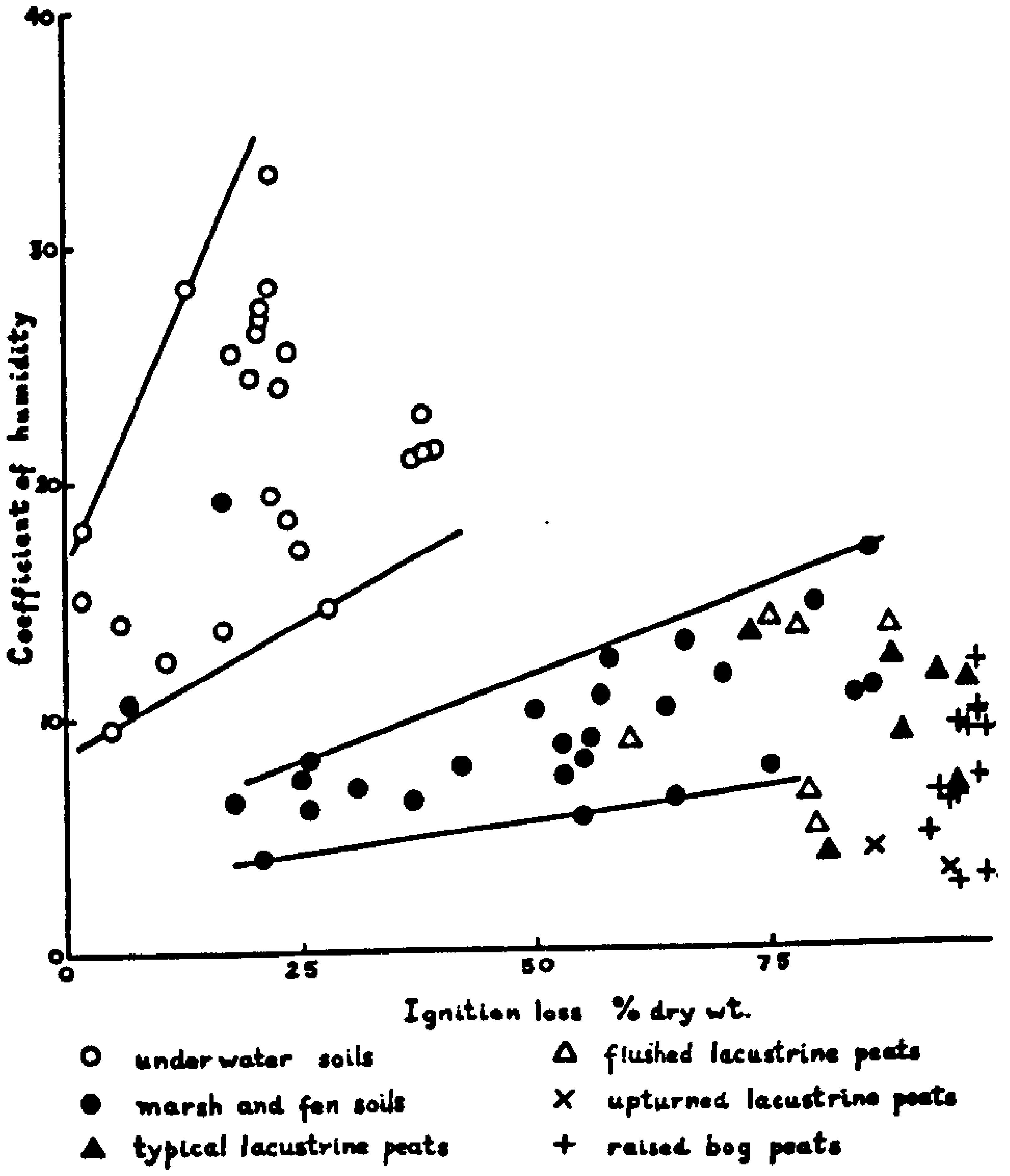


FIGURE I.

Coefficient of humidity in relation to humus content.

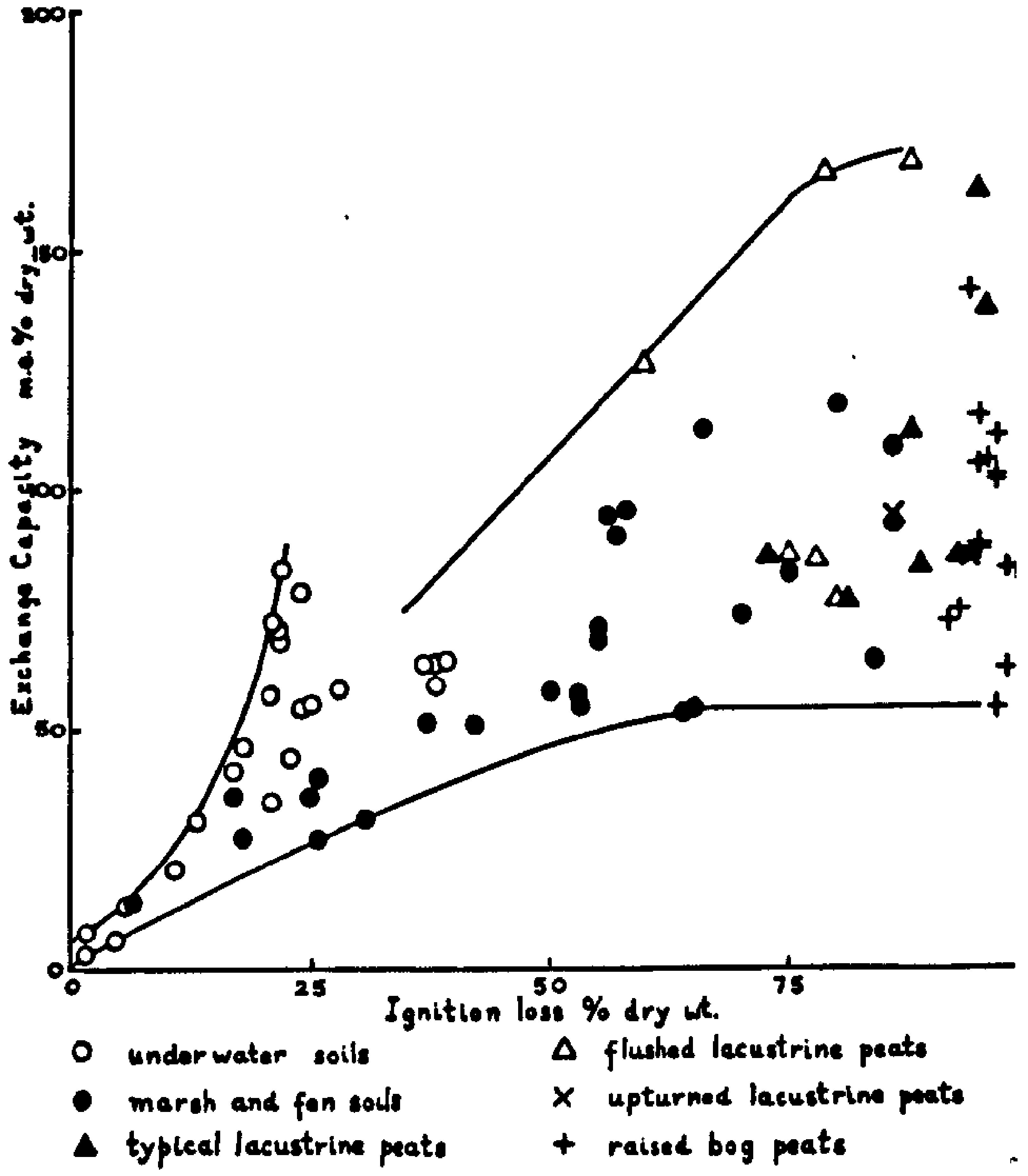


FIGURE II.

Exchange capacity in relation to humus content.

a very high value of 23 in one site almost unaffected by draining). There are of course seasonal variations also. In the underwater soils, and in those from marshes and fens, the coefficient tends to rise somewhat with increasing organic matter, in contrast to the drop generally found in woodland soils (Gorham, in prep.). In the latter case of course the peat, while very absorptive, may also offer a great deal of surface for evaporation.

The underwater soils seldom become very peaty. The maximum ignition loss found by the writer was 39%, and Misra (1938) in 68 analyses found only 5 samples with over 50%.

Exchange capacity (Figure II).

As can be seen in the figure, exchange capacity increases from less than 10 m.e. in the most inorganic soils to between 50 and 170 m.e. in the organic peats. In the latter group the high values presumably belong to the more decomposed samples; while the low values represent little decayed material which may in many cases contain much living root tissue. The two highest figures, 165 and 167 m.e., are for lacustrine bog peats from Blelham which may be flushed at times by moving water; and it is possible that since they are wholly base-saturated the high values may be due to base being free in solution. This, however, would not appear to account for the high values of 137 and 161 m.e. observed for ordinary lacustrine bog peats from Blelham, which were only 58 and 28% saturated with bases respectively.

The exchange capacities of over 70 m.e. in four lake muds with between 20 and 25% ignition loss appear to be very high. Assuming an approximate value of 8 m.e. for the inorganic fraction, a calculation of exchange capacity per 100 g ignition loss (= roughly organic matter) gives values ranging from about 275 to 340 m.e. These are still well below the maximum of 400 m.e. cited for humus colloids by Baver (1940). That the organic matter of lake muds may be highly colloidal is suggested by the gelatinous nature of many subaqueous peats and by the absence of recognizable plant remains. We may note here that the exchange capacity of the underwater muds is generally greater than that of marsh soils of similar organic content.

Even higher figures for exchange capacity were obtained on some black muds (starred in the table), due to extremely high contents of exchangeable base. The black color of these muds gave a clue to the results, they were apparently strongly reducing and contained precipitated ferrous sulphide. In the acetic acid solution of exchangeable base this compound dissolved to give erroneously high results. Passing a stream of oxygen through the most extreme of these samples reduced the exchangeable base from 143 m.e. to 62 m.e., while raising the exchangeable hydrogen from 11 to 14 m.e. Oxygenation of one of the brown and more highly organic muds from Pull Wyke had no significant effect, increasing exchangeable base by 5 m.e. and reducing exchangeable hydrogen by 1 m.e.

Total exchangeable bases (Figure III).

Underwater soils are relatively rich in bases as compared with the emergent marsh soils, as might be expected from their close contact with moving water. In the soils between 20 and 30% ignition loss, the former are all above 30m.e. while the latter are below this

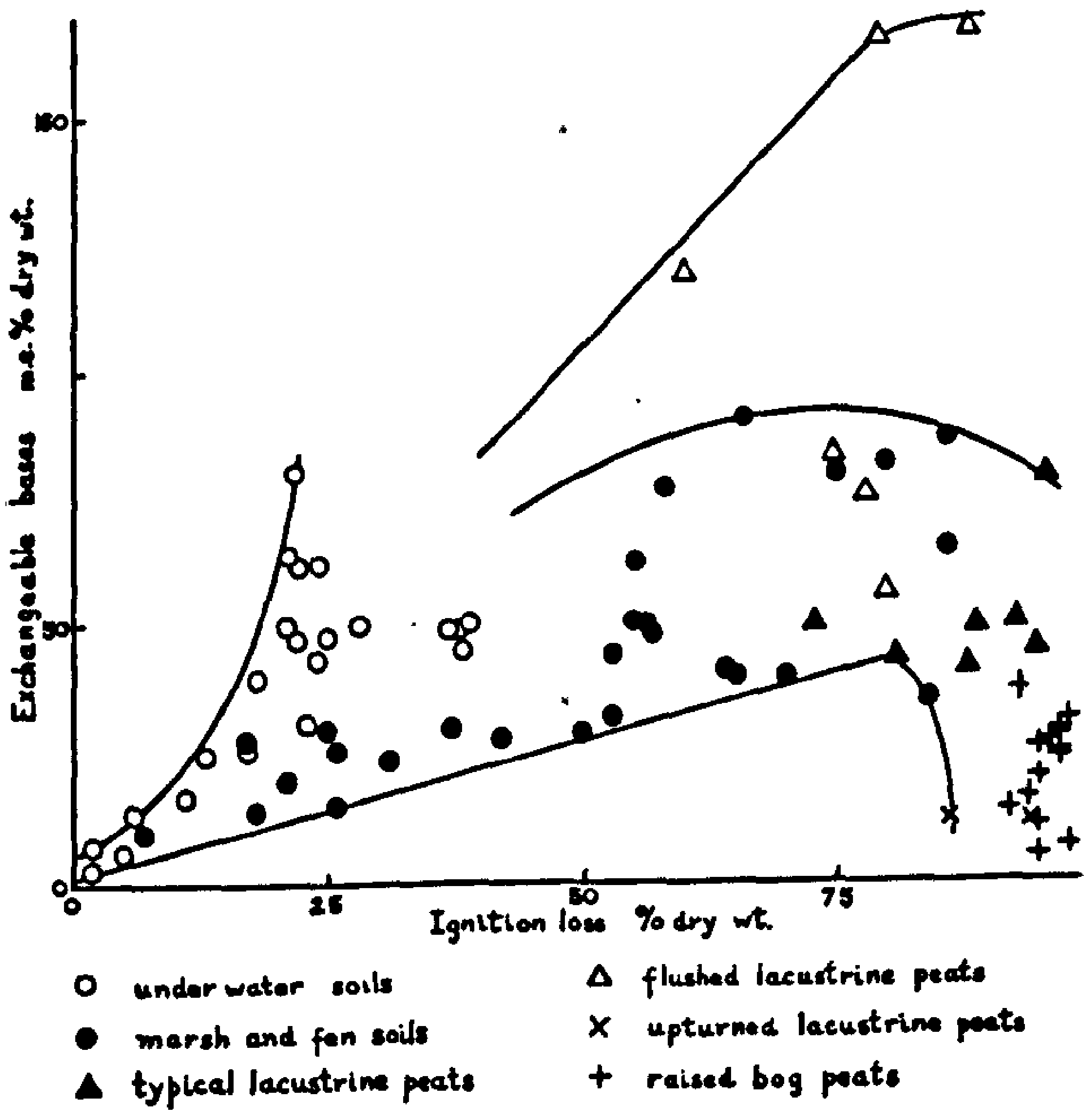


FIGURE III.

Total exchangeable bases in relation to humus content.

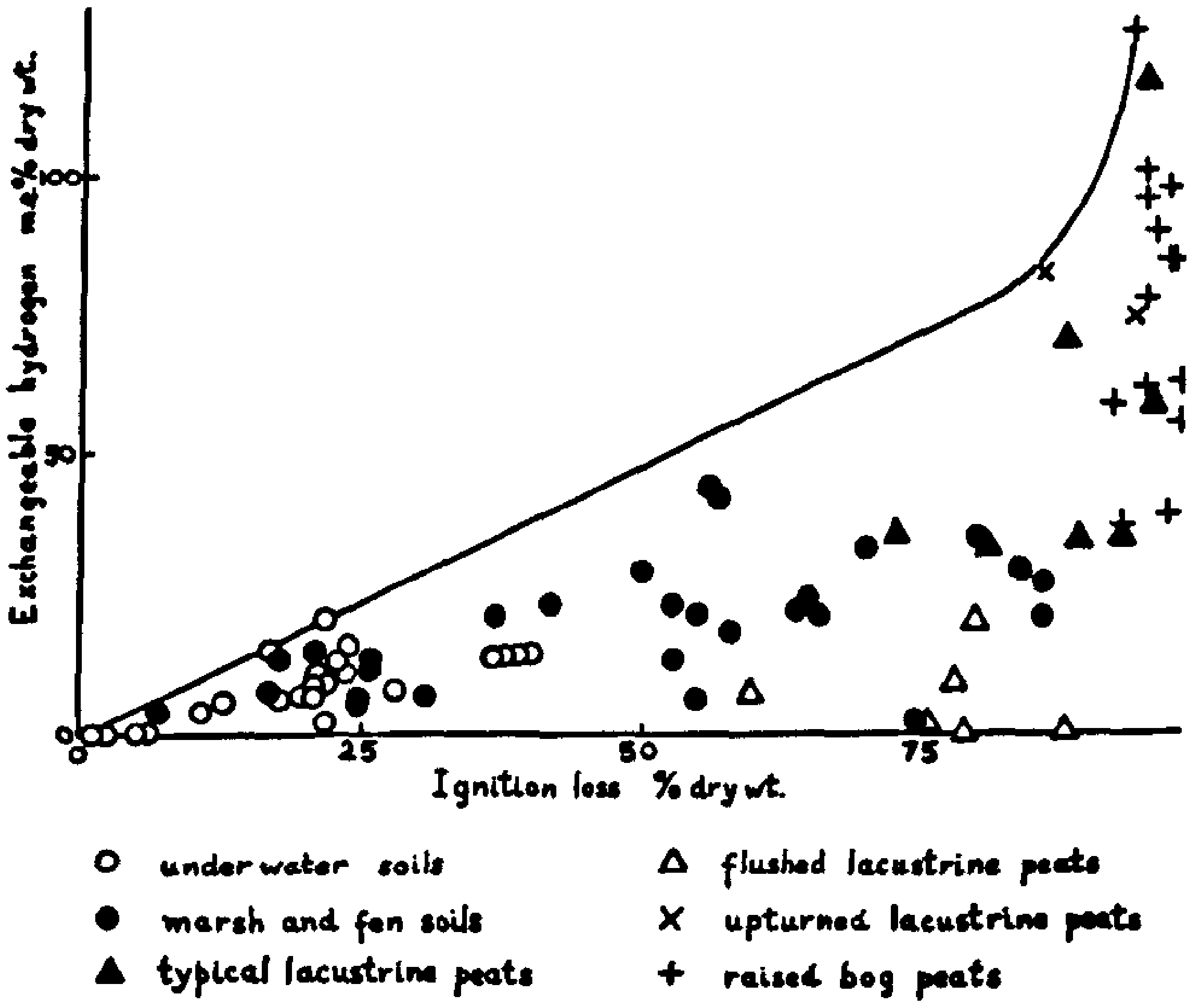


FIGURE IV.

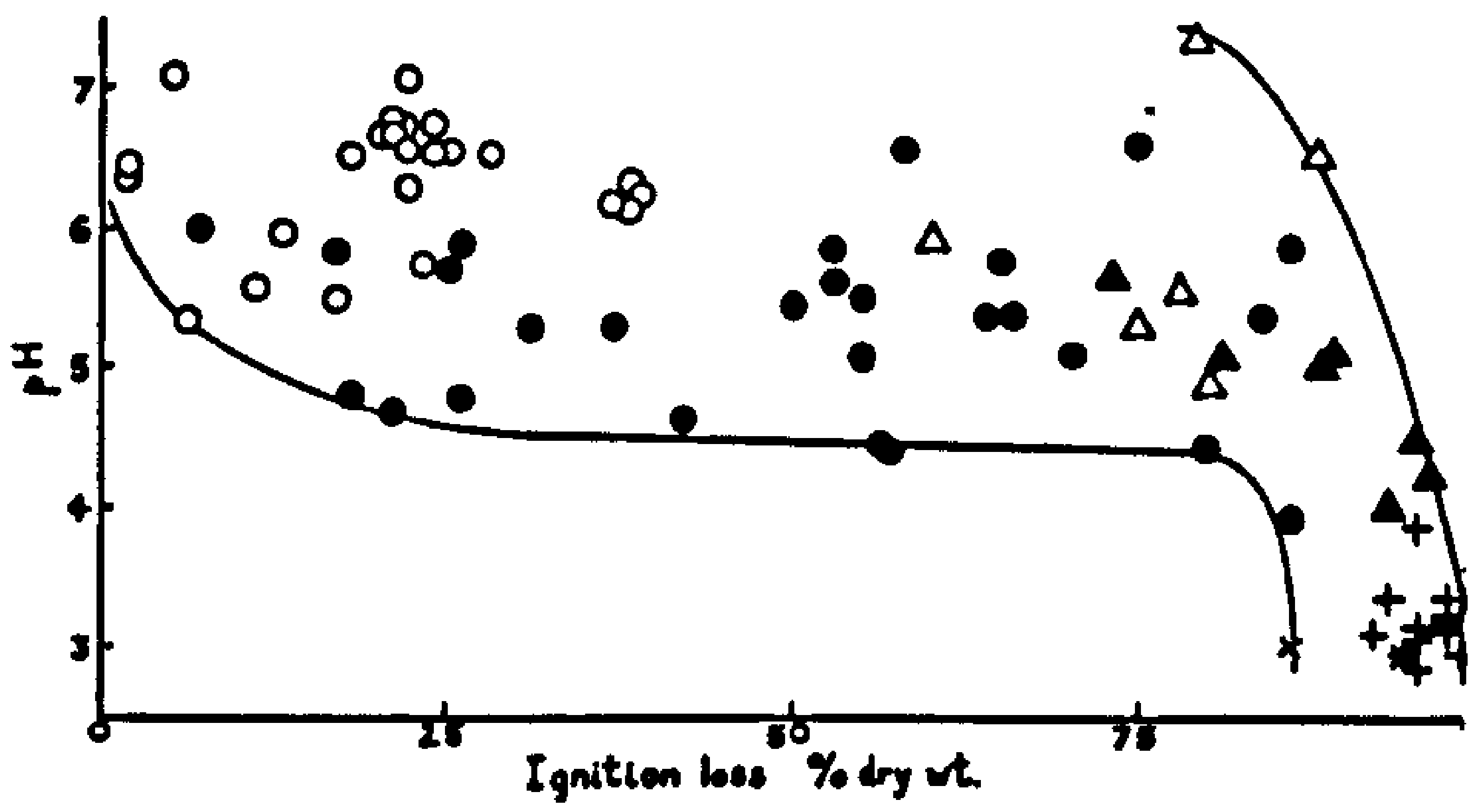
Exchangeable hydrogen in relation to humus content.

figure. The marsh and fen soils show a rise from 10 m.e. in the most inorganic to between 30 and 91 m.e. in the organic peaty soils with more than 50% ignition loss. The flushed lacustrine bog peats are also high in bases, ranging from 56 m.e. to 167 m.e. The more typical lacustrine bog peats tend to be rather low, six out of seven samples containing between 40 and 50 m.e. The two peat hummocks from Blelham resemble the raised bog peats in having a very low level of bases, only 11 and 12 m.e. as compared with a range of from 5 to 37 m.e. in the latter. In the raised bog group the two samples beneath actively growing _Sphagnum_ show the highest results, 26 and 37 m.e.; while the most disturbed sites on the other hand only contain from 5 to 16 m.e.

Exchangeable hydrogen (Figure IV).

The chief point of interest here is the rapid increase in exchangeable hydrogen consequent on bog development. The underwater soils contain up to 21 m.e., while the maximum amount in the fen soils is only 44 m.e. The typical lacustrine bog peats, however, range from 33 to 116 m.e.; while in the riased bog peats the lower limit~~s~~ is 37 m.e. and the upper limit 125 m.e. On the average the raised bog peats are highest. In these, the peats least affected by drainage are rather low, those apparently most affected range from rather low to the two highest values, possibly depending on the degree of decay. The lacustrine bog peats from the flushed margins are low in exchangeable hydrogen, ranging from 0 to 20 m.e.

FIGURE V. pH in relation to humus content.



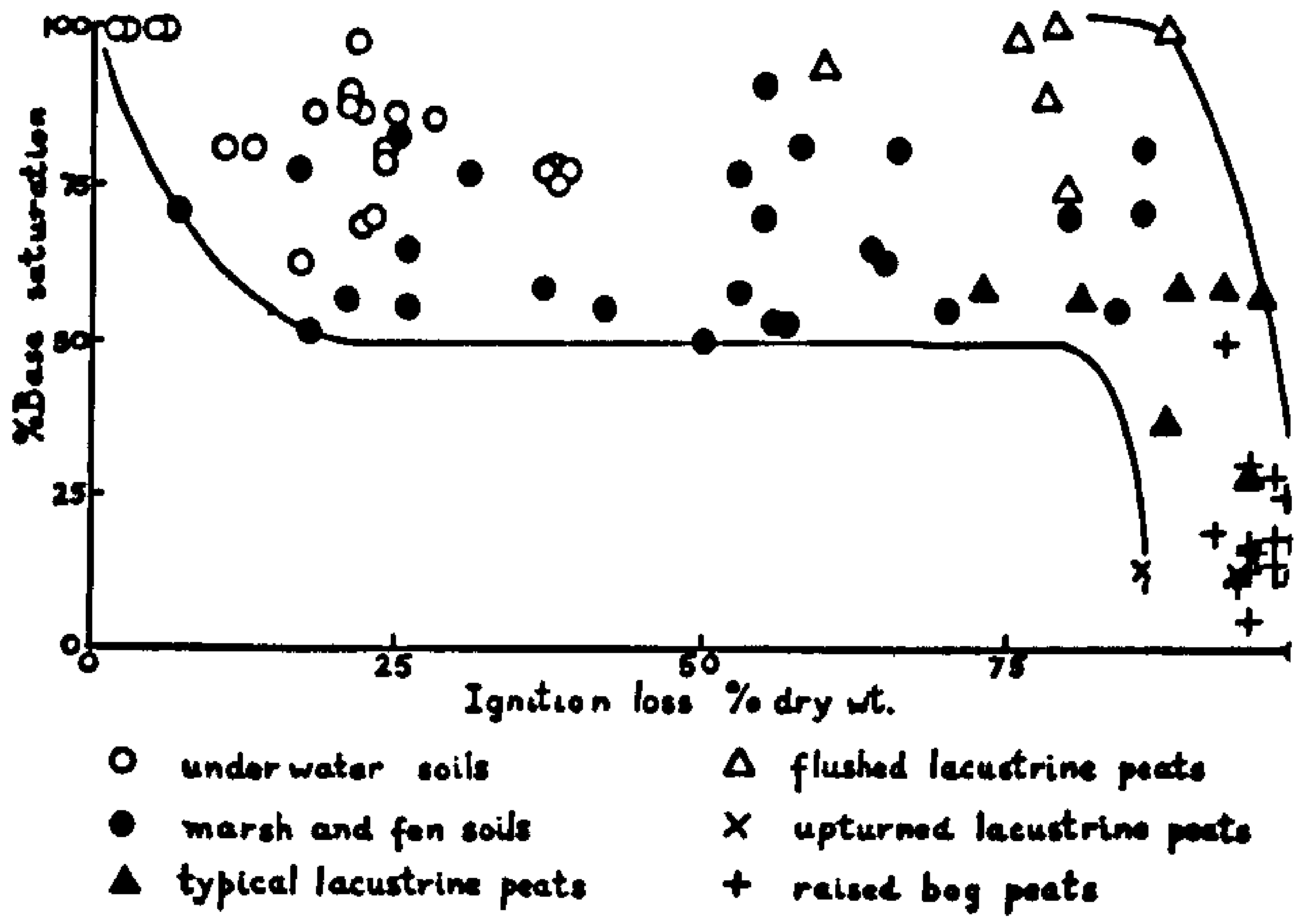


FIGURE VI. Base saturation in relation to humus content.

pH and % base saturation (Figure V and VI).

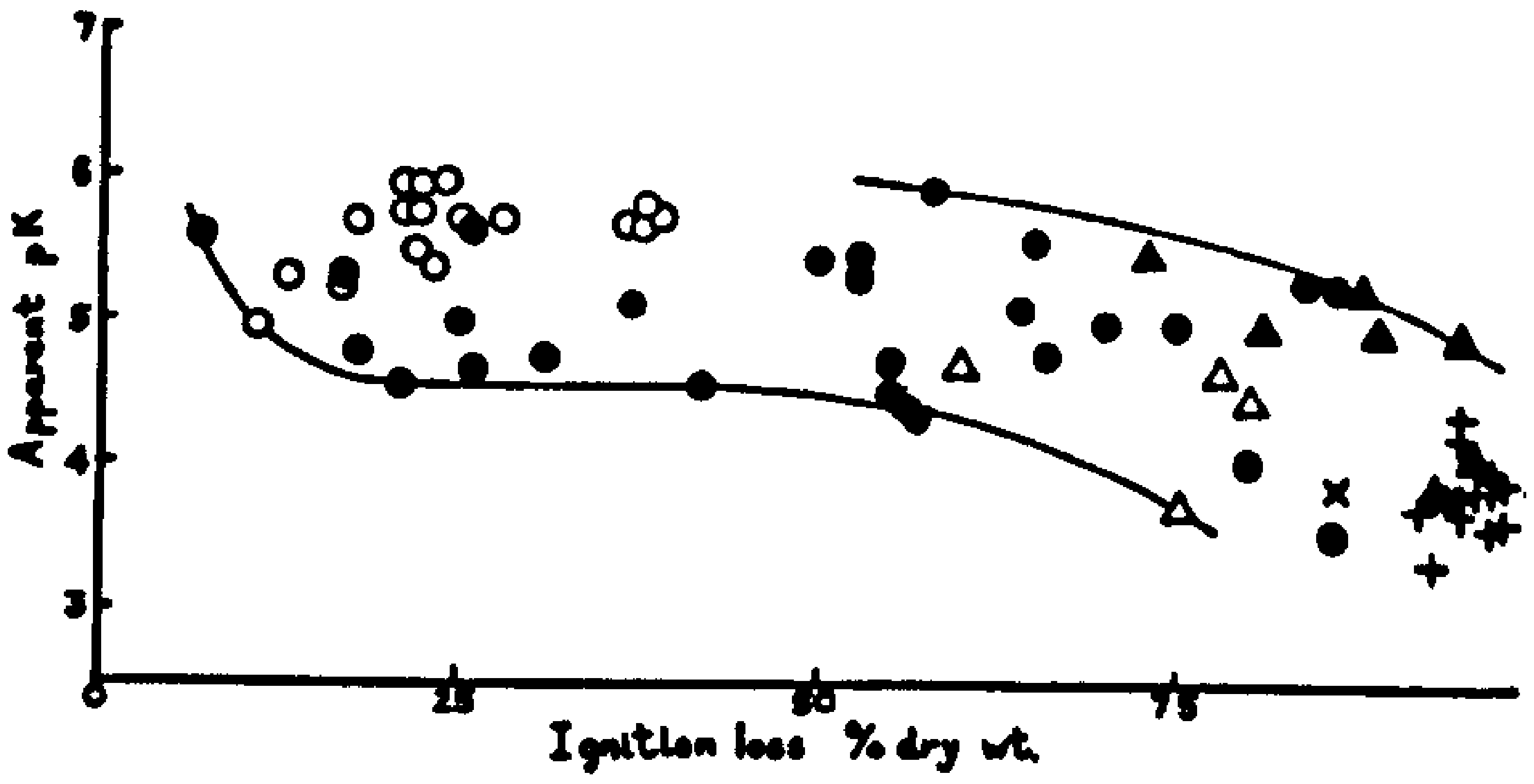
The trends for these two values follow similar lines. While both may remain high until the soil becomes very peaty, especially in situations where there is some water movement; there is a tendency for the lower limit to drop sharply between 0 and about 20 % ignition loss, presumably due to the production of hydrogen ions by decaying organic matter. The marsh soils are generally more acid and less base saturated than the underwater soils, chiefly due to the greater exchangeable base content and weaker acids of the latter, exchangeable hydrogen being quite similar in both series. This suggests that periodic aeration and stagnation are the important factors, the former perhaps tending to produce stronger acids (as suggested farther on) and the latter to prevent accession of bases.

Between about 20 and 85 % ignition loss pH remains more or less constant between 4.5 and 7; while base saturation remains between 50 and 100 %.

About 85% ignition loss both values drop sharply. In all but one of the raised bog peats pH has fallen to between 2.8 and 3.4; while base saturation goes well below the 50% level, to as low as 5%. The two relatively undisturbed bog sites show the highest pH and base saturation figures. Those areas most affected by drainage are the most acid and deficient in bases.

It may be noted here that the data provided by Pearsall (1938), on the pH of little altered raised bogs, fill in exactly the transition

FIGURE VII. Apparent pK in relation to humus content.



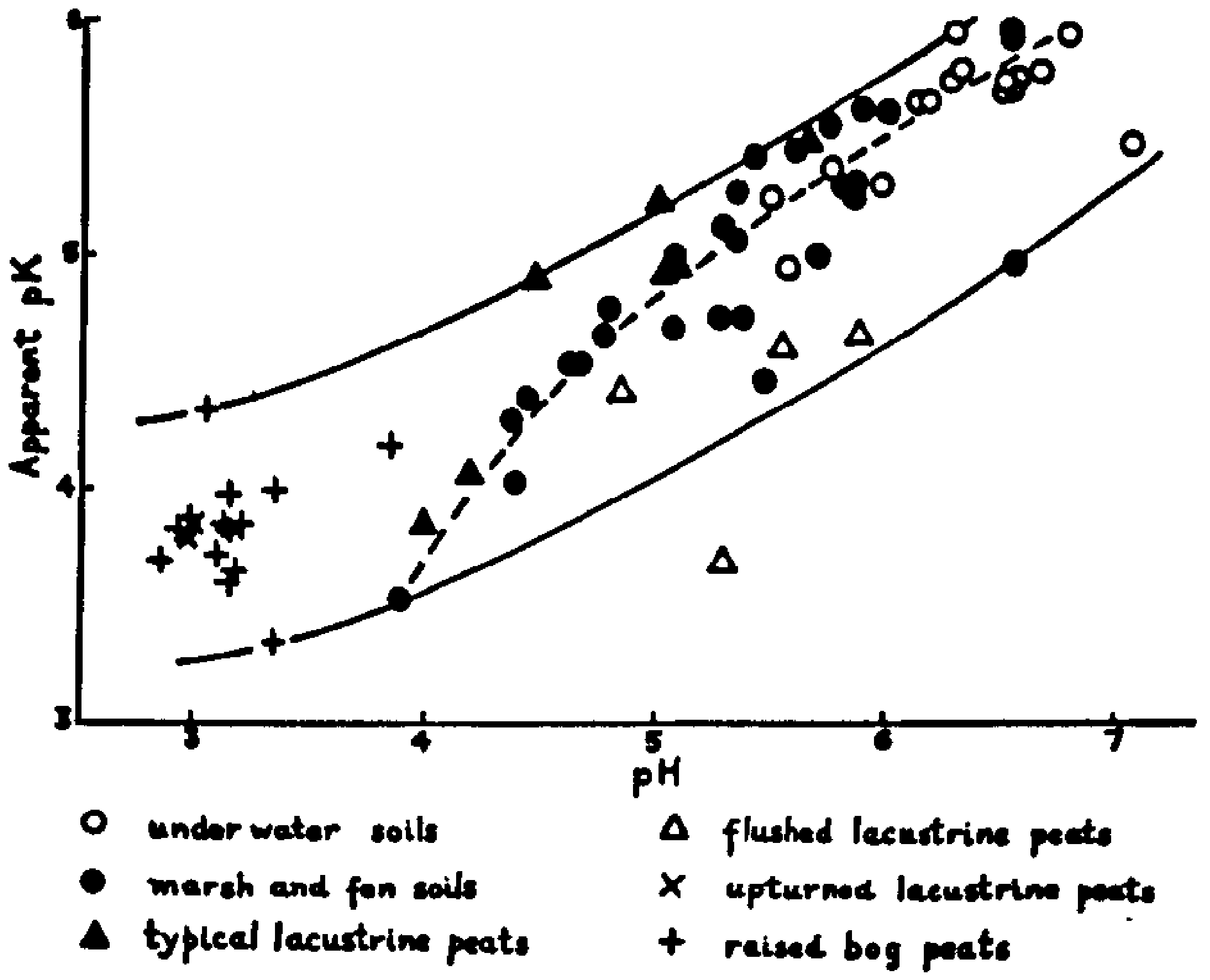


FIGURE VIII. Apparent pK in relation to pH.

between lacustrine bogs and the drained raised bogs in the Lake District. The Irish bogs, with a rainfall of about 85 to 120 in. per year, gave pH values of from 3.86 to 4.45. The English samples, from the Solway Firth and with a lower rainfall of from 60 to 80 in. per year, were somewhat more acid, between pH 3.40 and 3.68. In comparison, the lacustrine bog peats from the Lake District range down to pH 4.0; while the semi-drained and oxidized surfaces of the raised bogs show a pH range from 3.8 in the wettest sample to 2.8 in the driest.

Apparent pK (Figure VII and VIII).

As in the last two determinations, the lower limit for pK drops sharply with the first additions of organic matter to the soil, to about pK 4.5. The upper limit is about 6.0. Between 20 and 50% ignition loss pK remains within this range. In the more organic soils, however, it declines steadily to between 3.3 and 4.9 at about 95% ignition loss.

The underwater soils have relatively weak acids, pK being always above 4.9. The marsh and fen series range from 3.53 for a sample in a Carex inflata community to 5.92 in a zone dominated by Carex elata. The lacustrine bog peats exhibit a similar range of pK. The raised bog peats all have rather strong acids, with pK's between 3.34 and 4.34.

The relation of pK to pH is shown in Figure VIII. It appears that pK tends to drop with increasing acidity in the succession from underwater soils to lacustrine bog peats. However, once pH has dropped to between about 3.5 and 4.0 in the most acid fens and lacu-

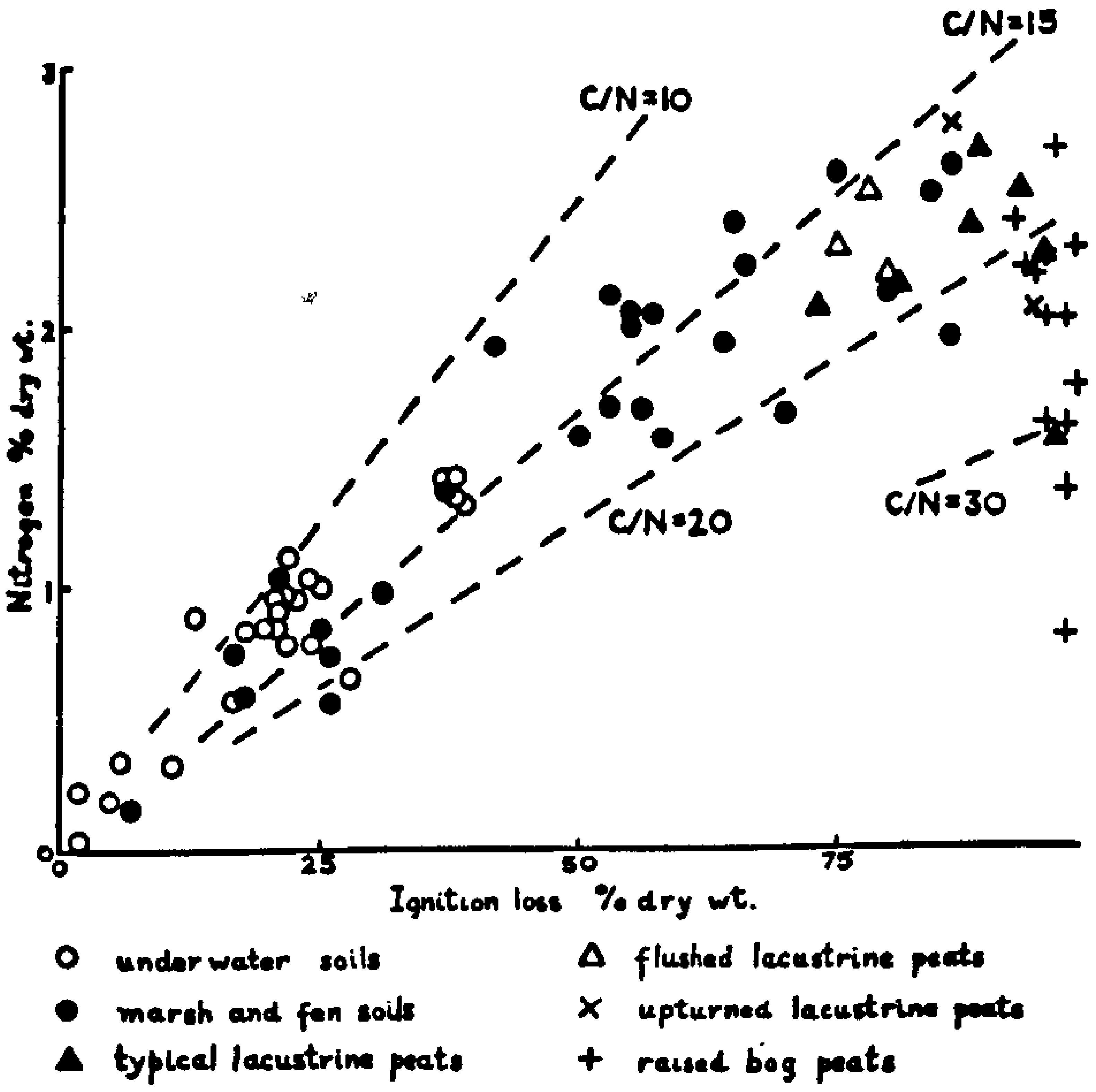


FIGURE IX.

Nitrogen in relation to humus content.

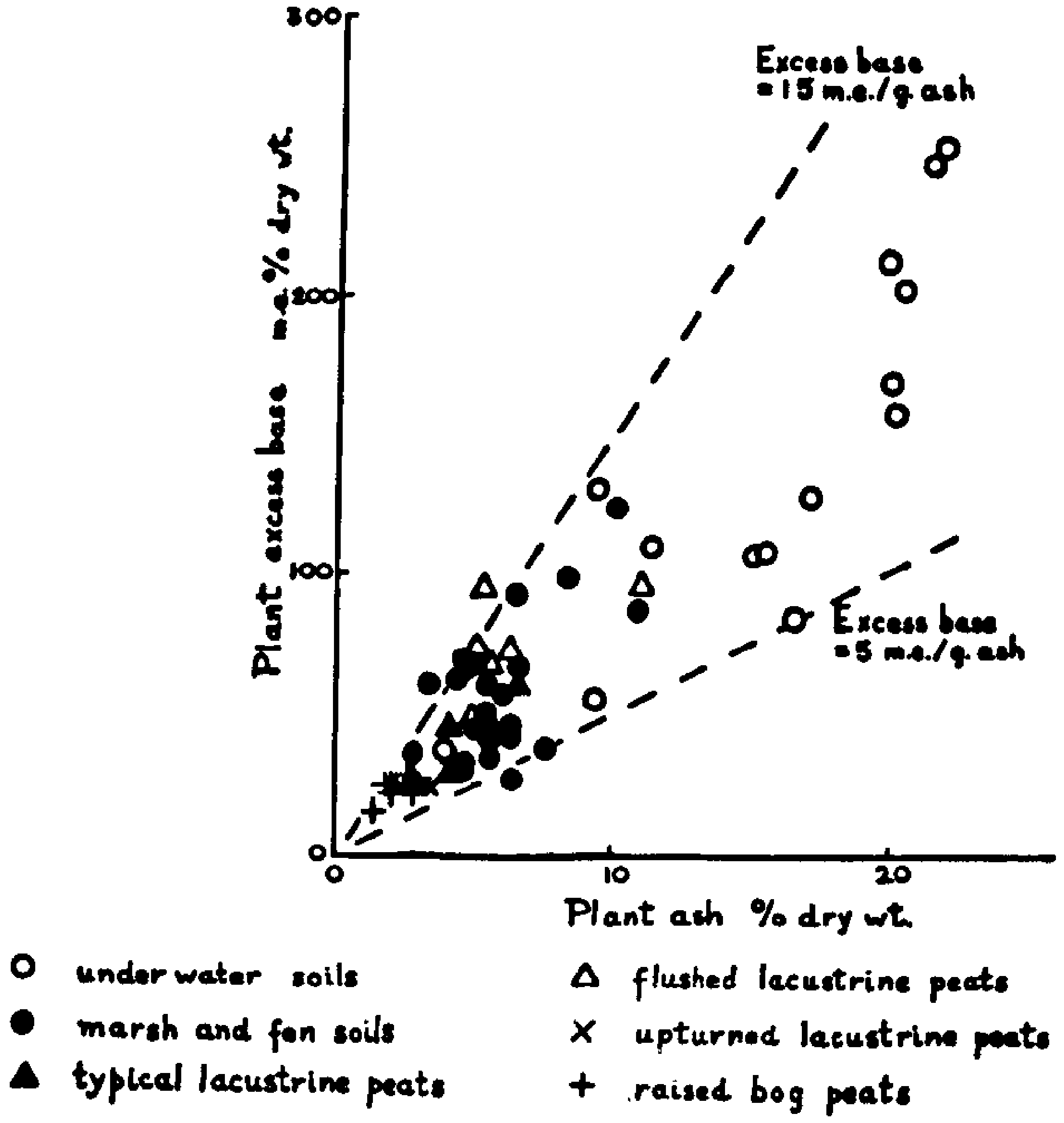


FIGURE X.

The relation of excess base to ash content in plants of wet soils.

strine bogs, there seems to be little further increase in acid strength consequent on raised bog development; nor is there much difference in the pK's of the three groups of more and less disturbed sites. Thus the low pH of the latter is chiefly due to the production of larger quantities of acid, rather than to the formation of stronger acids than those found in the most acid fens and lacustrine bogs. In the succession previous to raised bog development there is some indication (shown by the broken line in Figure VIII) of a more rapid decline of pK with increasing acidity.

<u>Nitrogen</u> (Figure IX).

The nitrogen content of the soil increases markedly from the inorganic to the peaty soils, as might be expected. At 25% ignition loss the percentage of nitrogen is between about 0.5 and 1.2% dry weight of soil, above 40% ignition loss the values range from 0.8 to 2.8% dry weight. While in general the trend in proceeding from the underwater and marsh soils to the fen and lacustrine bog peats takes the form of a steady increase in nitrogen, there would appear to be some tendency toward a drop in the raised bog peats. In the more organic of the former soils (between 75 and 95% ignition loss) the range for nitrogen is between about 2 and 2.8% dry weight; while in the raised bog surfaces it is between about 0.8 and 2.7%.

If nitrogen is calculated as % ignition loss, or approximately as % organic matter, the values fall with increasing humus content in the soil, as may be gathered by an inspection of Figure IX. In other words, as the soils become more organic, the amount of nitrogen per unit of humus decreases, i.e. the carbon/nitrogen ratio increases, as shown in Table V. The sharpest change occurs in the raised bog peats.

While the errors are liable to be considerable, by assuming organic carbon to contribute half the ignition loss we may estimate rather crudely the C/N ratios of these soils. In Figure IX the broken lines define certain constant levels of C/N ratio determined in this way. We see that C/N in these soils rises with increasing humus content. A majority of the values fall between about 10 and 15 in the inorganic soils, 15 and 20 in the highly organic fen and lacustrine bog peats, and about 20 and 30 in the raised bog peats.

Plants

The results for plants are given in the same tables as the soils data, and are also presented in Figure X.

Ash.

The total mineral uptake, as measured by the ash content, is highest in the group of plants growing on the underwater soils. Between 4 and 22% of the dry weight of these plants consists of mineral ash. It is interesting that the lowest figures are for the two species of *Typha*, which are emergent plants resembling the marsh species; and that the two plants with floating leaves, *Nuphar* and *Potamogeton natans*, tend to be intermediate. The totally submerged plants are all above 15%. The marsh and fen plants contain between 2.8 and 11.9% of ash, with no apparent relation to soil base status or organic matter. *Cladium*, a plant of calcareous tarns, seems strangely low in mineral matter, a finding confirmed by analyses on some Irish samples (Pearsall, private communication). The plants from the lacustrine bogs show a similar range of ash content to those of the fens, and we may observe that the Sphagna (which do not include the main raised bog formers) are not particularly low in minerals. The five species of plants from the raised bogs show a low range of ash content, from 1.4 to 4.4% dry weight.

Excess base.

This value gives an approximation of the excess of inorganic cations over inorganic anions, or roughly the inorganic cations which in the plant are balanced by organic anions. It is only a very approximate measure, however, because some plants may contain large amounts of organic sulphur and phosphorus, which on ignition tie up equivalent amounts of base. The data of Mattson & Karlsson (1944) on woodland plants from both damp and dry soils indicate that the excess base generally accounts for about 60 to 90% of the total calcium, magnesium and potassium in the plants; except in grasses, where it represents about 40%. Unfortunately, nothing is known of this relation in plants of waterlogged soils.

The results are similar to those for mineral ash. The submerged plants are high, with from 84 m.e. in Nitella to 253 m.e. in a specimen of Littorella. The marsh, fen and lacustrine bog plants fall between about 25 and 125 m.e., again with no apparent relation to soil characteristics. The five raised bog species are very low, ranging from 16 to 35 m.e.

In Figure X excess base has been plotted versus ash content, and we see that as the mineral uptake rises, excess base also increases. The broken lines indicate constant levels of excess base per unit of ash, and we find that most of the plants contain between 5 and 15 m.e. per g. of ash. Those approaching the former limit presumably contain larger amounts of silica, heavy metals which would not titrate as excess base, or sulphur and phosphorus, which on ignition would tend to neutralise the excess base. There are no apparent differences between the plants on different soil types.

Nitrogen.

As in the preceding two determinations, nitrogen is highest in the submerged plants and, with the exception of the *Sphagnum* species, lowest in the five species from the raised bogs. The submerged plants contain between about 2.8 and 5.0% nitrogen. The marsh, fen and lacustrine bog species (excepting *Sphagnum*) range from about 1.1 to 4.1%. The five plants from raised bogs are relatively low in nitrogen, with from about 1.1 to 2.1%. The *Sphagnum* species from the lacustrine bogs all contain less than 1.0% nitrogen, going as low as 0.7%.

If we calculate the *C/N* ratios for the plants in the same way as for the soils, the aquatic group range from about 9 to 14; the marsh, fen and lacustrine bog species (excluding *Sphagnum*) from about 11 to 46; and the raised bog plants from about 24 to 47. The *C/N* ratio of *Sphagnum* is very high, from 52 up to 71.

DISCUSSION

The main interest of these results lies in the picture they present of the chemical changes which take place in these wet soils in passing from the inorganic mineral soils to highly organic peat deposits. While the results themselves do not of course form a chronological series, they do allow us to construct a simplified picture of soil development, relatively unaffected by all the local variations which complicate the actual chronological succession in specific areas.

We may first consider this developmental trend from the point of view of acid-base relations. It is clear from the figures that soils may become highly organic and still retain a high base status, especially if there is fairly frequent moving water renewing the base supply, as in the marginal lacustrine bog peats. However, where the soil water is stagnant for most of the year acidity early develops, due to the production of hydrogen ions by organic decay. Thus at a level of about 25% ignition loss a minimum pH level of 4.5 is reached, and base saturation may be reduced to 50%. The marsh soils exhibit this tendency much more than the underwater soils in contact with freely moving water. (The writer is unable to accept the extremely low levels of base saturation reported for certain of these underwater soils by Misra in 1938, since it appears inconceivable that soils of pH 5.6 and 6.6 should be only 4 and 8% base saturated respectively).

The subsequent accumulation of organic matter does not markedly affect the base status until the soils have become almost wholly organic, presumably the inorganic silt fraction serves as a reservoir of bases tending to offset acid production. But once the soil is beyond reach of silting and becomes purely organic, there is in these Lake District peats a marked increase in the content of acids, as shown by the figures for exchangeable hydrogen, and a corresponding drop in exchangeable base. In this way pH may fall well below 4, and base saturation decline to very low levels.

This seems only to happen in areas where there is little or no contact with the ground water, that is, where the sole supply of moisture comes as rain. The supply of bases from the rain is presumably too low to maintain a high degree of saturation of the humus colloids. In this case the peats are said to be ombrogeneous, as opposed to topogenous or soligenous when the water supply comes from static or moving ground water (see Sjörs, 1950). The organic level above which the Lake District peats appear to progress toward the ombrogenous condition lies at about 85% ignition loss.

A most important point in regard to the acid-base relations of the present series is that extreme lowering of pH and base saturation in the raised bog peats is partly due to drainage and consequent surface aeration and oxidation, as has been demonstrated by Pearsall (1938). The pH values are with one exception below 3.5, whereas in undisturbed English bogs from a drier climatic area the pH ranged between 3.4 and 3.7. In Irish raised bogs under a higher rainfall (but still less than in the Lake District) the pH did not fall below 3.8, the same value as that of the wettest and most natural of the Lake

District samples. However, it is probably true to say that the lowering of pH from 4.5 to about 3.8 and a decline of base saturation below 50% does occur during the natural development of an ombrogenous condition in these bog surfaces. That the effect of drying is not merely one of concentration has been shown by Pearsall & Wright (private communication), who found that much of the increased hydrogen ion concentration produced during the drying of some waterlogged Sphagnum peats could not be removed by restoration of the original waterlogged condition.

The effect of drying and aeration on the lacustrine bog peats seems much the same as on those from the raised bogs. This is demonstrated by the results for the two samples taken from the peat hillock on the small bog at Blelham, which resemble those from raised bog samples much more closely than those from the waterlogged peats around them. And Pearsall's (1938a) studies of birchwoods on peat indicate a marked fall in pH ascribed to artificial drainage. Indeed, the most heavily drained birchwood sites, and the drained raised bog areas invaded by pinewood, appear to produce a soil hardly distinguishable (by the methods used in the present study) from the accumulations of mor humus found on many base-deficient terrestrial woodland soils.

If we next consider the pK values it is at once apparent that the underwater soils possess relatively weak acids as compared with the marsh soils, pK being generally higher in the former. After a level of 50% ignition loss is reached in the soil succession pK tends to decline steadily.

As noted before, the pK's of the wettest as well as the most drained raised bog series differ little from those of the most acid fen and lacustrine bog sites, suggesting that the differences in acidity are more quantitative than qualitative. In this connection we must remember that though the raised bog surfaces may have been partly oxidized, they are not always oxidizing, and anaerobic reducing conditions obtain on parts of these bogs for much of the year. The acidity production of the oxidation process is then largely irreversible, as mentioned previously. Also, the fen and lacustrine bog sites are occasionally dried out to some extent in the middle of dry summers. In those peats which have become almost wholly organic and silt-free this drying and aeration may also produce strong acids and thus account for the low pK of some samples. That there is some surface drying in both natural fens and undisturbed raised bogs is suggested by Pearsall's data (1938, 1941) indicating that permanently anaerobic waterlogged soils do not fall below pH 4.7 to 5.0.

Next we may take the question of nitrogen. While it is easily seen that the content of this element is dependent on the amount of humus in the soil, there remains the problem of the steady increase in C/N ratio with increasing peat development. It is probably partly at least due to the fact that in the highly organic soils there is often much unavoidable contamination with living root material. And since the decomposition process gives off carbon to the air while tending to conserve nitrogen, the consequence of decay is a decrease in C/N ratio. This will be most manifest in the soils with least contamination by living tissues, i.e. the relatively inorganic ones.

However, another factor of major importance is the C/N ratio of the plants forming the humus. For instance, the tendency of the raised bog peats to show a lower nitrogen content than the fen and lacustrine bog peats is no doubt largely due to the very low nitrogen content characteristic of *Sphagnum*, the main peat former in these bogs. (While there is much *Sphagnum* in the lacustrine bogs, the substratum on which it is growing has a large proportion of sedge peat).

This may be further illustrated if we compare the ranges of C/N ratio for the different groups of plants and soils, as has been done in Table V. Unfortunately no living raised bog *Sphagna* have been analysed, but they should hardly be higher in nitrogen than the lacustrine bog species. Two things emerge from this table. First, both plants and soils show an increased ratio in passing from the underwater to the semi-aquatic and finally to the raised bog habitats. Secondly, while the ratios of underwater plants and soils are very similar, the plant ratios increase more rapidly as the succession proceeds than do the soil ratios. The values for marsh, fen and lacustrine bog plants tend to be greater than those for their soils, and the C/N ratio of living *Sphagnum* (derived from the lacustrine bog species) is greatly in excess of that for the raised bog peats, which are largely built up by this moss (although different species, and in some cases with a good deal of admixture with Calluna and Eriophorum). To sum up, the relative nitrogen conservation of the decomposition process is important, as evidenced by the generally lower ratio in the terrestrial soils than in their plants, and probably also by the increase in ratio in the more organic soils contaminated by living tissues; but the nature of the plant residues is also fundamental. In the case of Sphagnum the low nitrogen content is undoubtedly a characteristic of the plant and not related to soil status to any marked extent.

The fact that soil C/N exceeds plant C/N in the underwater habitats is most interesting. The data of Birge and Juday (reported by Misra, 1938) indicate that planktonic C/N ratios are also low (about 6), and presumably bottom-living organisms would be similar. These facts may indicate a slight excess of nitrogen over carbon losses under these more anaerobic conditions. Differences in C/N ratio of various stages in the organic development of underwater soils, claimed by Misra (1938) from the same area, would in view of the scatter of data appear of little significance, especially in the most inorganic soils.

The plant nutrients show the influence of soil base status very clearly. The underwater soils, the most highly base saturated group, support a vegetation with high levels of both minerals and nitrogen. These high levels may, however, be partly due to a low proportion of carbonaceous supporting tissues. The most base deficient soils, the raised bog peats, also have the plant cover lowest in bases and (if we exclude the lacustrine bog *Sphagna*, or consider them as representing also raised bog *Sphagna*), in nitrogen. The proportion of excess base to the total mineral ash content of the plants is much the same, however, in all habitats.

The iron and manganese in these plants has also been investigated (Mayer & Gorham, in press). Both reach the highest levels in the underwater plants *Potamogeton alpinus* and *Sparganium minimum*, characteristic of the most organic lake muds. The manganese contents of these two plants were 288 and 378 mg. per 100 g. dry weight respectively; and the iron contents 303 and 562 mg. per 100 g. dry weight. The marsh, fen and lacustrine bog plants are on the average lower in these elements than the submerged plants, and are very variable. The raised bog plants are rather uniform, and on the average not greatly different from the marsh and fen plants; iron ranging between 10 and 21 mg. per 100 g.

of dry plant material and manganese between 35 and 59 mg. In these habitats as well as in woodland, mosses tend to concentrate iron in marked preference to manganese; the reverse is true of most other plants, especially the woody species.

SUMMARY

A study has been made of the nutrient status of some waterlogged soils and their plants, in the English Lake District. In passing from relatively inorganic underwater soils - through marsh, fen and lacustrine bog soils - to highly organic raised bog peats; both the amount and strength of soil acids increase, C/N ratio rises, and base saturation falls. This is reflected in the nutrient status of the plants; those from underwater habitats being highest in minerals and nitrogen, and those from raised bogs being low in both these constituents.

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TABLE I. Chemical characteristics of soils and plants from underwater habitats.

Soil									
Water % dry weight.	Ignition loss % dry weight.	Water/Ignition loss	pH	Apparent pK.	Exchangeable bases m.e. % dry weight.	Exchangeable hydrogen m.e. % dry weight.	Exchange capacity m.e. % dry weight.	% base saturation.	Nitrogen % dry weight.
30	2	15.0	6.44	-	3	0	3	100	0.04
36	2	18.0	6.40	-	8	0	8	100	0.24
48	5	9.6	7.09	-	6	0	6	100	0.20
/84	6	14.0	5.35	-	14	0	14	100	0.35
136	11	12.4	5.58	4.95	17	4	21	81	0.33
368	13	28.3	5.98	5.31	25	6	31	81	0.89
227	17	13.7	5.49	5.25	26	15	41	63	0.58
459	18	25.5	6.52	5.70	40	6	46	87	0.84
*487	20	24.4	6.68	-	-	7	-	-	0.85
564	21	26.9	6.80	5.95	50	7	57	88	0.86
-	-	-	-	-	-	-	-	-	-
572	21	27.2	6.68	5.78	64	8	72	89	0.96
*552	21	26.3	6.74	-	-	10	-	-	0.92
425	22	19.3	6.30	5.95	47	21	68	69	0.79
729	22	33.1	7.08	5.47	81	2	83	98	1.12
622	22	28.3	6.57	5.74	61	9	70	87	0.97
553	23	24.0	5.76	5.38	31	13	44	70	0.96
*613	24	25.5	6.76	-	ø62	ø16	ø78	ø79	1.03
438	24	18.3	6.56	5.97	43	11	54	80	0.79
424	25	17.0	6.54	5.70	48	7	55	87	1.00
406	28	14.5	6.52	5.72	50	8	58	86	0.66

Water % dry weight	Ignition loss % dry weight	Water/Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry weight	Exchangeable hydrogen m.e. % dry weight	Exchange capacity m.e. % dry weight	% base saturation	Nitrogen % dry weight.
767	37	20.7	6.18	5.64	49	14	63	78	1.39
801	38	21.1	6.32	5.78	49	14	63	78	1.33
863	38	22.7	6.16	5.65	45	14	59	76	1.41
823	39	21.1	6.27	5.72	50	14	64	78	1.31

/ on stiff clay, scattered plants

* black with ferrous sulphide

Ø black with ferrous sulphide, after oxygenation

Plant	Ash % dry weight.	Excess base m.e. % dry weight.	Nitrogen % dry weight.	Location
Nitella sp.	16.6	84	3.32	Windermere, Low Wood.
Littorella uniflora	20.4	203	3.21	Windermere, Troutbeck.
Isoetes lacustris	20.0	169	3.00	Windermere, Low Wood.
Littorella uniflora	21.8	253	-	Windermere, Troutbeck.
Nuphar lutea	11.4	110	4.44	Esthwaite Water, north end.
Littorella uniflora	21.4	247	2.80	Windermere, Pull Wyke.
Typha latifolia	9.3	56	2.69	Esthwaite Water, north end.
				Blelham Tarn.
				Blelham Tarn.
Potamogeton perfoliatus	17.0	128	4.67	Windermere, boat house.
Potamogeton crispus	15.5	108	4.97	
				Blelham Tarn.
				Esthwaite Water, west side.
Typha angustifolia	4.0	38	1.92	Blelham Tarn.
				Blelham Tarn.
				Blelham Tarn.
				Windermere, Pull Wyke.
				Blelham Tarn.
				Esthwaite, west side.
Potamogeton natans	9.4	131	3.53	Blelham fish pond.
Potamogeton alpinus	15.3	109	4.04	
Sparganium minimum	20.1	158	4.26	Windermere, Pull Wyke.
Elodea canadensis	19.8	213	4.01	

Plant	Ash % dry weight	Excess base m.e. % dry weight	Nitrogen % dry weight	Location
				Windermere, Pull Wyke
				Windermere, Pull Wyke
				Windermere, Pull Wyke
				Windermere, Pull Wyke

TABLE II. Chemical characteristics of soils and pl

marsh and fen habitats.

Soil

Water % dry wt.	Ignition loss % dry wt.	Water/Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
74	7	10.6	6.00	5.60	10	4	14	71	0.16
326	17	19.2	5.85	5.31	28	8	36	78	0.75
117	18	6.5	4.81	4.78	14	13	27	52	0.60
84	21	4.0	4.68	4.56	20	15	35	57	1.04
186	25	7.4	5.70	5.00	30	6	36	83	0.84
159	26	6.1	4.77	4.67	15	12	27	56	0.56
214	26	8.2	5.90	5.63	26	14	40	65	0.74
217	31	7.0	5.28	4.74	24	7	31	77	0.98
238	37	6.4	5.28	5.12	30	21	51	59	1.37
329	42	7.8	4.63	4.54	28	23	51	55	1.92
508*	50	10.2	5.43	5.43	29	29	58	50	1.57
466	53	8.8	5.60	5.46	32	23	55	58	1.69
393	53	7.4	5.84	5.31	44	13	57	77	2.12
443	55	8.1	5.48	4.47	62	6	68	91	2.00
315	55	5.7	5.07	4.69	50	21	71	70	2.06
507	56	9.0	4.46	4.40	50	44	94	53	1.68

Plant	Ash % dry wt.	Excess base m.e. % dry wt.	Nitrogen % dry wt.	Location
Eleocharis palustris	6.3	45	2.37	Esthwaite, east side.
Glyceria fluitans	7.6	39	2.75	Clay pond, Wray Castle.
Salix aurita	6.5	93	3.16	Windermere, Sandy Wyke.
Phalaris arundinacea	6.3	46	3.36	Esthwaite, north fen.
Molinia coerulea	4.7	34	2.61	Windermere, Red Nab.
Salix fragilis v. decipiens	6.6	67	2.46	Esthwaite, north fen.
Sparganium erectum	11.9	87	1.30	Blelham fish pond.
Juncus effusus	2.8	28	1.05	Windermere, High Wray bay.
Calamagrostis lanceolata	5.6	41	2.76	Esthwaite, north fen.
Alnus glutinosa	5.1	69	2.83	Esthwaite, north fen.
				Esthwaite, north fen.
Salix purpurea	4.6	64	1.81	Esthwaite, north fen.
Molinia coerulea	4.5	32	1.87	Esthwaite, north fen.
Filipendula ulmaria	8.3	99	3.79	Elterwater, north side.
Salix viminalis	4.9	68	2.44	Elterwater, north side.
Carex vesicaria	6.0	58	1.92	Esthwaite, north fen.
Carex paniculata	5.3	50	2.32	Esthwaite, north fen.
Carex elata	5.4	45	1.87	Elterwater, north side.

Soil

Water % dry wt.	Ignition loss % dry wt.	$\frac{\text{Water}}{\text{Ignition loss}}$	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
613	57	10.7	4.37	4.31	48	42	90	53	2.05
707	58	12.3	6.55	5.92	77	18	95	81	1.57
760	64	10.2	5.35	5.08	41	22	63	65	1.94
417	65	6.4	5.76	5.54	40	24	64	63	2.40
859	66	13.0	5.38	4.74	91	21	112	81	2.24
815	70	11.6	5.08	5.00	40	33	73	55	1.66
581	75	7.7	6.58	4.98	80	2	82	98	2.60
1166	80	14.5	4.40	4.03	82	35	117	70	2.13
896*	84	10.7	5.36	5.28	35	29	64	55	2.52
943	86	11.0	3.91	3.53	65	27	92	71	1.96
1444	86	16.8	5.86	5.24	87	21	108	81	2.62

* Sphagnum becoming dominant

Plant	Ash % dry wt.	Excess base m.e. % dry wt.	Nitrogen % dry wt.	Location
Salix atrocinerea	4.7	71	2.29	Esthwaite, north fen.
Hypnum cordifolium	3.5	61	2.80	Windermere, Congo bay.
Carex lasiocarpa	5.5	36	2.04	Esthwaite, north fen.
Phragmites communis	6.4	27	3.57	Priest Pot.
Cladium mariscus	2.9	37	1.55	Cunswick Tarn.
Carex canescens	5.5	61	1.42	Esthwaite, north fen.
				Esthwaite, north fen.
Carex inflata	5.0	46	1.72	Esthwaite, north fen.
Menyanthes trifoliata	10.1	124	4.13	Windermere, Congo bay.

TABLE III. Chemical characteristics of soils and plants from lacustrine bogs.

Soils

Water % dry wt.	Ignition loss % dry wt.	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
969	73	13.3	5.64	5.48	50	35	85	59	2.07
328	81	4.0	5.06	4.95	43	33	76	57	2.16
988	88	12.3	5.00	5.23	41	70	111	37	2.39
799	89	9.0	5.08	4.92	49	34	83	59	2.68
1069	93	11.5	4.00	3.84	50	35	85	59	2.53
651	95	6.9	4.48	4.89	45	116	161	28	2.27
1161	96	11.2	4.20	4.07	79	58	137	58	1.56
531	60	8.9	5.91	4.68	119	7	126	94	-
1039*	75	13.9	5.30	3.68	83	2	85	98	2.31
1054	78	13.5	5.55	4.63	75	9	84	89	2.52
524	79	6.6	7.32	-	165	0	165	100	-
407	80	5.1	4.85	4.43	56	20	76	74	2.20
999	88	13.5	6.53	-	167	0	167	100	-
358	86	4.2	3.01	3.85	12	82	94	13	2.78
299	94	3.2	2.98	3.81	11	74	85	12	2.06

* strongly marked iron flush.

Plant	Ash % dry wt.	Excess base m.e. % dry wt.	Nitrogen % dry wt.	Location	
				High Cross Tarn.	Typical
Molinia coerulea	4.2	30	2.40	Nor Moss.	
				Blelham.	
				Blelham.	
Sphagnum fimbriatum v. laxifolium	4.1	46	0.88	Nor Moss.	
				Blelham.	
Narthecium ossifragum	6.6	61	2.99	Blelham.	
Sphagnum teres	5.6	69	0.91	Blelham.	Stream-flushed
Potamogeton polygonifolius	11.0	96	2.45	Nor Moss.	
Sphagnum sp.	5.3	94	0.86	Nor Moss.	
Hypnum cuspidatum	5.0	72	1.40	Blelham.	
Thuidium tamariscinum	5.0	48	1.58	Blelham.	
Sphagnum plumulosum	6.3	73	0.66	Blelham.	
Myrica gale	2.9	25	2.75	Blelham.	Upturned
Molinia coerulea	3.3	25	2.87	Blelham.	

TABLE IV. Chemical characteristics of plants and peats from raised bogs.

Soils

Water % dry wt.	Ignition loss % dry wt.	Water / Ignition loss	pH	Apparent pK	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchange capacity m.e. % dry wt.	% base saturation	Nitrogen % dry wt.
614	93	6.6	3.34	3.34	37	37	74	50	2.23
2200	95	23.2	3.84	4.19	26	61	87	30	-
442	92	4.8	3.10	3.72	14	58	72	19	2.40
894	95	9.4	3.16	3.83	20	95	115	17	2.26
886	96	9.2	3.13	3.85	17	89	106	16	2.69
1160	97	12.0	3.34	3.99	19	84	103	18	1.61
685	97	7.1	3.18	3.59	15	39	54	28	2.03
973	97	10.0	3.14	3.98	14	97	111	14	1.36
947	97	9.8	3.19	3.86	18	84	102	18	0.82
906	98	9.2	3.18	3.65	21	62	83	25	1.76
580	94	6.2	2.93	3.82	16	125	141	11	2.20
251	95	2.6	2.86	3.70	11	77	88	13	2.03
609	95	6.4	3.04	4.34	5	100	105	5	1.62
307	98	3.1	2.98	3.88	7	55	62	11	2.30

Plants	Ash % dry wt.	Excess base m.e. % dry wt.	Nitrogen % dry wt.	Location	
Pinus sylvestris (seedling)	1.4	16	2.09	Striber's Moss.	Sphagnum dominant
				Striber's Moss.	
Scirpus caespitosus	2.7	23	1.61	Rusland Moss.	
Eriophorum vaginatum	2.0	25	1.05	Rusland Moss.	
Eriophorum vaginatum	2.1	25	1.21	Rusland Moss.	
Scirpus caespitosus	1.8	26	1.99	Rusland Moss.	
Eriophorum angustifolium	2.7	29	1.44	Rusland Moss.	
Eriophorum vaginatum	2.6	29	1.27	Rusland Moss.	
Eriophorum vaginatum	2.0	23	1.30	Rusland Moss.	
Eriophorum vaginatum	2.4	26	1.79	Rusland Moss.	
Eriophorum vaginatum	2.7	27	1.49	Rusland Moss, pinewood.	
Deschampsia flexuosa	4.4	35	1.78	Striber's Moss, pinewood.	
				Striber's Moss, pinewood.	
Scirpus caespitosus	2.6	34	2.06	Rusland Moss, pathway.	

TABLE V. C/N ratios of plants and soils.*

Habitat	Plant C/N	Soils C/N
Underwater	9-11-14 excluding emergent plants	4-13-25
Marsh and fen	11-22-46	10-16-24
Lacustrine bog	15-22-34 excluding Sphagnum 52-58-71 Sphagnum samples	12-19-31 mostly poor fen peat, with not much Sphagnum admixture; although Sphagnum now covers much of the area
Raised bog	24-32-47 no Sphagnum samples	18-27-59 mostly Sphagnum peat with some ericoid and cotton grass admixture.

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* The figure underlined is the average, those before and after give the range of values.

IV. A NOTE ON SOME CAIRN GORM SOILS

In the autumn of 1949 the writer, on a trip through Scotland, gathered a few samples of soil and peat from some upland granite areas, chiefly on Cairn Gorm. This was done with the aim of comparing the chemical changes consequent on humus accumulation with those taking place in other habitats already investigated, such as terrestrial woodland sites, and waterlogged soils and peats (Gorham, in prep.). The data obtained are not extensive, but there are certain points both of resemblance and difference to soil development in these other habitats, which may be of interest in view of the wide difference in most respects of the areas compared.

DESCRIPTION OF SAMPLES

Ten samples of surface soil were collected from the slopes of Cairn Gorm, between 2,000 and 4,000 feet; and five surface peats from other Scottish areas are also included. Some data on the sites are presented in Table I. While the peats from the lower altitudes may not be strictly comparable to the Cairn Gorm series as regards habitat, they correspond closely on the basis of chemical properties, and are also indistinguishable by texture and appearance from the more alpine samples. Most of the Cairn Gorm collections were made from sites of normal microtopography, but two were chosen to illustrate other than average conditions. Sample 7 was collected from a hollow receiving a flush of water from a ledge above. And sample 14 was collected from a severely eroded black patch of peat, highly decayed and amorphous, and completely without plant colonists. Both of these soils show deviations from the normal in regard to their chemical properties as well.

METHODS

The samples were collected in small 4 x 1" specimen tubes, corked, and after return to the laboratory stored in the refrigerator. Analyses were carried out some six months later, at which time the samples showed no sign of change from their original condition. Before analysis they were pressed through a sieve of twenty meshes to the inch, to remove stones and to provide a more homogeneous material. The following determinations were carried out:

pH - glass electrode on stored sample.

Water - dried at 110°C, results as % dry weight of soil.

Ignition loss - ashed at 525-550°C, results as % dry weight.

Total exchangeable bases - following the method of Brown (1943), results as milli-equivalents per 100 grams of dry soil.

Exchangeable hydrogen - method of Brown (1943), results both as milli-equivalents per 100 grams dry weight and per 100 grams ignition loss.

Nitrogen - micro-Kjeldahl technique on duplicate samples, results as % dry weight.

We may take the ignition loss in these sandy acid soils as almost entirely humus. From the sum of exchangeable bases and hydrogen we can derive the exchange (adsorptive) capacity, and exchangeable bases as a percentage of the exchange capacity constitutes the base saturation of the soil. The strength of the soil acids may be roughly approximated by the "apparent pK" (Chandler, 1939). This value is calculated by the equation

$$pK = pH - \log \frac{(\text{salt})}{(\text{acid})}$$

using exchangeable bases as (salt) and exchangeable hydrogen as (acid). Since pK is the pH of half base saturation, a decrease in pK indicates stronger and more dissociated acids. By assuming carbon to make up half the ignition loss of the soil, we can estimate crudely the carbon/nitrogen (C/N) ratio.

RESULTS

The results are given in Table II and presented graphically in Figures I to IV. The various chemical properties are plotted versus ignition loss, in order to show the changes following humus accumulation in the soil.

Water and humus.

The water content rises steadily with increasing humus content, as might be expected. There is however little change in the water/humus ratio, which averages about 3 for all soils. The inorganic sands range from about 1 to 5, while the peats lie mostly between 2 and 4, values comparable to those for many woodland soils.

Exchange constituents (Figure I).

There is a very close correlation between exchange capacity and humus content in these soils, the values ranging from about 12 m.e. % dry weight in the sands to between 100 and 125 m.e. % dry weight in the most organic peats. These levels are much the same as those found in

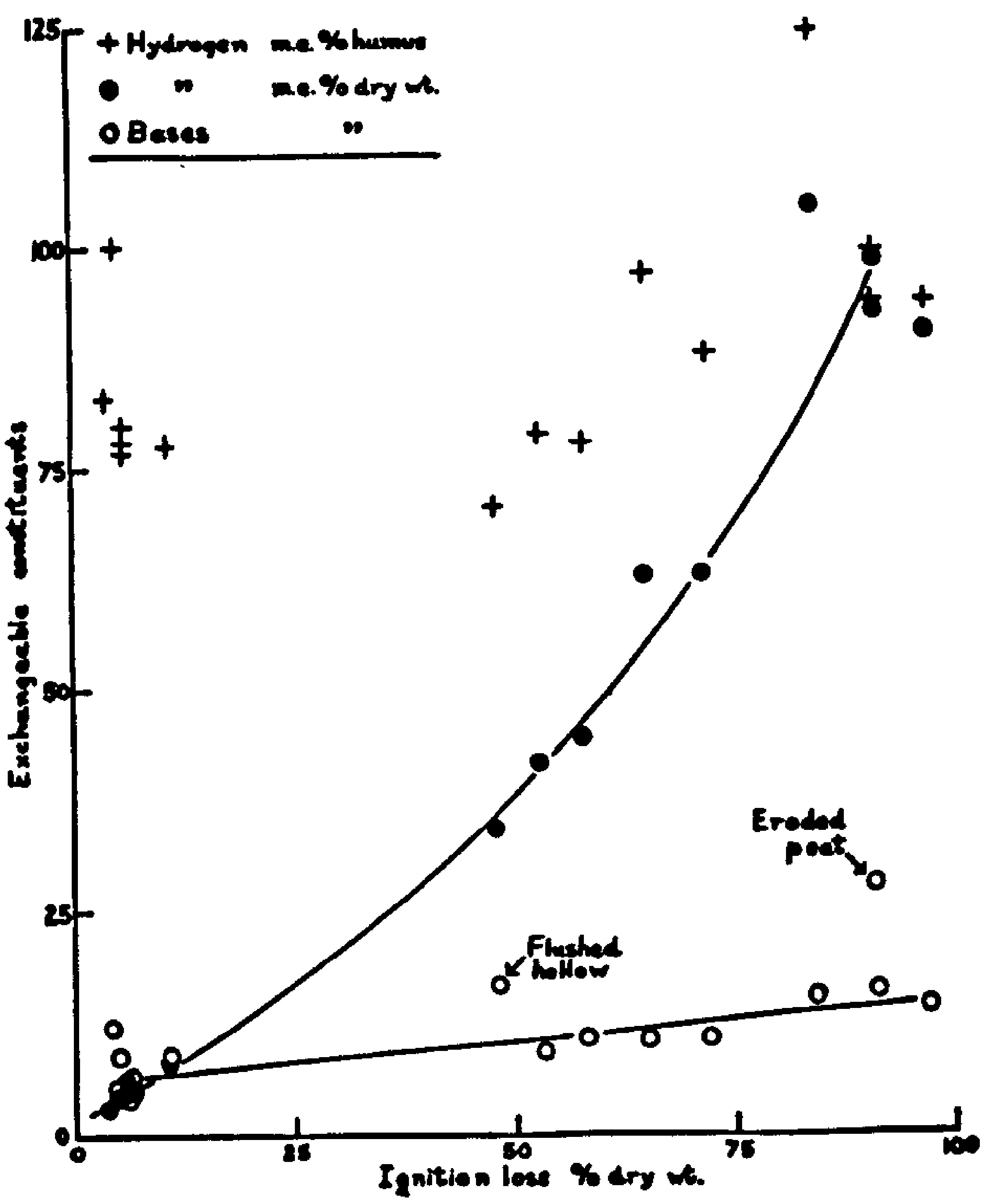

FIGURE I.

Total exchangeable bases and exchangeable hydrogen in relation to humus content.

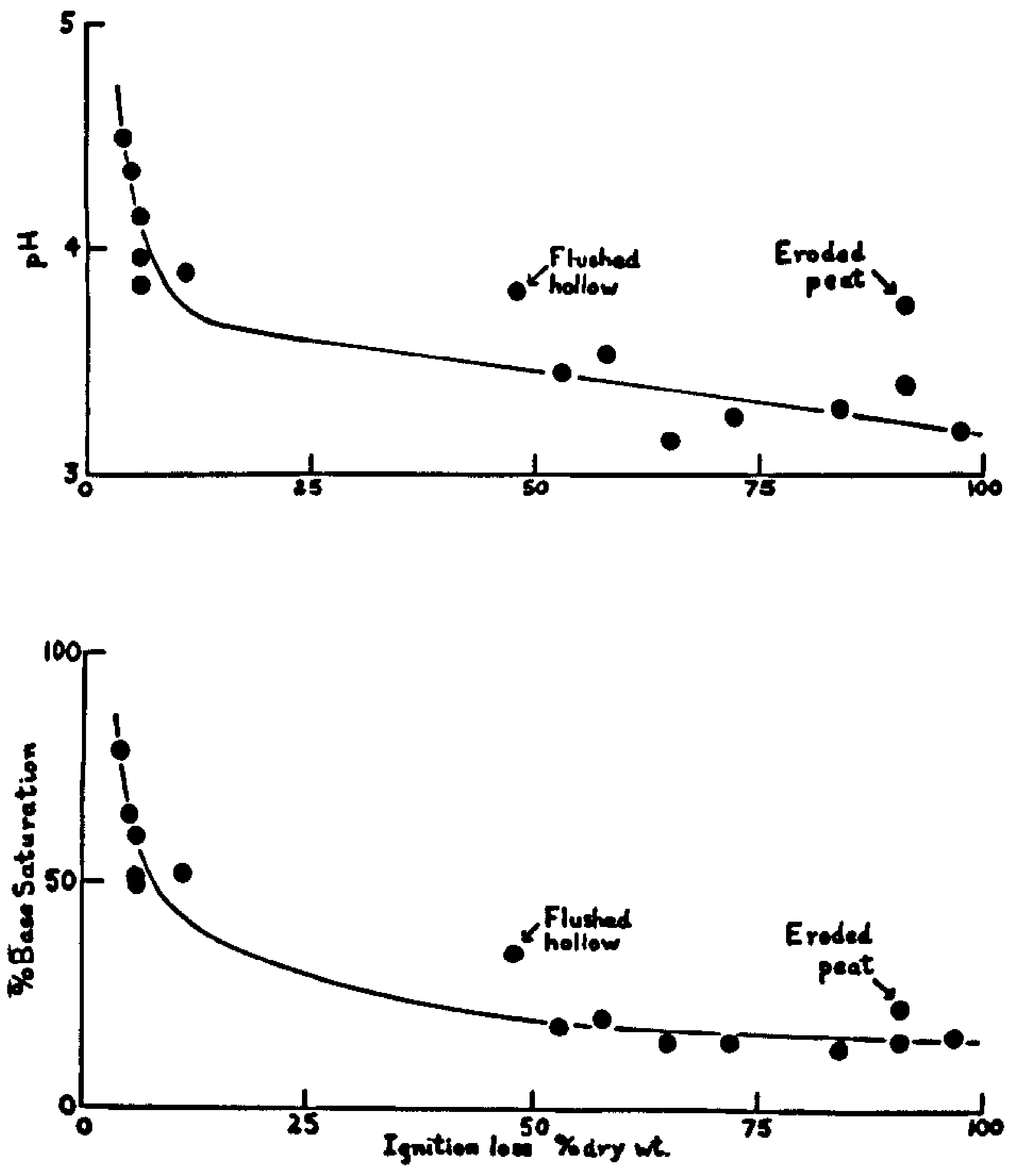

FIGURE II.

pH and base saturation in relation to humus content.

the more humified samples of <u>mor</u> from leached and acid woodlands, and in water-logged peats (Gorham, in prep.).

Exchangeable bases are low in the sandy soils, averaging about 8 m.e. % dry weight, and rise to about 15 m.e. in the most organic peats. The single sample from a flushed hollow gives a high value of 17 m.e. at 48% ignition loss. The highest content of exchangeable bases, 28 m.e. % dry weight, is found in the eroded and highly decomposed peat with no vegetation cover. Here organic decay seems to be proceeding faster than leaching can remove the released bases.

Most of the increased exchange capacity is saturated with hydrogen ions, as in woodland <u>mor</u> humus layers (Gorham, in prep.); and in the most organic samples there is almost 1 m.e. of hydrogen per gram of soil. If we consider the content of exchangeable hydrogen per unit of humus (since there is not sufficient clay to seriously affect the ignition loss), we find some increase in the most organic peats, as shown in Figure I. This is probably due to a higher degree of decomposition in these very organic soils, which also show a slightly higher exchange capacity per unit humus than the peats of about 50 to 70 % ignition loss. Probably the latter are still receiving additions of humus from the plant cover, while in the former decomposition is the dominating factor. This appears certainly to be the case in the eroded sample.

The very high exchange capacity of the most inorganic soils, if calculated on the basis of ignition loss, may indicate a high degree of organic decomposition; but may also be due to the presence of some bases free in solution, since exchangeable hydrogen per unit humus is not also high.

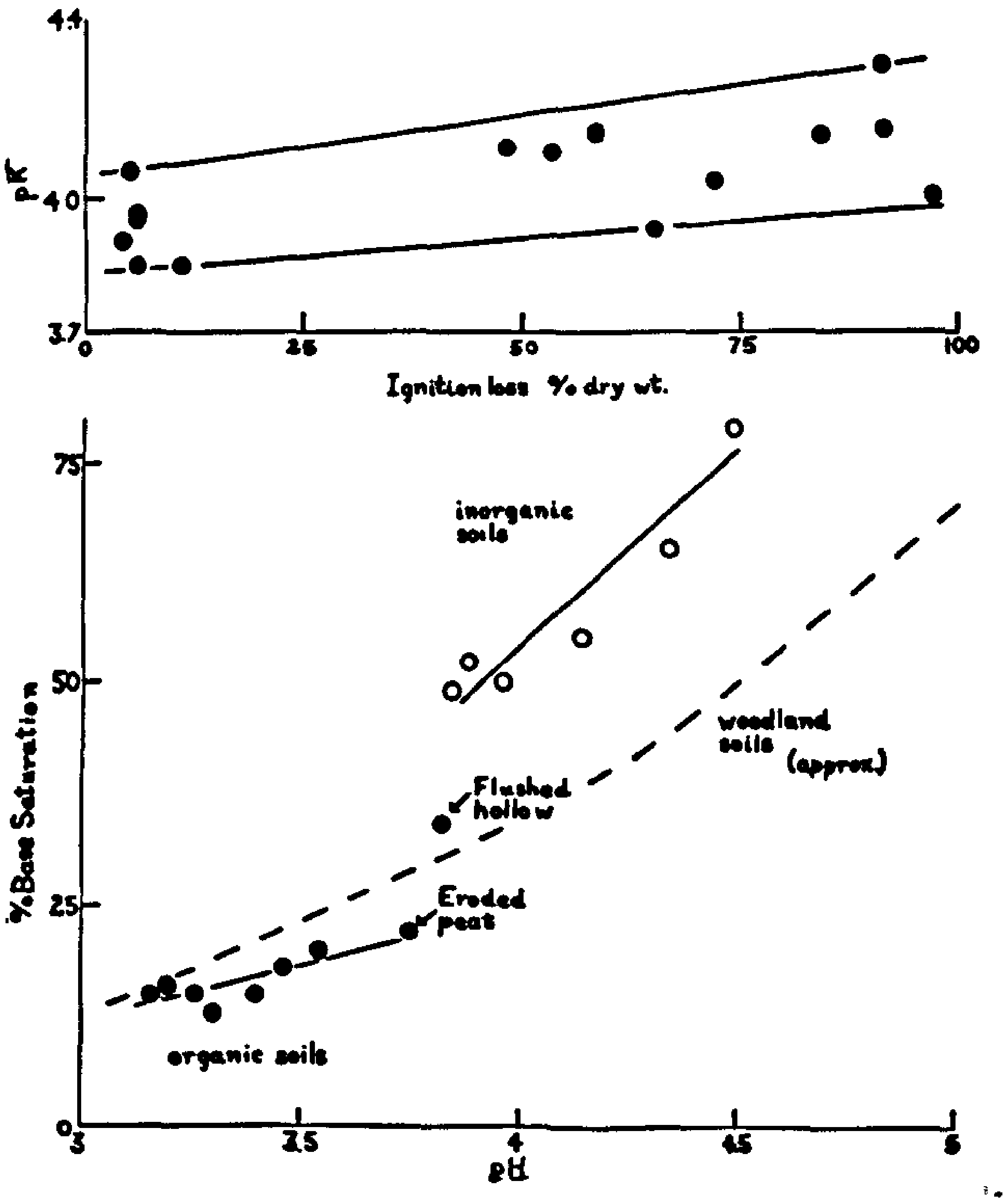

FIGURE III.

(a) Apparent pK in relation to humus content.

(b) Base saturation in relation to pH.

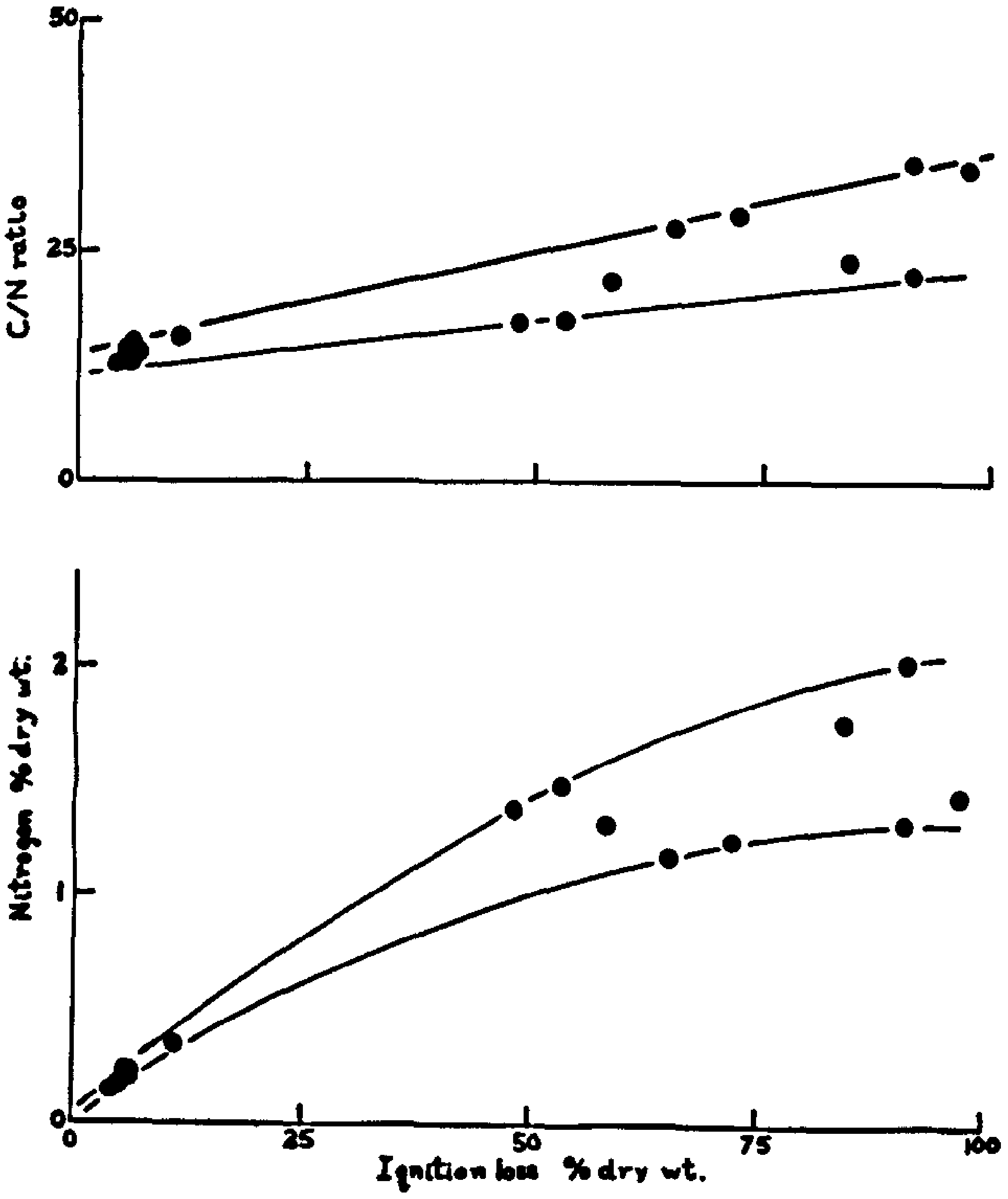

FIGURE IV.

Nitrogen and C/N ratio in relation to humus content.

pH and base saturation (Figure II).

In these soils, as in the woodland mors, both pH and base saturation fall with increasing humus content. The striking thing here is the sharpness of the drop in the early stages; pH falling from 4.48 to 3.84 and base saturation from 79 to 49% before a level of 10% organic matter is reached. Thereafter the decline is more gradual, until in the most organic peats we find pH values between 3.2 and 3.4, and base saturation at about 15%. These figures coincide almost exactly with those for highly organic soils both from leached woodlands and from drained and somewhat oxidized raised bog sites in the Lake District. The flushed sample and the eroded peat are higher than average, the former being 34% saturated at pH 3.82, and the latter 22% saturated at pH 3.75.

Apparent pK (Figure IIIa).

It appears that the acids in these soils are rather strong, especially in the more sandy samples. The pK range is from 3.85 to 4.07 in the inorganic soils, and from 3.93 to 4.30 in the peats. In contrast, the range for leached and inorganic woodland loams (in the Lake District) is from about 4 to 5, and in the highly organic woodland mors from about 3.30 to 4.10 (Gorham, in prep.). Thus in the Scottish soils pK is low in the sandy soils and increases slightly with humus accumulation; while in the clayey Lake District loams pK is higher at first, and decreases greatly as the soils become more organic.

We may obtain the same picture in another way by plotting % base saturation versus pH, as in Figure IIIb. The broken line represents roughly the average relation in the leached woodland soils from the Lake District, the acid soils being generally the more organic ones. We see that the Scottish peats are not much different from the woodland series, being slightly less base saturated on the average. But the sandy soils are much more base-saturated than the woodland series at similar pH levels. This is of course associated with greater strength and base binding power of the humus acids in the granitic sands, as denoted by their low pK values. The flushed site exhibits a rather high pK, and the highest value is that for the eroded peat.

Nitrogen (Figure IV).

As might be expected, nitrogen is closely correlated with humus content. It is about 0.2 % dry wt. in the sandy soils, and rises to between about 1.2 and 2% in the organic soils. If the C/N ratio is considered we find low values between 12 and 16 in the inorganic soils, which increase to between 17 and 34 in the peaty samples. Since the peats were generally amorphous and contained few recognizable plant remains, it would appear that their high values are not due to contamination by living root tissues.

The C/N ratios of the sandy soils are relatively low and similar to those of inorganic soils from both leached woodland and waterlogged habitats. These low ratios perhaps suggest a high degree of decay. The peat ratios are however higher than woodland mor values from the Lake District, and comparable to those of peats from drained raised bogs.

DISCUSSION

Our picture of soil development on the granitic detritus of these areas may well begin with a consideration of some work by Tamm (1924). He took gravel of crushed granite and rotated it in quartz flasks for 12 hours at 2-3°C, in carefully distilled water with and without the addition of carbon dioxide. This we may take as representing the primary physical and chemical weathering process. In all cases the pH, which in the beginning was about 7 without CO_2 and as low as 4 with CO_2 saturated water, rose to a higher level. In the pure water the final value was generally about pH 12, and in water with added CO_2 between 5.6 and 7.1, depending on the concentration of the gas. The amounts of base released by this treatment were determined by titration, and are as follows:

Without CO_2 - 0.06 to 0.11 m.e. per 100 g of granite.
With CO_2 - 0.07 to 0.28 " " " " "

These results show that the effect of weathering is a release of bases and a rise in pH. If the bases are removed by leaching and the pH is solely determined by the CO_2 dissolved in the rainwater, at 0 °C and atmospheric pressure this value will be above 5.5.

Evidently the low pH values found even in the least organic of the present granitic samples are well below those which might be accounted for by inorganic weathering factors. It then appears that the first addition of humus to these soils produces a severe drop in both pH and base saturation; and we see from the pK values that the acids responsible are relatively strong, slightly stronger indeed than those of the peaty soils in the area, and much stronger than the acids in Lake District woodland soils of comparable pH and humus content.

The above facts suggest that it is perhaps advantageous that the acids produced by the plants of this granitic detritus be strong. There is abundant room for colonization on the bare upper slopes of Cairn

Gorm, and it may be that the plants with relatively strong acidoids, and producing strong acids in their decaying humus, are better able to leach enough mineral nutrients from the rock to survive. This gains significance if we again consider that it takes twelve hours of constant rotation (forty times per minute) in water saturated with CO_2 to produce about 0.3 m.e. of bases from 100 grams of granite gravel.

It is probably also necessary that such plants have a low nutrient requirement. This is supported by the data on nutrient levels given by Mattson and Karlsson (1944) for some of the species characteristic of these soils. Their samples were taken from sandy or peaty soils below pH 4.0, and so are rather comparable. The ranges of mineral ash and calcium for Calluna, Vaccinium myrtillus, V. vitis-idaea, V. uliginosum and Empetrum nigrum are 3.3-6.2 % dry wt. for the former, and 19-42 m.e. % dry wt. for the latter. In comparison, the average ash content of brown earth vegetation quoted by the above authors is 11% dry wt., and the average calcium content 77 m.e. % dry wt. Potassium and magnesium show a similar relation. Plants in these habitats are also poor in nitrogen, a series of determinations in the area studied giving a range of from 0.6 to 1.9 % dry wt.; while the data of Mattson & Karlsson (1944) show a range of 0.8 to 1.8 % dry wt. for the plants mentioned above, and C/N ratios averaging 46. This may account for the rather low nitrogen content of the peats formed beneath them.

A further point in favor of the above hypothesis is the richer and more varied flora commonly found in the flushed habitats, where there is a constant renewal of bases by percolating water even though the concentration may be low. Floristically varied areas are well known to be usually found where there are rocks richer in lime, or where there is a good water-borne base supply, as has been abundantly illustrated by Pearsall (1950). Evidently then, mineral availability must be an important factor in the establishment of vegetation on such soils; and the monotonous and restricted flora of these granitic habitats testifies to their extreme deficiency in elements necessary for plant growth.

SUMMARY

A study has been made of some chemical characteristics of granitic soils and peats, chiefly from Cairn Gorm. It appears that the first addition of organic matter to the soil brings about a sharp increase in acidity and a marked fall in base saturation. The presence of comparatively strong acids in the humus produced by the colonizing plants is suggested as a possible advantage, in view of the difficulty of obtaining mineral nutrients from the granite substream.

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TABLE I. Details of localities and habitats sampled.

No.	Locality	Altitude (ft.)	Plant cover	Nature of sample
1.	Cairn Gorm	3,750	*Empetrum hermaphroditum* mat.	Fine sandy soil.
2.	" "	3,750	Sward of grass and rushes with *Lycopodium alpinum*.	Fine reddish brown sand.
3.	" "	4,000	Cushion of *Rhacomitrium lanuginosum* and *Juncus trifidus*.	Sandy granite debris
4.	" "	3,750	*Potentilla argentea*.	Granitic sand.
5.	" "	3,750	*Calluna vulgaris*, 1-2 inches high.	Sandy soil.
6.	" "	3,750	*Lycopodium selago*.	Granitic sand.
7.	" "	2,500	*Sphagnum*, *Nardus stricta*, *Scirpus caespitosus*, *Narthecium ossifragum*, and other spp. in sward.	Peaty sand in flushed hollow below ledge.
8.	" "	3,750	Dwarf *Vaccinium myrtillus* and *Empetrum hermaphroditum*.	Small peat deposit in shelter of boulder.
9.	Loch Rannoch	ca 1,000	*Calluna vulgaris* and *Cladonia* dominant.	Peat over podzolized sand, top of hill.
10.	" "	ca 500	*Calluna vulgaris*, *Hypnum schreberi* and *Scirpus caespitosus*.	Peat over steep rock slide.
11.	Cairn Gorm	2,000	Tufted *Scirpus caespitosus*.	Peat on flat terrace.
12.	Glenmore Forest	-	*Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea* and *Hylocomium splendens*.	Peat from podzolized sandy knoll.
13.	Rannoch Moor	-	*Calluna vulgaris* and *Myrica gale* dominant.	Peat from podzolized granitic knoll.

No. Locality	Altitude	Plant cover	Nature of sample
14. Cairn Gorm	2,000	Eroded, no vegetation.	Very black and amorphous peat.
15. Loch Rannoch	-	*Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*, and *Hylocomium splendens*.	Peat from podzolized knoll in the Black Wood.

TABLE II. Chemical characteristics of soils and peats from granitic areas.

No.	pH	Apparent pK	Water % dry wt.	Ignition loss % dry wt.	Exchangeable bases m.e. % dry wt.	Exchangeable hydrogen m.e. % dry wt.	Exchangeable hydrogen m.e. % humus.	Exchange capacity m.e. % dry wt.	Exchange capacity m.e. % humus	% base saturation	Nitrogen % dry wt.	C/N
1	4.48	3.91	11	4	12.3	3.3	83	15.6	390	79	0.155	12.9
2	4.34	4.07	24	5	9.3	5.0	100	14.3	286	65	0.170	14.7
3	3.84	3.85	6	6	4.7	4.8	80	9.5	158	49	0.194	15.5
4	3.96	3.96	20	6	4.6	4.6	77	9.2	153	50	0.235	12.8
5	4.14	3.97	13	6	7.0	4.7	78	11.7	195	60	0.215	14.0
6	3.88	3.85	28	11	9.2	8.6	78	17.8	162	52	0.345	15.9
7*	3.82	4.12	165	48	17.0	34.0	71	51.0	106	34	1.380	17.4
8	3.46	4.11	154	53	9.4	42.0	79	51.0	96	18	1.485	17.8
9	3.54	4.15	167	58	11.0	45.0	78	56.0	97	20	1.325	21.9
10	3.16	3.93	196	65	11.0	63.0	97	74.0	114	15	1.180	27.5
11	3.26	4.04	163	72	11.0	63.0	88	74.0	103	15	1.245	28.9
12	3.30	4.14	353	84	15.0	104.0	124	119.0	142	13	1.755	23.9
13	3.40	4.16	333	91	16.0	92.0	99	108.0	117	15	2.015	22.6
14**	3.75	4.30	313	91	28.0	98.0	93	126.0	138	22	1.325	34.3
15	3.20	4.01	290	97	14.0	90.0	93	104.0	107	16	1.435	33.8

* Flush   * Eroded peat