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THE VEGETATION OF FOOTPATHS, SIDEWALKS, CART-TRACKS AND GATEWAYS

By G. H. BATES.

(*With Plates XXXV–XXXVII.*)

I. Footpaths.

The contrast between the vegetation of footpaths traversing grassland and that of the surrounds has been commented upon by observers on numerous occasions, while graziers have recognised the fact that horses and sheep prefer to feed upon the footpath rather than the other parts of the field. Apart from a passing speculation by Darwin ((**1**), p. 10), no detailed examination of conditions or of the factors concerned appears to have been made, in spite of the possibility of the findings being of economic value.

The vegetation of the path is usually shorter than that of the surrounding areas, though this varies with the intensity of grazing. The most outstanding phenomenon is the dark green colour of the path in comparison with the other herbage. This deep colour is maintained throughout the year and is most conspicuous in winter when the path stands out in vivid contrast to the dead remains of plant life on each side.

With the exception of paths on very dry sandy soil, the dominant species are smooth-stalked meadow grass (*Poa pratensis*), perennial rye grass (*Lolium perenne*) and wild white clover (*Trifolium repens*). *Poa pratensis* is constant for all examples and *Lolium perenne* for the majority. *Trifolium repens* is extremely scarce in shaded positions, but is constant for all paths exposed to sunlight. Crested dogstail (*Cynosurus cristatus*), cocksfoot (*Dactylis glomerata*) and plantains (*Plantago* spp.) are fairly constant.

A distinct and constant zonation is found. In the centre of the path, if much used, is an area of bare earth. This is adjoined on either side by a zone of *Poa pratensis* followed by zones of *Lolium perenne* and *Trifolium repens*. An example is shown in Pl. XXXV, phot. 1, this being a path on a Lakeland fell. The surrounding vegetation is an *Agrostis-Festuca* association with *Briza media*, *Vaccinium myrtillus*, *Molinia caerulea* and *Nardus stricta* as sub-dominants. Pl. XXXV, phot. 2 shows a small area of this and is a typical example of the contrast which occurs.

On dry sandy heaths in districts of low rainfall the dominant species of the path are usually *Festuca ovina*, *Agrostis stolonifera*, *Galium* spp., *Plantago* spp. and *Hieracium* spp. On heavier soils and in moister situations, where puddling of the surface occurs in winter, it is notable that areas dominated by *Poa*

Phot. 2. Herbage on steep hillside adjoining footpath. Plants present are *Molinia caerulea*, *Agrostis stolonifera*, *Festuca ovina*, *Vaccinium myrtillus* and *Potentilla erecta*.

Phot. 1. Zonation on edge of footpath.

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pratensis and *Lolium perenne* are those where the surface is disturbed. The sward is not broken, but the mud oozes through and almost covers the surface.

Footpaths are obviously of varying lengths but the width is limited according to circumstances and may vary from a few inches, as on a mountain side, to several yards, as on a common. The lateral boundaries are not sharply defined, but merge gradually into the surrounds, for treading is not evenly distributed and is more concentrated in the centre. The boundary usually occurs where the *Lolium perenne* and *Trifolium repens* zone reaches its outer limit.

Floristic composition of the vegetation of footpaths.

The above statements with regard to the floristic composition of footpath vegetation and the arrangement of species into zones is so patent to everyday observation that elaboration in the form of statistical data is scarcely necessary.

To provide some illustration, however, eight examples are taken as follows:

Example 1. Sheep Walk. Tarn Hows, Lancashire.
,, 2. Larch Wood, Gooseyfoot Tarn, Lancashire.
,, 3. Mixed Wood, Walton, Derbyshire.
,, 4. Paddock, Ashgate, Derbyshire.
,, 5. Marsh Pasture, Terrington Marsh, Norfolk.
,, 6. Riverside, Gaywood, Norfolk.
,, 7. Chalk Heath, Massingham Heath, Norfolk.
,, 8. Sandy Heath, Wooton Heath, Norfolk.

Example 1 occurred on a hillside where the soil was very acid (*p*H 4) and the rainfall high. Example 2 occurred under similar conditions but in a shaded situation. Example 3 occurred on a medium loam with an acid reaction (*p*H 5). Example 4 occurred in the same neighbourhood as Example 3, but the soil was neutral in reaction owing to heavy liming. All forms of grazing animals, including rodents, were excluded from this site. Example 5 is found upon a pasture of renowned grazing value on the silt land bordering the Wash. Example 6 was upon a black alluvial riverside soil, neutral in reaction. Example 7 was that of a footpath traversing a heath overlying chalk, the soil being comparatively moist and neutral in reaction. Example 8 occurred upon a dry, sandy, acid heath (*p*H 5) overlying a Lower Greensand formation.

An intensive survey of the above examples was carried out both in summer and in winter. Quantitative data, both of areal percentage occupied and of frequency, were collected both from the footpath proper and also for comparative purposes from the surrounds. Qualitative data relating to constancy, exclusiveness, vitality and periodicity were obtained from 100 examples.

For the purposes of this article the publication of the whole of this information would be superfluous, and, as already stated, the phenomena are familiar or are easily accessible to the observer. For the purposes of the subsequent examination of the problem, however, the findings are summarised below.

Quantitative data.

(1) *Areal percentage.*

In all the eight examples bare ground occurred where treading was most severe, and occupied an average of approximately 18 per cent. of the ground covered by the path.

Poa pratensis occupied an average of 34 per cent. of the area of the paths in Examples 1–8, but only 2 per cent. of the area in Example 8 on dry sandy heath.

Lolium perenne occupied an average of 18 per cent. of the area of the paths in Examples 1–8, but only 1 per cent. in Example 8 and was absent in Example 2.

Trifolium repens occupied an average of 10 per cent. of the area of the paths in Examples 1–8, but was absent in Example 2 and only covered 2 per cent. of the area in Example 8.

Plantago spp. and *Bellis perennis* were present in two examples, and other species such as *Dactylis glomerata* and *Cynosurus cristatus* were present in others.

Poa pratensis, Lolium perenne and *Trifolium repens* were the dominants on the paths on which they occurred.

In all cases except Examples 5 and 8, the flora of the surrounds was mixed and none of the above species were dominants. In Example 5, however, *Poa pratensis, Lolium perenne* and *Trifolium repens* were co-dominants on the surrounds as well as on the path, and in Example 8 both the path and the surrounds consisted of an *Agrostis-Festuca* association containing *Galium saxatile* and *Plantago coronopus* as sub-dominants.

(2) *Frequency.*

This was determined by noting the number of times a species or a patch of bare ground occurred within a 10×10 in. quadrat frame thrown 100 times at random.

Bare ground occurred with an average frequency of 33 per cent. over the eight examples. *Poa pratensis* had an average frequency of 69 per cent., *Lolium perenne* 55 per cent. and *Trifolium repens* 35 per cent. over the eight examples. No other species possessed a frequency of any magnitude in comparison with the above. None of the above species displayed a high frequency on the surrounds except again in Example 5, where *Poa pratensis, Lolium perenne* and *Trifolium repens* were high and in Example 8 where *Agrostis* spp. and *Festuca ovina* had the highest frequency.

(3) *Constancy.*

Both *Poa pratensis* and *Lolium perenne* displayed 100 per cent. constancy upon paths, while *Trifolium repens* displayed 80 per cent. constancy. No other species was comparable with the above, the next in order being *Galium saxatile* 32 per cent., and *Bellis perennis* 25 per cent.

Qualitative data (from 100 *examples).*

Exclusiveness. No species could be described as exclusive to the footpath, but the following are preferential: *Poa pratensis, Lolium perenne, Trifolium repens, Bellis perennis, Hieracium* spp., *Plantago major* and *P. coronopus.*

Vitality. The following species regularly accomplish their complete life cycle: *Poa pratensis, Lolium perenne, Cynosurus cristatus, Trifolium repens, Galium saxatile, Plantago* spp. and *Luzula* spp. Many other species found on the paths only showed vegetative development.

Periodicity. The following species only were winter green: *Poa pratensis, Lolium perenne* and *Cynosurus cristatus.* Other species were dormant during the winter months.

Habitat factors.

(1) *Edaphic factors.*

General physical conditions. The soil of the footpath is in the first place similar to that of the surrounds, and would exhibit the same characters upon mechanical analysis. Any differences in the physical condition of the soil between path and surround are the result of treading upon the path.

It is obvious that the soil of the path possesses a greater density than that of the surrounds, and this has a secondary influence upon temperature and moisture conditions. Attempts to obtain definite measures of the respective densities were a failure and only approximations were possible. This was due to the difficulty of exact excavation, owing to plant roots and to stones. Several facts were, however, quite apparent from the investigation.

In the surrounds the top 5 cm. were of lower density than those below, owing to the lightening effect of plant roots, and also to the fact that there is no superimposed layer of soil, and that no treading occurs. On the footpath the surface soil is of greater or equal density to the lower soil. The lower soil of the paths was of about the same density as that of the lower soil of the surrounds.

It would appear that in the case of the footpath, the denser or consolidated condition of the soil, due to treading, exists only in about the first 3–5 cm., and that below that level conditions are comparable with those at a similar depth in the remainder of the field.

The exact arrangement or texture of the particles in the surface layer will differ according to whether the trodden soils contain a certain proportion of clay or not. Clay when trodden or "puddled" in the presence of moisture becomes altered physically, owing to deflocculation of the particles. The result of this action is the retention of moisture on the soil surface, and upon the soil drying by the evaporation of this moisture, a "baked" or "poached" condition arises, and a hard, "baked" crust of varying thickness is formed.

The proportion of clay in the soil of the footpath and the condition arising therefrom cannot be of any importance as a factor influencing the constitution

of the footpath community, for the community is the same in its main features on other types of soil, except in the extreme case of dry sandy heath.

Experiments were carried out in 1929 ((**2**), p. 587) on a heavy loam soil (Chesterfield, Derbyshire), and again in 1932 on light sandy loam (near King's Lynn, Norfolk) in an attempt to determine whether consolidation in itself exerted direct influence or selective influence on the species. A garden border was in each case divided into two, one half being consolidated and the other left loose. The following species were sown in rows (duplicated and randomised) across both loose and solid areas: *Lolium perenne*, *Poa pratensis*, *Holcus lanatus*, *Agrostis stolonifera*, *Festuca ovina*, *Trifolium repens* and *Plantago major*.

In the case of the 1929 experiment soil was consolidated to a depth of about 30 cm., by packing the soil layer upon layer. In this experiment it was found that all the species were reduced to about half the size and weight of those upon the loose soil. The root systems were also restricted by the solid soil.

In the 1932 experiment consolidation was carried out by surface pressure after the species were established, care being taken not to crush any of the leaves or stems of the plants. In this case the consolidation resembled the type effected on the footpath, i.e. only the first few centimetres of soil were affected. In this experiment little result was noted, except in the case of *Poa pratensis* which was reduced in size in the consolidated portion. *Holcus lanatus*, *Agrostis stolonifera* and *Festuca ovina* were slightly stunted. It is significant that these species are comparatively shallow-rooted.

From the above results there appears no reason to suppose that consolidation itself is responsible for the "footpath flora". *Poa pratensis* is the species most adversely affected, and yet this is the constant and most abundant species upon the consolidated portion of a path.

Soil moisture. On the whole the footpath is a moister habitat than the surrounds. The pressure of the soil particles into closer association should increase surface tension and consequently the power of a soil to retain moisture, though in recently published work (**3**) it has been shown that consolidation does not greatly affect water-holding capacity. The surface of the footpath, however, is pressed down to a lower level than the surrounds and gravitation will increase water supply in virtue of this fact. Another factor is that the vegetation of the surrounds is frequently matted, and this surface covering of root material retains water at the surface and renders the soil dry. On the footpath "mat" is eliminated by treading and a freer access of water is possible.

On the other hand a clay soil may, in the puddled state of the footpath, prohibit the access of moisture, and may bake very hard in dry weather. Moisture conditions will be worse, in such cases, on the path than on the surrounds, yet the footpath still possesses its distinctive vegetation.

The species of the footpath socies are not, as a whole, characteristic of a wet or dry habitat. *Lolium perenne* thrives under good moisture conditions, but is

deep rooted and fairly drought-resistant. *Poa pratensis* is shallow rooted, but possesses underground runners and is drought-resistant. This latter grass is recognised by agricultural botanists as one that tolerates dry situations. *Trifolium repens*, in virtue of its deep root system, is very drought-resistant, and it is often to be observed that when pastures are burnt dry, this species is still present in a green state. Actually a dry season favours the development of *Trifolium repens*.

In view of the above facts it does not appear that moisture in itself can be regarded as a factor which is directly responsible for the existence of a distinct footpath socies. It is asserted by some that the distinct green colour of the footpath in winter is due to moisture, but this may be explained by the fact that the species of the footpath are all winter green.

It is to be observed that the footpaths existing on dry sandy soil in districts of low rainfall do not possess the characteristic flora of paths in other situations (Example 8). Small colonies of *Poa pratensis* and *Lolium perenne* may be found in the damp hollows, but the dominant and subdominant species are *Festuca ovina*, *Agrostis stolonifera*, *Galium* spp., *Plantago* spp. (excluding *Plantago major*) and *Hieracium* spp. The phenomena were also noted where paths traversed a cinder track and a slag heap (**4**).

On all other types of soils in moister situations the characteristic footpath community exists on an area which coincides exactly with that which is puddled on the surface in winter. As already stated, the sward is not broken, but mud oozes through and becomes mixed with the herbage. The occurrence of the typical footpath community of *Poa pratensis*, *Lolium perenne* and *Trifolium repens* on puddled areas is highly significant and goes to show that a moist condition of the soil is important, though certainly an indirect factor. The presence of moisture and a suitable physical condition of the soil are essential to puddling. *Poa pratensis* and *Lolium perenne* can tolerate puddling, which is thus essential to the production of the footpath socies, because, as will be seen later, it is lethal to species not characteristic of the footpath.

Chemical composition. There is no reason why the chemical composition of the soil of the footpath should vary from that of the surrounds. There is in some cases a greater accumulation of organic matter from decayed vegetation on the surrounds than on the footpath, but this is not always the case. It is also notable that grazing animals prefer the footpath, and thus it may receive more droppings and urine than the surrounds. It is to be noted, however, that in the case of some paths, livestock and even rabbits are excluded, e.g. Example 4.

As regards soil acidity a number of investigations failed to reveal any significant difference in the *p*H value of the soil of the surrounds and the path, except where much "mat" was present on the surrounds, and here a difference was recorded, the earth below the "mat" being more acid than that of the path.

Light and aspect. Where a footpath traverses grassland there is a greater illumination on the path than on the surrounds, owing to the fact that the herbage is suppressed by treading, and its shading effect thereby removed. In many cases where a path runs from east to west the north margin of the path (which faces south) will be illuminated by the direct rays of the sun at its maximum intensity. The opposite side, especially where overshadowed by tall grass or raised ground, will be shaded. The difference in illumination determined by actinometer was for the shaded portion one-ninth that of the lighted northern side, in a typical example.

Light intensity exerts a marked influence upon *Trifolium repens.* In a shaded habitat, such as a wood or where other objects exclude sunlight, *Trifolium repens* is absent or very scanty, e.g. Example 2. Even aspect affects this species, and it will be found that where the southern side of a path is shaded from direct sunlight by tall grass or rising ground there is a considerably lower scale of abundance, frequency and dominance than on the opposite side. When *Trifolium repens* is in flower, the relative abundance of white flower-heads on the side of a path with a southern aspect compared with the shaded northern aspect on the opposite side is very conspicuous. Light intensity does not appear to exert any marked influence on the other species of the footpath, and they may all be found in shaded situations.

The influence of the biotic factor.

Grazing. It is notable that livestock prefer to graze the footpaths rather than the surrounds. This applies mostly to sheep and horses, as these animals bite closely. It must be obvious upon consideration that grazing is a secondary influence. The species of the footpath are the best pasture plants in the agricultural sense, and owing to their shortness they offer a succulent herbage. The droppings and urine from the animals are sometimes held responsible for the green colour of the path, as is the case with water supply. No difference is noted, however, on footpaths where grazing animals, including rabbits, are excluded, e.g. Example 4.

Treading. The effect of treading upon the flora of a community is threefold, and is both direct and indirect. The indirect action has already been studied, i.e. the consolidation of the soil and its influence upon the species. It has been shown that this is not responsible for the footpath socies.

The direct influences are those of treading and puddling upon the plant itself, and the mechanical effect or injury caused thereby. It is very obvious that many species are damaged and are often completely destroyed by the action of treading, while on the other hand the species of the footpath socies are comparatively immune to harm of this kind. The reason for this immunity or resistance must obviously be due to some peculiarity of structure which the species possess in common, and which is not possessed by the species susceptible to injury.

An examination of the habit of growth of the dominant gramineous species *Poa pratensis* and *Lolium perenne*, shows a very striking and significant character possessed by these species and not by the species of the surrounds, i.e. the conduplicate stem and folded leaf section as compared with the rolling of the leaf in other Gramineae (excepting *Poa* spp., *Dactylis glomerata* and *Cynosurus cristatus*). An examination of this structure of leaf and stem shows it to be an excellent adaptation to resist injury, for the leaf and stem offer a flat surface to the crushing action of the foot. The conduplicate arrangement of the shoot is of similar mechanical structure to the leaf springs of a carriage.

The life form of the gramineous species of the footpath is also distinct from that of the most frequent species of the surrounds. The gramineous species of the path constitute a synusia of cryptophytes, the buds being buried just below the level of the soil. The Gramineae of the surrounds are mainly hemicryptophytes, the buds being at ground level, and two of the species, *Agrostis* spp. and *Holcus mollis*, may be chamaephytes.

The arrangement of the gramineous species into life forms is a somewhat fine point. It might be argued that some species described in this thesis as cryptophytes or chamaephytes respectively might all be grouped as hemicryptophytes, but adhering rigidly to the position of their perennating organs as the criterion, there is no doubt as to which species tend to the cryptophytic habit and which to the chamaephytic.

It appears obvious that the double adaptation, i.e. the folded leaf and the conduplicate stem with the cryptophytic life form, enable the plant to withstand injury. The leaf and stem are resistant to injury, while the growing point is protected below the surface of the earth.

It has been noted that *Poa pratensis* occupies the zone of the most intense treading and is followed by *Lolium perenne* on the less trodden area. A comparison of the two species shows *Poa pratensis* to be better adapted than *Lolium perenne* to resist injury. In the former case the growing point is buried deeper in the soil and the plant propagates by underground stolons as well as by seed. The leaves of *Poa pratensis* are short, tough and concave in longitudinal and cross section. The leaves of *Lolium perenne* are longer and more flaccid.

It is notable that *Poa trivialis*, though possessing much the same foliage characters as *P. pratensis*, is very rare on the well-trodden portion of footpaths. This species is definitely chamaephytic in life form. It has also been noted that *P. annua* may occupy interstices where it is protected from treading, and it may also have a transient existence where treading is for some reason suspended ((**2**), p. 589). *P. annua* is a therophyte.

Of the non-gramineous species *Plantago major* is well adapted to withstand treading. The leaves are broad and tough and occur in rosette form, the upper ones protecting the lower. On the footpath the plant is an ecad occurring here as a cryptophyte, whereas on untrodden areas it is a hemicryptophyte with semi-erect leaves. The average size of the plant is smaller on the footpath than

on the surrounds. Similar phenomena are noted in the case of *Plantago media*, *P. lanceolata* and *P. Coronopus*.

Trifolium repens is least adapted to treading of any of the footpath species, and it is a significant fact that it occupies the outer zone and invades the footpath from the surrounds. Light appears to offer the greatest stimulus to this species and to account for its presence on the footpath. The plant is a chamaephyte with prostrate runners, and in virtue of the tough and prostrate nature of these runners exhibits a certain resistance to treading. The leaves are often injured by the process and are smaller in size upon trodden area (**4**). *Trifolium repens* is not injured by even pressure (as contrasted with treading) to the same extent as are the Gramineae.

Experiments upon the influence of treading.

An experiment was carried out to test the theory of resistance to injury possessed by certain species and not by others ((**2**), p. 589). The following grasses were grown in separate and repeated strips: *Poa pratensis*, *Dactylis glomerata*, *Lolium perenne*, *Anthoxanthum odoratum*, *Alopecurus pratensis* and *Agrostis vulgaris*. The ground was then utilised as a garden path and trodden daily. *Poa pratensis* assumed a low dense habit, *Dactylis glomerata* and *Lolium perenne* were suppressed but persisted. The three remaining species were exterminated by treading. The experiment was carried out in 1929 on a heavy loam (Chesterfield, Derbyshire). Puddling took place during wet weather, though the work was carried out in summer.

A further experiment was carried out on a light loam (King's Lynn, Norfolk). The following species were sown in rows and the trial duplicated. *Trifolium repens*, *Dactylis glomerata*, *Poa pratensis*, *Lolium perenne*, *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* (the latter was planted in the form of runners). A pathway was trodden through the plots and the species were subjected to a severe treading and puddling during a wet summer and autumn.

Trifolium repens was affected by the treading but not destroyed. *Dactylis glomerata*, *Poa pratensis* and *Lolium perenne* were somewhat restricted in development but persisted and quickly recovered from the bruising action of treading by making fresh growth during the resting stage. *Festuca elatior* offered some resistance, but eventually the buds in the centre of the plant, being above ground level, were destroyed. *Agrostis stolonifera* and *Agropyrum repens* were completely destroyed and in the latter case the runners appeared dead and shrunken.

It was noted that seedlings of *Poa pratensis* appeared all over the trodden areas, but were very dense in the region of the *P. pratensis* strips. It is possible that some of the seedlings were those of *P. annua*, but if so they did not persist beyond the seedling stage, as no mature plants were identifiable.

The exact effect of treading was as follows: The original plants were broken

down, and the leaves damaged in the case of all the species. In the case of *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* the buds at the base of the plants were trampled in the mud and damaged, but with *Dactylis glomerata*, *Poa pratensis* and *Lolium perenne*, these were protected beneath the surface of the soil. It appeared that the damage to the bared buds of *Festuca elatior*, *Agrostis stolonifera* and *Agropyrum repens* only took place when the earth was wet and treading produced a pulpy condition.

Special influence of treading.

Festuca ovina and *Agrostis stolonifera* appear capable of withstanding treading upon a dry footpath, but they do not tolerate puddling. The same applies to *Galium* spp. These plants are extremely stunted by the treading and the leaves are very fine. It is obvious that the stunted leaf of *Agrostis* and the setaceous leaf of *Festuca ovina* must be resistant to treading, and it is significant that these species are the dominants on dry footpaths. Many other cryptophytic species occur on the surrounds, but are not found on footpaths, and are all of a type which would be damaged by treading, i.e. upright or fragile.

While *Festuca ovina* and *Agrostis stolonifera* are able to withstand treading upon the leaf they are not able to withstand the slight surface disturbance caused by puddling, and the damage done by the bruising action of the foot or hoof when pressing into the surface soil. These two species are chamaephytes and their growing points are on the surface of the earth: furthermore they possess an extremely superficial root-system, forming a mat of root material at their base.

Large-scale experiment on the influence of puddling.

An experiment was carried out on a large scale in Hardwick Park, Derbyshire, illustrating the effect of puddling upon an association of *Agrostis* and *Festuca* (**5**). The aim was to imitate the action of the hoof in wet weather on about four acres of very matted grassland. The composition of the grassland, assessed on the percentage area basis, was:

Agrostis spp.	35·4
Cynosurus cristatus	24·6
Festuca ovina	23·1
Luzula campestris (agg.)	9·2
Lolium perenne, Trifolium repens, Ranunculus spp., Moss, Holcus lanatus	7·7
	100·0

The sward was cut frequently in two directions by a disc harrow, drawn by a tractor while the ground was very wet and rain was falling. The turf was worked into a morass of mud and presented a puddled appearance. It was then heavily rolled. The operation was carried out in March 1929, and in the following summer a complete change in the flora was noted. The analysis of the treated portion was then as follows:

Poa pratensis	50·9
Cynosurus cristatus	21·7
Agrostis spp.	9·1
Trifolium repens	12·0
Lolium perenne	1·0
Holcus lanatus, Festuca ovina, Ranunculus spp.	5·3
	100·0

The analyses of the herbage were carried out independently by Mr A. Roebuck of the Midland Agricultural and Dairy College.

The influence of this puddling action, carried out on a large scale, shows a result of such striking similarity to that observed on the footpath, as to need no elaboration. The astonishing acquirement of dominance by *Poa pratensis* in so short a time must be explained by very widespread presence of the seed over the area and the establishment of a peculiarly favourable seedbed by the "puddling" operation. The plants were young when examined in the summer, and hay had previously been fed to cattle on the area. As will be seen, the *Poa* mainly replaced *Festuca* and *Agrostis*, which were severely reduced.

It would appear probable that the evergreen or "winter green" condition of *Poa pratensis* and *Lolium perenne* may be a factor in their favour in the footpath community, in that they are in a growing state during the puddling process. This may exert some influence, but in the above experiment, the time of the operation (i.e. March in a moist warm spring) allowed a good chance for *Festuca ovina* and *Agrostis stolonifera* to recuperate.

Selective influence of treading and puddling.

From a consideration of the above data it would appear that the species which are found on footpaths, in wet or dry situations, are enabled to persist by virtue of their leaf structure. When, however, puddling becomes a factor, *Festuca ovina* and *Agrostis stolonifera* are obliterated, but all species possessing the cryptophytic life form are able to persist.

The influence of treading and puddling upon a gramineous community may be readily demonstrated by rubbing a given area with a rubber squeegee during wet weather or when the ground is in a wet condition. An experiment of this nature was carried out on Massingham Heath, Norfolk (August 1932). Three quadrats were chosen, each 1 sq. metre in area, with *Agrostis stolonifera*, *Festuca ovina*, and *Holcus lanatus* as co-dominants, and scattered individuals of *Lolium perenne*, *Trifolium repens* and *Plantago* spp. The areas were rubbed with a squeegee and with the foot until the vegetation was bruised and the surface pasted with mud. Several days later it was noted that the quadrats presented, as a whole, a dead appearance. It was observed, however, that while *Agrostis stolonifera*, *Festuca ovina*, and *Holcus lanatus* were apparently dead, the "stumps" of *Lolium perenne* and *Plantago* spp. stood out of the ground in a striking manner and were still green. The runners of *Trifolium*

repens also remained green. A fortnight later it was noted that some of the *Agrostis stolonifera* showed signs of recovery, a few fresh green shoots having arisen, but *Festuca ovina* had not recovered and *Holcus lanatus* was obliterated beyond recognition. *Lolium perenne* had made a good recovery, having grown leaves up to 10 cm. long. *Trifolium repens* was developing leaves and so was *Plantago* spp.

The formation of the footpath socies.

In the years 1929–30, in a grass paddock (Hawkshead Hill), attempts were made to study the formation of a footpath socies, by observations carried out on several areas when the footpath was diverted to fresh ground. Permanent quadrats were unfortunately obliterated, but the following facts were revealed from close observation.

Existing species not typical of the footpath synusia were suppressed and bare ground populated by *Poa pratensis* which in some cases sprang from seed, but in others proliferated from pre-existing individuals. *Plantago* spp. also appeared as seedlings upon this central area and grew to maturity. *Lolium perenne* did not appear as seedlings in the first place, but pre-existing specimens persisted and proliferated, and in the second year seedlings were observed. *Trifolium repens* invaded the outer margins of the path vegetatively. The runners appeared to be attracted towards the unshaded area from individuals existing in the surrounds. Runners of *T. repens* were defoliated by the action of treading and were pressed into the puddled ground, but in many cases recuperated.

II. FLAGGED FOOTPATHS.

Several types of flagged pavements are in existence, the commonest being the ordinary street sidewalk. In this case the flags may be of stone or concrete, but in both cases interstices exist between the flags. Garden paths and field paths are sometimes flagged and even asphalt paths possess a curb which is composed of individual stones. Cobbled paths and roadways are now of uncommon occurrence.

Except in the centre of large cities or in the presence of chemical fumes or similar agents destructive to plant life, all flagged pavements possess vegetation, though this is in many cases extremely scanty. Lower forms of plant life such as mosses and algae may cover the flags or exist in the interstices, but their distribution is not considered in this paper.

The complete floristic list of the habitat is indefinitely large and ranges from seedling trees to grasses, but the frequency of the majority is of so low an order as to be negligible. They are accidentals, occurring in odd sheltered or protected places.

The remarkable character of the vegetation of this type of habitat is the predominance of *Poa pratensis* over all other species. This grass occupies the

interstices between the flags, sometimes dominating this area and sometimes occurring in scattered colonies. It is practically constant for all examples occurring on flagged pavements in the most varied localities. It has been observed as the dominant species of flags and kerbstones for miles along a road crossing Derbyshire moors, on the promenades of seaside resorts, and in the suburbs of cities in all parts of the country. Subdominant species are *Galium* spp. and *Sagina procumbens*.

Where the flagged path borders a bank or wayside the latter situations may be populated by a large variety of species, yet *Poa pratensis* still dominates all the interstices of the flags. In a survey of twenty examples it was found that whereas *P. pratensis* occupied an average area of only 5 per cent. of the vegetation of the surrounds, it composed 95 per cent. of the vegetation of the interstices assessed on an area basis ((**2**), p. 585).

There appear to be two reasons for the dominance of this species, firstly the ability to invade the interstices by means of its runners, and secondly the adaptation to resist the injury caused by the very severe and concentrated treading. This power of resistance is due to life form and leaf and stem structure and has already been fully described.

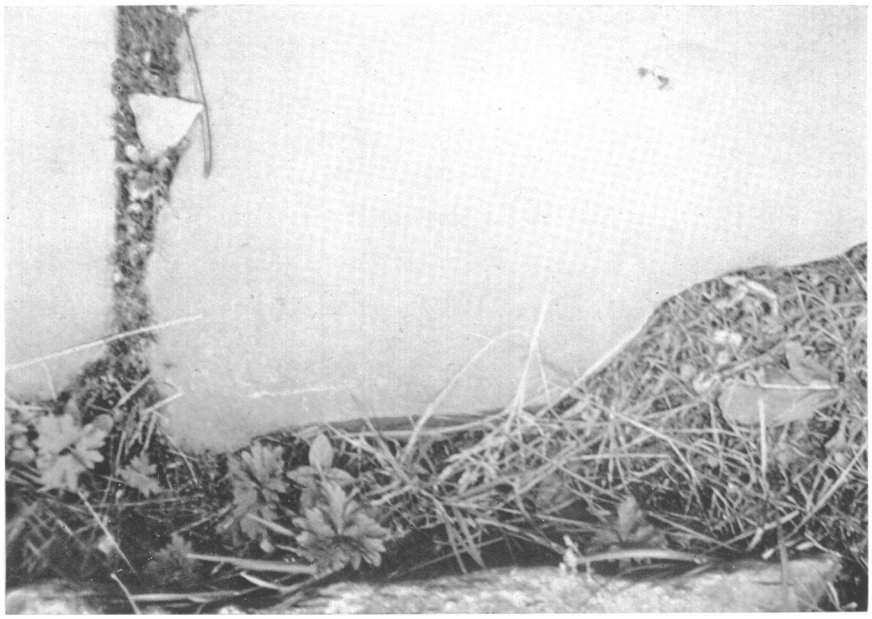
In the case of disused flagged paths or those rarely trodden, the flora may be extremely varied and possess no distinct characters; this also applies to cobbled paths. The colonisation of a newly laid flagged path takes place by seed infection of the soil of the interstices and by invasion from the surrounds of runner-bearing species. The commonest ubiquitous annuals may appear together with *Agrostis* or *Agropyrum*. *Poa pratensis* may appear as isolated seedlings in the interstices or from runners invading from the surrounds. The mechanical effect of treading soon exerts its selective influence, *Poa pratensis* surviving on the closely trodden portions.

Pl. XXXVI, phot. 3 shows the domination of an interstice by *Poa pratensis* while the immediate surrounds Pl. XXXVI, phot. 4 contain a mixed flora.

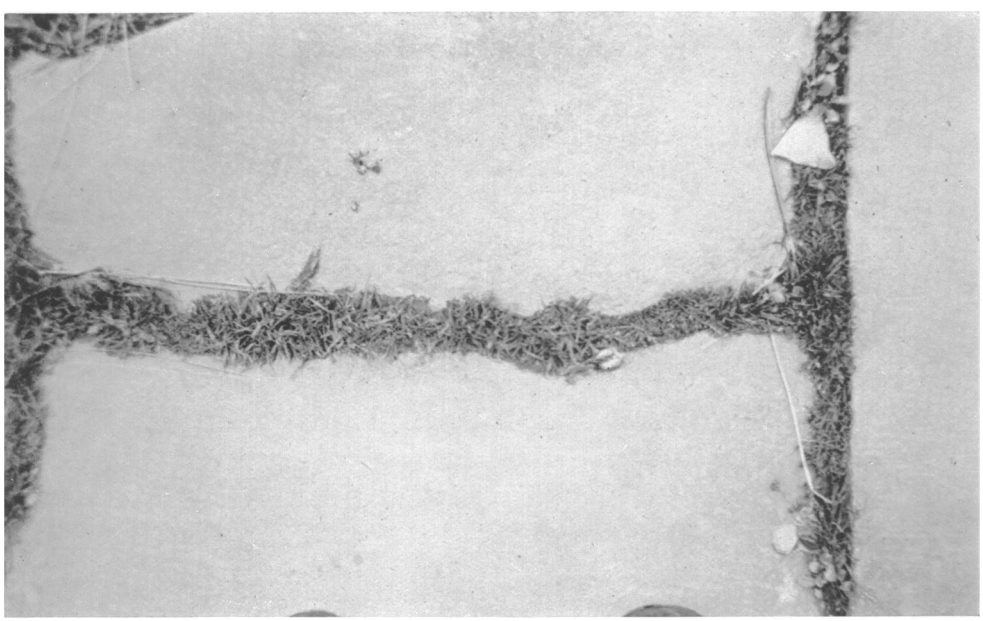
III. Cart-tracks and gateways.

Cart-tracks, frequently used lanes, fen droves and gateways cover a large area of the countryside, probably of greater magnitude than that occupied by footpaths. They are all subjected to the same mechanical influences, i.e. human treading, and in addition the deep disturbance and churning action of horses' hoofs and of cart-wheels during wet weather. In summer the surface may be hard and stable, but in winter certain parts of it will become a morass.

On cart-tracks and fen droves the characteristic species are knotgrass (*Polygonum aviculare*), swinescress (*Senebiera Coronopus*), silverweed (*Potentilla anserina*), greater plantain (*Plantago major*), rayless chamomile (*Matricaria suaveolens*). The grasses are *Poa annua*, *P. pratensis*, *Lolium perenne*, while associated with these there may be *Trifolium repens*. Distinct zonation exists on these areas, and upon examination it is found that the most disturbed



Phot. 3. Surrounds of flagged path. *Agrostis stolonifera, Festuca ovina, Ranunculus* spp. and *Circaea lutetiana.*



Phot. 4. Flagged path, interstices dominated by *Poa pratensis.*

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regions are dominated by the annuals, while perennials dominate the more stable regions. The most severely trodden and compressed portion of the stable surface do not, as a rule, support grasses, but the less trodden and compressed part of the stable surface and the margins of the habitat may be dominated by the perennial grasses and by *Trifolium repens*.

This community may usually be defined as an associes. The magnitude of the area and its separation by ditches or hedges from the surrounding communities should entitle it to this rank. It contains consocies, socies and colonies. It is obviously in an unstable state.

Gateways exhibit a somewhat similar flora and the constancy of the species is the same throughout the country. The obvious reason is that the mechanical factor is again the most potent. The phenomenon of zonation is also observed, especially where a gateway enters a grass field, and this zonation gives an excellent example of specific changes in response to varying intensity of compression. In the actual gateway midway between the posts is an area of bare ground where disturbance and treading are so severe that no species can exist while these continue. Following upon this is a zone in which *Polygonum aviculare* and *Matricaria suaveolens* are dominants. Intermixed with the latter species, but extending further out, *Plantago major* is a constant.

Transient individuals of *Poa annua* may occur over any part of the area at certain seasons, most commonly in winter and spring. In the gateway of a pasture, grasses exhibit a zonation consisting of the same species together with *Trifolium repens* and arranged in the same way as on footpaths. The grass zones are furthest from the gateway and merge into the pasture.

Gateway communities may also be described as associes, being subordinate communities in the midst of cultivated or semi-cultivated vegetation communities.

Quantitative data. In five examples composed of two gateways, two cart-tracks, and one fen drove a survey revealed the following data. The species *Plantago major*, *Polygonum aviculare*, *Matricaria suaveolens*, *Senebiera Coronopus*, *Potentilla anserina*, *Poa pratensis* and *Agrostis stolonifera* were present in all cases with the exception of one gateway where *Potentilla anserina* was absent. The relative abundance, and also the areal percentage occupied varied greatly with each example, for the size of the individual plants was extremely variable. Frequency did not vary to quite the same extent, which was probably due to a certain amount of zonation of the species. The fact that the above species were the co-dominants is revealed by the fact that other species, grouped as miscellaneous, only showed an average abundance of 3·6 per cent. of the total.

In a hundred examples the following percentage constancy of the species was recorded: *Plantago major* 100, *Polygonum aviculare* 92, *Matricaria suaveolens* 89, *Senebiera Coronopus* 79, *Potentilla anserina* 60. *Poa pratensis* 94, *Agrostis stolonifera* 54. One or more other species occurred in all the examples.

Qualitative data. No species could be described as exclusive to the community, but the first five in the above list could be classed as preferential.

As regards vitality, miscellaneous species were accidental and did not multiply. *Agrostis stolonifera*, originating from adjoining situations on stable ground, showed restricted vegetative development. The remaining species of the community regularly completed their life cycle.

The periodicity of the species varied, in that *Poa pratensis* was winter green while the other species were dormant (or absent in the case of therophytes) in the winter aspect. *Polygonum aviculare* and *Matricaria suaveolens* do not appear as seedlings until late in the spring aspect.

The distribution within the community, apart from the phenomena of zonation, showed one outstanding feature, i.e. that perennials do not exist upon the areas which have been disturbed and puddled in winter, except in a seedling or "maiden" state. These areas are dominated by the annuals *Matricaria suaveolens* and *Polygonum aviculare* and in some cases by seedlings and immature plants of *Plantago major*.

Habitat factors.

The habitat of the community under consideration bears some features of resemblance to that of the footpath, in that it is a disturbed area, and the disturbance is due to puddling. In this case, however, the disturbance is of a much more violent nature, the soil being puddled and disturbed to depths of several inches, or in the case of cart-ruts even to the depths of the axles. Certain parts of the area are disturbed during winter months when the ground is soft, other parts, as, for example, the region between the cart-wheels and the horse's hoofs, remain undisturbed. During summer the ground becomes hard, and though still subjected to pressure, comparatively or quite stable.

Edaphic factors.

Since the gateway and footpath communities are constant for all types of soil, the chemical composition of the soil and to a certain extent its physical condition, i.e. humus, clay, sand or chalk content, cannot have any definite influence upon the flora. On sandy heaths (Bawsey and Snettisham, Norfolk, Greensand formation) the same flora is found as upon heavy clays. On soils containing a clay fraction "poaching" and deflocculation of the clay particles occurs, but this is not the case on sands.

Light.

Owing to the absence of other vegetation the habitat is fully illuminated, as was the footpath. There appears to be some connection between the light factor and the vegetation, as all the species except *Matricaria suaveolens* are prostrate or straggling, and unable to compete for light in other habitats. *Matricaria suaveolens* is a Composite with dissected leaves, and it is well known that species of that family and with that type of foliage are extremely intolerant of shade.

Phot. 5. Fen drove, aestival-autumnal aspect. *Polygonum aviculare* is dominant between the tracks.

Phot. 6. Fen drove with *Potentilla anserina* and *Plantago major* dominating the undisturbed region between the cart-tracks.

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In the above connection observations were made in several localities on the reaction of *Matricaria suaveolens* to light. The first three were cart-roads running east and west. When the hedge was dense or the ground overshadowed by it or by trees, *Matricaria suaveolens* was absent or scanty. In one example, at Castle Rising, Norfolk, a building shaded the sidewalk up to the inner edge of the kerb. A little *Matricaria suaveolens* grew under the wall and on the sidewalk, but it was abundant upon the kerb.

It is a significant fact that *Matricaria suaveolens*, *Senebiera Coronopus* and *Polygonum aviculare*, all germinate comparatively late when most places are overshadowed by vegetation. Seedlings of these species are not to be observed on cart-tracks or in gateways until the end of May. It is highly probable that these are the only habitats offering light and a suitable situation for germination at this season.

Thus it appears that light is a contributing factor to the existence of the cart-track and gateway community.

Disturbance and compression.

It is obvious that the chief factor influencing the habitat is that of disturbance of the ground during winter and compression of the surface in summer when the ground is dry. The effect of the winter disturbance is to destroy all species which have become established during summer. These species consist of the annuals *Polygonum aviculare*, *Matricaria suaveolens*, *Senebiera Coronopus*, and the seedlings and first year plants of *Plantago major*, together with a few miscellaneous seedling perennials. The annuals would obviously die irrespective of the disturbance, but the perennials are also destroyed. Observation shows that runner-bearing perennials are crushed beneath the wet soil, while *Plantago major* is squeezed out and left upon the surface to be destroyed by frost or other agencies. In any of these communities the perennials of more than one year's standing are found on parts of the habitat which are stable during winter.

Potentilla anserina, having its main rootstocks established upon stable undisturbed ground, may during summer send runners over an area which was disturbed during winter. It does not, however, tolerate much treading.

Pl. XXXVII, phot. 5, shows the aestival-autumnal aspect of a fen drove; the surface is colonised by *Polygonum aviculare*: in winter it was a morass devoid of vegetation. Pl. XXXVII, phot. 6 shows *Potentilla anserina* and *Plantago major* dominating an undisturbed region between cart-tracks.

The structural resistance to treading.

Plantago major, *Matricaria suaveolens*, *Polygonum aviculare*, *Senebiera Coronopus* and *Poa pratensis* are all resistant to treading. The resistance of *Poa pratensis* and *Plantago major* in virtue of their life form and structure has already been discussed (p. 477). The remaining species are also adapted to this influence.

Polygonum aviculare has hard wiry stems which resist treading, and the prostrate form prevents snapping of the stem at any given point. The leaves are small and become much smaller when the plant is subjected to treading. The flowers are minute and are protected in the axils of the leaves. *Senebiera Coronopus* is prostrate, has small scale-like leaves and small flowers and thus survives compression. *Matricaria suaveolens* is normally an upright plant but can become prostrate. The ability of this species to resist treading appears to be due to the small area of finely dissected leaves, and the extremely pliable nature of the stem, which is tough and fibrous and does not snap if bent double. The flower heads are comparatively large, but if compressed they splay out and appear to escape injury.

It must be made clear that the species of the community do not flourish under compression, but are severely stunted in growth both with regard to the shoot and the root system. They are also altered in habit, being converted from the upright or semi-upright to the prostrate habit. In spite of this severe stunting they are, however, capable of completing their life cycle.

General summary.

I. The chief factor concerned in the production of the footpath socies from the grassland community is the mechanical effect of treading and puddling. This exerts a selective influence on the grasses, eliminating those not structurally adapted to withstand the injury of treading and puddling. The species adapted by virtue of life form and leaf and stem structure are able to persist. These dominants are zoned according to the intensity of treading. Under dry conditions where no puddling occurs, treading alone produces little change.

The plantains are governed by the same factor as the grasses and owe their existence to their life form. *Trifolium repens* does not exhibit as great a resistance to treading as do the grasses and hence occupies only the outer zone of the footpath. Light appears to be a decisive factor with this species, shading being eliminated by the treading down of taller species.

II. The interstices of flagged paths and sidewalks are dominated by *Poa pratensis*. This is because this species can invade the area by means of runners coupled with its structural adaptations to resist injury by treading.

III. The characteristic flora of a cart-track or gateway community, owes its existence to a peculiar combination of circumstances. Severe disturbance and churning of the ground in winter exterminates all perennial species which have seeded during summer, annuals dying naturally or as a result of this disturbance. During summer the disturbed area becomes hard and stable, but is still subjected to surface pressure, and is therefore populated by annuals or by seedling perennials (chiefly *Plantago major* and *Poa pratensis*). In virtue of their life form and habit, these are able to resist the injury of treading to a sufficient degree to continue their existence through the summer and autumn. Other species than the above may appear during spring and summer as acci-

dentals, but succumb to treading. The undisturbed areas between or around the disturbed region are populated by perennials which may resist a severe degree of treading, but cannot survive disturbance and churning of the ground during winter.

All the species are ill adapted to compete for light and the habitat offers illumination without competition. It also favours species which germinate comparatively late in spring.

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