FACTORS OF MULL AND MOR DEVELOPMENT IN TEMPERATE GRASSLANDS

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DEFINITION OF MULL AND MOR

The humus forms of soil profiles have been defined as the group of A horizons in which organic matter is concentrated (Barratt 1964). They are generally the first parts of soil profiles to respond to changes in soil-forming factors and they are particularly worthy of study in the temperate grasslands of Great Britain and New Zealand where grasslands have largely developed on former forest soils.

Grassland humus forms have been investigated morphologically in the field and with the microscope (Barratt 1960, 1964). They are divisible into two main groups: mulls and mors. In mulls, organic residues are finely comminuted and intimately mixed with the colloidal-sized fraction of the mineral soil. In mors, organic residues accumulate predominantly above the mineral soil surface, but show progressive decomposition with increasing proximity to the mineral soil, and typically three layers are produced.

- L layer of little-decomposed leafy residues.
- F layer of fragmented or partially decomposed but still recognisable residues.
- H layer of decomposed and finely comminuted organic material generally with a sharp boundary over the mineral soil.

Intergrades termed mor-like mulls are recognised where mulls are very high in organic matter and low in clay, so that they are difficult to distinguish from mors in the field. Their true nature can be determined microscopically.

Peat develops by accumulation of organic residues to form virtually the whole of the soil profile. It is generally distinguished from mor by its great thickness, but another character that generally distinguishes peat from mor is its weak humification in lower layers (Taylor and Pohlen 1962).

FORMS OF MULL AND MOR UNDER GRASSLAND

Mulls and mors are further subdivided on a basis of horizon thickness, structure and consistence into a number of forms, each with one or more characteristic microstructures. These forms are conveniently placed into four groups in relation to the degree of litter breakdown and incorporation:—

A. *Strongly Granular, Weakly Granular and Massive Mulls* in which intimate organic matter is incorporated with the mineral soil in thick A_1* horizons.

B. *Fine and Morlike Mulls* in which intimate organic matter is concentrated largely towards the surface of the mineral soil.

C. *Massive, Matted and Granular Mors* in which L and F horizons are thin and comminuted organic residues in thick H horizons, overlie the mineral soil.

D. *Laminated Mors* in which L and F horizons are thick and contain little-decomposed organic residues resting upon H horizons that are generally thin.

MICROSTRUCTURES OR FABRICS

Each of the horizons or layers of the humus form may have a different microstructure or fabric (Fig. 1). The five most commonly encountered fabrics in Great Britain and New Zealand with specific variants in highly calcareous or waterlogged soils are:

1. *Strong mull humus*, a continuous fabric of worm-cast origin with irregular cavities. It is dark-coloured with an intimate association of clay and decomposed organic matter.
2. *Weak mull humus*, a continuous fabric with sharp-walled unconnected cavities. It is light in colour because of a low content of organic matter intimately associated with the clay.

* For an explanation of soil horizon nomenclature see Taylor and Pohlen (1962) p. 69.

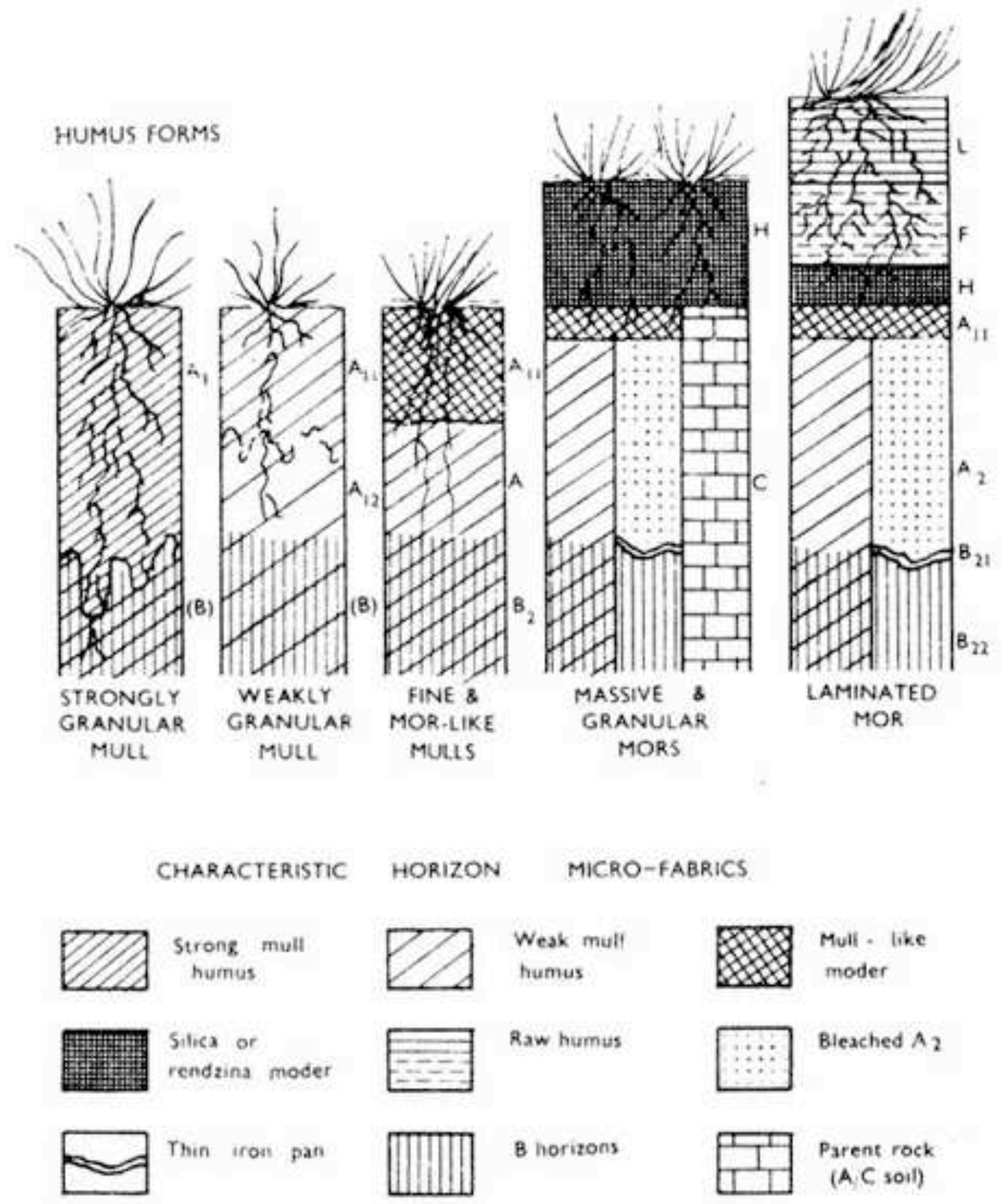

FIGURE 1. *Diagrammatic representation of humus forms under grass, showing their characteristic micro-fabrics.*

3. *Mull-like moder*, of discrete loosely-aggregated faecal pellets, generally 0.15–0.2 mm. in diameter, resembling those of enchytraeids, but coarser in some samples. It otherwise generally resembles strong mull humus but may contain a very high proportion of finely comminuted organic matter in association with the clay.
4. *Silica moder and rendzina moder*. Silica moder is generally composed of small blackish-brown organic faecal pellets, less than 0.1 mm. diam., such as those produced by Acarina (mites) and Collembola (springtails) but coarse moders with discrete pellets up to 2.0 mm. long are also encountered. Plant fragments are bitten into cavities and are held loosely in the mass, as are mineral grains, which are predominantly quartz. In rendzina moder the fabric is similar but calcite grains occur in place of quartz.
5. *Raw humus* consists of little-decayed leafy residues and in places cells have orange-brown resin-like contents which appear to be very resistant to decomposition. In some samples the residues show evidence of attack by fungi. (For illustrations of microfabrics see Barratt 1964.)

NATURE AND OCCURRENCE OF GRASS HUMUS FORMS

A. GRANULAR MULLS

1. *Strongly Granular Mulls*

These are characteristic of dark brown topsoils rich in organic matter, slightly to moderately acid, pH 5.5–6.0, with strongly granular to crumb structures and deep penetration of the lower boundary into the subsoils along earthworm channels. The microfabric of their A_1 horizons is predominantly strong mull humus.

They occur under topdressed pastures of moderately leached southern and central yellow-brown earths in New Zealand and brown earths in England. However, where parent materials are highly calcareous these mulls extend up to the cool humid zone of blanket peat. They support fleshy, nutrient-demanding swards that usually include clover and have moderate to high grazing value. Below ground these swards have deep freely branching roots; active populations of burrowing earthworms are supported which help to promote the deep organic cycle.

2. *Weakly Granular Mulls*

These are generally of light brown colour and weak structure, strongly to moderately acid, pH 4.9–5.9, with little penetration into subsoil horizons. The microfabric of their A_1 horizons is characteristically a weak mull humus.

They occur in brown-grey and yellow-grey earths, the topsoils of which become dry in summer. In Great Britain they have been found in experimental lowland hayfields that have been cropped continuously without addition of fertilisers for up to 100 years.

In soils with this form grass yields are low and rooting systems are correspondingly weak; little organic matter is supplied to the soil in the form of plant residues and the organic regime is only weakly impressed on the mineral soil.

B. FINE AND MOR-LIKE MULLS

Characteristically, these humus forms are rather thin, dark brown in colour, almost black in the mor-like mulls, and have a finely granular structure. They overlie horizons that are lighter in colour and coarser in structure. In these A_{11} horizons the microfabrics are generally mull-like moder, generally underlain by weak mull humus in the A_{12} horizons.

They occur under native tussock and pastures of the upland and high-country yellow-brown earths of New Zealand. In the British uplands they have been found over brown earths from andesite and from strongly acid leached calcareous soils, pH 4.5–5.0. They also occur over hard chalky limestone with a near-neutral pH of 6.7 in Southern England where the thin topsoil dries out in summer. They also form in the above mentioned hayfields with a long-term manurial treatment of farmyard manure but are there underlaid by horizons with strong mull humus microfabrics.

The soils generally support a somewhat fibrous herbage including bent *(Agrostis)* and fescue *(Festuca)* species of rather low grazing value and with a tendency to form a shallow root mat. Few earthworms occur in these horizons but enchytraeid worms and arthropod larvae are very active.

C. MASSIVE, MATTED AND GRANULAR MORS

In all of these forms little litter remains unfragmented and their thick black H horizons may have massive to medium granular structure, with silica moder or rendzina moder microfabrics.

They occur in soils liable to become either very wet or very dry, such as the podzolised southern yellow-brown earths, or in peats that are beginning to decompose after drainage, or in skeletal soils where the thin black soil penetrates between fissures in the rock. These soils can be extremely acid, pH 4.0, as in the podzols or neutral to alkaline as in skeletal soils over limestone.

The vegetation may contain fibrous, acid-tolerant grasses such as *Nardus stricta* (matgrass) over the podzols, or prostrate mosses and cushion plants over the skeletal soils. In these sites the only fauna capable of tolerating the limiting soil conditions are surface-feeding forms adapted to the habitat, such as mites (Acarina) with their chitinous exoskeletons and springtails (Collembola). Where conditions are not so limiting coarser moders containing arthropod larvae and small earthworms tend to occur.

D. LAMINATED MORS

In these humus forms organic residues, predominantly leafy, accumulate at the soil surface to form thick L and F horizons, extremely acid, pH 3.5–4.5, with raw humus microfabrics, that generally overlie thin H horizons with silica moders. The H horizons pass in some sites to mull-like moders and weak mull humus fabrics in A_{11} and A_{12} horizons, or bleached mineral soil in A_2 horizons.

They characterise untopdressed British uplands with their cool moist climate but are also found in acid and gleyed soils of lowlands. They have been induced in hayfields by long-term treatment with acid ammonium sulphate on soils where mulls develop in the absence of the acid treatment. In New Zealand they have so far been found under pastures on the coarse-textured pumice soils such as *Taupo sandy loam* where few earthworms are present to mix the soil.

The humus forms develop generally under fibrous acid-tolerant grasses such as matgrass *(Nardus stricta)* with their roots in the humus layers, so that a shallow organic cycle is favoured. As their microfabrics might indicate, they are almost devoid of fauna in their L and F layers and the little decomposition occurring appears to be fungal, although mesofauna may be active in the H and A_{11} horizons.

DEVELOPMENTAL FACTORS

Humus forms are part of the soil profile and are thus subject to the same soil-forming factors, set out by Taylor and Pohlen (1962) as: Climate, topography, soil parent materials, organisms (including the vegetation) and age of the site (including modifications by man).

Condensation of the organic cycle towards the soil surface and the transition from mull to mor are associated with definite trends in site factors.

Climate and Topography

There is an increasing tendency for mor development as climate becomes cooler and more humid throughout the year with increased altitude and latitude, and this is well shown in untopdressed British uplands below the zone of blanket peat (Fig. 2a). At the lowest altitudes granular mulls are found over brown earths of high base status, but with rising altitudes these pass progressively to fine, matted and leafy laminated mulls and laminated mors over podzolic brown earths and podzols, Crompton (1958), Stapledon (1936). In New Zealand, with its wide climatic range and wide range of zonal soils, all gradations from weakly granular mulls to laminated mors occur (Fig. 2b).

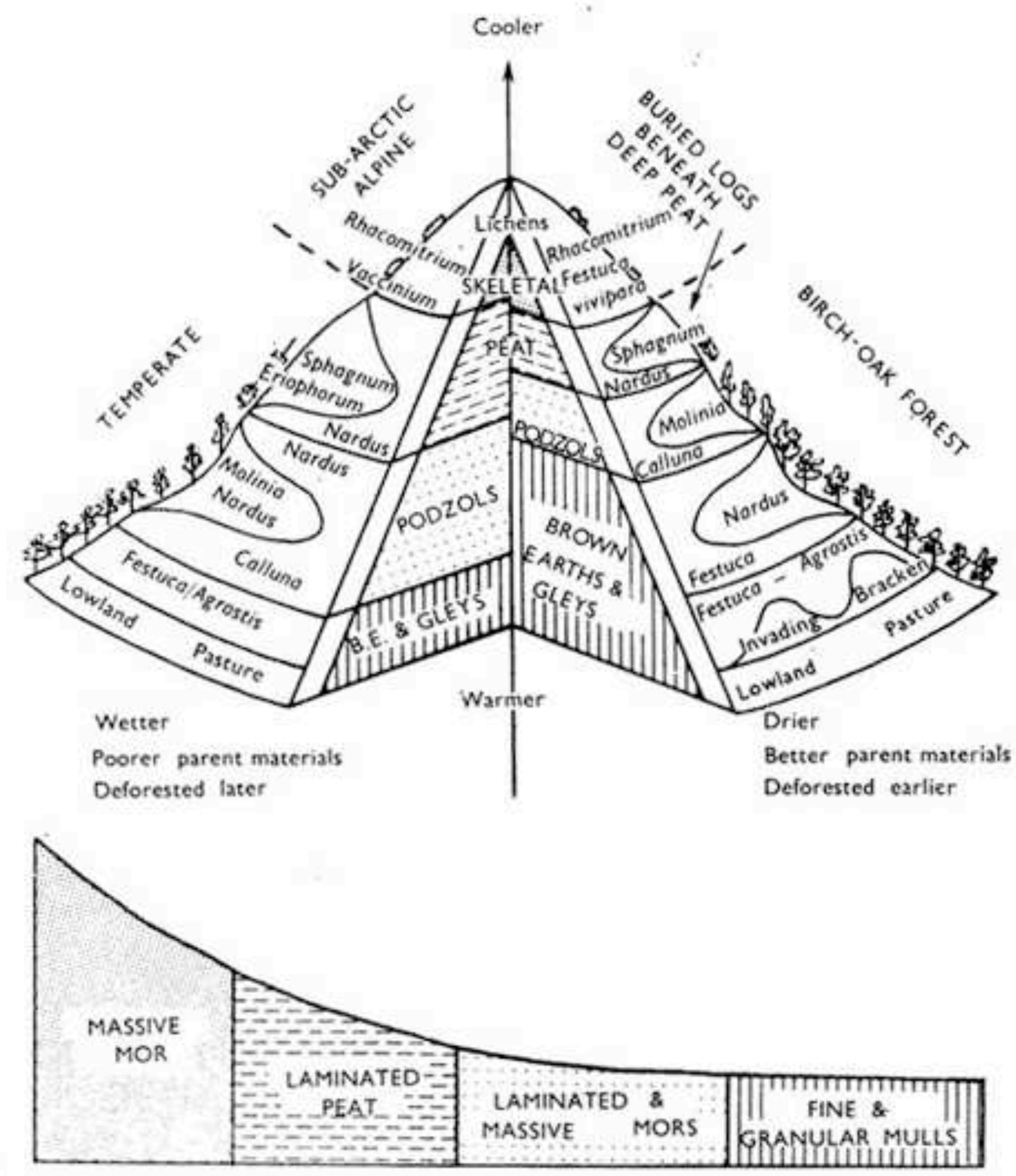

FIGURE 2a: *Idealised diagram showing the broad distribution of humus forms in relation to climate, soils and vegetation, in Great Britain.*

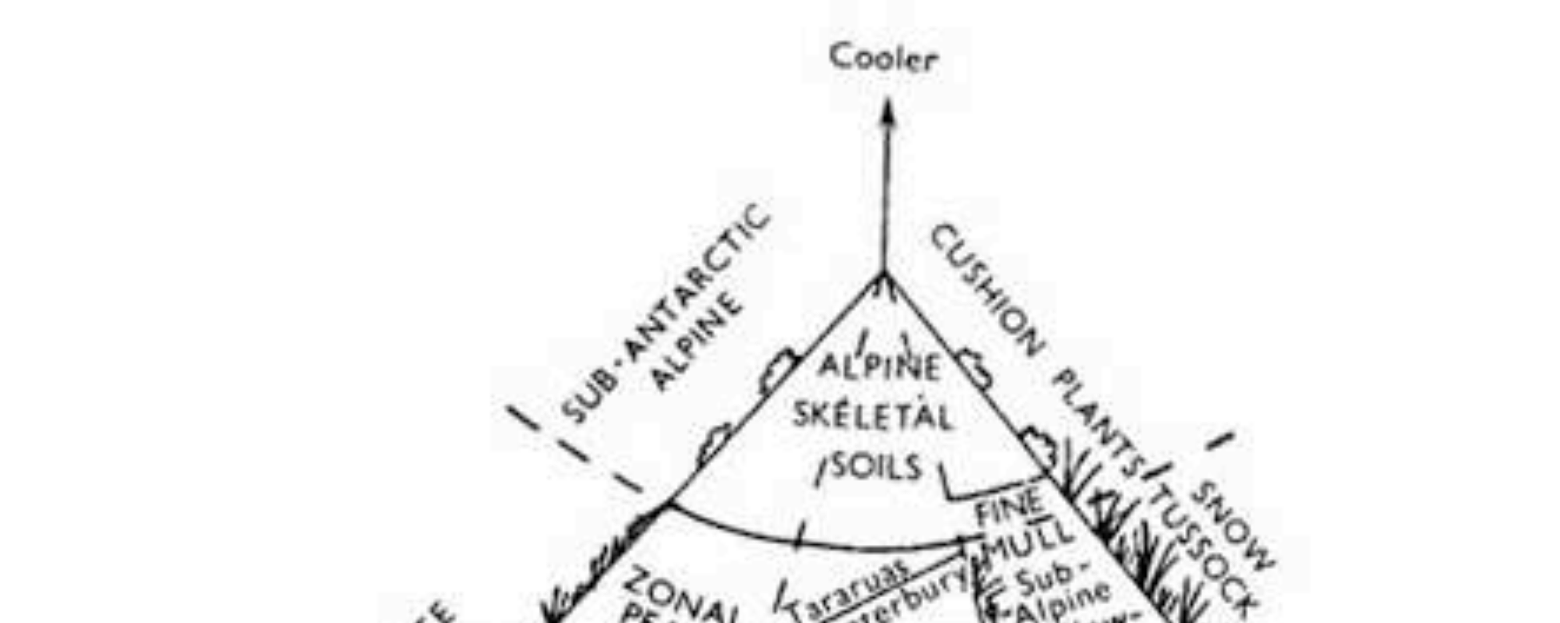

FIGURE 2b: *Idealised diagram showing the broad distribution of humus forms in relation to climate, soils and vegetation, in New Zealand.*

Soil climate is severe at alpine elevations, at subantarctic latitudes and on skeletal soil slopes, so that plant growth and chemical rock weathering are minimised. Soils survive wind action mainly in the protection of crevices, and they are thin, with massive mors. In the drier climate of the brown-grey and yellow-grey earths, by contrast, organic activity is suppressed more than rock weathering and accumulation so that the organic cycle has a rather weak effect on the mineral soil. This is reflected in their weakly-developed mulls.

Parent Material and Drainage

In many places the broad climatic sequence from mull to mor is greatly modified by parent material and drainage. On lime-rich parent materials mulls have been found almost up to the blanket peat zone in the northern Pennines; conversely, in uncultivated wastelands or heaths of the lowlands, laminated mors have been found over acid, coarse-textured and badly drained profiles.

Vegetation

In England hill soils which now carry untopdressed pasture once supported oak *(Quercus)* and birch *(Betula)* forest over brown earths with mull. However, under grass, with its shallower organic cycle, there is an inevitable tendency towards mor development. This is accentuated with rising altitude, or on poorer soils, by changes in sward composition. The sward becomes progressively more fibrous, lower in feeding value, shallow-rooting and acid-tolerant in a sequence from bent *(Agrostis)* with *Festuca ovina* over the brown earths, to matgrass *(Nardus)* or common heather *(Calluna vulgaris)* over podzols and flying bent *(Molinia caerulea)* on the more poorly drained sites (Stapledon 1936). In the alpine and skeletal soils however, prostrate and cushion plants are characteristic, with low herbage production and thin soils tending to form under the little protection afforded by the vegetation.

In much of New Zealand, by contrast, grasses seem to be promoting mull in some soils that formerly supported mor-forming forest. In the alpine and subalpine tussock country of the Torlesse range of Canterbury, for example, Molloy (1964) has shown buried beech forest profiles with mor where fine mulls have since developed under tussock. In North Auckland, original kauri mors now appear as massive mulls under grass, although their mixed comminuted raw humus with bleached clay microfabrics give evidence of their former condition.

Soil Organisms

Soil organisms occur in a definite sequence from mull to mor that is closely related to the microfabrics they help to produce. Strongly granular mulls are characterised by an active population of burrowing earthworms (Van Rhee 1963) such as *Allolobophora longa, A. caliginosa* and *Lumbricus terrestris* whose need for adequate moisture, and association with fleshy herbage and lime have been shown by Satchell (1955). Smaller and shallower-working fauna such as small earthworms e.g. *Lumbricus rubellus* (Lee 1959), arthropod larvae, potworms *(Enchytraeidae)*, mites and springtails, promote finely-granular mulls, mor-like mull intergrades and massive mors. In these, conditions are too acid, periodically too wet or too dry, or textures too coarse to support burrowing earthworms. Under the more acid and generally wetter conditions in laminated mors with a fibrous herbage of low nutrient value, only fungi appear to be active. Comparisons of mull and mor have shown greater microbial activity, as measured by CO_2 evolution, and higher bacterial numbers in mull (Kirkwood 1964).

Time and Modifications Caused by Man

Generally speaking, in the course of time the tendency in temperate latitudes is for soils to become leached with the eventual development of podzols with mor humus. Man's action is to retard or accelerate this process through his influence on the soil-forming factors.

By replacing some of the mor-forming forests by grass, man is promoting mull. This is probably because of increases in soil moisture, ground flora and soil faunal activity when the canopy is opened. In most districts, however, the shallower organic cycle maintained under shallow-rooting grasses tends to promote mor.

This is offset by topdressing in most parts of New Zealand and in the intensively farmed British lowlands. However, in the unfenced common grazings of the British uplands and moorlands or heaths, soils which once mainly supported oak forest are becoming leached under a fibrous herbage of low grazing value. Forest regeneration in these rough grazings is prevented by light grazing at rates of the order of one sheep to five acres. On the poorest soils *Calluna* heath is maintained by repeated firing for grouse shooting and sheep grazing.

These upland and heath soils support mor humus and exhibit podzolisation in various stages, but examination of the soil profiles in many districts reveals the original forest or cultivated mull humus form beneath the present mor humus (Crompton 1953). The original forest brown earth profile has also been revealed beneath Bronze Age and more recent earthworks in various parts of the country now occupied by heather podzols (see Dimbleby 1962).

In many places the trend from mull to mor appears to be reversible. This is shown by the sharp contrast between swards within shelters or topdressed paddocks close to farm buildings and surrounding moorland or heath. In such places close-grazed swards of better grazing value with their associated mull humus forms contrast with poorly grazed moorland species of low grazing value and their associated mor humus forms.

CONCLUSION

Humus forms can give a rapid and reliable indication of biological changes occurring in the soil. When these changes are unfavourable they can be reversed before the profile as a whole becomes seriously affected. This study shows that neither vegetation nor any other factor should be considered in isolation when attempting to account for mull and mor development. All five soil-forming factors must be considered when assessing their relative importance at a given site.

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SOME OBSERVATIONS ON THE ECOLOGY OF *CANDIDA ALBICANS*, A POTENTIAL MAMMALIAN PATHOGEN

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INTRODUCTION

Candida albicans is a yeast-like organism, belonging to the Family Cryptococcaceae. Its normal habitat is found in the alimentary tract of warm-blooded vertebrates, where it lives as a budding yeast on the mucosal surface and in the mucosal secretions. The organism is, however, an opportunist pathogen. When alterations occur in its environment, through changes in the host tissues or in the microbial community exploiting them, *Candida albicans* becomes invasive and penetrates the living layers of the substrate. This invasiveness is associated with a change in morphology, so that branching filamentous hyphae to a great extent replace the budding yeast-like form.

Although *C. albicans* must be constantly inoculated onto the skin and its appendages it only rarely establishes itself in this habitat and, when it does so, usually behaves like a pathogen. In the following paragraphs only the colonisation of the skin is considered. The results of invasion of the intestinal wall and the deeper organs are much more serious for the host, but the factors involved in the pathogenesis of systematic candidiasis are too complex to be summarised in this paper.

HEADQUARTERS AND RANGE

Candida albicans is found as a member of the normal flora of a large number of mammals and possibly of birds, and it seems reasonable to designate the alimentary tract of mammals as the headquarters of this yeast. Van Uden (1960) has divided the intestinal yeasts into 3 groups:

(1) obligate saprophytes
(2) facultative saprophytes
(3) passers-by

He includes *C. albicans* in the first group, defined as organisms which have a natural habitat exclusively in the mammalian gut. Table 1 shows the distribution of *C. albicans* in the intestinal tract of some New Zealand mammals, other than man. It is clear that a number of mammals can be carriers of this yeast. It may not however be present in the alimentary tracts of all species, for Parle (1957) failed to recover it in samples taken from cows, guinea pigs, mice or rats.