DOCTOR OF PHILOSOPHY

The effects of trampling and vehicles on natural vegetation.

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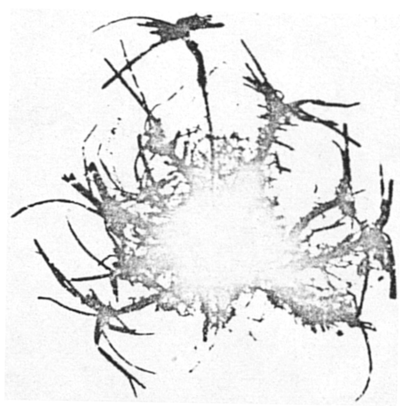
POA PRATENSIS L.

Response to trampling damage



Collected from tall vegetation

Collected from a car track

THE EFFECTS OF TRAMPLING AND VEHICLES ON NATURAL VEGETATION

A thesis presented for the degree of
Philosophiae-Doctor
in the University of Wales

by

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CONTENTS

ABSTRACT

Track and footpath conditions were investigated on the Aberffraw sand dunes, Anglesey. Soil bulk density and penetration resistance were related to the number of passages by cars or walkers and was increased on tracks and footpaths; compaction was examined to 50 cm depth. Trampling increased soil moisture in dry areas and compaction *per se* was probably beneficial to plants.

Vegetation was shown by multivariate analysis to be related to the soil parameters. Light trampling favoured dicotyledonous species but they were later eliminated and monocotyledonous species survived with a reduction in biomass and species number. Track occurrence ~~preference~~ indices were calculated for the common species and survival strategies considered; tillering capacity may be more important than protected meristems.

Trampling and wear by vehicles was applied to undamaged vegetation and the effect measured before and after recovery. Intensity was found to be more important than the effect of frequency. 1820 walkers or 200 vehicles reduced cover to 50% in the summer; vehicles were more destructive in winter. Physical carrying capacity was calculated and relative vulnerability of various habitats was estimated from data of other workers.

Soils were found to decompress when traffic was removed but vegetation initially inhibited the process. Tillage, seeding and the effects of fertiliser on vegetation regeneration were studied; the first inhibiting and the latter two treatments accelerating the process. Turves in greenhouse conditions were used to predict the results. The desirable end point was considered from the management point of view.

The effect of a track on the microclimate was studied with emphasis on thermal characteristics: vegetation removal had a greater effect than soil compaction. The effect on plants in relation to their distribution and morphology was discussed.

Models describing the ecological changes caused by trampling and the physical carrying capacity of sand dune pasture were constructed.

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M.J. Liddle.

INTRODUCTION

Three million years ago the Olduvi cave-dwellers (Le Gros Clark 1965) probably used the home centre reference system and may have retraced familiar routes and hence created paths (Gatty 1958). From Britain there is evidence of pathways made 4,860 years ago (Coles & Hibbert 1968). In general, increases in human trampling must be correlated with increases in the size and mobility of populations (Hippisley-Cox 1934, Watkins 1933), although the surfacing of roads and tracks will have led to a reduction in the trampling of vegetation, especially towards the end of the industrial revolution. Recently great increases in leisure time, private vehicle ownership and population have led to 'aesthetic and even physical erosion of resources' for recreation (Patmore 1970). There is, therefore, a need for the study of the impact of outdoor recreation on the semi-natural environment (Burdon & Randerson 1972), especially in sand dune areas (Ranwell 1969, 1972), Beattie (1967), Richards (1970) and Westhoff (1967).

In an early qualitative study which included the flora of footpaths Jeffreys (1917) noted that paths were usually lower and consequently wetter than the surrounding vegetation, the path species being less xeromorphic. Brittle-stemmed species such as _Pteridium aquilinum_ were excluded from the path flora but small forms of _Festuca rubra_ and _Agrostis tenuis_ were present. The association between animal trampling and fertility noted by Thompson (1858) was used by Jeffreys (1917) to account for the presence on paths of _Poa annua_ and _Lolium perenne_. Although Shantz (1917) published an account of the regeneration of vegetation on abandoned roads and Meinecke (1928) carried out an investigation into the effects of trampling on root branching and rootlet production by Redwoods, it was Bates (1934, 1935) who began the systematic study of the effects of trampling.

Using quantitative methods of measuring vegetation and soils, Bates (1935) pointed out that treading had both direct mechanical effects on the vegetation and indirect effects through soil changes; he examined the possibility of different strategies involving either quick colonisation and complete life cycle during a period of low disturbance or vegetative survival of perennials under trampling stress; he set up trampling experiments although he did not record the precise amount of wear applied to the plants, and apparently he was the first to record the process of path formation.

From this pioneer work it is possible to segregate several aspects of trampling and although they are interrelated they are worthy of individual attention as main effects.

Trampling agencies can be divided into three categories on the basis of the mechanisms of damage. They are animal trampling (this is usually associated with grazing effects except in the work of D.B. Edmond), human trampling and the effect of vehicles. Spedding (1971) stated that animals cause damage because of the hooves' sharp cutting edges and a ground pressure which may be as high as 1,600 $g.cm^{-2}$. Bates (1936) noted that the human foot has a twisting action which imposes horizontal as well as vertical forces on the plants; the vertical forces are ca 1,971 $g.cm^{-2}$ (Lull 1959). Harper et al (1961) found a mean vertical pressure of 1,478 $g.cm^{-2}$ and the mean horizontal forces were 21% of the body weight in straight walking and up to 32% when turning.

The vertical pressures under tractors can be as high as 3,520 $g.cm^{-2}$. Cohron (1971) and Reaves & Cooper (1960) have recorded stresses imposed by vehicles to a depth of 113 cm below the soil surface. The horizontal forces of powered vehicles can also cause considerable damage to plants.

Bates (1934) noted that trampling reduced the leaf size of Trifolium repens which in turn reduced root growth which then became limiting. He considered that changes in vegetation were due to the mechanical effects of treading and the puddling of the soil and, that under dry conditions, treading alone produced little change (Bates 1935). Later Bates (1938) argued that the life form of the plant is of primary importance in the survival of path species. This was also the opinion of Gillham (1956) when she stated that trampling was more likely to affect taller plants because of the vulnerability of the meristematic zones. Pearce & Gillmore (1949) found that trampling damaged the leaves of Endymion nonscriptus and they attributed the death of plants to the loss of photosynthetic organs, a view also held by Edmond (1966) who considered burial of leaves an important factor. Gillham (1956) suggested that mechanical damdge by trampling increased the transpiration rate causing desiccation and possibly death.

Trampling alters the dynamic balance between species in a natural community. Bates (1935) believed that trampling had no beneficial action and Gillham (1956) extended this view and suggested that the mechanism of vegetation change operates through a process of selective suppression and that species that thrive under trampling simply take advantage of the removal of competitors. However, Davies (1938) contended that treading was directly advantageous to some species and Edmond (1958) reported increases in dry weight, tiller number and leaf number of Lolium perenne grown in compacted soils. Bayfield (1971) recorded similar increases ~~of these parameters~~ in Phleum pratense in response to low levels of artificial trampling.

Trampling usually occurs in the form of a gradient of intensity and many relatively rare species are associated with the low intensity regions (Westhoff 1967). Van der Maarel (1971) has argued that intermediate levels of trampling increase diversity in a species rich area and decrease it in a poor one, but that the sudden introduction of trampling will at first decrease diversity in any area.

The soil change most commonly found as a result of trampling is an increase of bulk density which is the result of a reduction in pore space. Recorded increases in bulk density include 0.37 $g.cm^{-3}$ in trampled sands (Lutz 1945); 0.33 $g.cm^{-3}$ in a chalk grassland soil (Chappell et al 1971) and 0.68 $g.cm^{-3}$ to a maximum bulk density of 2.05 $g.cm^{-3}$ in a gravelly sandy loam (Dotzenko et al 1967). Arndt & Rose (1966) found an increase of 0.22 $g.cm^{-3}$ after six passages of a tractor on an agricultural soil.

Jeffreys (1917) and Bates (1935) both stated that footpaths were a moister habitat than the surrounds although Gupta (1933) contended that consolidation did not greatly affect the water holding capacity of soil. Lutz (1945) reported an increase of 8.9% (volumetric) in the field capacity of a trampled sandy soil, and Burden (1970) found an increase in the proportion of water filled pores in recently compacted soil. Under low rainfall conditions trampling can create water shortage (Thomas 1960). Dotzenko <u>et al</u> (1967), working with relatively dry soils (below 16% gravimetric), found a negative correlation between moisture content and bulk density. Chappell <u>et al</u> (1971) and Goldsmith <u>et al</u> (1970) both found negative correlations with increased wear, the former giving gravimetric estimations. A possible cause of the differences between these studies may be the fact that water will be squeezed out of a very wet soil. Compaction reduces the amount of water at high moisture levels and increases it volumetrically when the level is low (Warkentin 1971); this may increase the availability of water to plants (Jamison 1953). The difference between gravimetric and volumetric measurement of water contents should also be noted.

There has apparently been very little work on the changes in gas relations of trampled soils although

Bates (1935) attached great importance to the puddling of soils which may inhibit gas exchange and Edmond (1957) noted gleying of trampled soil, suggesting an oxygen shortage. However, work in the agricultural context has shown that smaller pore size will reduce air mass flow and diffusion and that, below a porosity of about 10%, oxygen content of soil air is reduced (Grable & Siemer 1968).

Bates (1935) commented that greater density has an effect on soil temperature and Chappell _et al_ (1971) found that the exposed soil froze to a depth of 4 cm but it was not frozen under deeper vegetation. Specific heat is increased by compaction unless water is expelled; conductivity increases with increasing water up to 12% or 16% (volume) and then decreases (Lowery 1970). Thermal diffusivity depends on the ratio of conductivity to specific heat, but in dry soils it increases with increasing compaction (Willis & Raney 1971) and as a result temperature fluctuations increase.

Jeffreys (1917) and Davies (1938) both suggested that a greater nutrient supply was likely to be available from manure on animal paths and Streeter (1971) found increases in nitrogen and phosphorus correlated with reduced pore space in a recreation area. Compaction can lower the mass flow and the diffusion of nutrients in soil water (Kemperer et al 1971) and the mineralisation of organic matter may be reduced by lower soil oxygen (Whisler et al 1965). Soil penetration resistance rises with compaction but is reduced by increasing water content (Chancellor 1971). The American Society of Agricultural Engineers (1971) have produced an excellent monograph on the 'Compaction of Agricultural Soils' which covers this topic in greater detail.

Soil compaction affects plants differently at different stages of their life cycle. Aeration, light, water content and movement, availability of nutrients and soil temperatures may all affect germination (Mayer & Poljakoff-Mayber 1963). The effects may depend on whether the seed is above or below the soil surface. Germination may, therefore, be inhibited or assisted by soil compaction. Seedling establishment is probably more difficult in compacted soil as a result of reduced mass flow of water, lower oxygen tension in the root zone and increased soil strength. Higher water content will, however, aid root penetration and lower the extreme temperatures at the soil surface (Trouse 1971). Arndt (1965) showed that plants with epigeal cotyledons had to push out a larger cone of compacted soil than monocotyledons and this may have a significant effect on path flora. As the size of the plant increases the mass flow of water and the availability of nutrients and oxygen may become more important. Edmond (1958) found that puddling inhibited growth of short rotation rye grass, whereas compaction alone stimulated production.

There would appear to be two major strategies for the survival of species on paths. The first is that of a short life cycle; these species germinate, establish, grow, flower and set seed at a time when conditions are relatively favourable. Bates (1935) included Polygonum aviculare, Matricaria matricarioides, Coronopus squamatus and Poa annua in this group. The other major strategy depends on an intrinsic resistance to the effects of trampling. In this group are Poa pratensis and Rumex obtusifolius (Bates 1935), Poa annua when it behaves as a perennial (Davies 1938), Lolium perenne and Trifolium repens (Edmond 1964), and unspecified Agrostis and Juncus (LePage 1967). Trifolium repens, however, is probably a member of the first group invading by vegetative means rather than by seed (Bates 1935).

The study of plants on existing pathways must take into account the effects of both mechanical damage and changed soil characteristics. A reduced vegetation biomass has been reported from a trampled area (Randerson 1969) and a negative correlation exists between vegetation height and wear (Goldsmith _et al_ 1970); LaPage (1967) reported that surviving species were usually small. Both Bates (1935) and Jeffreys (1917) noted that smaller forms of species tended to occur on pathways and Lock (1972) found that tussock forming grasses are favoured by grazing and trampling of hippopotamuses. Conduplicate or dissected leaves are resistant to trampling (Bates 1935); Bates (1935) and Edmond (1962) both consider that deep rooting is also an advantage.

Succulence is a characteristic that makes plants vulnerable to damage by trampling (Gillham 1956) and high levels of soil nitrogen can increase the succulence of _Lolium perenne_ causing it to be more readily damaged by trampling (Schothorst 1965). Edmond (1962) found that greater damage was caused by trampling in wet conditions and Wagar (1965) observed that camp grounds were more vulnerable to damage if they had been watered just before use; wet tundra sites are also more readily damaged than dry areas (Bellamy _et al_ 1971).

The position of a path may move laterally over a period of time (Bates 1951, Thomas 1959); this may be the result of the old route becoming impossible (Bayfield 1971a), of being 'lost' under a snow covering (Bates 1951), of gradual solufluction under the trampling pressure (Thomas 1959) or of the avoidance of an obstacle such as badly designed steps (Huxley 1970). This may alter a plant's position on the path and consequently an 'edge' species may exist for a short period in an area subject to high levels of wear and it could be mistaken for a resistant species.

Although Bates (1935) carried out trampling experiments he did not report the level of trampling or the quantity of plants damaged or surviving the treatment. Bayfield (1971a) trampled a _Calluna-Trichophorum_ heath at 650 m above sea level in the Cairngorm, Scotland and found that 240 passages created about 19% bare ground and caused considerable damage to the vegetation, especially to _Sphagnum_ of which 66% was damaged. Morrish & Harrison (1948) carried out a similar experiment with vehicles on plots of sown grasses and clovers; 200 passages with a 1,523 kg car produced an increase of 59% in the area of bare ground. On Canadian tundra a 3,864 kg tracked vehicle could produce 100% damage after 20 passages (Bellamy _et al_ 1971). Edmond (1958, 1962, 1966) carried out trampling trials with sheep and Bayfield (1971a) and Wagar (1964) have experimented with an artificial trampler to standardise the wear applied, while Cieslinski & Wagar (1970) used a corrugated roller, but unfortunately none of these fully reproduces the action of human feet.

A study of the regeneration of trampled vegetation was carried out by Shantz (1917) on abandoned roads in Colorado. He found that annuals such as *Polygonum aviculare* were the first colonisers, being replaced later by perennial species. Bayfield (1971a) found that his experimentally trampled areas regained nearly full cover in three years, although *Sphagnum* and lichens were still in a damaged condition. LaPage (1967) found that the cover of a site newly exposed to trampling was reduced to 55% but as more resistant species spread the cover increased to *ca* 70% at the end of the third year of use.

Studies of positive management of areas of 'natural vegetation' subjected to trampling have been reported from American camping sites. Wagar (1965) found that fertilisers had a most beneficial effect on ground cover and that watering aided the establishment of grasses. Herrington & Beardsley (1970), taking a more agricultural approach, sowed a seed mixture and used water and fertiliser as treatments. There was a positive interaction giving best cover when all treatments were combined. The importance of water may be related to the low annual rainfall (37 cm) and dry summers experienced at the experimental site. Rehabilitation of the compacted soil by the addition of organic matter, tillage or rotation was suggested by Lutz (1945). Lull (1959) has reviewed the crops, including mustard, alfalfa, sweet clover, sericea (Lespedeza cuneata), deep rooted legumes and perennial grasses, that have been used to reduce soil compaction. Even explosives have been used in special cases. Bayfield (1971b) used a mixture of perennial and annual grasses with fertiliser and a soil stabiliser as a nurse crop in the Cairngorm to prevent erosion during the slow recovery of natural vegetation.

The research needs for management of recreation areas have been defined by Brotherton (1972) as the identification of ecological change resulting from the interaction between the way an ecosystem is used and the management methods employed, the development of rapid survey systems for assessing the biological interest of sites, the development of techniques to increase vegetation resistance and recovery from trampling, including the selection of trampling resistant strains, and the management of surrounding areas of vegetation not subject to the direct effect of visitors.

Burden & Randerson (1972), in reviewing the approaches to the study of human trampling, have classified them as either experimental or analytical. Experimental studies can be either long term or short term. Analytical studies involve the study of an area already trampled with the estimation of wear from the condition of the vegetation or soils. Speight (1973) has given a wide ranging reference list in his review of the ecological effects of recreation.

This thesis is presented in the form of five separate papers and a final conclusion. The first two papers contain a survey of selected trampled areas of a sand dune system. Similar quantitative surveys of the effects of trampling on vegetation and soils have been made on chalk grassland (Streeter 1971, Chappell et al, 1971, and Perring 1967), and coastal heath (Goldsmith et al 1970). Sand dune areas are relatively unstable habitats; being aesthetically pleasing and situated on the coast they are subject to increasing recreation pressures; therefore, management data are urgently required. The soils also have the advantage that they are not affected by puddling and compaction effects may be more readily understood.

Paper three is an account of an experiment where known levels of wear are achieved by walking and driving vehicles for short periods of time; the effects of wear and the rate of recovery of the vegetation and soils were measured. By applying wear to previously untrodden vegetation it is possible to identify which members of the 'natural' flora are trampling resistant and, from the recovery data, which species occur on paths by virtue of their quick colonising ability. In this paper a model that defines the physical carrying capacity of the sand dune pasture is presented and the relative vulnerability of some different habitats is also discussed.

Paper four is a record of a study of the effectiveness of various management techniques for vegetation recovery in the sand dune habitat, some of which were tried by Wagar (1965) and Harrington & Beardsley (1970). This work was also carried out with the increasing pressure of recreationalists on this habitat in mind. The aim of management for this type of use involves an attempt to cater for the aesthetic requirements of people visiting these areas and for this reason ecological measures such as species richness and diversity are used as a means by which to assess the effectiveness of the regeneration treatments. This work also allows further study of some of the colonising strategists on paths and tracks.

In paper five the microclimates of some paths and tracks are reported. Previous authors (e.g. Bates 1935, Chappell et al 1971) have commented on the microclimatic effects of path creation but apparently no work has been carried out in the track situation.

The conclusion is in two parts, an ecological discussion of the various investigations and section devoted to the management implications of this work. Since each paper has its own introduction no attempt has been made to provide a complete literature review in this general introduction.

Throughout this introduction the nomenclature has followed that of Clapham, Tutin & Warburg (1962).

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PAPER 1

THE TRACK AND PATH SOILS IN THE ABERFFRAW SAND DUNES

CONTENTS

THE TRACK AND PATH SOILS IN THE ABERFFRAW SAND DUNES

INTRODUCTION

The field work presented in this thesis was carried out at the Aberffraw sand dunes, Anglesey, North Wales. This dune system is 3.2 km long and 1 km wide and is situated with its long axis running north east perpendicular to the coast, 4 km north west of the Newborough Warren National Nature Reserve described in Ranwell (1958). The area is composed of blown sand and the seaward end is exposed to the prevailing south west winds, but Ranwell (1958) considers the area to be relatively stable. The pH of the soil is generally between 7 and 8 and there is a high level of calcium carbonate (Pemadasa 1973). The whole dune system is open to the public who were able to drive vehicles off the roads at many points, and there has been a large increase in paths and tracks between 1960 and 1970 (Figs.1-1a & b).The sides of the landward road (A 4080) have now been banked and lay-bys are placed at about 300 m intervals where it crosses the system; cattle and sheep graze the area throughout the year. The survey and experimental areas were all in slack vegetation.

There have recently been a number of studies of

Fig.1-1

The Aberffraw sand dune system drawn from aerial photographs.

a) 1960 3.2 km of track and 2.2 km of footpaths

b) 1970 11.7 km of track and 16.5 km of footpaths.
(the smaller footpaths have been omitted)

c) 1970 with experimental sites indicated
a-j, n-w survey sites, 1-8 experimental sites

surfaced roads

tracks

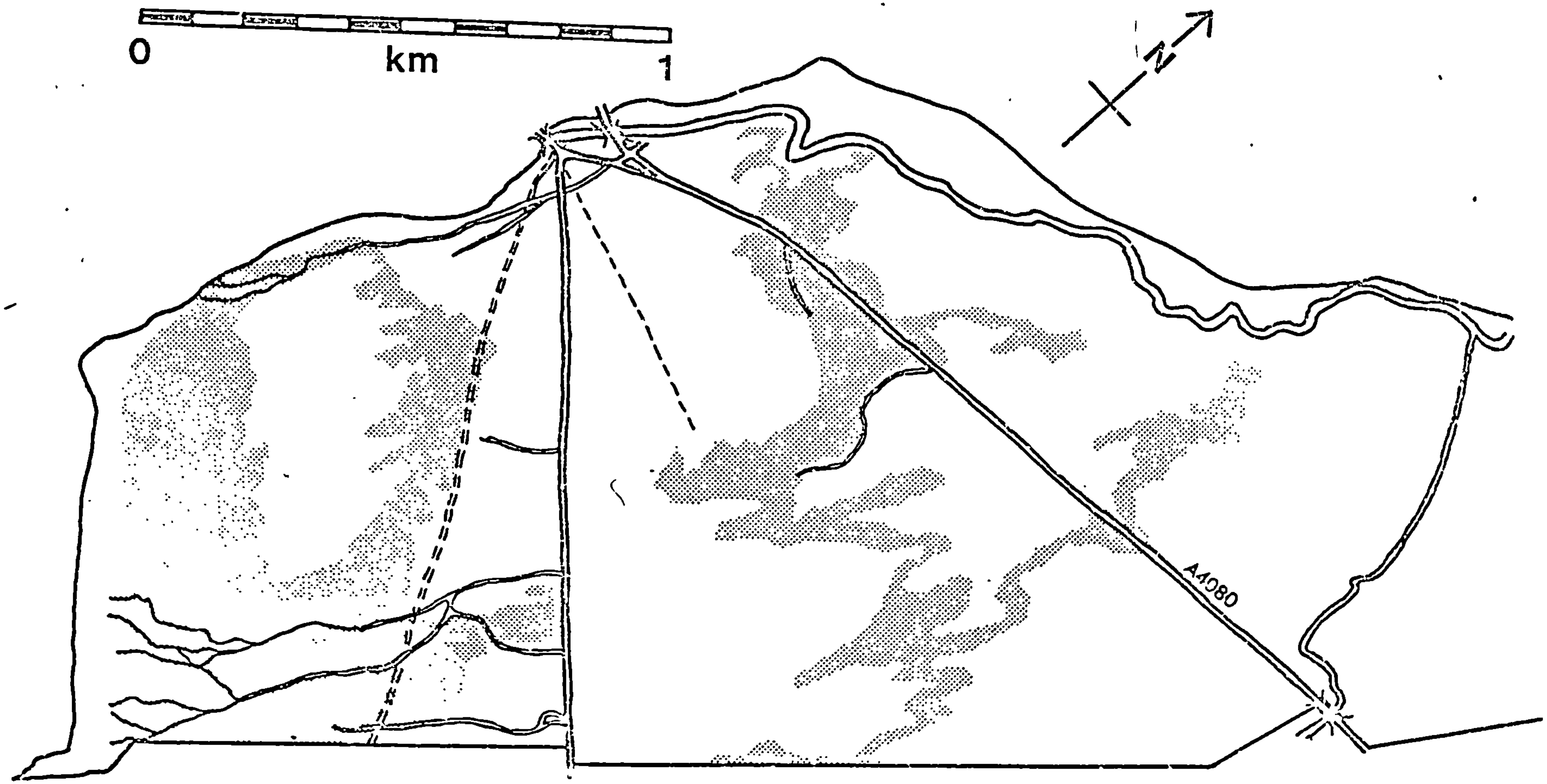
footpaths

disused tracks

disused footpaths

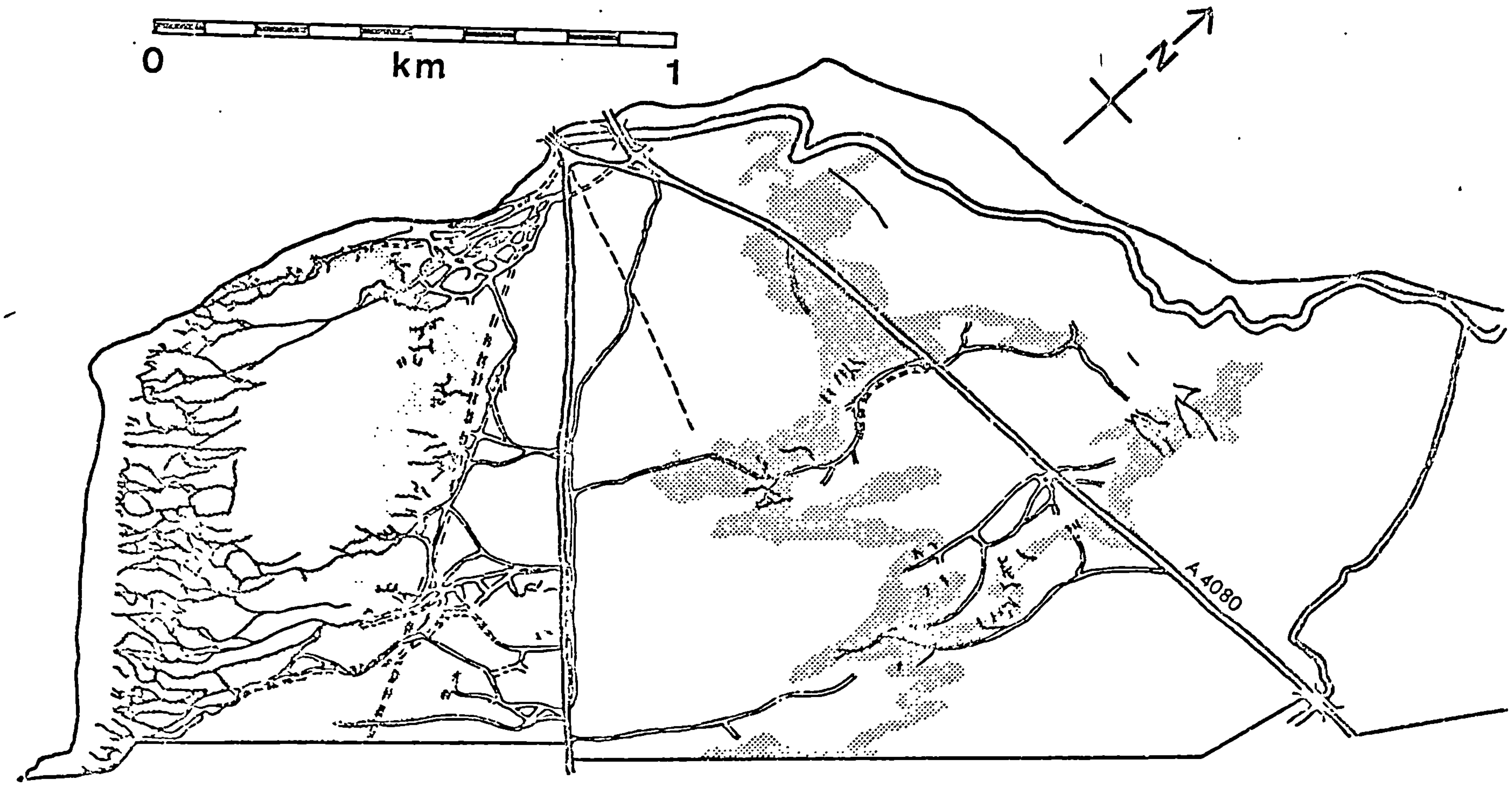
sand dunes

ABERFFRAW 1960



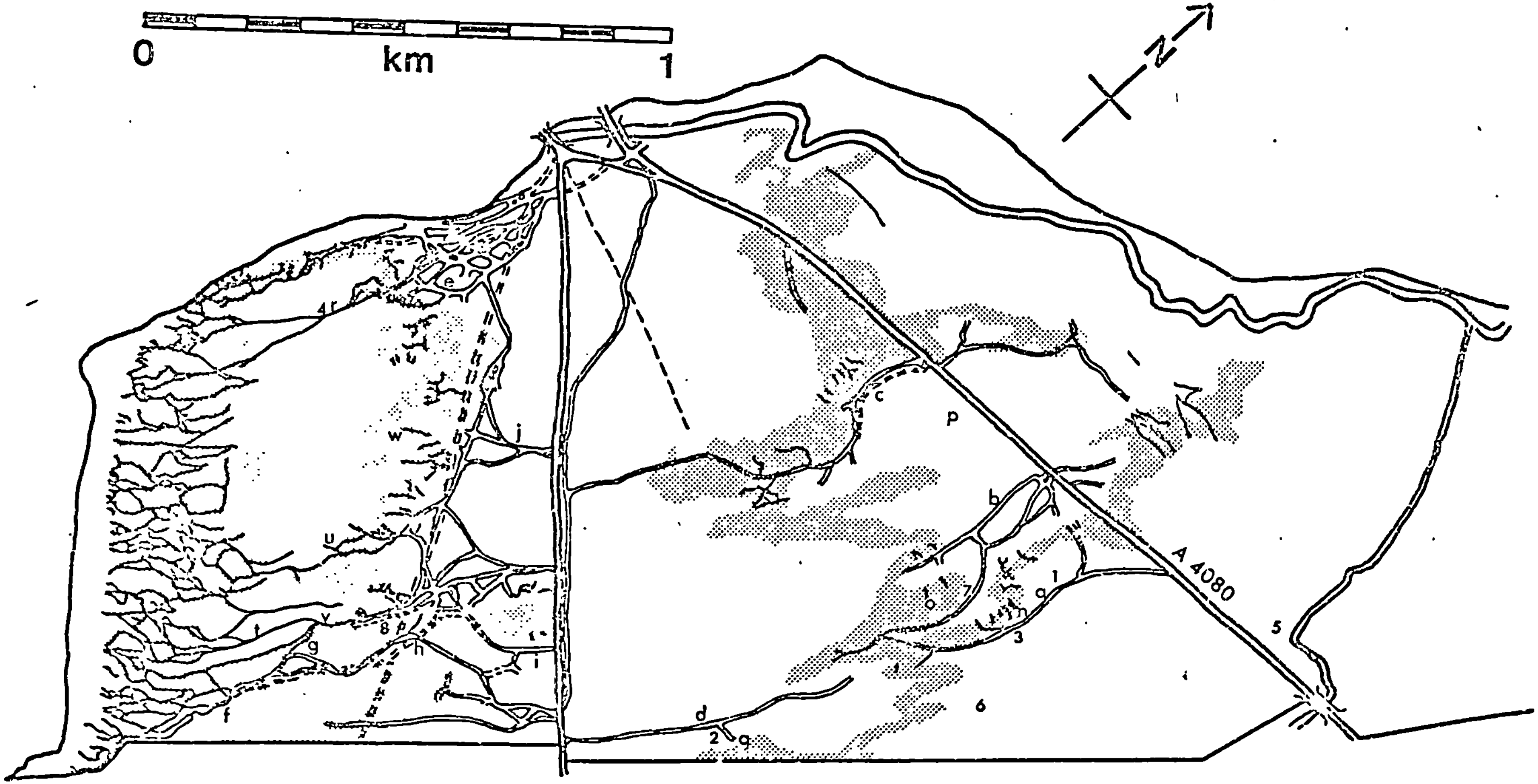
1-1a

ABERFFRAW 1970



1-1b

ABERFFRAW 1970



1 - 1C

the effect of trampling where both soil physical characteristics and vegetation were measured. Streeter (1970) working on chalk grassland found a decrease of porosity in the areas subject to high levels of trampling for a long period of time; a similar effect has also been recorded after a short period of intense use (Burdén 1970). Chappell _et al_ (1971) demonstrated a difference of 0.33 $g.cm^{-3}$ between trampled and unworn areas at depths of 0 to 25 mm in a similar habitat. Working in sands and sandy loam Lutz (1945) found increases in bulk density of 0.37 $g.cm^{-3}$ at depths of 0 to 10 cm; at 10 to 20 cm depths the increase was only 0.18 $g.cm^{-3}$. However, he only gives qualitative comments on the vegetation.

With the exception of that of Burdén (1970) the approaches mentioned above are all measurements of areas subject to an unknown amount of trampling and tending towards an equilibrium with this factor. The areas were subject only to human trampling except that studied by Chappell _et al_ (1971) which was open to vehicles. Arndt & Ross (1966) working with tractors on an agricultural clay loam soil found an increase in bulk density of 0.22 $g.cm^{-3}$ at 5 cm depth after six vehicle passages, but there was no significant change after double this number. They also observed that vehicles tended to pulverise the soil surface. Increases in soil penetration resistance of a maximum of 18 times between used and unused areas were found by La Page (1962) but Freitag (1971) states that the mechanics of penetration tests are not fully understood so the results must be considered empirical. He also comments that 'there has been little standardisation of the size, shape or method of use of penetrometers' so these must be carefully described. However, Tanner & Mamaril (1959) found that bulk density was less sensitive to changes in compaction than soil penetration resistance. The recording of absolute force required for penetration involves the use of a relatively complex instrument in which the speed of penetration is held constant, e.g. Mathieu & Toogood (1958), but Malcolm (1964) successfully used an impact penetrometer to detect hard pans due to ploughing. When an impact penetrometer is used the rate of loading is uncontrolled and the measurements are less sensitive in consequence (Freitag 1971). The impact machines are, however, cheap to construct and quick to use so that readings may be replicated and a very low variance in the data achieved: they are also capable of making readings to a considerable depth.

Soil moisture has been studied in relation to the other effects of compaction. A drop in gravimetric water content from 38.8% to 20.5% in the most worn areas was recorded by Chappell et al (1971) and Goldsmith et al (1970) working in the summer on an acid coastal heath found a negative correlation between wear and soil moisture content. However, Lutz (1945) did not record any changes of water content in compacted Merrimac sands and there was an increase of 8.9% volumetric water content in sandy loams. Burdén (1970) found that there was an increase in the percentage of water filled pores of recently trampled soil. There was no change in gravimetric water content when a clay loam soil was compacted by 0.22 $g.cm^{-3}$ but the volumetric water content increased by 4% (Arndt & Rose 1966). These differences may be partially due to differences between gravimetric and volumetric measurements and in the case of Chappell et al (1971) to the higher soil water content. Packard (1957) considered that moisture properties of soils are only seen correctly on a volume basis and gravimetric comparisons can lead to erroneous conclusions.

A laboratory study showed that a compressed sand will hold more water at suctions of 0.1 to 15 bar than uncompressed sand (Hill & Sumner 1967); this is in the range where it is available to plants (Warkentin 1971). Russell (1937) also suggests that available water depends on amount held per unit volume of soil and states that it is not very dependent on soil texture but may be increased by organic content, especially in light soils. The possible beneficial effects of increased soil water may be offset by inhibition of drainage and consequent lack of oxygen (Grable 1971) and a slower mass flow of water and dissolved nutrients (Kemper et al 1971).

The effects of mechanical damage by trampling may stimulate an increase in plant yield in dry weather (Lambert 1962) and possibly stimulate tillering (Langer 1963) as will a reduction in plant density (Lazenby & Rogers 1962); extreme damage may, however, kill the plants.

Section One of this paper describes the results of a survey of the primary soil characteristics of soil bulk density and penetration resistance of the tracks and paths in the Aberffraw dune system. (Paper Two gives an account of the distribution of the associated vegetation). This is followed by a report of a field experiment to determine the relationship between these characteristics and a known amount of wear.

Section Two considers the secondary effect of compaction on soil water as reflected by the survey and a more detailed examination of soils from a limited area. This is followed by an experiment to discover the effects of compaction on the availability of water to plants.

Finally, an experiment to assess the relative effects of compaction and mechanical damage is described.

GENERAL MATERIALS AND METHODS

Soil sampling. Soil cores were obtained, after surface vegetation had been removed, by driving metal cylinders into the soil; they were 6 cm deep and 7.4 cm in diameter. An anvil was fitted over the top of the cylinders which were driven in until they were level with the soil surface. The cores were extracted by cutting away the soil from around the cylinders and levelling their bases with a knife.

To prevent loss of water before weighing, each core was kept in the cylinder and placed between plastic petri dishes held with elastic bands, and the whole put in a polythene bag sealed with a wire fastener.

Measurement of soil characteristics. The field water content was calculated from the difference in weight between the collected soil immediately after removal from the polythene bag and the oven dry soil. It was expressed as a percentage of the weight of the oven dry soil or percentage volume of the cylinder. The weight of the soil was determined after drying for 48 hours at 105°C and bulk density was expressed as grams of oven dry soil ~~per~~ cm^{-3}.

Penetrometer. Measurement of soil penetration resistance was carried out using an impact penetrometer based on that described in Malcolm (1964). This isillustrated in photo 1-1. The mode of action is similar to that of a pile driver and the distance penetrated at each impact is recorded.

The central rod A (Fig.1-2) is free to travel vertically and passes through the centre of the cylindrical anvil B to which it is welded and the hammer C which can slide freely up and down the central rod. In action, the hammer is lifted by hand to the upper adjustable stop D and allowed to fall on to the anvil; a drop of 10 cm was used throughout this work. The force produced drives the point of the rod G into the ground, the distance penetrated is recorded by rotating the pencil holder E which rests on stop D around the central rod to mark its position on the record sheet F. The shape of the 'point' is shown in photo 1-2.

The penetrometer record Fig.1-3 was analysed in two ways -

A) For comparison with soil characters and site characterisation, the total number of impacts needed to reach a depth of 6 cm were counted. This is the depth of the soil samples used for the other measurements.

B) When the 'profile' was examined the number of impacts to penetrate each successive centimetre or six centimetres was counted.

Photo 1-1

Impact penetrometer showing hammer, anvil and recording mechanism.

Note extendable tripod legs.

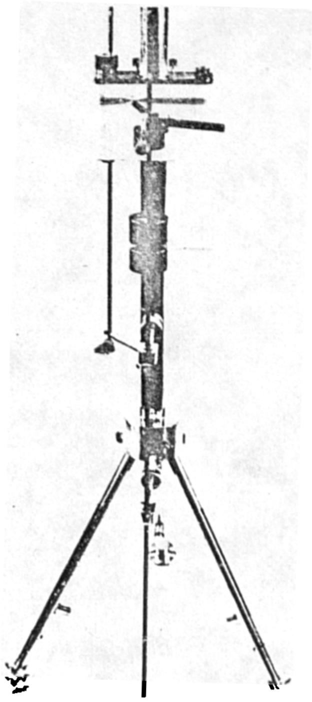


Photo 1-2

Profile of hemi-spherical penetrometer point.

Note that the shaft has reduced diameter to minimise the increase of friction against the soil with greater depths.

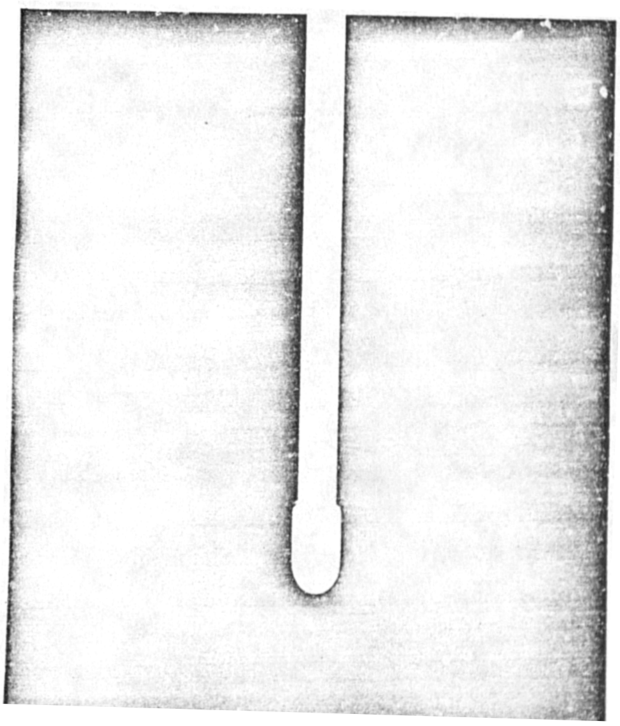


Fig.1-2

Impact penetrometer.

A central rod

B anvil

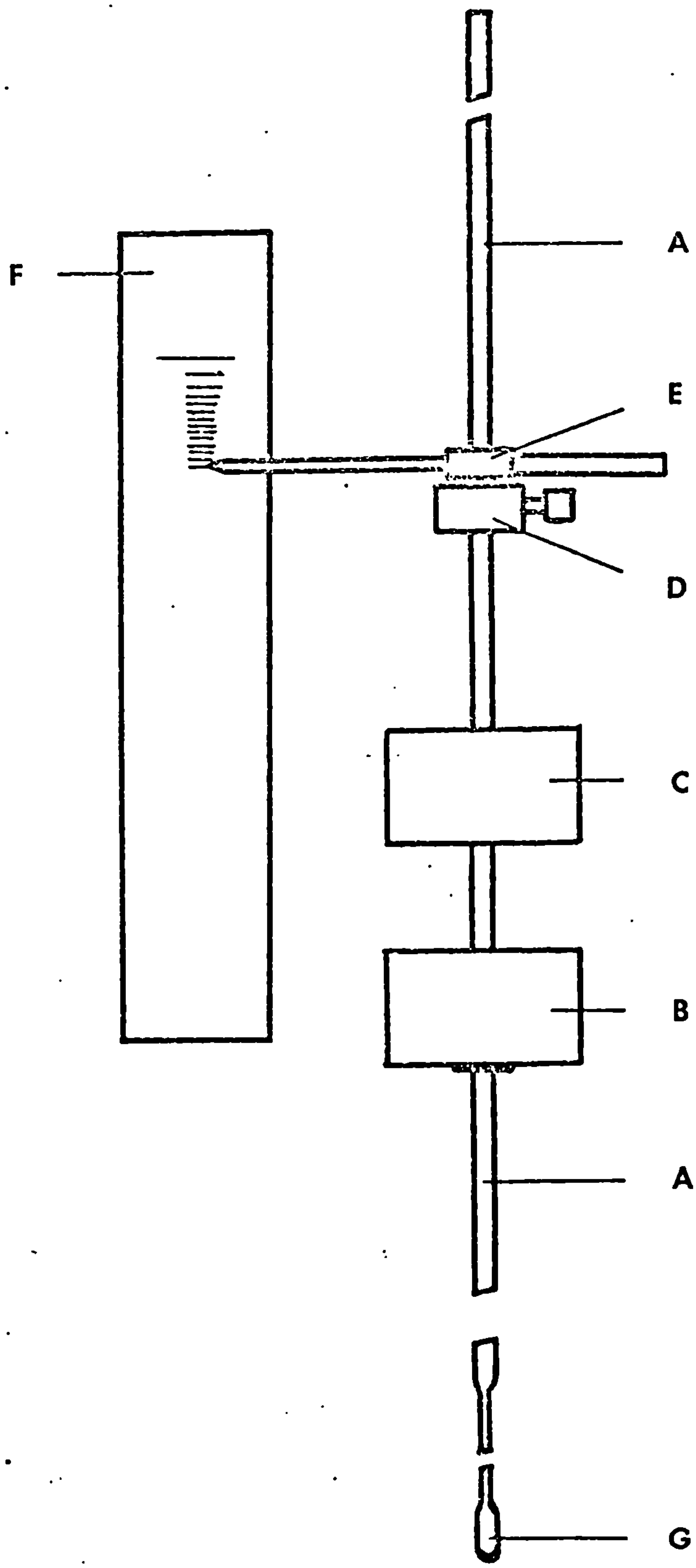
C sliding hammer

D hammer stop

E pencil holder

F record paper

G hemispherical point



1 – 2

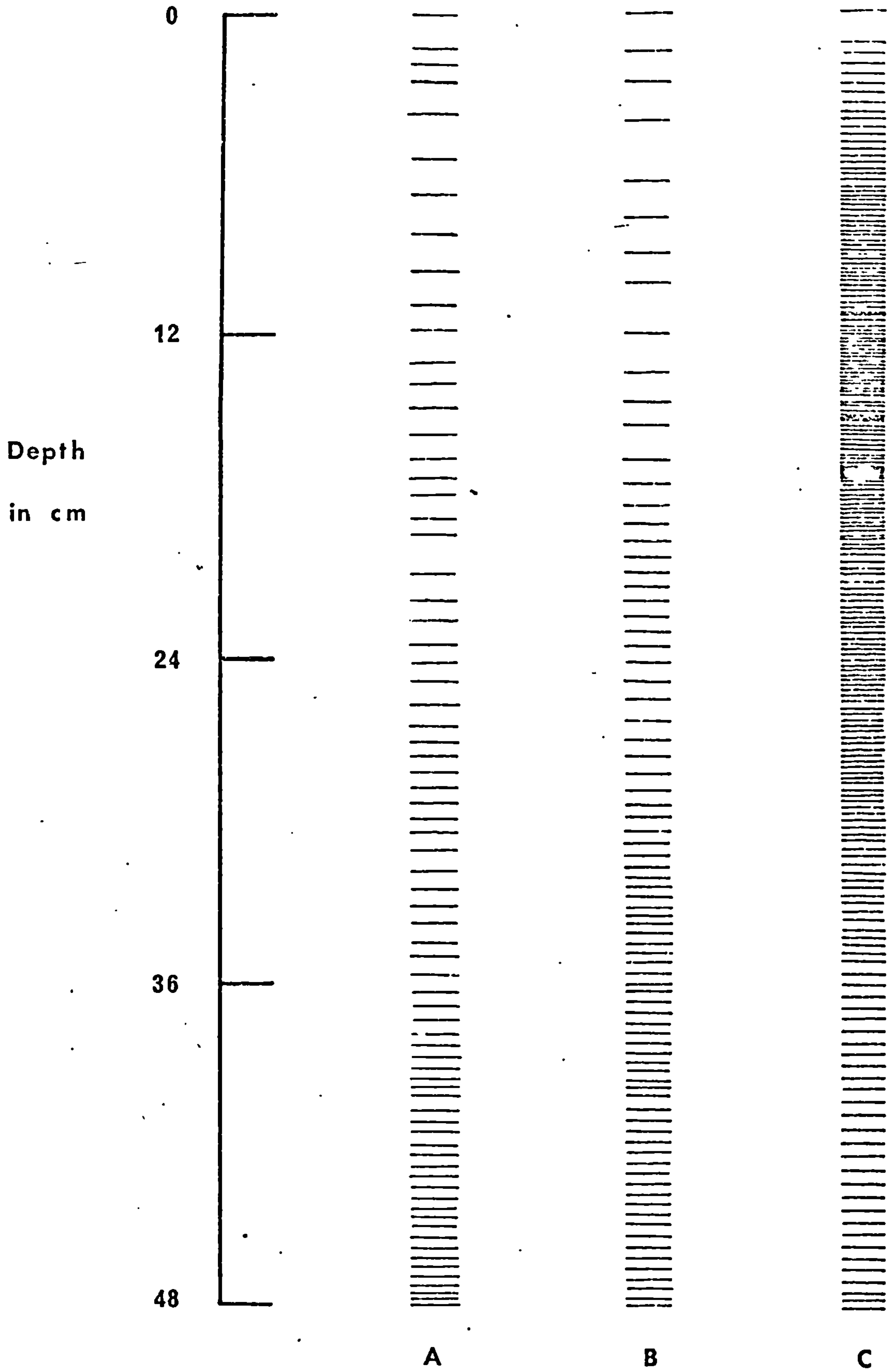
Fig.1-3

Penetrometer records from three points in a transect across a track (transect I, paper 2).

A in undisturbed vegetation

B vegetation undisturbed but some transmitted soil compaction below 36 cm

C vegetation almost absent from wheel track



1 - 3

Location of stands for general survey. Twenty sites were selected, ten on car tracks (coded a to j) and ten on footpaths (coded n to w); these are shown on Fig. 1-1c. Five of each were on dry areas and five on wet areas. The wet areas were selected on the basis of the presence of prostrate *Salix repens* and of *Hydrocotyle vulgaris* (cf. Ranwell 1959). Sites were chosen where relatively large areas of similar 'natural' vegetation occurred on both sides of the track or path.

Three stands were placed at each track site, one on the worn areas (No.1 to 10, 'Group' A), one on part worn picnic areas adjacent to the track, (No.11 to 20, 'Group' B) and one in adjacent 'natural' vegetation (No.21 to 30, 'Group' C). Two stands were used at each path site, one on the path (No.31 to 40, 'Group' D) and one in adjacent natural vegetation (No.41 to 50, 'Group' E). There were, therefore, 50 stands in all. Each stand included an area of one half of a square metre, composed either of one 100 x 50 cm quadrat, or of two 100 x 25 cm quadrats, as the wheel tracks were generally about 25 cm wide.

Penetrometer readings were replicated sixteen times in each stand. The quadrats were sub-divided into 16 areas of 12.5 x 25 cm at each stand and one reading was taken at a random position within each area. The sides of each area were divided into ten units so that the precise position could be determined by the use of pairs of random numbers. Eight soil cores were taken from each stand and the position was determined in the same manner as for the penetrometer readings except that there were eight sample areas each 25 x 25 cm.

SECTION 1

CHANGES IN SOIL BULK DENSITY AND PENETRATION RESISTANCE

MATERIALS AND METHODS

Soil particle analysis. This was carried out on soil samples from six stands, three with a high soil penetration resistance (Nos.12, 14 and 17) and three with a low resistance (Nos.29, 30 and 36). Three dried cores were taken from the original eight collected from each stand, they were passed through a 2,000 μ mesh sieve which separated the root material from the rest of the soil allowing the percentage root content to be calculated. Two hundred grammes of sieved soil from each core were passed through a series of sieves of 1,000 μ, 500 μ, 250 μ, 125 μ, 90 μ and 45 μ mesh sizes. The soils were sieved dry with the three large mesh sieves and washed through the three smaller mesh sieves. The proportion of the 200 g retained by each sieve was weighed and expressed as a percentage of the total; the very little remainder of sizes smaller than 45 μ was not included in Fig.1-6.

The resulting percentage fractions were divided by the log interval between the sieve sizes, i.e. the range of sizes retained by that particular sieve; this was in order to correct for the small range of 35 μ between the 90 μ and 125 μ sieves (see Bagnold 1941 for an account of this method).

The effect of car and foot traffic on soil bulk density and penetration resistance. For this experiment a site was chosen in the dune slack area (Photo 1-3, and 1 on Fig.1-1c) where there was some relict *Ammophila arenaria* and a considerable moss flora. A track 40 feet long was laid out and the car was driven along it in alternate directions. The weight distribution on soft ground was about 950 $g.cm^{-2}$ and 1,500 $g.cm^{-2}$ on hard ground. Soil mensurations were made at each time interval (see Table 1-1a), using 10 centimetre square quadrats, two of which were placed randomly in each wheel track. Four penetrometer readings were taken near the edge of each quadrat, the zero point in each case being the surface of the compressed soil and not its original level. The vegetation was then removed and a soil core obtained. The work was carried out over a period of three days and there was heavy rain after the second day.

For the estimation of the effect of foot traffic a series of stepping areas 10" x 15" were laid out at two foot intervals in two parallel rows 14 feet long. Wear was applied and samples taken at intervals as shown in Table 1-1b. The areas were sampled systematically starting at the west end and centre of the north row and at the east end and centre of the south row. The

Photo 1-3

View from south end of experimental track after 256 runs in the car (site 1, Fig.1-1c). All wear experiments were carried out in similar vegetation.

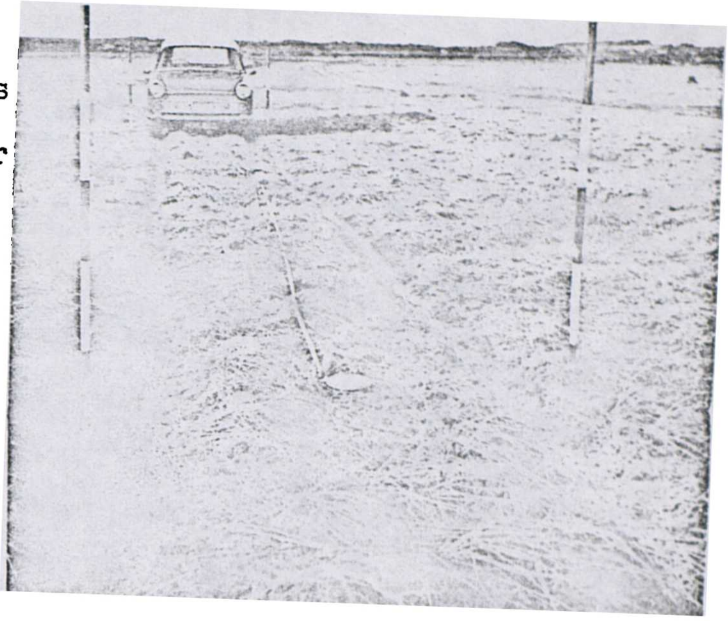


Photo 1-4

Separation of the effects of shoot damage and soil compaction. Pots in position for carrying out damage treatment. Simulated soil 'surface' only in place on right hand steel plate.

Table 1-1a

Sequence of treatments in wear experiment (car)

Direction north or south	Number of runs	No. of runs at which hardness measured and soil cores taken
0	0	0
S	1	1
N	2	3
S	1	4
S	2	+
N	2	8
N	4	
S	4	16
S	8	
N	8	32

From here on 8 runs were taken in alternate directions to reach the numbers shown in the last column.

+
64
128
192 *
256

+ overnight stops

* only hardness measured

Table 1-1b

Sequence of treatments in wear experiment (walking)

Direction east or west	Number of steps on each quadrat	No. of steps at which hardness measured and soil cores taken
0	0	0
E	2	
W	2	4
E	6	
W	6	16
E	10	
W	10	
From here onwards 10 steps were made in alternate directions to reach the numbers shown in the last column. After 256 the total was made by six people all making 30 steps before changing direction		64 + 256 1024

+ overnight stop

10 centimetre square quadrat was placed once in the most worn part of each stepping area and soil penetration resistance was measured and cores extracted as described above. There was no rain during this experiment.

RESULTS AND DISCUSSION

The rapid increase in wear on the dunes is clear from a comparison of the maps, Figs.1-1a and 1-1b. There is no need for further comment on the requirement for information upon which management of these areas can be based.

<u>General Survey. Soil bulk density and penetration resistance</u>. The two direct effects of soil compaction, increase bulk density and soil penetration resistance both showed a marked increase on tracks and paths. (Figs. 1-4a and b). The mean bulk density on tracks (Group A) is 1.34 g.cm^{-3} and in natural vegetation (Group C) it is 1.09 g.cm^{-3}, a statistically significant increase of 0.25 g.cm^{-3}. That of 'picnic' areas subject to wear by cars and other activities (Group B) is 0.17 g.cm^{-3} greater than the adjacent untrampled areas. Footpaths not accessible to cars (Group D) show a rise from 1.11 g.cm^{-3} in natural vegetation (Group E) to 1.28 g.cm^{-3}, an increase of 0.17 g.cm^{-3} (Fig.1-4a). The footpaths are ~~0.15~~ 0.06 g.cm^{-3} less than the tracks. These are all statistically significant differences, and the range of variation is reduced in compact areas. The stand soil data are all presented in Table 1-2.

The soil penetration resistance shows the same trends as bulk density: the increase found on tracks

TABLE 1-2

GENERAL SURVEY SOIL DATA

Stand number	Log penetration resistance		Bulk density $g.cm^{-3}$		Percentage water content	
	Mean	SE	Mean	SE	Gravimetric mean	Volumetric mean
1	1.4636	0.0215	1.365	0.011	9.184	12.45
2	1.4313	0.0083	1.165	0.033	38.843	44.86
3	1.1857	0.0128	1.405	0.009	11.679	16.40
4	1.3084	0.0352	1.327	0.024	13.250	17.45
5	1.1519	0.0162	1.286	0.015	4.244	5.46
6	1.3137	0.0130	1.421	0.011	10.934	15.54
7	1.4725	0.0106	1.180	0.014	34.630	40.86
8	1.2896	0.0133	1.432	0.010	15.086	21.60
9	1.1670	0.0714	1.395	0.009	3.605	5.02
10	1.0436	0.0383	1.421	0.015	9.539	13.56
11	1.3076	0.0784	1.207	0.017	8.786	10.51
12	1.4687	0.0161	1.121	0.029	39.901	44.73
13	1.2405	0.0153	1.343	0.008	4.335	5.86
14	1.5344	0.0324	1.244	0.024	13.241	16.47
15	1.2003	0.0137	1.214	0.012	5.170	6.28
16	1.1023	0.0214	1.368	0.011	11.518	15.64
17	1.4865	0.0087	1.158	0.019	35.972	41.30
18	0.8200	0.0416	1.316	0.015	7.428	9.78
19	1.0157	0.0288	1.228	0.014	3.319	4.10
20	0.9813	0.0430	1.384	0.013	9.434	13.06
21	1.0112	0.0355	1.016	0.019	4.667	4.74
22	1.0520	0.0181	0.868	0.010	54.244	46.54
23	0.7671	0.0348	1.129	0.025	3.679	4.14
24	1.0412	0.0276	1.092	0.032	13.326	14.56
25	0.6293	0.0537	1.121	0.021	3.732	4.18
26	1.2206	0.0183	1.324	0.009	6.966	9.21
27	1.0461	0.0240	0.890	0.020	44.621	39.71
28	1.1686	0.0280	1.159	0.020	12.114	13.92
29	0.3538	0.0862	1.109	0.020	3.159	3.49
30	0.3514	0.0627	1.201	0.020	3.667	4.40
31	1.0330	0.0233	1.262	0.025	8.146	10.27
32	1.2843	0.0165	1.196	0.012	24.698	34.46
33	1.2331	0.0125	1.240	0.017	12.545	15.56
34	1.2351	0.0142	1.214	0.017	12.068	14.64
35	1.2923	0.0124	1.151	0.021	10.790	12.42
36	0.5295	0.0335	1.410	0.015	4.554	6.42
37	1.1784	0.0200	1.161	0.015	8.410	9.76
38	1.3394	0.0197	1.303	0.022	23.166	30.19
39	0.8660	0.0192	1.366	0.012	6.221	8.44
40	1.0320	0.0152	1.324	0.018	12.381	16.39
41	0.6887	0.0355	1.119	0.015	4.286	4.80
42	1.0738	0.0161	1.290	0.021	22.506	29.03
43	1.0881	0.0193	1.134	0.018	7.317	6.32
44	0.7019	0.0453	0.946	0.024	6.514	6.10
45	0.8875	0.0526	0.957	0.030	5.858	5.54
46	0.1721	0.0541	1.304	0.021	6.034	7.87
47	0.9217	0.0333	0.905	0.021	8.884	7.98
48	0.9734	0.0375	1.093	0.020	23.822	25.94
49	-0.0064	0.0531	1.165	0.015	3.256	3.72
50	0.8123	0.0179	1.242	0.012	15.756	19.56

Fig.1-4

Primary physical soil parameters from general survey.

a) Bulk density $g.cm^{-3}$

b) Log of penetrometer impacts (L.P.I.)

A Track stands

B Picnic area stands

C Adjacent 'natural vegetation' stands

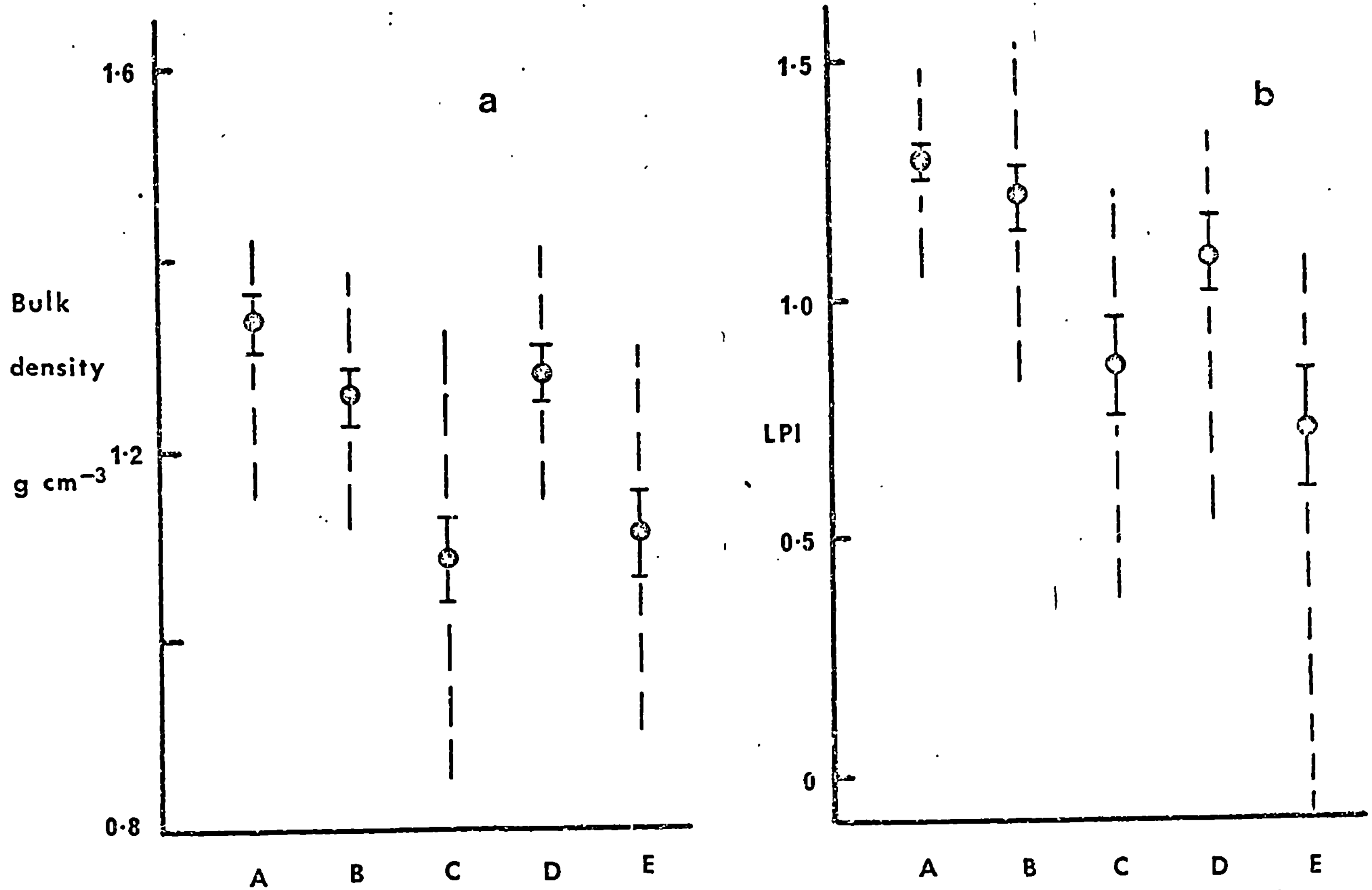
D Footpath stands

E Adjacent 'natural vegetation' stands

Mean

2 standard errors

Range



1 – 4

was 0·43 log penetrometer impacts (L.P.I.) and the increase on footpaths was 0.38 L.P.I. (Fig.1-4b). The difference between footpaths and tracks was 0.19 L.P.I. and these differences are also all statistically significant.

The increase in bulk density of 0.25 $g.cm^{-3}$ caused by the presence of tracks at Aberffraw is less than the increase of 0.36 $g.cm^{-3}$ reported in Lutz (1945) on a sandy soil, but there is not a statistically significant difference between his highest records and those presented here. The difference between the lowest records each including one standard error is only 0.02 $g.cm^{-3}$, so the degree of compaction can, therefore, be considered essentially the same. Chappell et al (1971) found a similar degree of compaction on a clay loam over chalk but his densities of 0.68 $g.cm^{-3}$ to 1.02 $g.cm^{-3}$ were lower than the sandy soils. The reason may be that their soils were sampled in November whereas the Aberffraw samples were taken in June and July when the area was subject to intense use; both areas were open to vehicles and Aberffraw was also grazed by cattle and sheep. Arndt & Rose (1966) found that the surface layer was pulverised by vehicles on clay loam; at Aberffraw the dry areas had a loose surface but there was a crust on the tracks and paths in the wet slacks.

The increase of 18 times soil penetration resistance found by LaPage (1962) in trampled areas was much greater than that recorded here where the mean sand dune compaction was only 2.6 times the uncompacted area. However, he may have chosen the extreme situations which compare with the greatest difference found in the sand dunes of 37 times (L.P.I. of -0.10 to 1.47).

To understand the effects of these soil changes on the vegetation it is necessary to examine their interrelationships. The mean of the group bulk densities and soil penetrability show that the footpaths (E) and their associated vegetation (D) are uniformly displaced from groups B and A (Fig.1-5). Soil samples from three stands in group B and two from E and one from D together were analysed for mechanical properties. They had a mean difference in penetration resistance of 1.18 L.P.I. and a difference of only 0.11 $g.cm^{-3}$ in bulk density (Fig.1-5). The mean root content and particle size distribution of these samples (Fig.1-6) show that the stands with a high L.P.I. had almost one and a half times the amount of plant root over 2 mm and that the particle sizes were slightly more evenly distributed, i.e. the soil was poorly graded in the low L.P.I. stands (cf. Harris 1971 for terminology). The mean particle size corresponds with that of the lee slope of an

Fig.1-5

Relationship between bulk density and L.P.I. of grouped survey stands.

a) Bulk density g.cm^{-3} X axis

b) Log of penetrometer impacts (L.P.I.) Y axis

A Track stands

B Picnic area stands

C Adjacent 'natural vegetation' stands

D Footpath stands

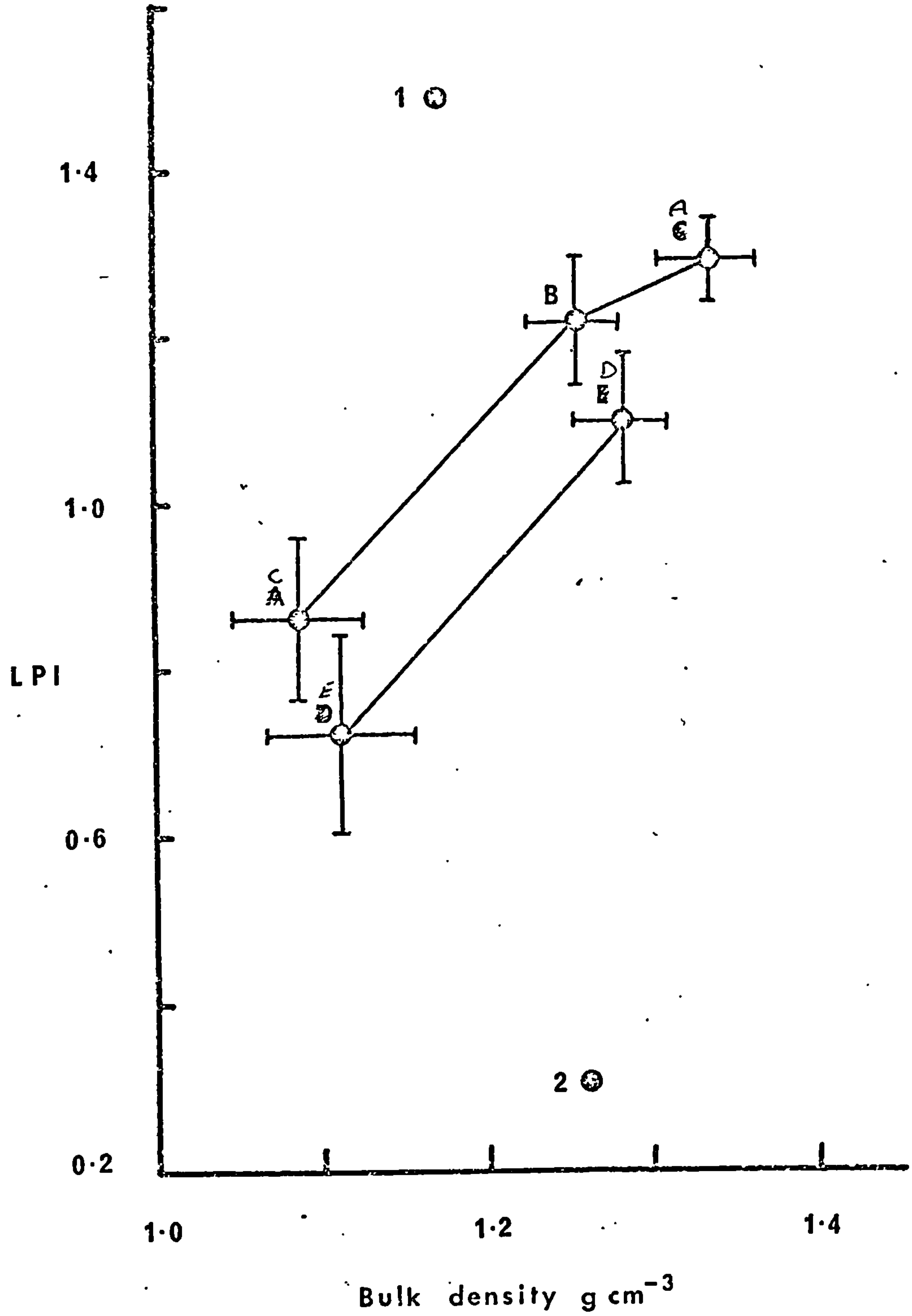
E Adjacent 'natural vegetation' stands

⊖ Mean

2 standard errors

Range

Point 1 is the mean position of high L.P.I. stands and point 2 is the mean position of low L.P.I. stands analysed for root content and mechanical composition of soil.

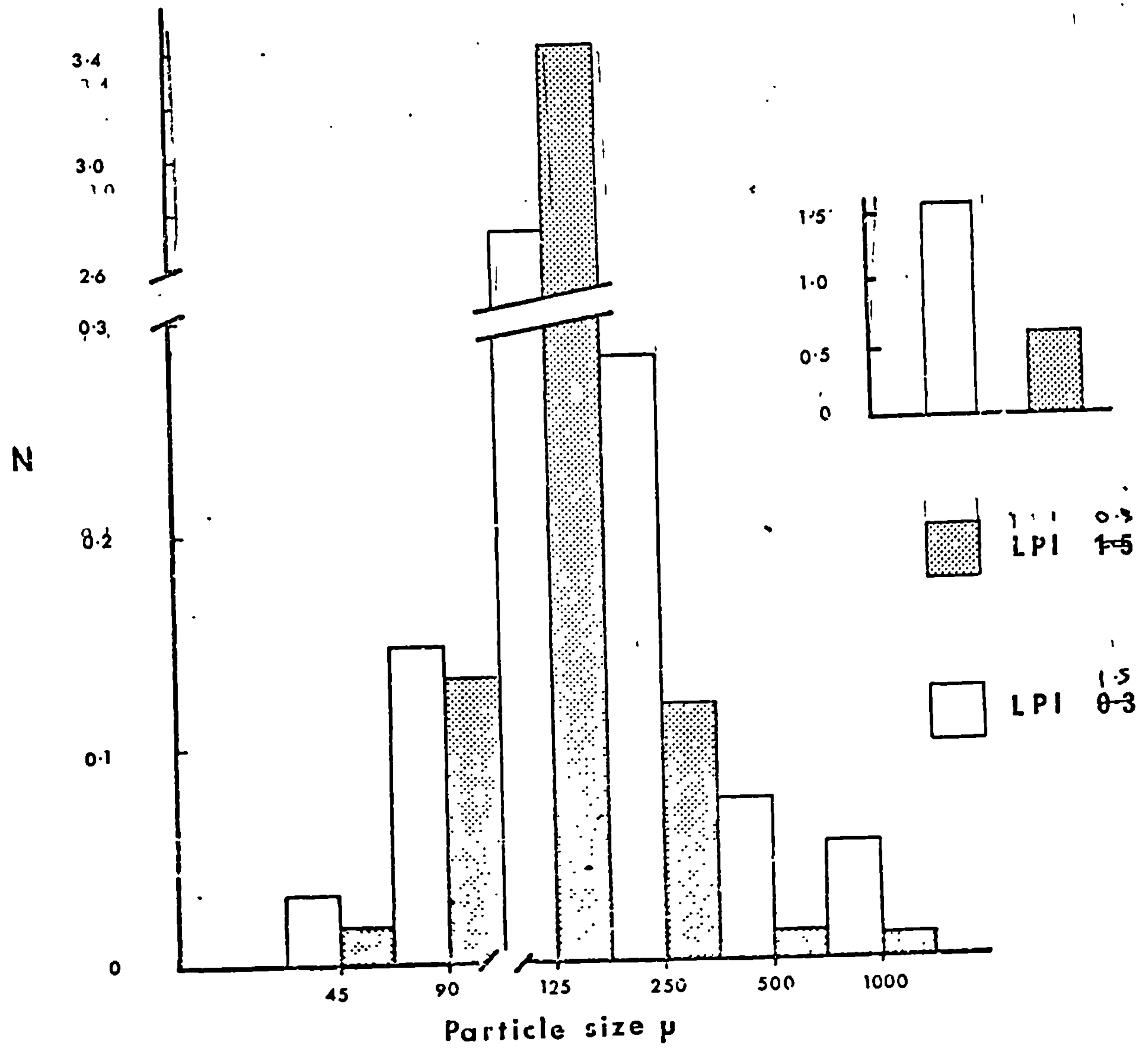


1 – 5

Fig.1-6

Mechanical composition and root content of high and low L.P.I. stands. See text, page 34, for explanation.

$$N = \frac{\%\ \text{weight of fraction}}{\text{Log sieve size interval}}$$


N
3·4
3·0
2·6
0·3
0·2
0·1
0
45
90
125
250
500
1000
Particle size μ
1·5
1·0
0·5
0
LPI 1·5
LPI 0·3

1–6

Ammophila dune at Braunton Burrows (Willis *et al* 1959).

The high L.P.I. samples were all from dry areas that had been subject to wear by vehicles and the low L.P.I. samples were all from wet stands that had not been exposed to this treatment. Harris (1971) states that poor grading leads to lower resistance to sheer-induced motion of soil particles and Freitag (1971) gives data showing that penetration resistance decreases as water content rises. The higher L.P.I. could, therefore, be due to higher root content, better graded soil or lower levels of soil water. However, this explanation needs to be treated with caution as readings from wet and dry portions of another track showed the reverse of the expected relationship with L.P.I.s of 1.43 and 1.25 respectively, while the bulk densities were 1.21 $g.cm^{-3}$ and 1.41 $g.cm^{-3}$.

The fact that the higher root content and better grading, which increases capillary water content, are also associated with wear by cars suggests that vehicles may have a beneficial effect on plants at low levels of use in these dry soils. The soil water content is, however, also significantly higher on footpaths which do not show this particle size distribution effect.

<u>The effect of car and foot traffic on soil bulk density and penetration resistance</u>. The results of these experiments show that both soil bulk density and penetration resistance are directly related to the amount of traffic when this occurs over a short time period. (Figs.1-7a, b, c and d). Bulk density has a straight line relationship with the log of the traffic intensity (R^2 = 0.91 (car), R^2 = 0.86 (foot), $P < 0.01$ (Figs.1-7a and b)); the increase for 256 passages was 0.2 $g.cm^{-3}$ as a result of wear by both car and walkers. The log of penetrometer impacts also has a straight line relationship with the log of number of car passages (Fig.1-7c) and log number of steps (Fig.1-7d) (R^2 = 0.93 (car), R^2 = 0.95 (foot), $P < 0.01$). The increase for 256 passages was 0.6 L.P.I. as a result of wear by car and 0.42 L.P.I. as a result of walkers. Judged on the basis of the correlations the penetrometer is slightly more efficient as an instrument for measuring wear and the standard errors of L.P.I. at each intensity are relatively smaller than those of bulk density.

The degree of soil compaction varies with depth. The uncompacted soils were slightly more penetration resistant in the upper 2 cm than in the next 2 cm (Figs. 1-8a and b). This is in contrast to the findings of Chappell *et al* (1971) where their uncompacted area had

Fig.1-7

The relationship between number of passages by car and walking and the changes in soil bulk density and L.P.I.

a) Number of passages in car and changes in soil bulk density

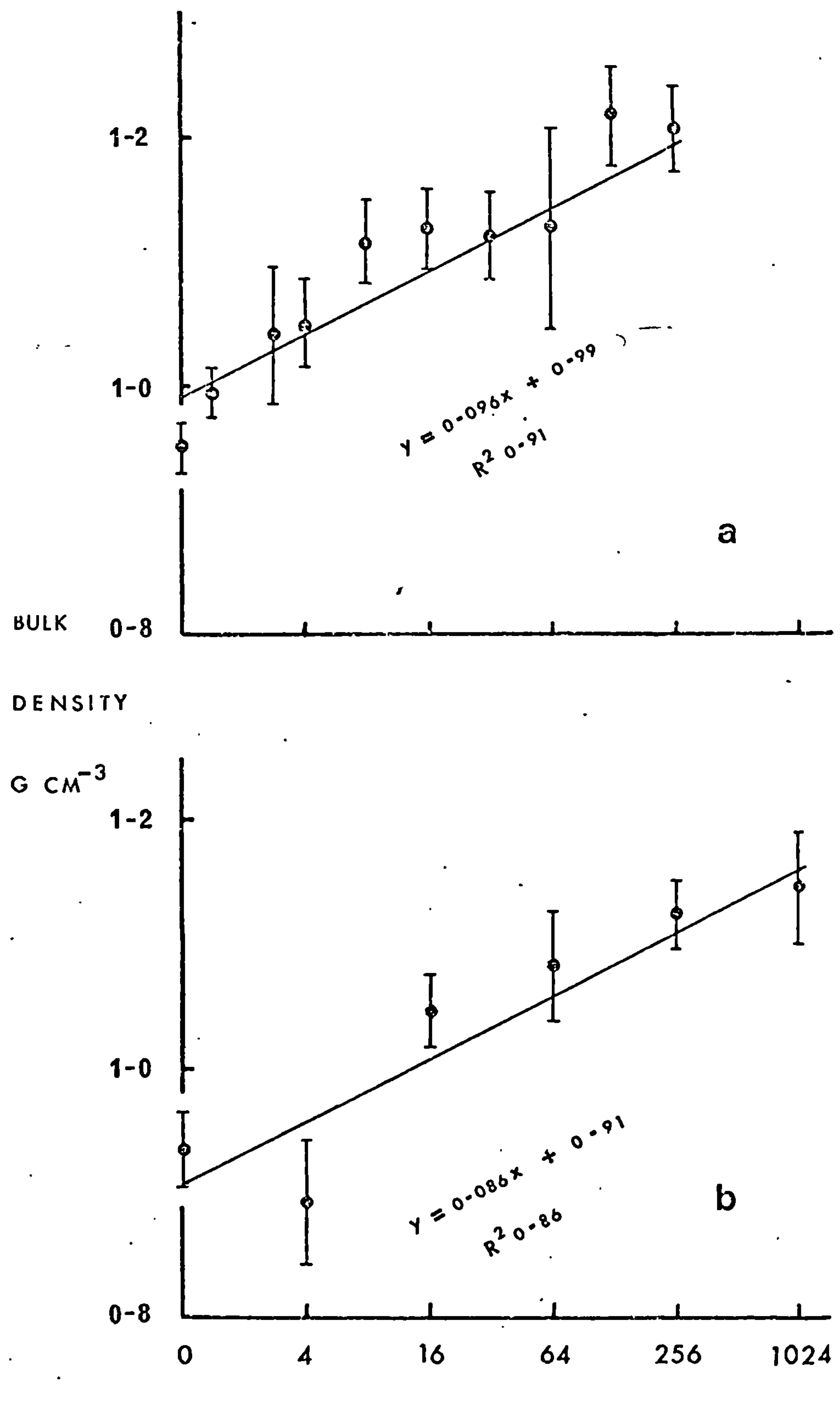
b) Number of passages walking and changes in soil bulk density

c) Number of passages in car and changes in L.P.I.

d) Number of passages walking and changes in L.P.I.

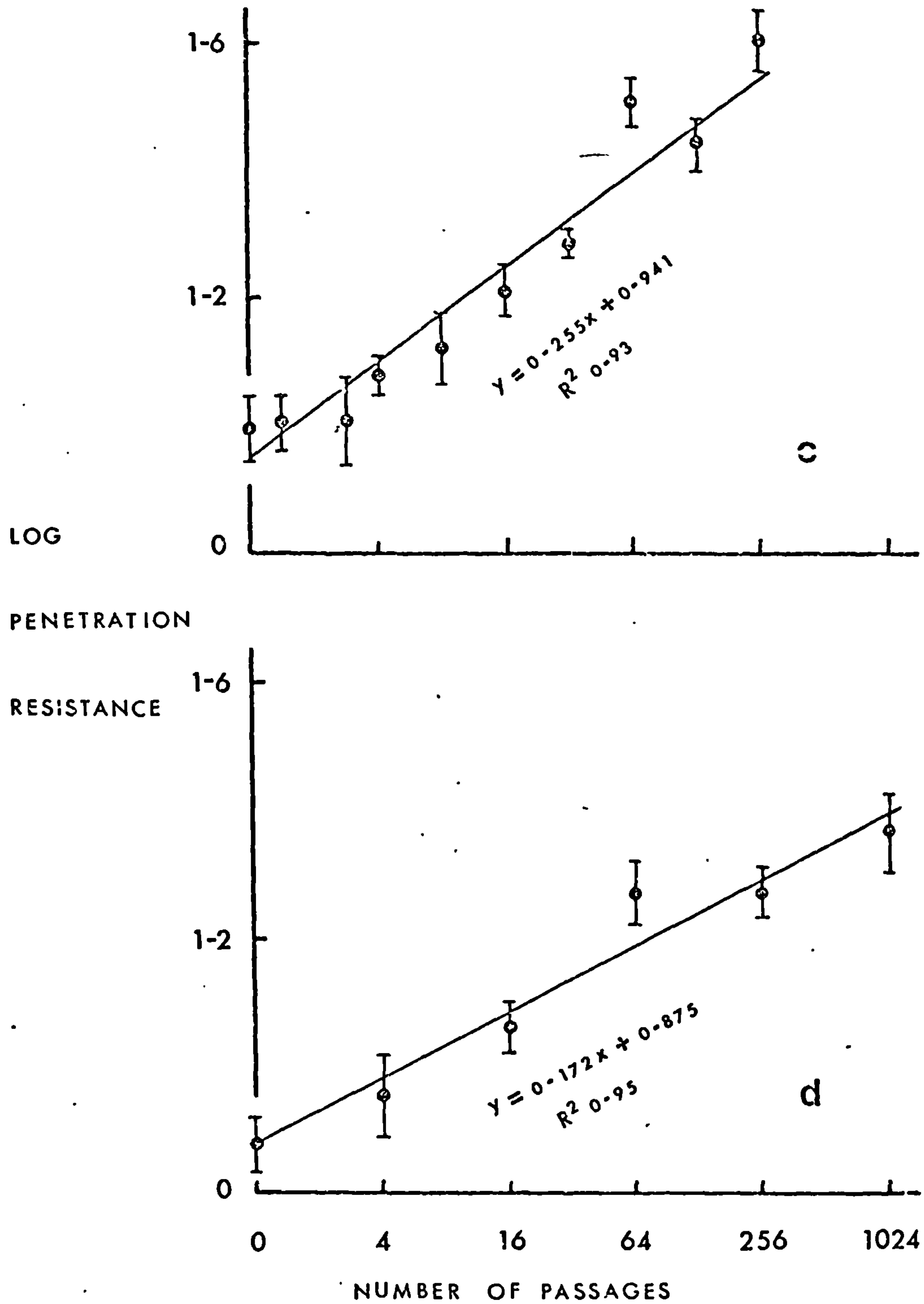
⊙ Mean

I 2 standard errors



1-2
1-0
Y = 0-096x + 0-99
R2 0-91
a
BULK 0-8
DENSITY
G CM-3
1-2
1-0
Y = 0-086x + 0-91
R2 0-86
b
0-8
0
4
16
64
256
1024

1 -7



LOG PENETRATION RESISTANCE
1-6
1-2
0
Y = 0-255x + 0-941
R² 0-93
c
1-6
1-2
0
Y = 0-172x + 0-875
R² 0-95
d
0
4
16
64
256
1024
NUMBER OF PASSAGES

a lower bulk density in the upper two layers. However, the compacted soils at the worn sites used by Chappell _et al_ (1971) and at Aberffraw were both more compressed in the upper layers. This evidence suggests that the grazing animals may have partially compacted the 'untrampled' Aberffraw soils.

The soils subject to wear by car have their most resistant layer in the first centimetre, Fig.1-8a, whereas the trampled sites have the most resistant layer in the second centimetre, Fig.1-8b. This suggests that the car has compacted the surface vegetation into the soil and formed a crust, whereas the screwing action of human feet has displaced the broken vegetation (cf. Harper _et al_ 1961 and Davies 1938). The car has also caused a 4.5 cm depression below the original surface, photo 1-6. A maximum compaction layer was found at 10 cm depth by Arndt & Rose (1966) and Lutz (1945) reported that bulk density in the 10 to 20 cm layer was greater than in the surface 10 cm. This suggests that the profiles shown here are atypical as a result of wear occurring over a short period of time.

The relationship between the effect of cars and walkers requires quantitative definition for management purposes. The various parameters in this experiment must, therefore, be adjusted in terms of the number of

Fig.1-8

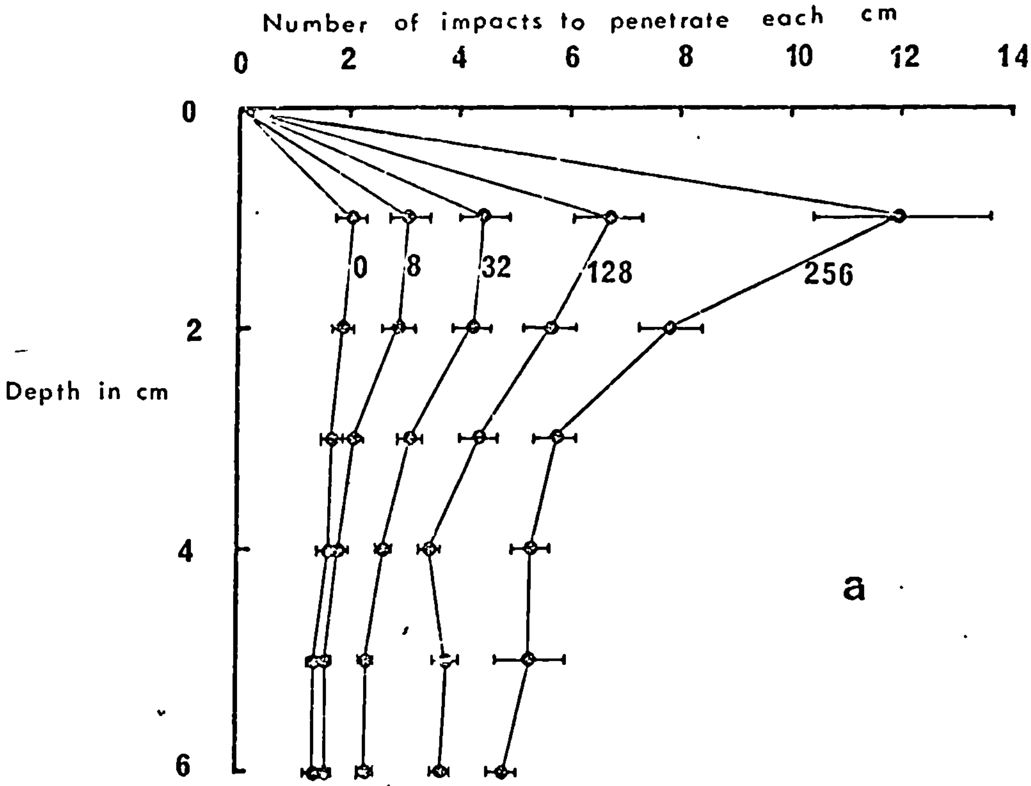
Soil penetration resistance for each centimetre depth to 6 cm.

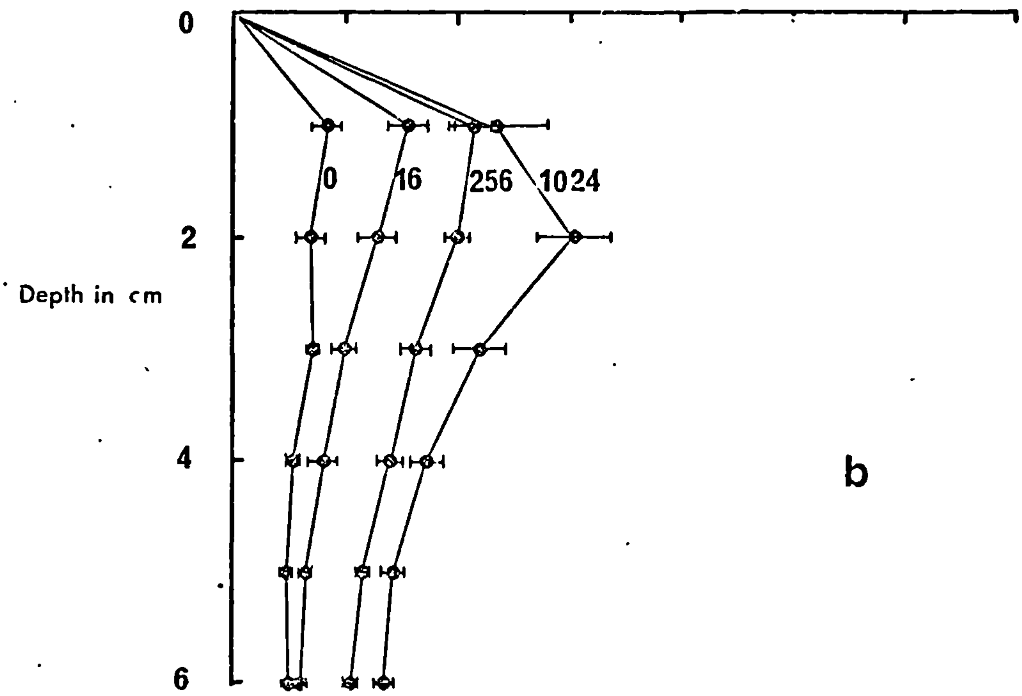
a) After increasing number of passages in car

b) After increasing number of 'steps'

● mean

|——| 2 standard errors


Number of impacts to penetrate each cm
0
2
4
6
8
10
12
14
Depth in cm
0
2
4
6
0
8
32
128
256
a


Depth in cm
0
2
4
6
0
16
256
1024
b

people either walking or in a car as this is the unit required for control of wear. In this experiment the car used was heavier than average (1,282 kg including the driver) but it only contained one person. Data in Patmore (1970) (p.116-118) provides an average of 2.89 to 2.99 people per car when visiting rural beauty spots. The heavy car and one driver is, therefore, approximately the same weight as the average 'holiday' car with three passengers and will be considered as such in this comparison.

The area of ground trodden in this experiment was approximately 12% of a normal 450 mm wide single file path (Huxley 1970) and the 125 mm wide car rut was about 50% of the 250 mm width of a normal straight wheel track measured in the same area. In order to adjust the results of this experiment to a more natural distribution the effects of human trampling should, therefore, be divided by 8.5 and those of the car by 2.

The measured increase of bulk density for the same number of passages was 0.2 $g.cm^{-3}$ in both cases. Bringing all these factors together -

	Measured $g.cm^{-3}$		Correction for No. of people		Area correction		Corrected B.D.
Walking	0.2	÷	1	x	0.12	=	0.023
Car	0.2	÷	3	x	0.5	=	0.033

And for L.P.I.

	Measured L.P.I.						Corrected L.P.I.
Walking	0.42	÷	1	x	0.12	=	0.05
Car	0.6	÷	3	x	0.4	=	0.08

Cars cause a 30% greater increase in bulk density and L.P.I. than is caused by walkers and the area damaged by cars will be much greater especially at the corners of tracks and in picnic areas. Finally, observation suggests that the organic soil crust is rarely destroyed by walkers but is frequently broken on car tracks in dune slack areas.

SECTION 2

CHANGES IN SOIL MOISTURE AND OTHER PARAMETERS

MATERIALS AND METHODS

General survey. The materials and methods are described in Section One.

The relationships between soil factors. Samples for this survey were collected from the track at site 1 and the track and footpath at site 2 (Fig.1-1c) at the end of December 1969. The quadrats were placed randomly on transects in the part-worn and unworn areas, but on the tracks and footpath the most worn parts were selected. Soil penetration resistance was measured and cores obtained in the manner described for the previous experiment.

To measure the water content of the saturated cores the bases were covered with muslin and a filter paper and allowed to equilibrate overnight in one inch of water. They were then weighed and water content taken as the difference from oven-dry soil. The pore space was determined and expressed in the same way except that the water was level with the top of the cylinder. The field capacity was calculated from the water content of the soil cores after saturation and draining for an arbitrary period of 48 hours.

The root content was measured by drying the soil at room temperature for eight days and sieving through a 2 mm sieve: the material that did not pass through the sieve consisted of roots and was devoid of stones. This was expressed as a percentage of total air dry weight of soil and roots.

The effect of soil compaction on survival during drought.

The experiment was carried out in 6" pots with a soil of 2 parts by volume acid washed silica sand and one part John Innes No.1 Compost. Half the pots had their soil compressed before, the seed was sown and the plant used was *Festuca rubra*, 'Danish Red Fescue'. Five blocks were arranged randomly on the bench, each with five pairs of pots, one compressed and one uncompressed in each pair; the bulk densities were 1.36 $g.cm^{-3}$ SE 0.02 and 1.08 $g.cm^{-3}$ SE 0.02 respectively. Ten plants in each pot were allowed to establish for 42 days. The soils were completely saturated on the last day and weighed and transferred to a dry capillary table, under a polythene 'cloche' and no further water applied. The temperature averaged about 17°C. and the relative humidity fluctuated between 55% and 75% for the duration of the wilting period.

One pair of pots taken randomly from each block was removed from the cloche and watered at 0, 15, 20, 25 and 30 days. They were all harvested one week after the end of the 30 day period. The tiller number per plant was recorded and the plant material sorted into dead and live fractions and fresh and dry weights were determined. The soils were weighed and dried and weighed again so that initial and final water content could be calculated. The means and standard errors of the various parameters were calculated separately for each wilting period.

RESULTS AND DISCUSSION

General survey, soil water measurements. There is no statistically significant difference between the volumetric or gravimetric water content of the five groups of stands. Fig.1-9a and Table 1-3 respectively. However, when these groups were sub-divided into wet and dry stands on the basis of the field assessment significant differences were found. The dry track and path stands had higher water contents than the adjacent undisturbed areas, 6.4% and 4.5% volumetric or 3.9% and 3.1% gravimetric respectively (Fig.1-9b and Table 1-3). This is similar to the report by Packard (1957) that Taupo Pumice soils with very low bulk densities of 0.36 $g.cm^{-3}$ improved their moisture properties when compacted to 1.23 $g.cm^{-3}$ under pasture. There were no significant differences between any of the wet stand groups (Fig.1-9c and Table 1-3). If the mean of the gravimetric water content of the two wettest track stands, 36.7%, is compared with that of the adjacent areas, 49.4%, then it can be said that the very wet track soils hold 12.7% less water. (Table 1-2 Nos.2 and 7 and 22 and 27). However, the volumetric comparison (44.9 and 43.1%) reverses this relationship.

Lutz (1945) found no significant increase of volumetric water content in his sands but the compacted sandy

Fig.1-9

Volumetric water content of groups of stands

a) Means of all stands in each group

b) Means of five dry stands in each group

c) Means of five wet stands in each group

A Track stands

B Picnic area stands

C Adjacent 'natural vegetation' stands

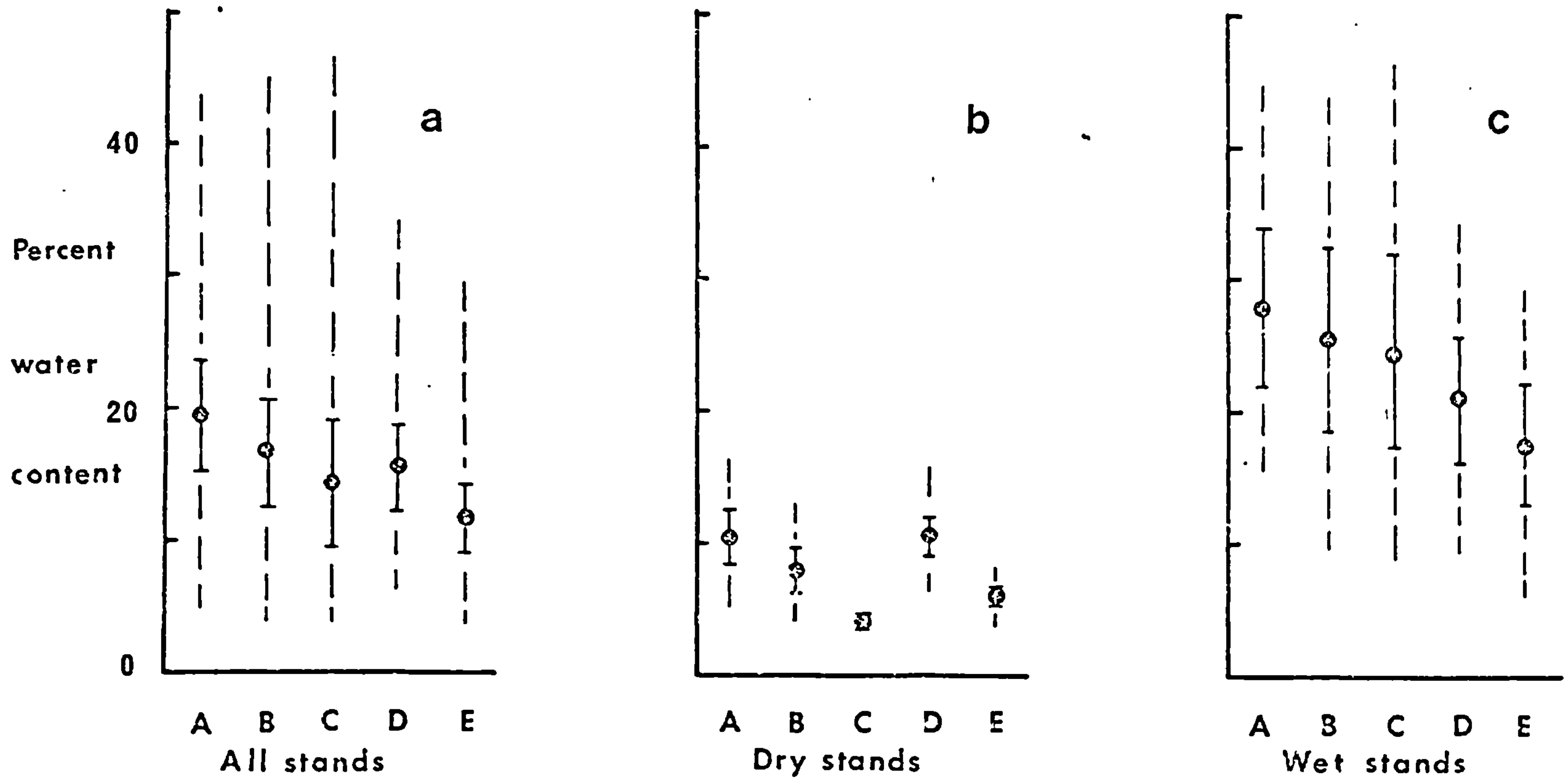
D Footpath stands

E Adjacent 'natural vegetation' stands

⊙ Mean

2 standard errors

Range



a
b
c
Percent
water
content
40
20
0
A B C D E
All stands
A B C D E
Dry stands
A B C D E
Wet stands

1 – 9

Table 1-3

Gravimetric soil water content (%)

		$\bar{x}$	S.E.
All Stands			
	A	15.10	3.79
	B	13.92	4.13
	C	15.02	5.89
	D	12.30	2.12
	E	10.42	2.38
Dry Stands			
	A	7.65	1.58
	B	6.22	1.22
	C	3.78	0.25
	D	8.45	1.46
	E	5.35	0.71
Wet Stands			
	A	22.55	5.87
	B	21.61	6.76
	C	26.25	9.64
	D	16.14	3.26
	E	15.49	3.49

Fig.1-10

Relationship between the bulk densities and L.P.I. of wet and dry stands in each group.

a) Bulk density $g.cm^{-3}$

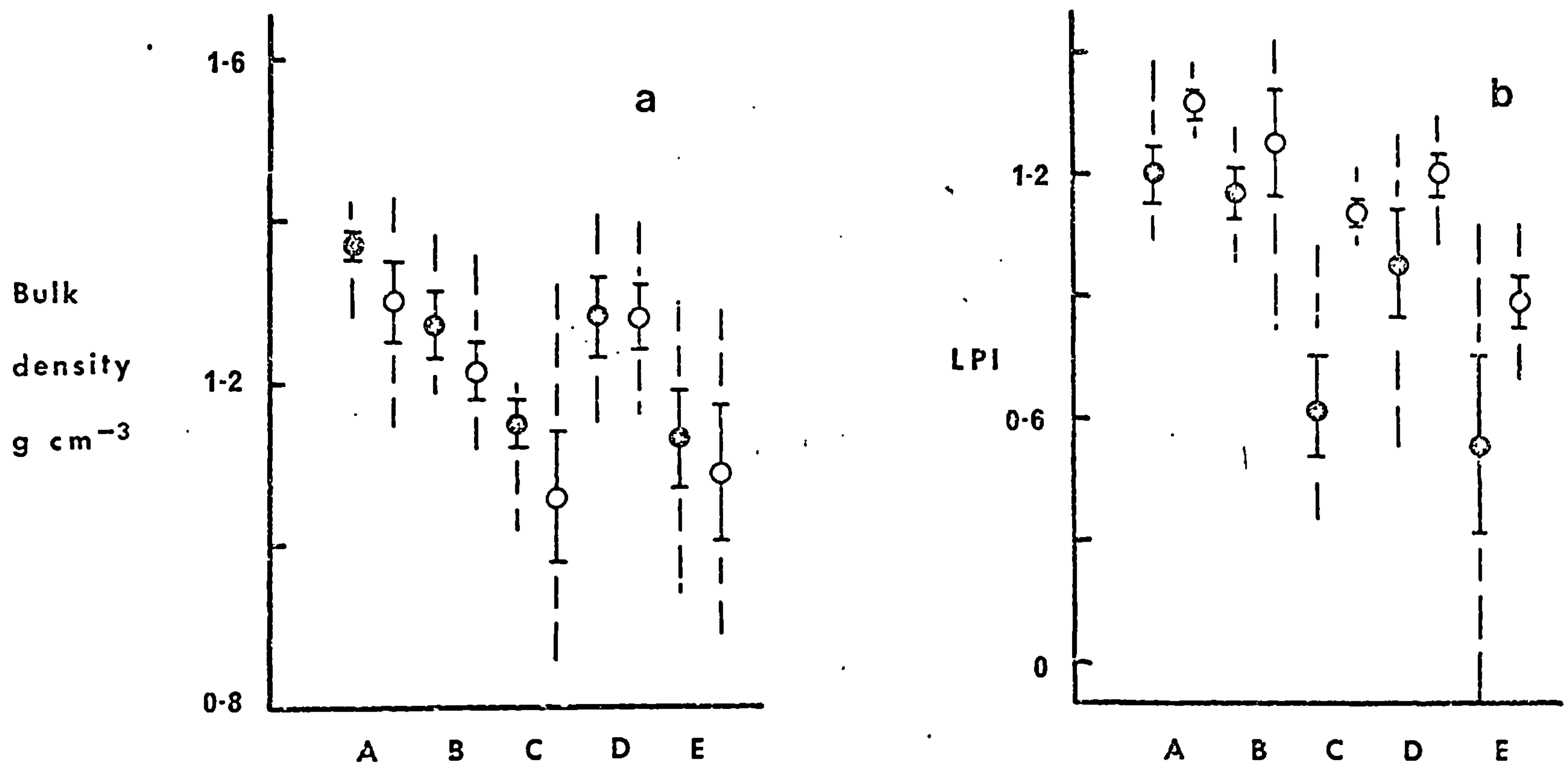
b) L.P.I.

⊙ mean of dry stands

○ mean of wet stands

2 standard errors

range



1 – 10

loam had an increase of 8.4%; this is higher than the 6.4% found at Aberffraw. The decrease of 18.3% (gravimetric) reported by Chappell _et al_ (1971) is probably the result of a decrease in total pore space and compares with the gravimetric measurements of the very wet stands at Aberffraw. The undisturbed wet dune soils were probably not saturated during the summer when the soil was sampled. The increase in volumetric water content of 6.4% in the compressed dry soils may have a direct effect on the plants and an indirect one via the thermal properties of the soils.

The two measures of primary soil characteristics have different relationships with soil water. Bulk density has a negative correlation with gravimetric water up to 1.3 $g.cm^{-3}$; it then becomes slightly positive. The R^2 value of the regression was, however, only 0.09 ($P < 0.051$) and there was no significant correlation with volumetric soil water. However, the soil penetration resistance has a positive correlation with volumetric soil water, $R^2 = 0.31$ ($P < 0.001$). When the primary soil parameters were divided into wet and dry groups, Fig.1-10, this opposite relationship was emphasised. The L.P.I. of the dry track, footpaths and the natural vegetation were all significantly lower than the wet stands from the same groups. (Fig.1-10b). As suggested by the regressions the bulk densities of the dry stands tended to be higher than those of the wet stands of the same group but the only significant difference occurred on the tracks (Fig.1-10a).

These results indicate that the L.P.I. is related to soil water content to a greater extent than is bulk density. But the compacted wet slack soils appeared to have a hard crust that was not present in dry areas and the penetrometer may be affected by this feature of soil structure associated with water content.

<u>The relationships between various soil factors</u>. The difference between the water content of the soil when collected and the measured field capacity of the soil core in isolation (Fig.1-11a) gives an indication of the field drainage situation. In this case, the track soil water contents were above their intrinsic field capacity. Compaction is either hindering drainage (Warkentin 1971) or aiding capillary rise from the water table (Ranwell 1959). An alternative possibility is that the vegetation on the non-track areas had withdrawn the water from these soils but this is unlikely in midwinter when the measurements were made. Warkentin (1971) suggests that sands will reach equilibrium after 12 hours of drainage. Since these cores were allowed to drain for 48 hours the 'field capacity' (or arbitrary point on the time-

Fig.1-11

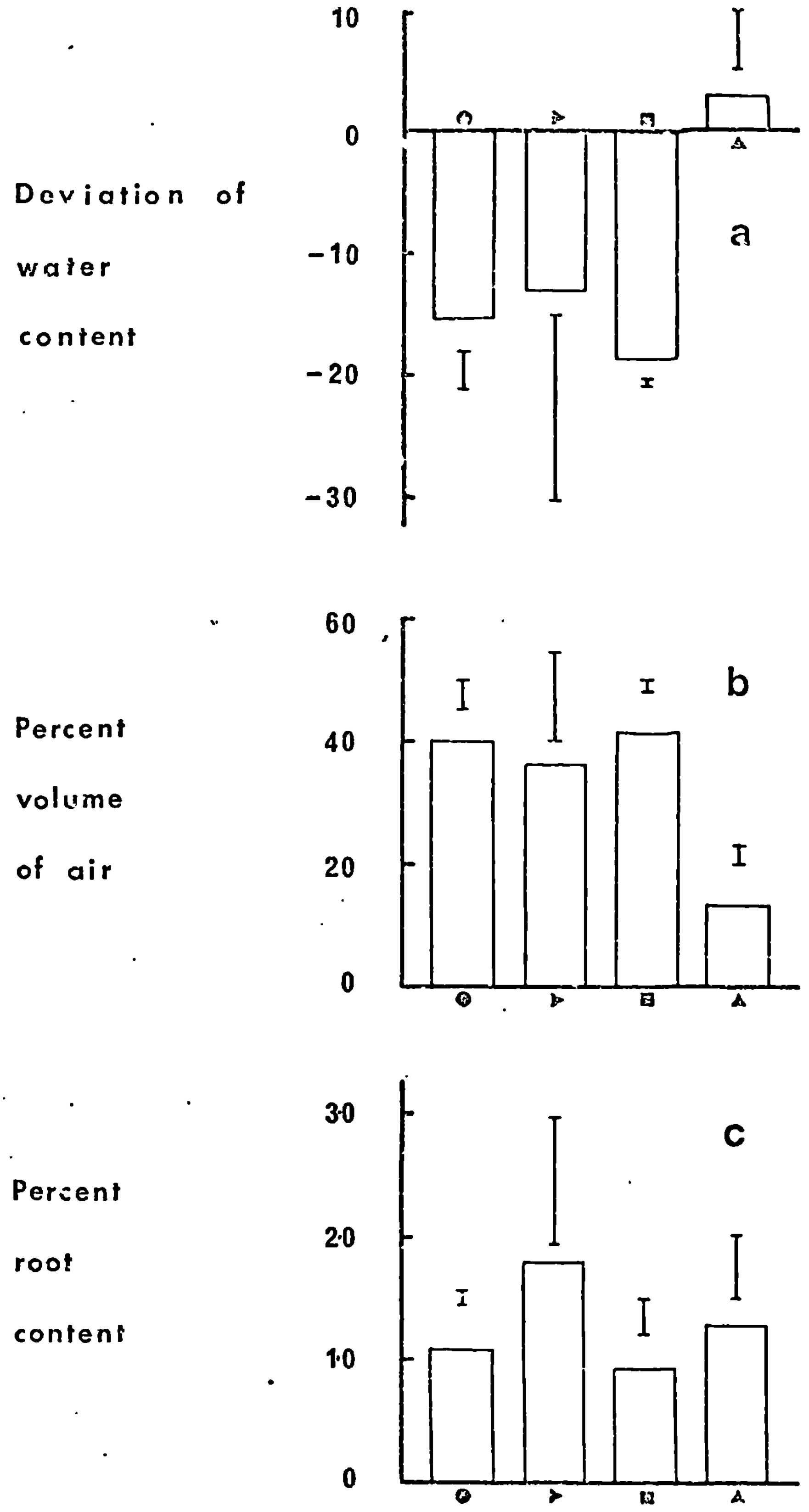
Detailed examination of soil characteristics

a) Percentage deviation of collected field water content from field capacity

b) Percentage volume of air in field condition

c) Root content, percentage of total dry weight

- ⊕ 'natural vegetation'
- ► footpaths
- ◘ picnic areas
- ▲ tracks
- I two standard errors


Deviation of water content
10
0
-10
-20
-30
a
Percent volume of air
60
40
20
0
b
Percent root content
3·0
2·0
1·0
0
c

drainage curve) measured here may be rather low.

The increased water content reduced the air porosity in track soils, in this case to a mean of 13.1% (Fig.1-11b). This level is low enough to hinder diffusion and restrict soil respiration rates in some soils (Grable 1971). It is, therefore, possible that the root growth of winter annuals will be inhibited by oxygen deficiencies in wet but not flooded slacks.

The percentage root content was highest in the footpath (1.79%) and track soils (1.25%) compared with 1.09% in the adjacent areas; these differences are only significant in the case of the footpaths (Fig.1-11c). This suggests that the total effect of compaction may be beneficial to plant growth at least in the summer.

<u>The effect of soil compaction on survival during drought</u>.

The plants grown in compacted soil maintained a greater percentage of live tissue under drought conditions than the plants grown in uncompacted soil (Fig.1-12a). They also had a 40% higher tiller number (Fig.1-12b) and a 45% higher fresh weight at the start of the wilting period (10.5 g S.E.0.8 and 7.9 g S.E.0.4 fresh weight respectively). The gravimetric water content of the soil and roots was the same for both treatments at all stages of wilting but the volumetric content at the starting time was 30% in the compressed and only 24.3%

Fig.1-12

The effect of soil compaction on the survival of plants in drought conditions.

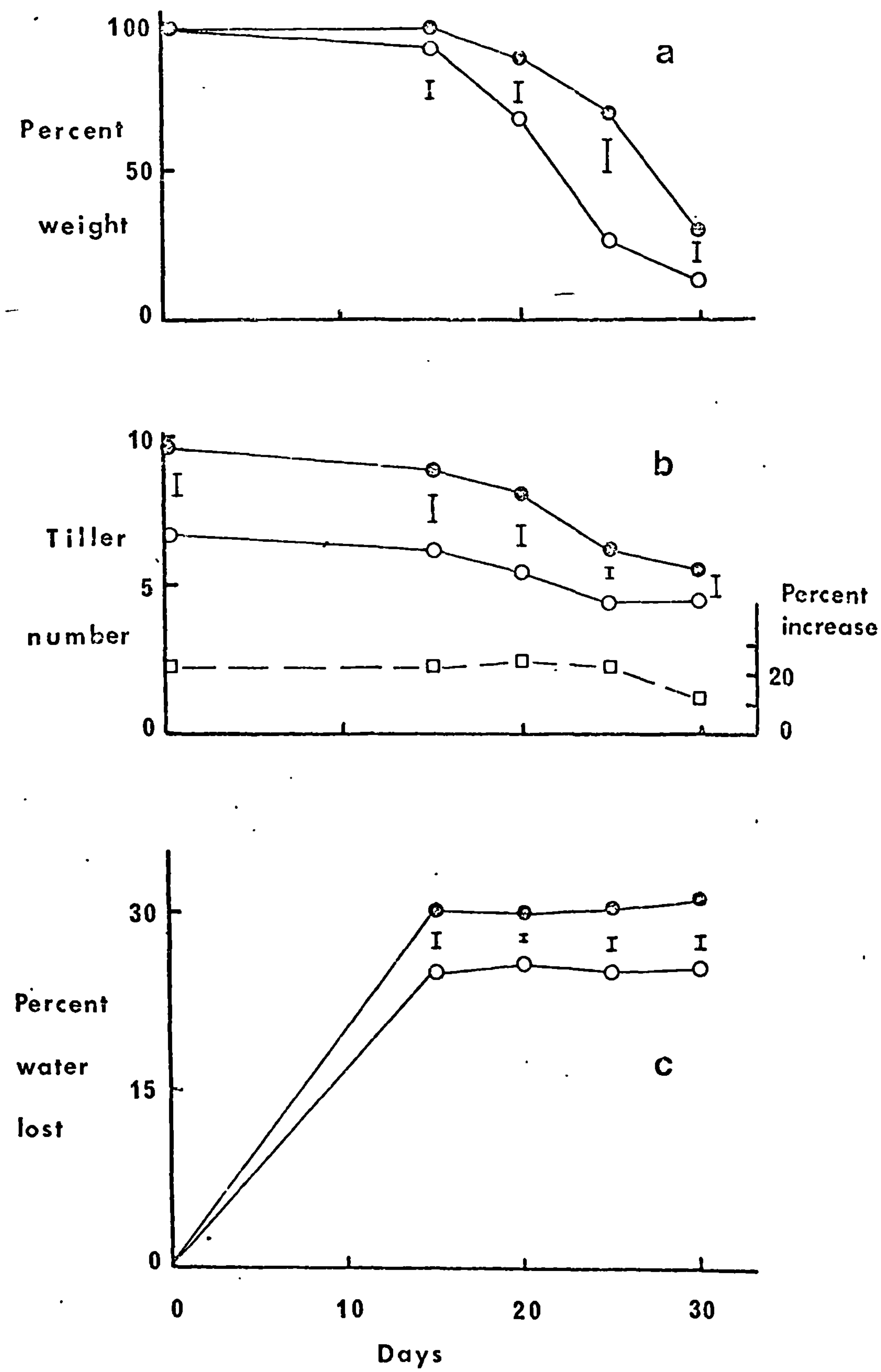
a) Change in percentage of live fresh weight of total plant fresh weight plotted against days of drought.

b) Number of tillers per plant plotted against days of drought.

c) Percentage volume of water lost from pots plotted against days of drought.

● Compacted

○ Un compacted



100
Percent
50
weight
0
a
10
Tiller
5
number
0
b
Percent
increase
20
0
30
Percent
water
15
lost
0
c
0
10
20
30
Days

in the uncompressed soils.

The volume of water lost during wilting was also greater in the case of the compressed soils (Fig.1-12c). These results show that at least for these artificial conditions Warkentin's statement that compacted soils have an increased amount of available water is correct (Warkentin 1971). They also indicate that volumetric water content should be used when discussing soil water in relation to plants. The difference in compaction between the two treatments is equivalent to 256 passages of the car when compared with the bulk density measurements of the wear experiment.

These data, together with the previous field measurements, suggest that compaction <u>per se</u> may have a beneficial effect on plant growth in the Aberffraw sand dune pastures. Seedling establishment may, however, be adversely affected.

SECTION 3

SEPARATION OF THE EFFECTS OF SHOOT DAMAGE AND SOIL COMPACTION BY VEHICLES

MATERIALS AND METHODS

The plants were grown in 6" pots each having a ½" thick, polyurethane varnished, steel plate over the top and were placed in 2.5 cm diameter central holes, see Photo 1-4. Three *Festuca rubra* plants were sown in each pot and allowed to establish for 112 days. Seven blocks were laid out, each of four pots. One from each block was an untreated control, one had the shoot damaged by driving over it eight times with a van that weighed 840 kg including the driver (ground pressure 1,218 $g.cm^{-2}$), one had the soil compressed by tamping with a 1" square block of wood and both treatments were given to the final pot. The driving treatment was carried out by placing the pots below ground level so that the steel plates rested in a frame at the soil surface; this prevented soil compression when the van was driven over it. (Photo 1-5). The soil bulk densities were 1.12 $g.cm^{-3}$, 1.16 $g.cm^{-3}$, 1.37 $g.cm^{-3}$ and 1.39 $g.cm^{-3}$ respectively and the differences were statistically significant between all except the last two treatments.

The plants were given a two week recovery period before harvesting so that the dead material could dis-

Photo 1-5

Method of carrying out damage treatment to shoots.

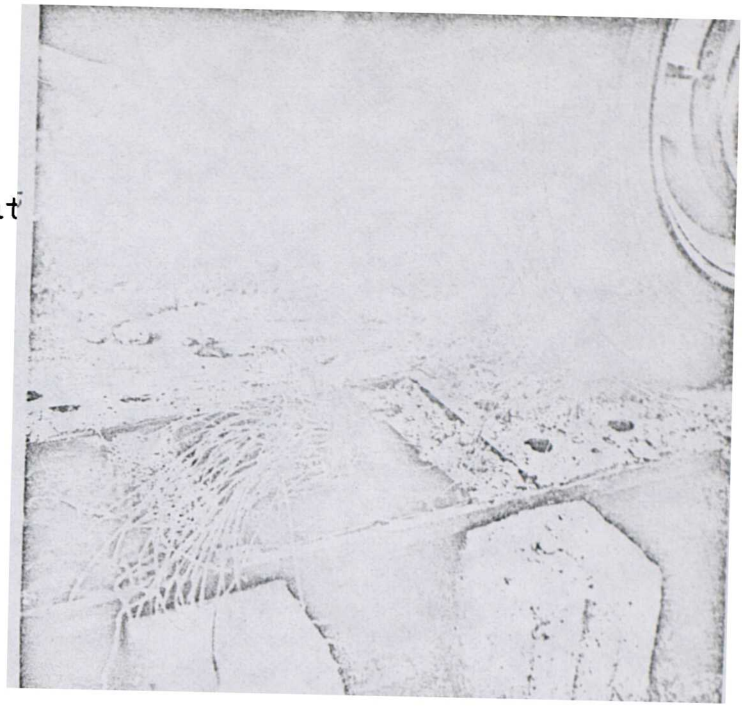
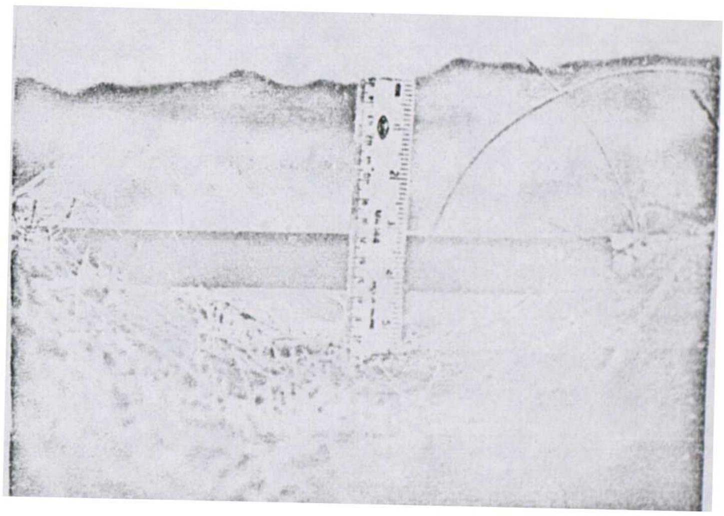


Photo 1-6

Point in car rut after 256 runs on previously uncompressed soil. Approximately 4 cm depression has occurred.



colour and be readily separated from live parts of the plants. The effect on shoot only was measured as it would not have been easy to separate live from dead roots. The results were analysed using analysis of variance.

RESULTS AND DISCUSSION

Damage to the shoots of the Festuca rubra by eight passages of the van caused a 42% increase in the number of tillers. Compaction of the soils caused a 37% rise but the two treatments together only caused a gain of 19% in tiller numbers (Fig.1-13a). An increase in tiller number has been recorded as a response to shoot damage or defoliation by Lambert (1962) and for compaction of the soil in isolation by Edmond (1958). However, the number of vehicle passages and the change in soil bulk density are not strictly comparable as this degree of compaction is equivalent to 2,480 passages of the car on the basis of the field experiment.

The shoot damage reduced fresh weight of live tissue by 17% while soil compaction increased it by 16%, a marked beneficial effect (Fig.1-13b). The two treatments together reduced the weight by 31%. The negative interaction suggests that the effect of compaction is both beneficial and harmful, the former effect outweighing the latter when no other stress is imposed,

Fig.1-13

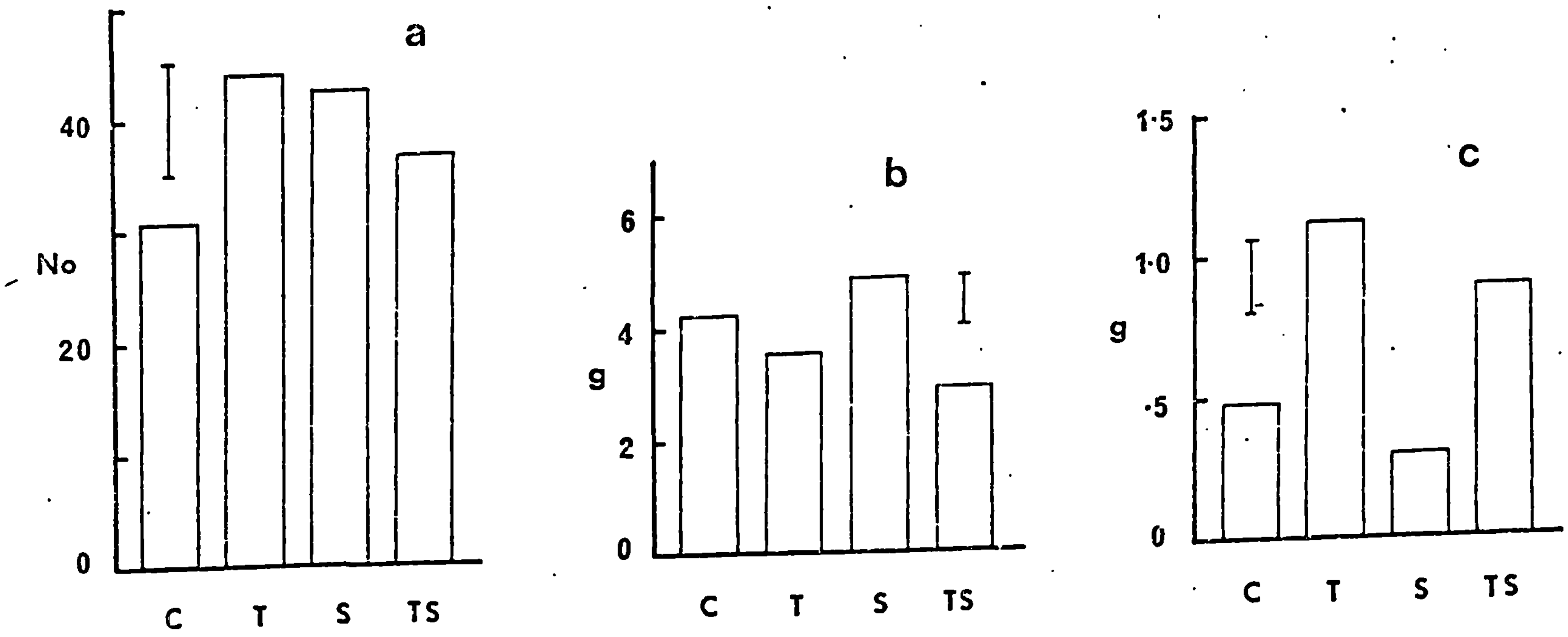
Effect of shoot damage and soil compaction on the growth of <u>Festuca rubra</u>.

a) Tillers per plant

b) Fresh weight of live tissue per pot

c) Fresh weight of dead tissue per pot

I 2 SE.



C control T top damage S soil compressed

1 – 13

but the reverse relationship dominating when the shoot is also damaged. Since soil water was unlikely to be limiting in greenhouse conditions another explanation for the beneficial action must be found. There may have been a greater availability of nutrients in compressed soils and the negative effect may have been root damage. The fresh weight of dead material reacted to the treatments in precisely the opposite way from that of the live material (Fig.1-13c).

These results show that compaction alone is beneficial to established plants, but that mechanical damage reduces biomass although tiller numbers are increased.

GENERAL DISCUSSION

The bulk density of soils on sand dune paths and tracks was measured and the average found to be 1.~~34~~28 g.cm^{-3} and 1.~~28~~34 g.cm^{-3} respectively. There was a straight line relationship between bulk density or the log of penetrometer impacts and the log of the number of passages, and the increase in bulk density of undisturbed soils caused by 256 passages of walkers or cars was 0.2 g.cm^{-3} and the L.P.I. rose by 0.42 and 0.6 respectively. An average car with three passengers caused 1.5 times the amount of soil compaction in terms of bulk density as three people walking and the effect is spread over a wider area.

The increase in compacted soil water content may be an important factor in dry periods in such well drained soils as those at Aberffraw; especially when combined with lower withdrawal by the reduced plant cover it may make the difference between death and survival. The increase in plant roots found in these soils suggests that plants are able to take advantage of this water. However, Barley & Greacen (1967) consider that there is evidence that mechanical properties of compacted soil may restrict root growth directly as well as indirectly by interacting with water and oxygen.

The damage caused by shoot compression and bending is shown to be greater than the effect of root damage by soil compression alone, which is apparently associated with some beneficial changes. Damage to the shoots does, however, stimulate a greater tiller production.

The crusted, more penetration resistant, wet slack soils are probably similar to the platey structures reported by Robinson & Alderfar (1952) and are likely to hold plant shoots more firmly than uncompressed soil. When they are pressed over against the ground by treading or tyres the length of stem that has to accommodate the bend is reduced as its base cannot move in the soil, also overall compression forces acting on the shoot will be greater than those occurring on soft soils which can 'mould' to accommodate the plant. This will lead to greater damage especially to those plants that grow in a completely vertical position. One may, therefore, expect that dune slack plants that survive trampling will emerge at an acute angle from the soil.

The survival problem in the softer dry areas may be that of resistance to surface abrasion by sand particles while the plant body is cushioned from the effects of direct compression.

Management implications of these data must centre around the critical level of compaction and wear for plant growth: this is discussed more fully in Paper 2. The improvement in water supply to plants in compacted soils may have an effect on the regeneration of dry areas. In more extreme conditions of wear the prevention of crust destruction will become important. Regeneration techniques must also consider the relation of the compacted state of the soil to damage mechanisms if the area is to be used again; they may involve treatments to ameliorate surface hardness.

The penetrometer experiments suggest that it is a suitable tool to use when assessing compaction differences inadjacent sand dune areas at any one time; however, care must be taken to avoid or measure changes in soil moisture due to rainfall and to see that comparisons are only made within one soil type. Bulk density in $g.cm^{-3}$ is probably a better general measure for site comparison over large areas.

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APPENDIX 1

A possible method by which penetrometer readings could be corrected for errors due to soil water content was investigated.

The regression of L.P.I. on B.D. gave an R^2 value of 0.33 ($P < 0.01$). The residual L.P.I. values from this regression were then regressed on the gravimetric soil water content and this gave an R^2 of 0.71 ($P < 0.001$) significance. The constants from this equation can then be used to correct the penetrometer reading, e.g.

correction factor = -0.6875 + 0.0262 x the soil water content

When this was subtracted from the original L.P.I.s and the remainder plotted against bulk density, an improved correlation coefficient of 0.70 ($P < 0.001$) was obtained. (See Appendix Table A1-1 and A1-2). When the same sequence was followed using volumetric water content the corrected L.P.I. R^2 value was only 0.56, so the gravimetric water measurement is apparently the best parameter to use for this correction.

This method could only be used in a restricted area and further field tests are required before it can be applied with confidence.

TABLE A1-1

SOIL DATA

Subjective category	Quadrat number	Penetration resistance	Bulk density	Collected water content %		Field capacity %		Deviation of collected water content from field capacity %	
		N° of impacts	$g\ cm^{-3}$	Gravimetric	Volumetric	Gravimetric	Volumetric	Gravimetric	Volumetric
▲	1	39.800	1.4412	16.05	22.83	16.13	22.96	-0.08	-0.13
▲	2	24.605	1.0431	23.56	24.58	36.34	37.91	-12.78	-13.33
▲	11	40.375	1.1543	32.54	37.55	26.40	30.37	6.14	7.18
▲	12	41.950	1.0857	37.00	40.21	31.02	33.71	5.98	6.50
▲	13	44.875	1.1274	35.93	40.51	30.48	34.36	5.45	6.15
▲	14	45.075	1.0952	37.43	40.99	31.56	34.56	5.87	6.43
▲	15	40.700	0.9060	43.20	43.03	38.37	38.21	4.83	4.82
▲	16	47.975	1.2882	27.60	35.56	23.94	30.84	3.66	4.72
□	3	10.550	1.0185	17.20	17.52	35.41	36.07	-18.21	-18.55
□	4	6.825	1.0287	17.55	18.05	35.61	36.63	-18.06	-18.58
□	5	7.450	1.0680	17.50	18.52	35.93	38.02	-18.43	-19.50
□	6	6.050	1.0199	16.57	16.90	34.30	35.78	-17.73	-18.88
▶	22	13.825	0.8122	26.06	21.17	52.19	42.39	-26.13	-21.12
▶	23	27.150	1.0457	26.69	27.64	32.45	33.31	-5.76	-5.67
○	7	7.300	0.9388	18.18	17.61	35.10	34.01	-16.92	-16.40
○	8	9.175	0.9943	21.11	21.00	41.63	41.41	-20.52	-20.41
○	9	10.300	0.9850	21.78	21.24	40.68	39.66	-18.90	-18.42
○	10	7.500	0.9025	23.04	20.80	43.82	38.53	-20.78	-17.73
○	17	17.825	0.9510	37.45	35.64	41.98	39.92	-4.52	-4.28
○	18	12.175	1.0739	25.65	27.55	35.81	38.46	-10.16	-10.91
○	19	14.670	0.8009	42.74	34.23	50.59	40.52	-7.85	-6.29
○	20	10.625	0.7965	27.76	21.11	49.91	38.75	-22.15	-17.64
○	21	13.075	0.8072	23.05	18.60	47.70	38.50	-24.65	-19.90
○	24	9.550	0.8275	24.62	20.37	52.25	43.24	-27.63	-22.87
○	25	7.475	0.9609	19.44	18.57	41.27	39.48	-21.83	-20.91

▲ track, □ picnic area, ▶ footpaths, ○ 'natural vegetation'

TABLE A1-1 (continued)

Subjective category	Quadrat number	Pore space % vol.	Root content % wt.	Vol. collected air space %	Log penetration resistance D' of impacts	Residual penetration resistance calculated from regression on bulk density	Correction factor	Corrected log penetration resistance: on gravimetric water %	Corrected log penetration resistance: on volumetric water %
▲	1	39.84	0.75	17.01	1.5999	-0.1282	-0.2076	1.8375	1.6329
▲	2	44.18	2.23	19.60	1.3911	0.1472	-0.0711	1.4622	1.2001
▲	11	49.79	1.21	12.24	1.6062	0.2298	0.1638	1.4424	1.6332
▲	12	51.40	1.16	11.19	1.6227	0.3238	0.2804	1.3455	1.6277
▲	13	50.02	1.74	9.51	1.6511	0.3068	0.2525	1.3005	1.6731
▲	14	51.49	0.87	10.50	1.6538	0.3478	0.2917	1.3621	1.6558
▲	15	55.61	1.92	13.58	1.6096	0.4218	0.4426	1.1670	1.5856
▲	16	46.45	0.13	10.89	1.6810	0.1451	0.0345	1.6555	1.7590
■	3	59.58	1.26	42.06	1.0233	-0.1913	-0.2375	1.2608	1.0053
■	4	57.72	1.06	39.67	0.8341	-0.3927	-0.2234	1.0625	1.0301
■	5	58.39	0.57	39.87	0.8722	-0.3695	-0.2297	1.1019	1.0852
■	6	60.75	0.58	43.85	0.7818	-0.4345	-0.2540	1.0308	0.9918
▶	22	64.49	2.33	43.21	1.1409	0.1721	-0.0057	1.1453	0.8449
▶	23	56.57	1.26	28.93	1.4338	0.2087	0.0107	1.4231	1.2628
⊖	7	62.91	0.74	45.30	0.8633	-0.2921	-0.2119	1.0752	0.9463
⊖	8	63.92	1.41	42.92	0.9719	-0.2145	-0.1152	1.1071	1.0679
⊖	9	62.48	1.05	41.24	1.0128	-0.1500	-0.1277	1.1305	1.0408
⊖	10	64.51	1.39	43.71	0.8751	-0.2013	-0.0843	0.9633	0.9411
⊖	17	60.47	0.96	24.83	1.2511	0.1169	0.2925	0.9636	1.3591
⊖	18	58.69	0.89	31.04	1.0927	-0.1979	-0.0265	1.1022	1.3057
⊖	19	63.45	1.01	29.22	1.1065	0.2111	0.4306	0.7159	1.1375
⊖	20	64.66	1.14	43.55	1.0265	0.0754	0.0387	0.9878	0.8245
⊖	21	66.36	1.07	47.76	1.1134	0.1505	-0.0345	1.2079	0.7864
⊖	24	65.67	1.21	46.30	0.9734	-0.0117	-0.0414	1.0188	0.8444
⊖	25	60.68	1.08	42.11	0.8736	-0.2776	-0.1789	1.0523	0.9566

▲ track, ■ picnic area, ▶ footpaths, ⊖ 'natural vegetation'

TABLE A1-2

Multiple regression data from Experiment II

	R^2	Significance	Constant	b
Log hardness on :				
Bulk density	0.33	1%	0.001	1.191
Collected water	0.40	0.1%	0.581	0.024
Root content	0.02	N.S.	1.106	0.086
Pore space	0.56	0.1%	3.013	-0.031
Deviation of collected water from field capacity	0.78	0.1%	1.475	0.024
Bulk density and collected water	0.82	0.1%	-0.868	1.360 0.027
Bulk density, collected water and root content	0.86	5.0%	-1.145	1.516 0.025 0.144
Field capacity on :				
Bulk density	0.93	0.1%	95.490	-57.259
Residual hardness on :				
Collected water content	0.71	0.1%	-0.688	0.026
Corrected log hardness on :				
Bulk density	0.70	0.1%	-0.171	1.359
Pore space on :				
Bulk density	0.73	0.1%	101.342	-42.974

PAPER 2

THE TRACK AND PATH VEGETATION IN THE ABERFFRAW SAND DUNES

CONTENTS

THE TRACK AND PATH VEGETATION IN THE ABERFFRAW SAND DUNES

INTRODUCTION

Surveys of both 'natural vegetation' and soils in relation to trampling are important as 'each is part of the environment of the other' (Tansley 1935). These have been carried out by Perring (1967), Streeter (1971) and Chappell _et al_ (1971) in chalk grasslands, by Goldsmith et al (1970) on coastal heath and by Bates (1935) mainly in acidic grasslands. All of these, except Goldsmith _et al_ (1970) and Perring (1967) have used soil bulk density as an indicator of the degree of wear. Willis _et al_ (1959) and Ranwell (1959) found that soil water was a major factor influencing the distribution of dune plants and it was considered important that any modification of this factor that may be caused by trampling should also be investigated; these data have been reported in Paper 1.

Many authors make some reference to the drastic effects of wear on sand dune vegetation, e.g. Ranwell (1969), Beattie (1967), Richards (1970) and Westhoff (1967), but there have apparently been no comprehensive surveys of the effects of trampling on the dune slack habitat.

Transects across paths have been investigated by a number of authors. Changes in profiles of a path surface during a short period of intensive use were examined by Burden (1970), an estimate of species distribution in relation to roads was made by Bates (1938b), cover measurements of certain species in relation to sheep tracks were presented by Thomas (1959), and Klecka (1937) describes estimates of abundance of common species across a path. Three recent papers give more detailed quantitative data. A series of paths for which percentage cover of damage to plants, cover of certain species and distribution of people estimated by tramplometer is described by Bayfield (1971). Streeter (1971) gives details of a number of transects in which total cover, cover of certain selected species, soil nitrogen, phosphorus and porosity were measured. Goldsmith et al (1970) present a very thorough description of a transect across a coastal path on the island of Tresco for which the frequency of each species, the surface profile, pH, conductivity, moisture content and vegetation height were all measured, and an estimate was made of the distribution of people. They also consider in detail the relationships between certain species and the environmental factors.

This paper describes the vegetation on the Aberffraw sand dunes in relation to the effects of trampling and vehicles. Two approaches have been adopted: in the first, a general survey was carried out; the soil data from this were presented in Paper 1 and the associated vegetation is described here. The second approach was to examine selected path and track transects in detail.

MATERIALS AND METHODS

General Survey

Site selection. The area chosen was the Aberffraw dune system (Fig.1-1, Paper 1) on the west coast of Anglesey, North Wales. There is free access by car and on foot and the whole of the area except the extreme N.E is traversed by car tracks and footpaths, some of which are shown in Fig.1-1b (Paper 1).

Vegetation sampling. The stand sizes and selection methods are described in Paper 1 and the designation of the categories is as follows :

- A On car tracks (stands 1 to 10)
- B Worn by cars and walking - 'Picnic areas' (stands 11 to 20)
- C Natural vegetation associated with tracks (stands 21 to 30)
- D On footpaths (stands 31 to 40)
- E Natural vegetation associated with paths (stands 41 to 50)

Phytosociological analysis techniques were chosen so that a summary of the vegetational diversity could be considered in relation to environmental variables. The techniques employed were ordination by principal components analysis using a correlation matrix between species, and by reciprocal averaging (Hill 1973), and classification by association analysis (Williams & Lambert 1959), using $\sqrt{\frac{\chi}{n}}$ as the division parameter and a stopping rule of max $\chi^2 = 5$. Since presence or absence record is considered to give nearly as much information as quantitative measures (Greig-Smith 1971), the species were recorded in this manner. Diversity was expressed as the reciprocal of Simpson's diversity index, N_2 (Hill 1973b).

Transect Records

Site selection. The transects were placed where the wear was graded across the path. Similarity of unworn vegetation on both sides of the track or path was also required as evidence that the whole transect had been homogeneous before wear occurred. Three transects were recorded, one on a car track (site 3), one on a path (site 4) and one on a sheep track (site 5).

Surface profile. The surface profile of the transect was recorded using a topograph and theodolite in the manner described by Boorman & Woodell (1966).

Penetrometer. Quadrats 25 x 25 centimetres were placed contiguously along the transect; the starting point was so arranged that abrupt changes in vegetation at path or track edges coincided as near as possible with boundaries between quadrats. Three penetrometer positions were arranged at right angles to the main transect line at each quadrat position, one in the centre and one 5 cm away from each side of the quadrat. The penetrometer was driven in to 10 cm depth and the top 5 cm of earth removed, the point was then driven in a further 5 cm and a further 5 cm of soil removed. This process was repeated until the point reached a depth of over 48 cm below the surface. In the case of the centre reading the turf was left in position and the earth was removed by 'mining' from outside the quadrat.

The average number of hits over each 6 cm depth was recorded for each quadrat and these figures were then written in vertical columns on the transect diagram under the appropriate surface levels. The lines connecting areas with similar hardness were then fitted by eye. The fact that the horizontal changes in hardness were of the same magnitude as the vertical changes is considered to justify the placing of vertical contours, although no horizontal readings of hardness were made.

Vegetation sampling. The 25 cm square turves were removed by cutting around the outside and then undercutting from one end with a large knife. They were then placed in polythene bags and kept in a deep freeze at below -20°C. until the above ground portions of the species could be separated, dried and weighed.

Nomenclature of the dicotyledons follows Clapham, Tutin & Warburg (1962); sedges, Jermy & Tutin (1968); grasses, Hubbard (1968); bryophytes, Watson (1966); and lichens, Dahl (1968).

RESULTS AND DISCUSSION

General Survey

Ordination. The stands were first ordinated to examine the degree of vegetational homogeneity of the site samples and their relationship with the environmental parameters, in particular with the factors that reflect the degree of trampling. Principal components analysis using a correlation matrix between species was chosen for the first analysis because of its known characteristic of centring around stands of low species number. It was thought that one of the ways that trampling would become apparent was by the death of the unresistant species and consequent reduction of species number in worn stands. The use of a correlation matrix between species has the advantage that a species ordination is also available for use in the autecological studies. The reciprocal averaging technique was used as a polythetic non-hierarchical classification method to separate the wet from the dry stands.

P.C.A. ordination of all stands. The first two axes of the principal components stand ordination are shown in Fig.2-1. The stands from the same sites are connected by lines with arrows pointing from undisturbed stands towards the associated worn areas. As shown in the schematic diagram in Fig.2-1a, the effect of trampling,

Fig.2-1

Ordinations of survey vegetation data.

a) to d) Principal components ordination of all survey stands.

a) Stand numbers. The lines connect stands that were situated at the same site and arrows point towards the stands subject to most wear. Continuous lines indicate track sites and dotted lines indicate footpath sites.

b) Soil bulk density $g.cm^{-3}$, given to first decimal place.

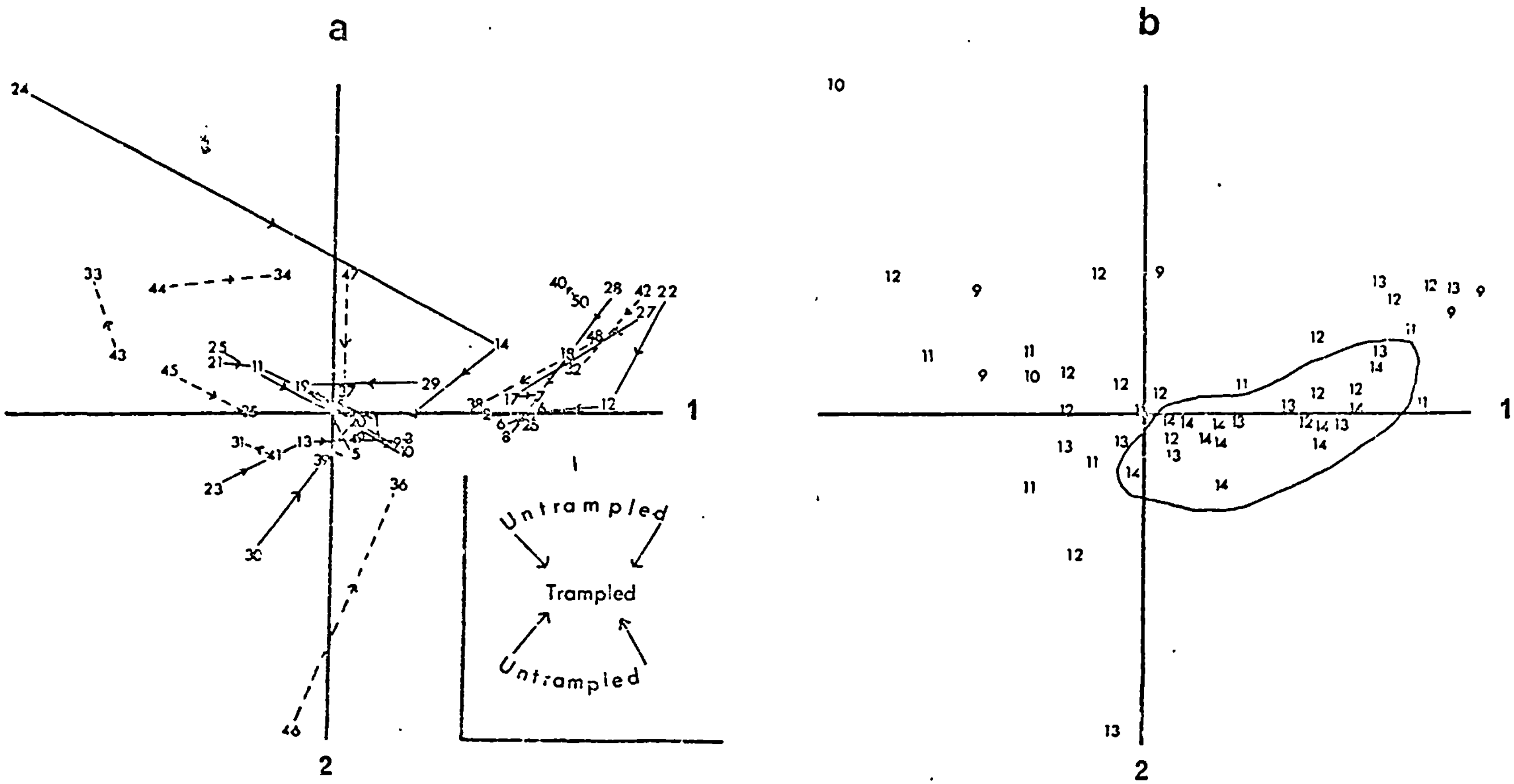
c) Percentage volume of soil water content.

d) Soil penetration resistance in L.P.I. given to first decimal place.

e) and f) Reciprocal averaging ordination of all survey stands.

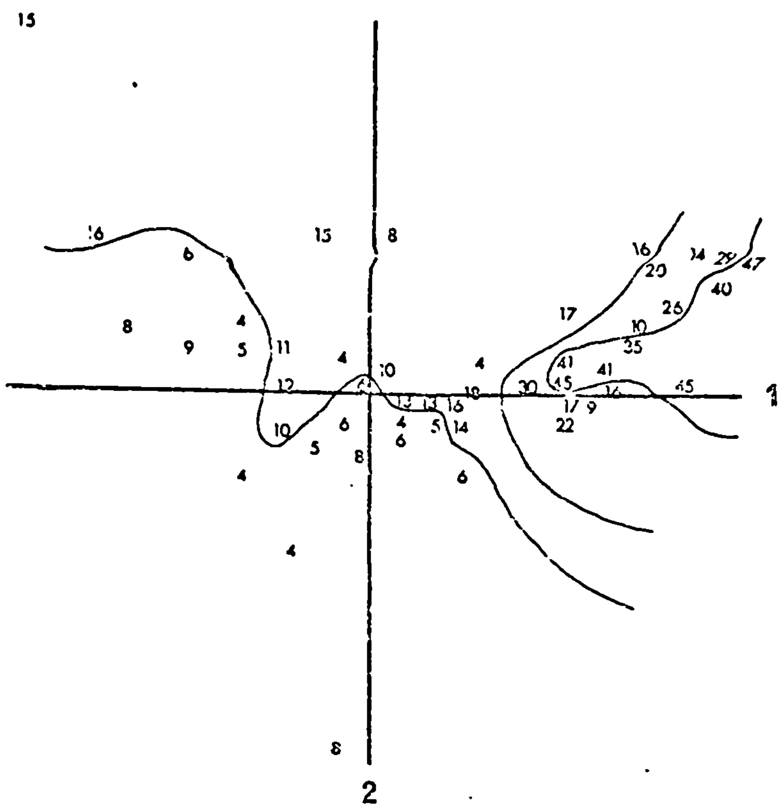
e) Stand numbers.

f) Percentage volume of soil water content.

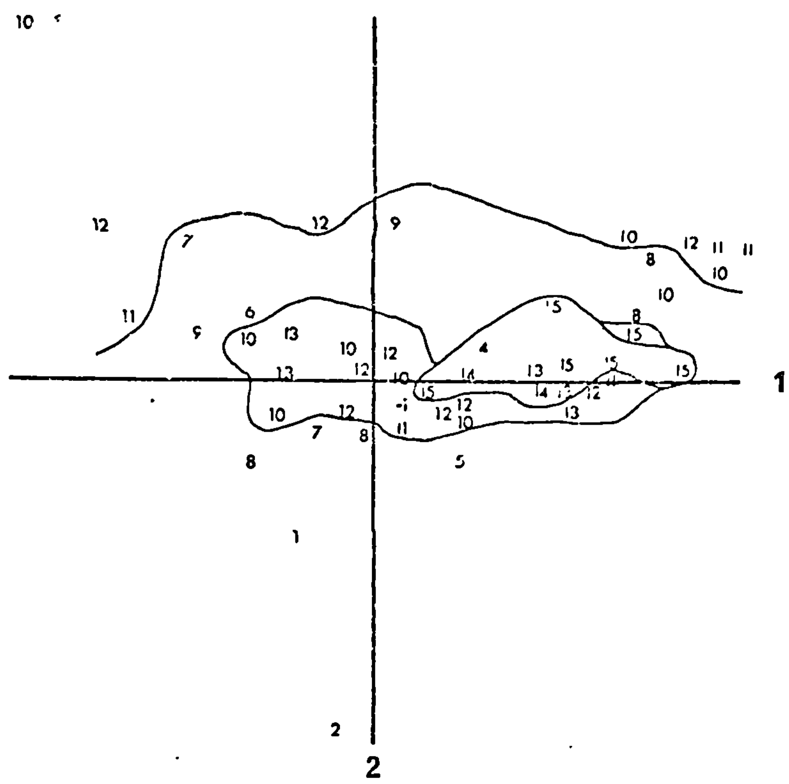


2 – 1

c

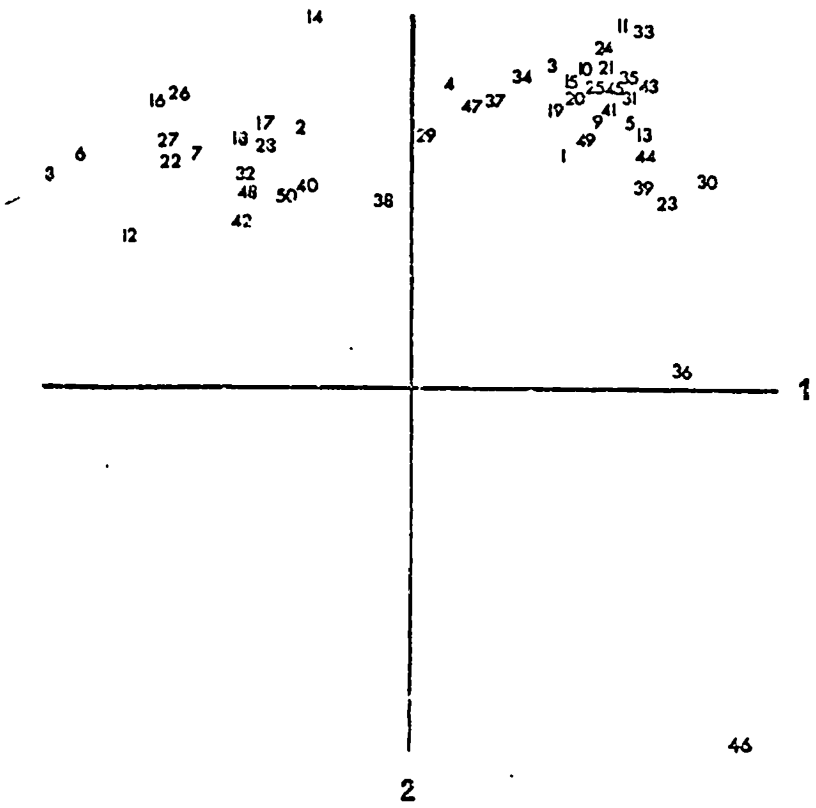


d

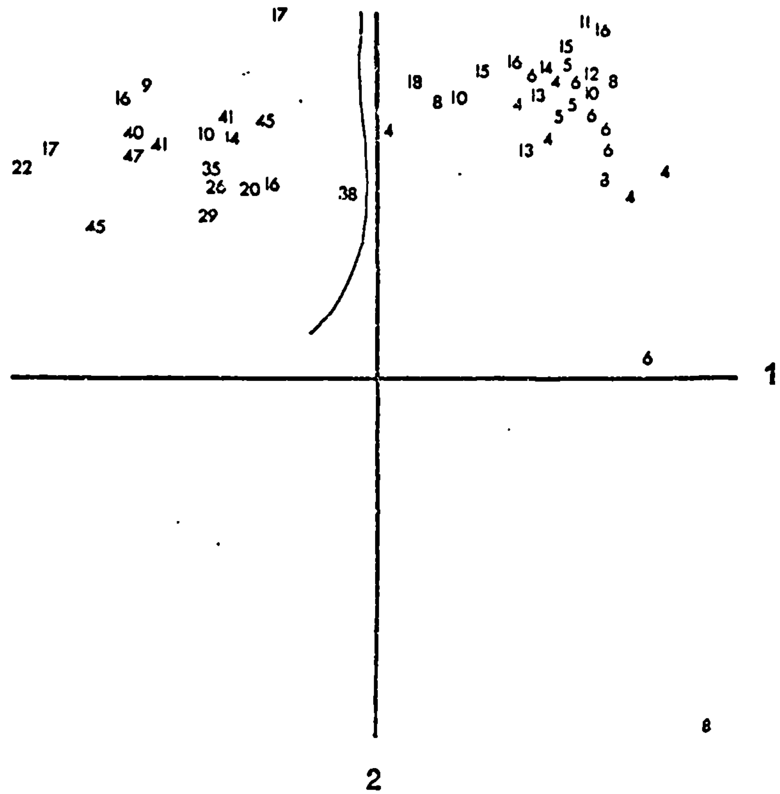


2 - 1

e



f



2 – 1

with few exceptions, is to drive the stands towards the centre of the ordination. This means that the environmental parameters whose contours are arranged concentrically around the ordination centre are associated with trampling while those with contours that traverse the centre are independent of this factor.

The extreme stand 46 was a natural area adjacent to a footpath through the fore dunes (stand 36) and contained five unique species. It is interesting to note that even in this extreme site trampling has produced a path stand that is comparable with the other dry path stands. Stand 24 at the other extreme was very species rich, having 38 species of which four were unique. (See the Species/Stand matrix, Appendix 1). In Fig.2-1b the bulk density contour including all stands over 1.4 $g.cm^{-3}$ is concentric to the centre of the ordination, while the collected water content contours (Fig.2-1c) tend to be perpendicular to the bulk density contours. This suggests that bulk density is associated with species number and hence the effect of trampling and vehicles, while the soil water content is more independent of this factor in the low bulk density areas but tends to be influenced by it in the region of the high bulk density stands. The division of stands into subjective groups of different types of wear (Paper 1, Fig.1-4) is not reflected in this analysis of the vegetation but wear itself has a clear influence.

The second point to emerge is that water content and bulk density both appear to be associated with the distribution of stands, the implication being that in the areas investigated trampling is at least as important ecologically as water content.

Stand log penetrometer impacts (Fig.2-1d) are distributed in a similar manner to stand bulk density but the areas of an L.P.I. over 1.0 tend to be twisted towards alignment with the water contours. This is expected in view of the known influence of soil water on penetrometer readings. Principal Components Ordination of all stands except the three extreme ones (24, 36 and 46) did not improve on the original ordination.

Reciprocal averaging ordination of all stands. This technique produced two clusters of stands arranged along a wet to dry gradient corresponding with axis 1 (Figs. 2-1e and f). The second axis produced a cluster with the two fore dune stands (36 and 46) separated from the rest. Axis three spread out the wet stands and tended to be associated with hardness and species numbers. The principal components ordination was judged to be better for the interpretation of trampling effects but Reciprocal Averaging provided a good classification into wet and dry stands for separate analysis; the division was made at the mid point of axis 1. This grouping was in good agreement with the subjective classification into wet and dry stands based on the vegetation, see Table 2-1.

Principal Components Ordination of wet and dry stands separately. The dry stands were ordinated without the aberrant stands 24 and 46 and the wet ones without stand 14. The associated stands are shown in Fig.2-2a; there is a tendency for the most worn stands to form groups, at the left side of the dry stand ordination, (i), and in the top right hand corner of the wet stand ordination, (ii). The bulk density contours in Fig.2-2b run at right angles to the 'direction' of wear as was the case in the ordination of all stands. The L.P.I. contour in Fig.2-2c tends to be similar in the wet stands (ii) but is almost at right angles to those of bulk density in the dry stands (i). This suggests that some factor other than bulk density was affecting the L.P.I. in the dry areas. That this factor is likely to be water content, or some phenomena associated with it is shown by the fact that the contour dividing the dry stands into those with more or less than 9% water content (Fig.2-2d (i)) is similar to the L.P.I. contour. However, the lines representing the effect of wear (Fig.2-2a) all cross from low to high water contents except that

Table 2-1

Division of stands into wet and dry groups according to various criteria

	Dry stands					Wet stands				
1. Subjective	1	11	21	31	41	2	12	22	32	42
field	3	13	23	33	43	4	14	24	34	44
assessment	5	15	25	35	45	6	16	26	37	47
	9	19	29	36	46	7	17	27	38	48
	10	20	30	39	49	8	18	28	40	50
	1	11	21	31	41	2	12	22	32	42
2. Measured	-	13	23	-	42	3	-	-	33	-
soil water	-	-	-	-	44	4	14	24	34	-
content	5	15	25	-	45	6	16	-	35	-
	-	18	26	36	46	7	17	27	-	-
	9	19	29	37	47	8	-	28	38	48
	10	20	30	39	49	-	-	-	40	50
3. Phytosocio-	1	11	21	31	41	2	12	22	32	42
logical	3	13	23	33	43	-	14	-	-	-
Reciprocal	4	-	24	34	44	6	16	26	-	-
averaging	5	15	25	35	45	7	17	27	38	48
ordination	9	19	29	36	46	8	18	28	40	50
	10	20	30	37	47	-	-	-	-	-
	-	-	-	39	49	-	-	-	-	-
4. Phytosocio-	1	11	21	31	41	2	12	22	32	42
logical	-	13	23	33	43	3	-	-	-	-
Association	-	-	24	34	44	4	14	-	-	-
analysis.	5	15	25	35	45	6	16	26	36	46
Williams and	-	-	-	37	47	7	17	27	-	-
Lambert	-	19	29	39	49	8	18	28	38	48
(1959)	-	20	30	40	-	9	-	-	-	-
						10	-	-	-	50

Dry stands sampled when raining

3 13 23

10 20 30 36 46

Fig.2-2

Principal components ordination of wet and dry stands separately.

a) Stand numbers. The lines connect stands that were situated at the same site and arrows point towards the stands most affected by trampling. Continuous lines indicate track sites and dotted lines indicate footpath sites.

b) Soil bulk density in $g.cm^{-3}$ given to first decimal place.

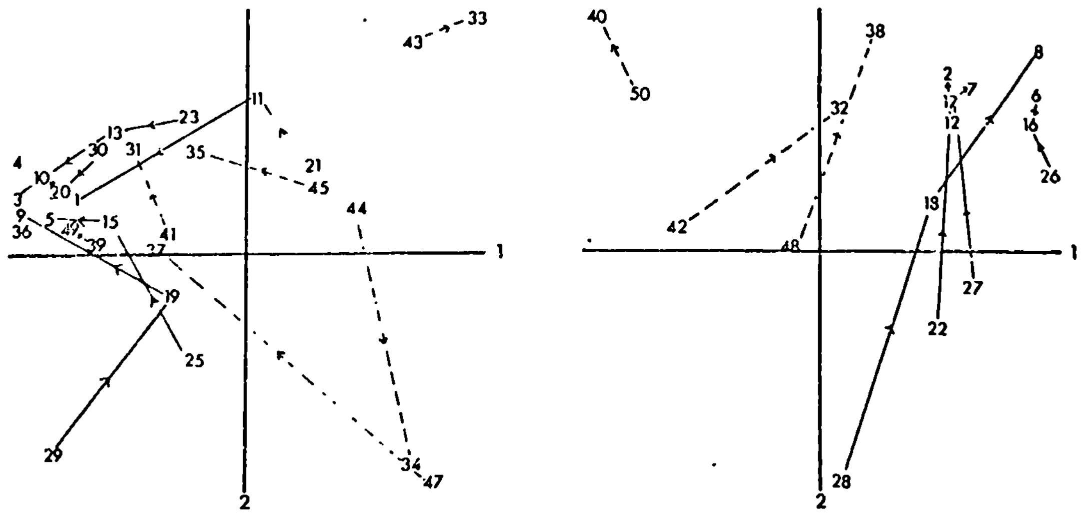
c) Soil penetration resistance in L.P.I. given to first decimal place.

d) Percentage volume of soil water content.

(i) Dry stands

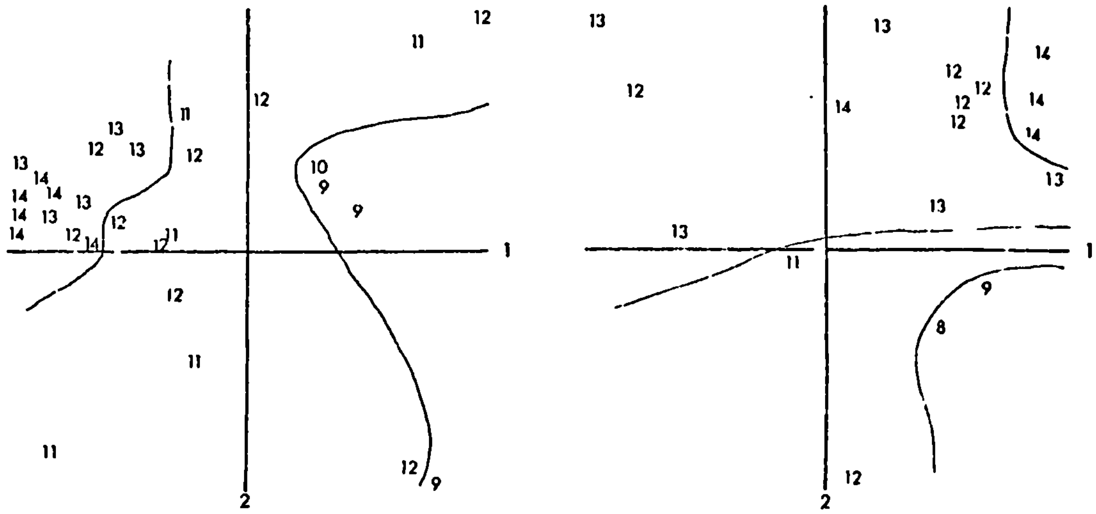
(ii) Wet stands

a



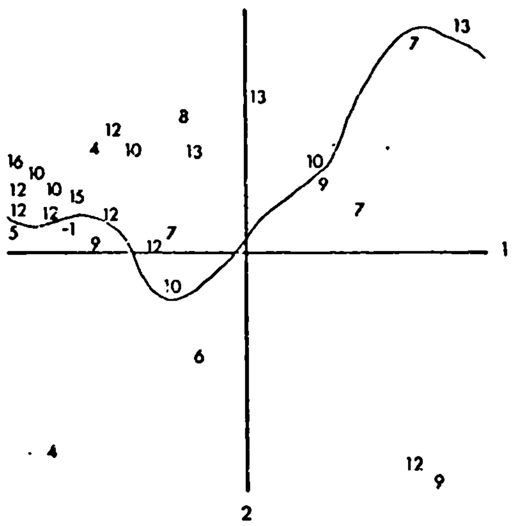
i ii

b

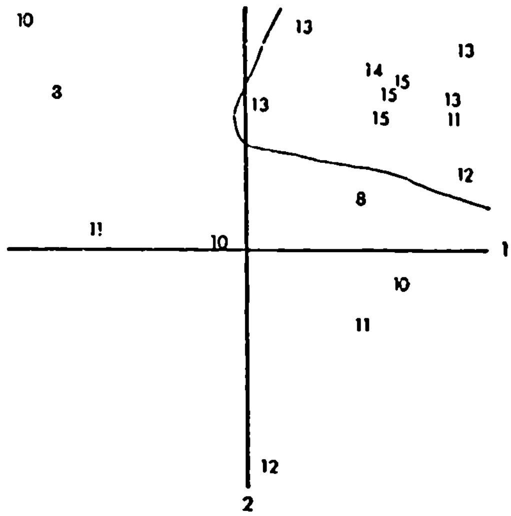


i ii

c

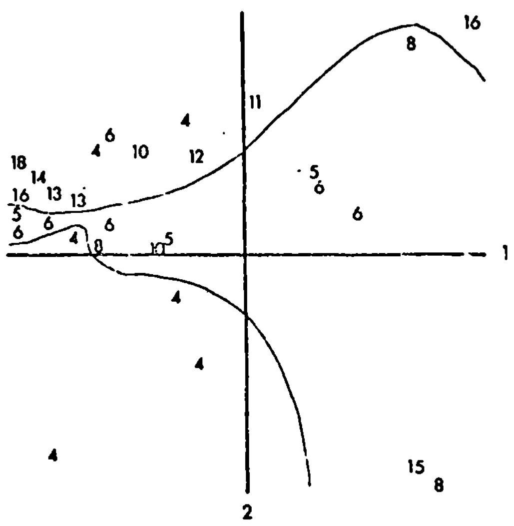


i

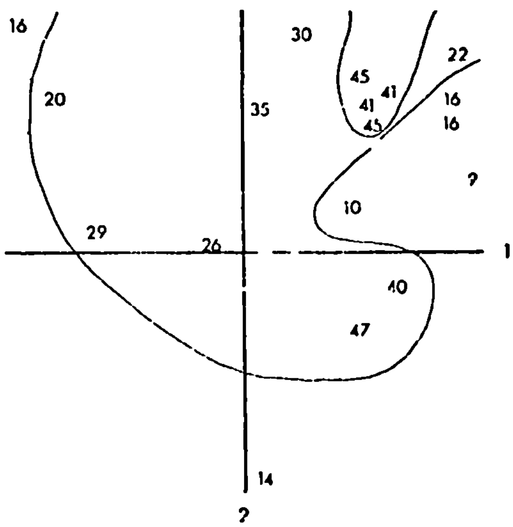


ii

d



i



ii

between stands 40 and 50. It should be noted that water content is associated with opposite effects on the L.P.I. and bulk density of the subjective groups, (see Figs.1-10a and b).

The fact that these differences are reflected in the ordination suggests that the vegetation may be influenced by trampling in a different way in the wet and dry areas.

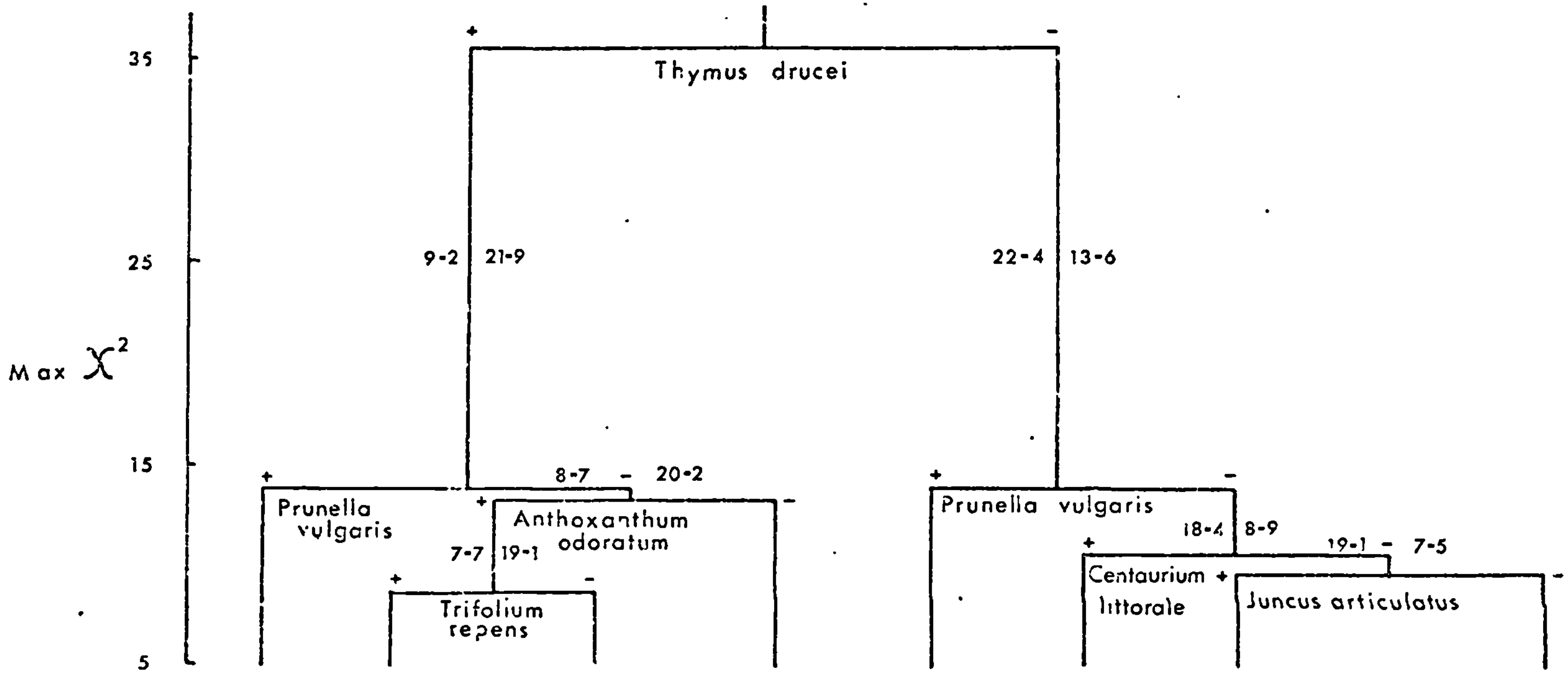
Classification

Association analysis. This classification again emphasised the importance of the two factors of water supply and trampling shown by the ordinations, and gave some information about the species upon which divisions were made (Fig.2-3).

The first division was made on *Thymus drucei*. This species is known to occur in ~~prefer~~ drier areas (Willis *et al* 1959) and tends to be associated with stands containing higher numbers of species. Both the second divisions on *Prunella vulgaris* tend to correct 'errors' introduced by the combination of dry stands with high species numbers at the first division; the dry groups are now associated with low species numbers. The + *Prunella* groups include half of tho twenty undisturbed stands and none of the ten severely worn stands. It should be noted that stands 12 and 14 which occur in the right hand

Fig.2-3

Association analysis with stand numbers, mean percentage volume soil water content and mean species number per stand. Figures on left of columns give mean volumetric water content and those on the right give mean species number.



Stand number	24 29 34 40 47	15 19 25 37	5 13 23 30 31 39 41 49	1 11 20 21 33 35 43 44 45	12 14 22 27 28 32 42 48 50	46	2 6 7 8 16 17 18 38	3 4 9 10 26 36
Mean number of species per stand	27-4	22	17-6	22-6	21-3	21	8-1	8
Mean water content	11-4	6-1	8-6	9-9	30	7-9	25	11-3

2 – 3

+ Prunella group were not in use by cars at the time of the survey, although the ground was compressed and rutted. Thus the first two ranks of the hierarchy have reinforced the importance of the water and trampling factors and incidentally shown that Prunella vulgaris is a moisture loving plant, very sensitive to trampling.

The division of the dry stands on Anthoxanthum odoratum associates this species with disturbed areas, and the right hand division of the wet stands separates the single aberrant fore dune stand 46 from the highly worn group.

The division of the + Anthoxanthum stands on Trifolium repens again separates lower from higher species numbers and may reflect variation in the amount of wear received by the stands as 15 and 37 were apparently not subject to heavy usage. The division of the - Centaurium stands on Juncus articulatus separates dry from wet worn stands all with low species numbers.

The classification tends to confirm a subjective assessment of the stands and it emphasises the relationship of Anthoxanthum odoratum with disturbance, a point that was not clear from previous data.

Subjective site categories. Many workers have found it convenient to divide vegetation wear into subjective categories based on a visual estimate of wear and in this case the amount of vegetation cover and species number (Figs.2-4a and b) show that these groups are also distinct in respect of these parameters. The same point has been made about the soils in Paper 1 so it is reasonable to use these categories as a means of grouping the species.

The picnic areas and footpaths showed similar soil characteristics to the car tracks but their vegetational data group them more closely with the unworn natural vegetation. This suggests that the vegetation is more affected by the superficial wear and mechanical damage imposed by cars than by the soil bulk density and hardness changes associated with trampling and vehicles.

Species number. The fact that the species number and total cover of each group have a similar pattern, Fig. 2-4, suggests that either measure would tend to give similar results; this, together with comments of previous workers, adds weight to the decision to use presence/absence data for this survey. This measure does not, however, reflect the behaviour of any one species in different stands.

There is a slight tendency for fewer species to occur in wet areas, but it is only significant in the B (Picnic) areas, Table 2-2. There is also a greater variability in the D (Footpath) areas, probably due to

Fig.2-4

Vegetation data of the subjective stand groups.

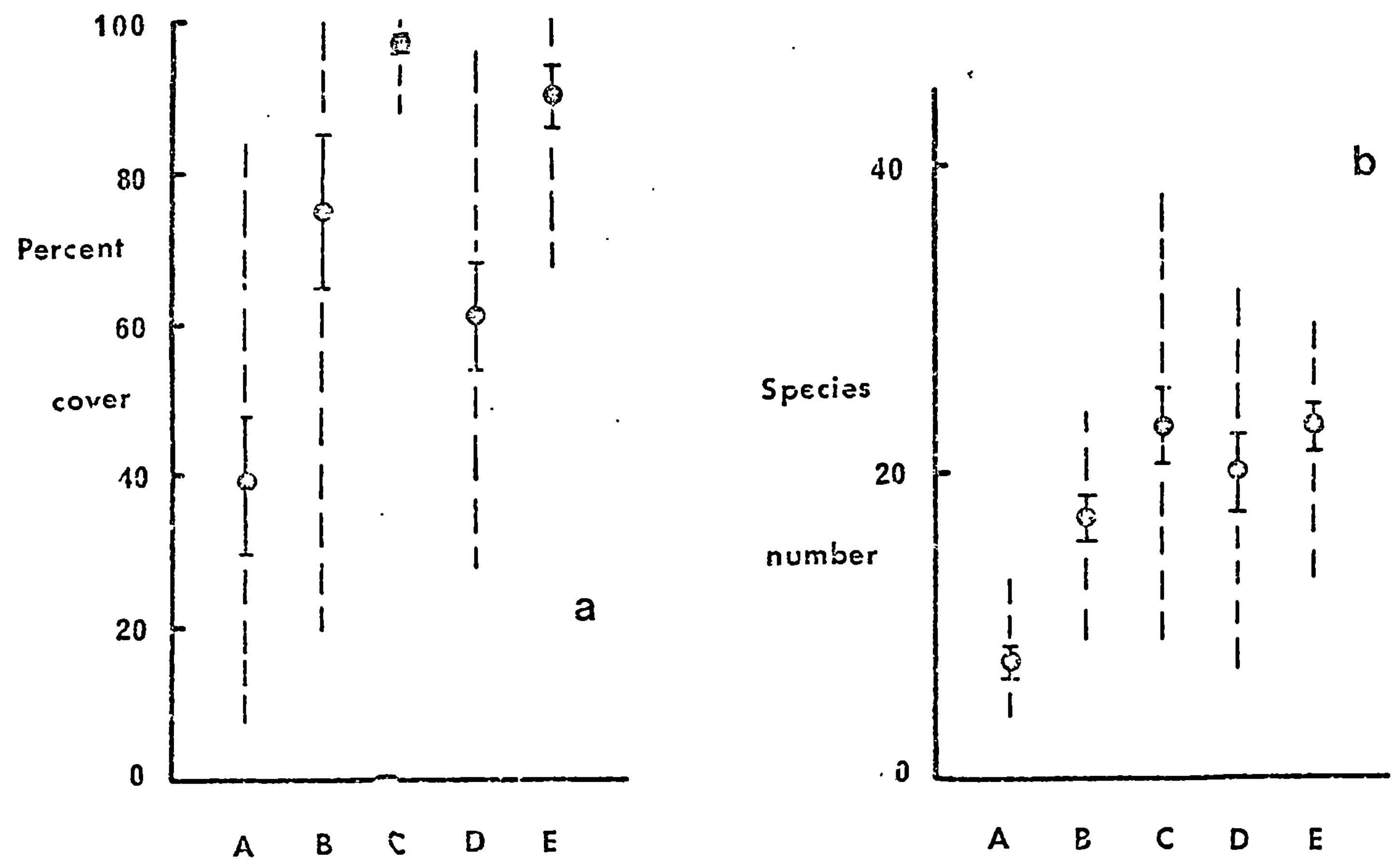
a) Percentage cover

b) Species number

mean

two standard errors

range



2 - 4

Table 2-2

Species number in relation to soil water

		Subjective site category				
		A	B	C	D	E
Dry	$\bar{x}$	8.3	17.8	22.2	21.0	24
Stands	S.E.	1.1	1.7	1.8	3.2	2.6
Wet	$\bar{x}$	6.3	12.5	20.3	23.3	22.3
Stands	S.E.	1.4	1.6	3.8	5.2	2.2

A track

B picnic areas

C adjacent 'natural vegetation'

D footpaths

E adjacent 'natural vegetation'

differences in intensity of use. Bellamy <u>et al</u> (1971) found that vehicles caused greater damage to vegetation in wetter areas and this finding agrees with theirs. In the sand dunes, however, when the water table is near the soil surface it prevents the formation of large blow outs and the total effect of wear on the environment is, in fact, more severe in the drier areas.

<u>The distribution of species in relation to trampling.</u>

The mean bulk density and volumetric water content of the soils in which the common species occurred was plotted on the species ordination and this was used as a basis for grouping the plants into those associated with high or low bulk densities, 87 and 36 species respectively, and low (48 species), medium (42 species) or high (3$\overset{3}{2}$ species) water contents, Table 2-3. The large number in the high bulk density class suggests that many species are able to survive or establish in the trampled areas.

The species occurrence in the five subjective classes and the frequency in the dry or wet stands of each class is given in Table 2-4. The species distribution was as follows : on tracks (A), 32 species; on footpaths but not on tracks (D-A), 45 species; on picnic areas but not tracks or footpaths (B-(A + D)), 16 species; only in untrampled vegetation (C + E)-(B + A + D), 30 species. The tracks

TABLE 2-3

Species groups based on principal components ordination of species

	High Bulk Density > 1.5	Low Bulk Density < 1.5
	Equisetum palustre	Veronica chamaedrys
	Viola canina	Senecio jacobaea
	Viola tricolor	Luzula campestris
	Cerastium atrovirens	Climacium dendroides
	Honkenya peploides	Pseudoscleropodium purum
	Arenaria leptoclados	Hypnum cupressiforme
	Ononis repens	Rhytidiadelphus triquetrus
	Trifolium dubium	Rhytidiadelphus squarrosus
	Trifolium arvense	Cladonia furcata
	Sedum anglicum	Peltigera canina
	Euphorbia portlandica	Cladonia ~~spp~~ indet
	Euphorbia paralias	
	Centaurium erythraea	
	Thymus drucei	
	Galium verum	
Water	Cirsium arvense	
	Crepis ~~spp~~ indet.	
content	Taraxacum officinale	
	Taraxacum laevigatum	
less	Veronica ~~spp~~ indet	
	Bromus mollis	
than	Festuca ovina	
	Festuca rubra	
10%	Vulpia membranacea	
	Catapodium marinum	
	Aira praecox	
	Ammophila arenaria	
	Agrostis tenuis	
	Phleum arenarium	
	Ditrichum flexicaule	
	Tortula ruraliformis	
	Thuidium abietinum	
	Thuidium philibertii	
	Amblystegium serpens	
	Camptothecium lutescens	
	Brachythecium albicans	
	Lophocolea bidentata	

TABLE 2-3 CONTINUED

	High Bulk Density > 1.5	Low Bulk Density < 1.5
Water content more than 10% and less than 20%	Sagina nodosa	Ranunculus bulbosus
	Erodium glutinosum	Polygala vulgaris
	Rubus fruticosa agg.	Cerastium holosteoides
	Centaurium littorale	Linum catharticum
	Plantago major	Trifolium repens
	Plantago coronopus	Lotus corniculatus
	Bellis perennis	Lotus pedunculatus
	Leontodon autumnalis	Potentilla reptans
	Leontodon taraxacoides	Rumex acetosella
	Cf.Souchus oleraceus	Anagallis arvensis
	Heiracium pilosella	Veronica officinalis
	Crepis capillaris	Euphrasia brevipila
	Poa pratensis	Plantago lanceolata
	Cynosaurus cristatus	Crepis vesicaria
	Koeleria cristata	Carex arenaria
	Sieglingia decumbens	Poa subcaerulea
	Ceratodon purpureus	Aira caryophyllea
	Bryum argenteum	Anthoxanthum odoratum
	Brachythecium rutabulum	Dicranum scoparium
	Riccardia pinguis	Frullania tamarisci
	Pellia endivifolia	Cladonia rangiferina
Water content over 20%	Equisetum variegatum	Prunella vulgaris
	Equisetum arvense	Preissia quadrata
	Ranunculus flammula	Liocolea badensis
	Ranunculus repens	Evernia prunastri
	Anthyllis vulneraria	
	Potentilla anserina	
	Hydrocotyle vulgaris	
	Salix repens	
	Anagallis tenella	
	Gentianella amarella	
	Mentha aquatica	
	Galium palustre	
	Hypochoeris radicata	
	Juncus bufonius	
	Juncus articulatus	
	Eleocharis quinqueflora	
	Eleocharis multicaulis	

TABLE 2-3 CONTINUED

	High Bulk Density>1.5	Low Bulk Density<1.5
Water content over 20%	Isolepis setacea Carex flacca Carex nigra Poa annua Holcus lanatus Agrostis canina Agrostis stolonifera Bryum pseudotriquetrum Cratoneuron filicinum Acrocladium cuspidatum Brachythecium glareosum Riccardia sinuata	

TABLE 2-4

Number of occurrences of species in each subjective group

A tracks, B picnic areas, C adjacent vegetation, D footpaths, E adjacent vegetation, d dry stands, w wet stands

Species that occurred on tracks										
Place of occurrence	A		B		C		D		E	
	d	w	d	w	d	w	d	w	d	w
Viola canina	1	–	2	–	3	4	5	1	5	2
Sagina nodosa	–	1	–	1	–	2	–	–	–	1
Ononis repens	2	–	2	–	2	–	2	–	1	–
Trifolium repens	–	2	4	3	1	4	2	3	2	3
Lotus corniculatus	1	–	4	–	2	4	2	3	1	4
Potentilla anserina	1	2	–	4	–	3	–	1	–	2
Potentilla reptans	–	2	–	1	–	5	–	1	1	2
Thymus drucei	2	–	5	–	5	1	4	3	1	3
Plantago major	–	1	–	2	–	1	–	–	–	–
Galium verum	3	1	4	–	5	1	4	2	4	2
Bellis perennis	2	3	5	4	1	2	3	4	1	4
Leontodon autumnalis	1	1	1	3	1	4	–	2	1	2
Leontodon taraxacoides	2	1	5	3	5	3	5	5	4	5
Cf. Sonchus oleraceous	–	1	3	2	–	–	3	1	1	1
Taraxacum officinalis	1	1	3	2	3	1	2	1	4	–
Taraxacum laevigatum	2	1	1	–	1	–	3	1	2	2
Juncus articulatus	–	4	–	5	–	3	–	3	–	2
Carex flacca	–	3	–	4	2	4	–	5	–	4
Carex arenaria	3	–	3	1	4	4	5	4	4	5
Festuca rubra	5	2	5	2	5	2	5	5	5	4
Poa annua	–	1	–	1	–	–	1	1	–	–
Poa pratensis	4	4	4	3	1	3	4	5	1	2
Anthoxanthum odoratum	1	–	2	–	1	1	2	1	2	3
Ammophila arenaria	2	–	2	–	5	1	4	2	5	3
Agrostis tenuis	1	1	3	1	3	1	3	–	2	1
Agrostis stolonifera	–	2	2	4	3	4	1	4	2	4
Sieglingia decumbens	–	1	–	1	–	–	–	–	–	–
Tortula ruraliformis	1	–	3	–	2	–	2	1	3	1
Acrocladium cuspidatum	–	1	–	1	–	2	–	–	–	–
Camptothecium lutescens	1	–	1	–	3	–	2	2	4	1
Brachythecium albicans	2	–	2	1	1	–	2	1	4	–
Brachythecium rutabulum	–	1	1	2	–	2	–	–	1	–

TABLE 2-4 CONTINUED

Species that occurred on footpaths but not on tracks	A		B		C		D		E	
	d	w	d	w	d	w	d	w	d	w
Equisetum varigatum	–	–	–	1	–	3	–	2	–	2
Equisetum arvense	–	–	–	1	1	3	–	–	–	–
Ranunculus bulbosus	–	–	1	–	–	2	2	1	–	–
Viola tricolor	–	–	1	–	2	1	2	–	4	–
Polygala vulgaris	–	–	1	–	2	1	1	2	1	1
Cerastium atrovirens	–	–	1	–	2	–	1	2	3	–
Linum catharticum	–	–	–	–	2	1	–	2	2	4
Trifolium dubium	–	–	–	–	1	–	2	1	1	–
Trifolium arvense	–	–	–	–	3	1	3	–	–	–
Lotus pedunculatus	–	–	–	–	–	–	–	1	–	–
Sedum anglicum	–	–	–	–	2	–	1	–	1	–
Rumex acetosella	–	–	–	–	–	–	–	1	–	1
Salix repens	–	–	–	–	–	1	–	3	–	4
Anagallis tenella	–	–	–	–	–	1	–	1	–	1
Anagallis arvensis	–	–	–	1	–	–	–	1	–	–
Centaurium littorale	–	–	–	–	–	1	–	2	1	2
Veronica officinalis	–	–	–	–	–	1	1	1	–	2
Euphrasia brevipila	–	–	1	–	–	1	–	1	–	4
Prunella vulgaris	–	–	–	2	1	4	–	3	–	4
Plantago coronopus	–	–	–	2	–	1	–	1	–	1
Senecio jacobaea	–	–	4	–	2	1	1	–	3	1
Crepis capillaris	–	–	1	2	3	–	1	1	–	1
Veronica ~~spp~~ indet	–	–	–	–	–	–	1	–	–	–
Luzula campestris	–	–	1	–	2	1	2	2	2	2
Carex nigra	–	–	–	2	1	1	–	1	–	1
Bromus mollis	–	–	2	–	2	–	1	–	–	–
Festuca ovina	–	–	1	–	2	–	–	1	2	–
Poa subcaerulea	–	–	2	1	4	3	3	1	3	2
Holcus lanatus	–	–	–	–	–	1	–	3	–	3
Phleum arenarium	–	–	–	–	–	–	2	–	1	–
Dicranum scoparium	–	–	–	–	–	1	–	1	–	1
Climacium dendroides	–	–	–	–	1	–	1	–	1	–
Thuidium philibertii	–	–	1	–	1	–	1	–	1	–
Brachythecium glareosum	–	–	–	–	1	1	–	1	–	–
Hypnum cupressiforme	–	–	–	1	–	1	1	–	2	–
Rhytidiadelphus triquetrus	–	–	–	–	–	1	1	–	1	1
Rhytidiadelphus squarrosus	–	–	–	–	–	–	1	–	1	1
Preissia quadrata	–	–	–	–	–	–	–	1	–	–
Riccardia pinguis	–	–	–	1	–	–	–	1	1	2
Leiocolea badensis	–	–	–	–	–	–	–	1	–	–

TABLE 2-4 CONTINUED

	A		B		C		D		E	
	d	w	d	w	d	w	d	w	d	w
Lophocolea bidentata	–	–	–	–	–	–	1	–	1	–
Cladonia furcata	–	–	–	1	2	1	1	–	1	1
Evernia prunastri	–	–	–	–	–	–	–	1	–	–
Peltigera canina	–	–	1	–	–	–	1	–	–	–
Cladonia ~~spp~~ indet	–	–	–	–	–	1	1	–	–	–
Species that occurred on picnic areas but not on tracks or footpaths										
Equisetum arvense	–	–	–	1	1	3	–	–	–	–
Erodium glutinosum	–	–	–	1	–	–	–	–	–	–
Hydrocotyle vulgaris	–	–	–	1	–	3	–	–	–	2
Centaurium erythraea	–	–	1	–	–	–	–	–	–	–
Plantago lanceolata	–	–	1	1	1	1	–	–	1	–
Hieracium pilosella	–	–	1	–	–	–	–	–	–	–
Juncus bufonius	–	–	–	2	–	1	–	–	–	–
Eleocharis quinqueflora	–	–	–	2	–	1	–	–	–	–
Isolepis setacea	–	–	–	1	–	–	–	–	–	–
Cynosurus cristatus	–	–	–	1	–	–	–	–	–	–
Koeleria cristata	–	–	2	–	–	1	–	–	–	–
Aira praecox	–	–	1	–	1	1	–	–	1	–
Ceratodon purpureus	–	–	–	1	–	–	–	–	–	–
Bryum argenteum	–	–	1	–	–	–	–	–	1	1
Pseudoscleropodium purum	–	–	1	–	1	1	–	–	–	1
Pellia endivifolia	–	–	1	–	–	–	–	–	–	1

TABLE 2-4 CONTINUED

Species that only occurred in 'natural vegetation'	A		B		C		D		E	
	d	w	d	w	d	w	d	w	d	w
Ranunculus flammula	-	-	-	-	-	1	-	-	-	-
Ranunculus repens	-	-	-	-	-	1	-	-	-	-
Cerastium holosteoides	-	-	-	-	1	1	-	-	-	-
Arenaria leptoclados	-	-	-	-	1	-	-	-	2	-
Anthyllis vulneraria	-	-	-	-	1	1	-	-	-	-
Rubus fruticosus agg	-	-	-	-	1	1	-	-	-	-
Euphorbia portlandica	-	-	-	-	1	-	-	-	-	-
Euphorbia paralias	-	-	-	-	1	-	-	-	-	-
Gentianella amarella	-	-	-	-	-	-	-	-	-	1
Veronica chamaedrys	-	-	-	-	-	1	-	-	1	1
Mentha aquatica	-	-	-	-	-	1	-	-	-	-
Galium palustre	-	-	-	-	-	1	-	-	-	-
Cirsium arvense	-	-	-	-	1	-	-	-	1	1
Hypochoeris radicata	-	-	-	-	-	-	-	-	-	1
Crepis vesicaria	-	-	-	-	1	1	-	-	1	-
Crepis ~~spp~~ indet.	-	-	-	-	1	-	-	-	-	-
Eleocharis multicaulis	-	-	-	-	-	1	-	-	-	-
Vulpia membranacea	-	-	-	-	-	-	-	-	1	-
Catapodium marinum	-	-	-	-	-	-	-	-	1	-
Aira caryophyllea	-	-	-	-	-	1	-	-	-	-
Agrostis canina	-	-	-	-	-	-	-	-	-	1
Ditrichum flexicaule	-	-	-	-	1	-	-	-	-	-
Bryum pseudotriquetrum	-	-	-	-	-	1	-	-	-	2
Thuidium abietinum	-	-	-	-	1	-	-	-	1	-
Cratoneuron filicinum	-	-	-	-	-	-	-	-	-	1
Amblystegium serpens	-	-	-	-	1	-	-	-	-	-
Riccardia sinuata	-	-	-	-	-	-	-	-	-	2
Frullania tamarisci	-	-	-	-	-	1	-	-	-	-
Cladonia rangiferina	-	-	-	-	-	1	-	-	-	-

and footpaths (A and D) together have 77 species which again suggests that many occur 'casually' in this situation. However, as 29 of A and D group of species are not in the high bulk density group from the ordination and the efficiency of the subjective grouping has been checked on other criteria this will be used for further discussion.

Track and path ~~preference~~ occurrence index. This figure is based on the ratio of occurrences of the plants on worn areas to occurrences on unworn areas, the occurrence on tracks being given a 2 x weighting as they require particular resistance to survive these conditions. The index is expressed on a scale of 0 to 1.0 and is only valid for comparisons within the group from which it was derived (i.e. the data from this survey). The calculation was carried out as follows :

The total occurrences of the species (or group) are listed under the site categories in which they appear. (See Tables 2-4 and 2-6). The ratio of occurrences on worn areas to total occurrences is then expressed as a fraction with a 2 x weighting on the A group, i.e. e.g.

$$\frac{2A + B + D}{2A + B + C + D + E}$$

The lowest resultant figure in the group was then subtracted from all the figures giving a range of figures starting from 0. Each figure was then expressed as a fraction of the highest in the group and rounded off to 0.1 of a unit, thus giving a ~~preference~~ occurrence index ranging from 0.0 to 1.0. The fact that the subjective categories have been shown to represent ecological groups suggests that the index is a meaningful figure.

When considering these ~~preference~~ occurrence indices, it must be borne in mind that there is no indication of how well a species is growing. Observation and comments by Wright (1967) suggest that if this were considered, _Festuca rubra_ would appear as the most resistant species. Poor representation in natural vegetation will give a species a higher index than one that does equally well on paths but better in natural conditions.

~~Preference~~ Occurrence index of various life forms. The index (Table 2-5) was calculated on occurrence of all species recorded in the survey, each one being classified according to the life form system of Raunkiaer (1934) as indicated by Clapham, Tutin & Warburg (1962). It must, however, be remembered that the ~~preference~~ occurrence index of species included in the same life form group may vary markedly as in the case of _Bellis perennis_ and _Potentilla reptans_, both of which are grouped as rosette hemicryptophytes, but individually have ~~preference~~ occurrence indices of 1.0 and 0.4.

TABLE 2-5

Occurrence ~~PREFERENCE~~ INDEX OF LIFE FORMS OR CLASSIFICATORY GROUPS

Group	No. of occurrences in each stand group					Calculation of occurrence ~~preference~~ index			
	A	B	C	D	E	$\frac{2xA+B+D}{2xA+B+C+D+E}$	=	−0.26	÷0.35 = P.I.
N.	0	0	3	3	4	3/10	0.30	0.04	0.1
Chw.	2	5	6	7	6	16/28	0.57	0.31	0.9
Chh.	5	13	18	15	17	38/73	0.52	0.26	0.7
Hp.	13	27	45	40	48	93/186	0.50	0.24	0.7
Hs.	28	49	55	60	51	165/271	0.61	0.35	1.0
Hr.	21	42	41	31	37	115/193	0.60	0.34	1.0
Gr. + Grh.	0	2	8	3	6	5/19	0.26	0.00	0.0
Th.	0	9	21	16	23	25/69	0.36	0.10	0.3
Mosses Acrocarps	1	5	5	4	9	11/25	0.44	0.18	0.5
Pleurocarps	5	11	18	13	21	34/73	0.47	0.21	0.6
Liverworts	0	2	1	4	7	6/14	0.43	0.17	0.5
Lichens	0	2	5	4	2	6/13	0.46	0.20	0.6

~~Preference~~ Occurrence index 0.8 to 1.0. The high index value of most of the hemicryptophytes is not unexpected; Bates (1935 and 1938a) considers that this is probably due to the protected position of the buds, and in the case of the grasses to protected growing apex. But the increase in tiller numbers as a response to trampling (Paper 1, Fig.1-13) suggests that the apex may be damaged and survival be due to high tillering capacity. The high resistance of woody chamaephytes is not expected and is due to the fact that this group is represented by one moderately resistant species, *Thymus drucei*. A discussion of its characteristics can be found in Appendix 2.

~~Preference~~ Occurrence index 0.5 to 0.7. This group contains many vascular plants and all bryophytes and lichens: these are all affected by trampling to some extent. The lower resistance of acrocarpous mosses when compared with pleurocarpous mosses is probably due to the former's upright habit, making the stem more liable to breakage. The P.I. of lichens is higher than expected, the resistant species being *Cladonia furcata* and *Peltigera canina*. This may in part be due to the flexibility of these structures when wet; *Peltigera canina* has been observed to survive considerable trampling in this condition.

~~Preference~~ Occurrence index 0.0 to 0.4. The geophytes in this survey were all *Equisetum spp* and their very low resistance is probably due to the brittle nature of the stem which may well be irreparably damaged by a single tread.

The single nanophanerophyte was <u>Salix repens</u>. The relatively upright habit exposes this plant to the full mechanical effects of vehicles and treading and this, together with the liability of woody branches to snap, could account for its low resistance.

The low value for therophytes may be an artefact as the survey was carried out in June/August after the majority had flowered. They may, however, owe their low resistance to shallow, easily displaced rooting systems, especially in dry areas, and the fact that the seedling roots have to penetrate the hard soil surface which is very marked on tracks in wet areas.

This life form study agrees with the general theories of previous workers such as Bates (1938a).

<u>Transect records</u>. The surface profiles of the track (transect I), footpath (transect II) and cattle and sheep path (transect III) show the lateral distribution characteristic of these features (Figs.2-5, 2-6 and 2-7). The deep impression and the two wheel ruts with ill-defined edges can be seen on most car tracks in dry areas (Fig.2-5). The wide lateral spread of the footpath (Fig.2-6) with a central slightly depressed region shows a similar distribution to that of people on footpaths

Fig.2-5

Transect I car track.

a) Surface profile and vertical contours of equal soil penetration resistance. Number of hits for each 6 cm depth indicated by contours. Vertical scale exaggerated 25 times. 'Wheel' diagram shows width of average car.

b) *Galium verum*

c) *Thymus drucei*

d) *Carex arenaria*

e) *Festuca rubra*

f) *Poa pratensis*

g) *Agrostis tenuis*

h) ——— *Camptothecium lutescens* - - - *Brachythecium albicans*

i) Percentage of total dry weight ——— *Festuca rubra* - - - *Poa pratensis* ····· *Agrostis tenuis*

j) Rosette plants

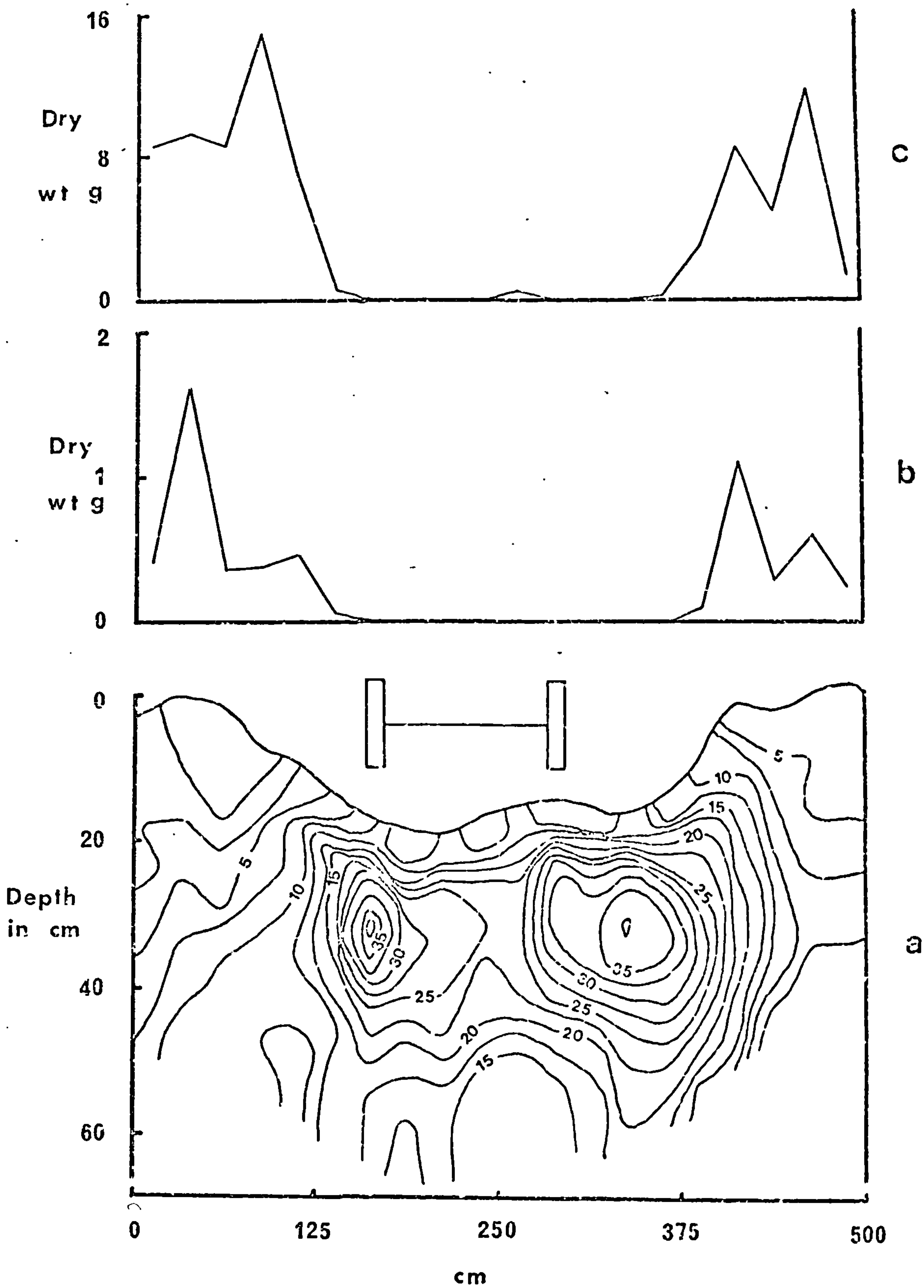
K) Percentage monocotyledonous species

l) Percentage dicotyledonous species

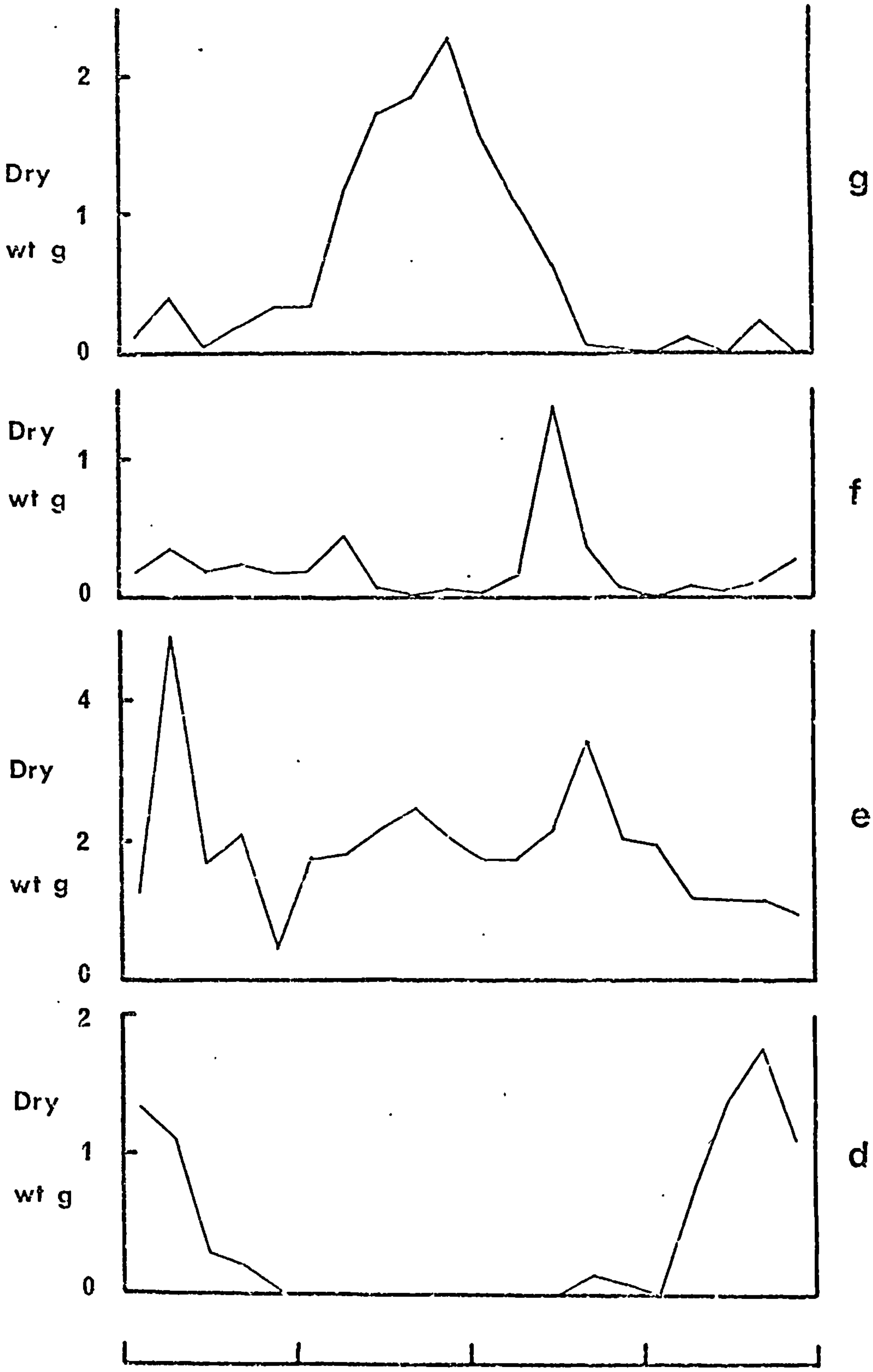
m) ——— species number - - - - diversity index

n) Total biomass dry weight

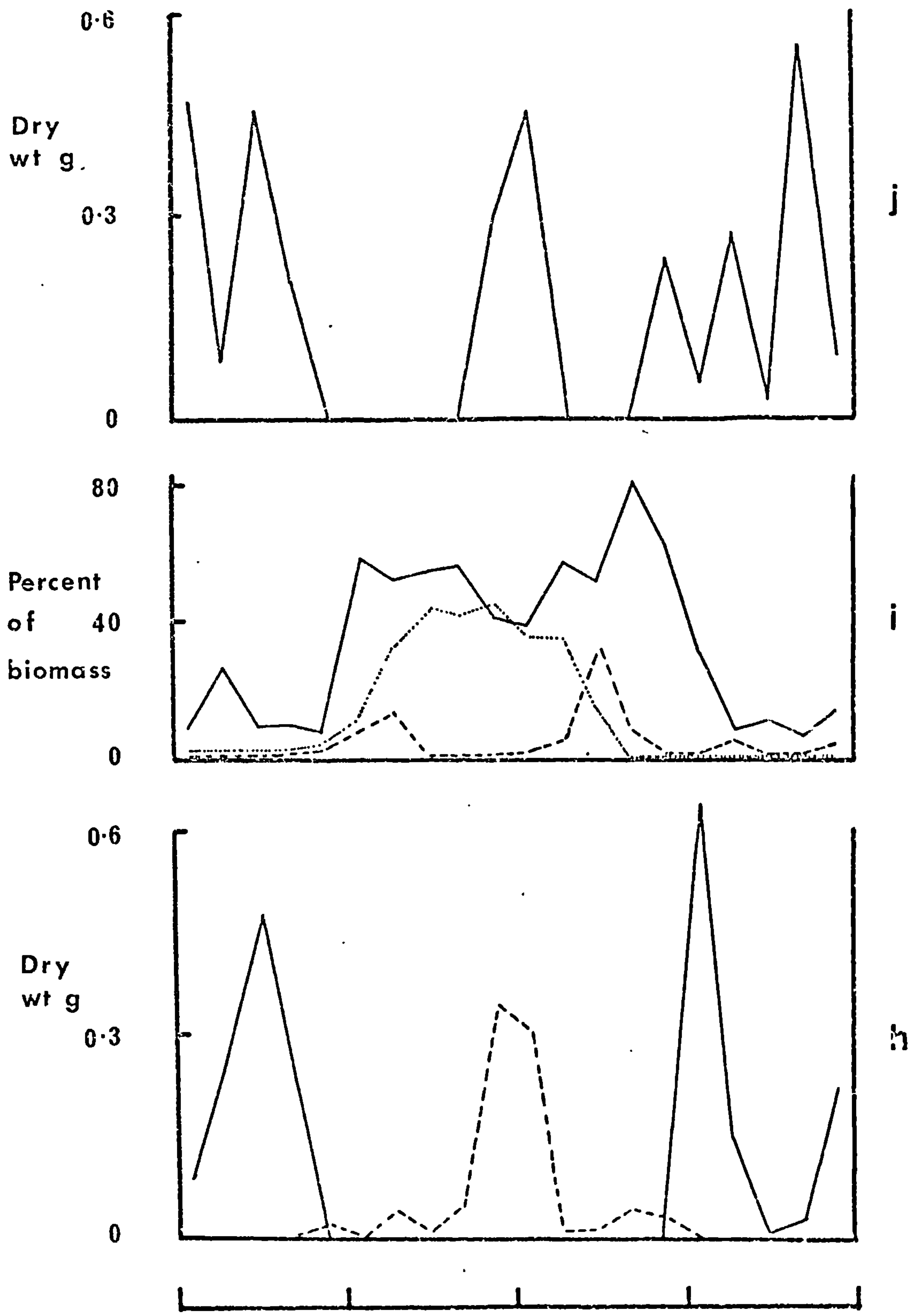
o) Percentage of resistant species

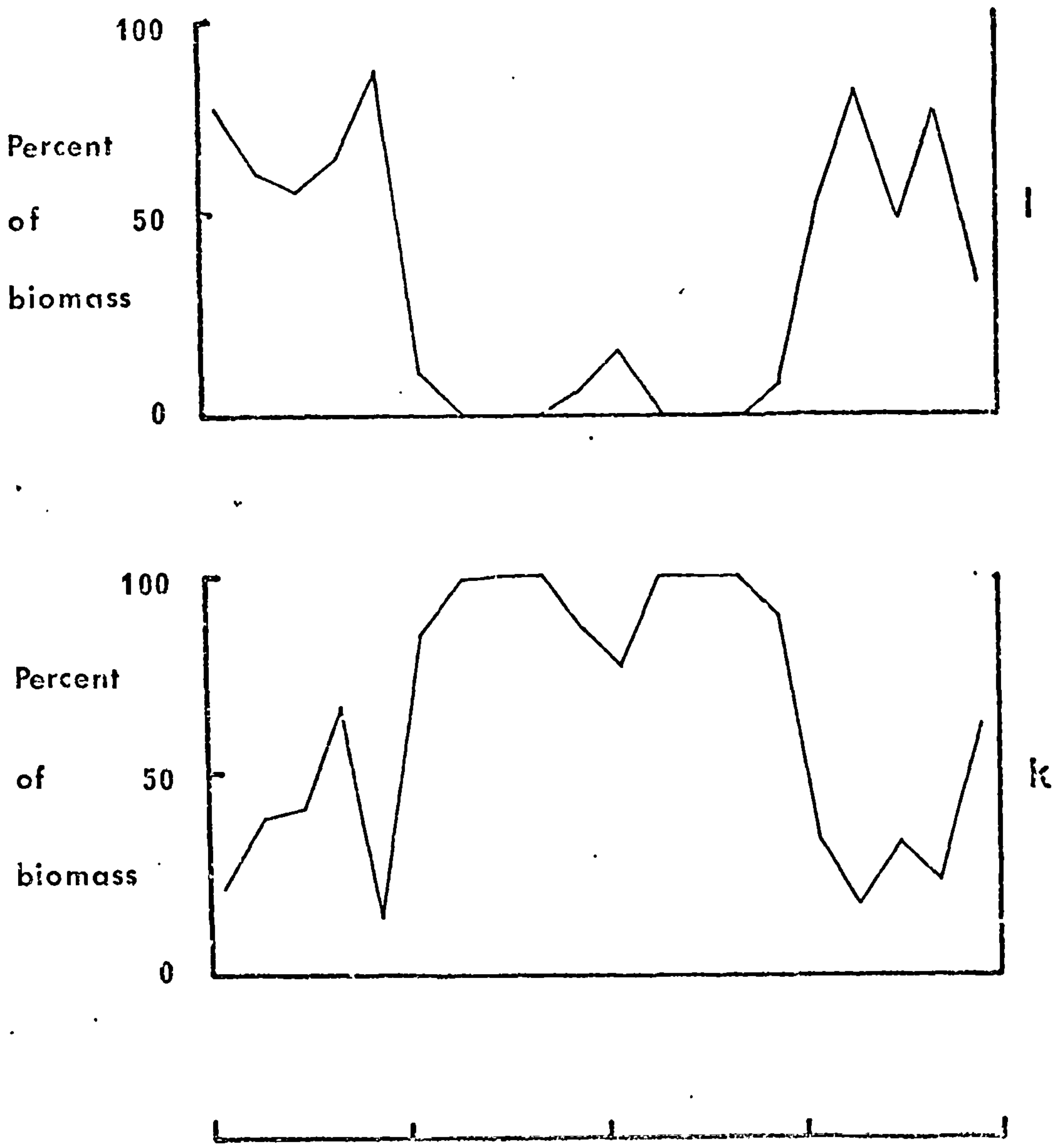


16
Dry
8
wt g
0
c
2
Dry
1
wt g
0
b
0
20
Depth
in cm
40
60
a
5
10
15
20
25
30
35
0
125
250
375
500
cm



2
Dry
1
wt g
0
g
Dry
1
wt g
0
f
4
Dry
2
wt g
0
e
2
Dry
1
wt g
0
d


0·6
Dry
wt g.
0·3
0
j
80
Percent
of 40
biomass
0
i
0·6
Dry
wt g
0·3
0
h


100
Percent
of
50
biomass
0
l
100
Percent
of
50
biomass
0
k

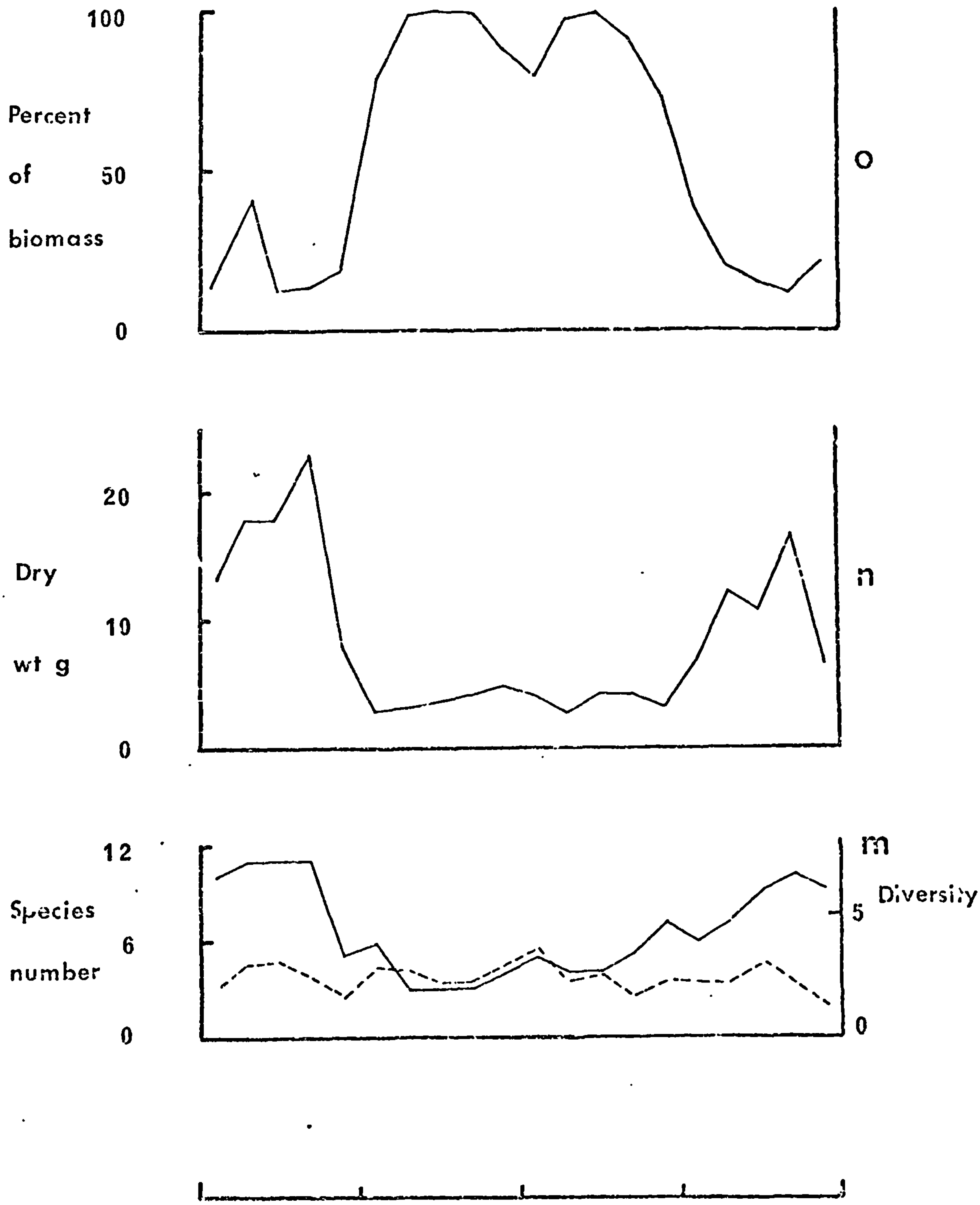

100
Percent
of
50
biomass
0
o
20
Dry
10
wt g
0
n
12
Species
number
6
0
m
Diversity
5
0

Fig.2-6

TransectII footpath.

a) Surface profile and vertical contours of equal soil penetration resistance. Number of hits for each 6 cm depth indicated by contours. Vertical scale exaggerated 25 times.

b) Bellis perennis

c) Galium verum

d) Trifolium repens

e) Thymus drucei

f) Luzula campestris

g) ——— Carex flacca - - - - Carex arenaria

h) Festuca rubra

i) Poa pratensis

j) Ammophila arenaria

k) Agrostis tenuis

l) ——— Camptothecium lutescens - - - Bryum spp
-·-·-· Tortula ruraliformis

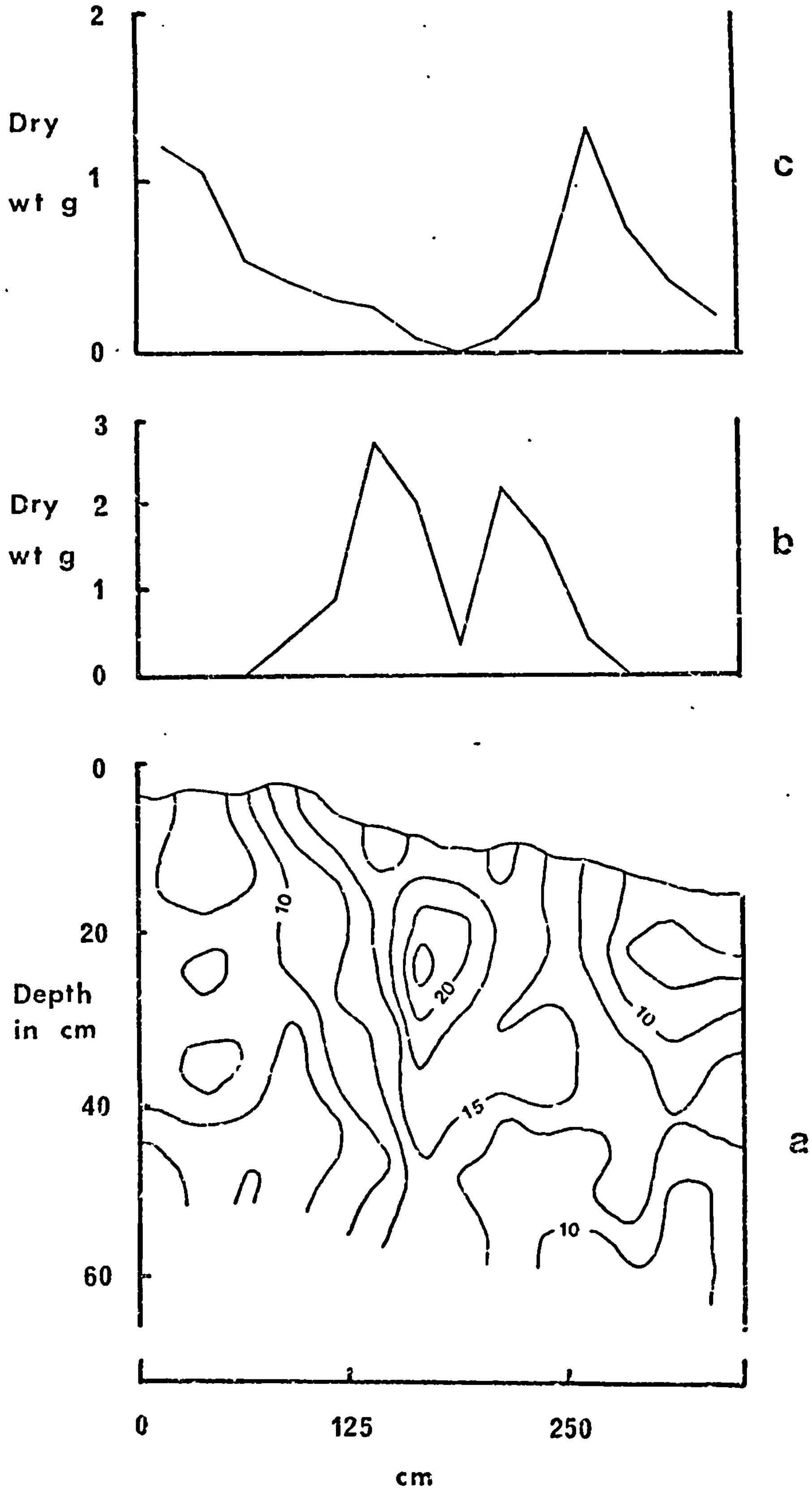
m) Percentage monocotyledonous species

n) Percentage dicotyledonous species

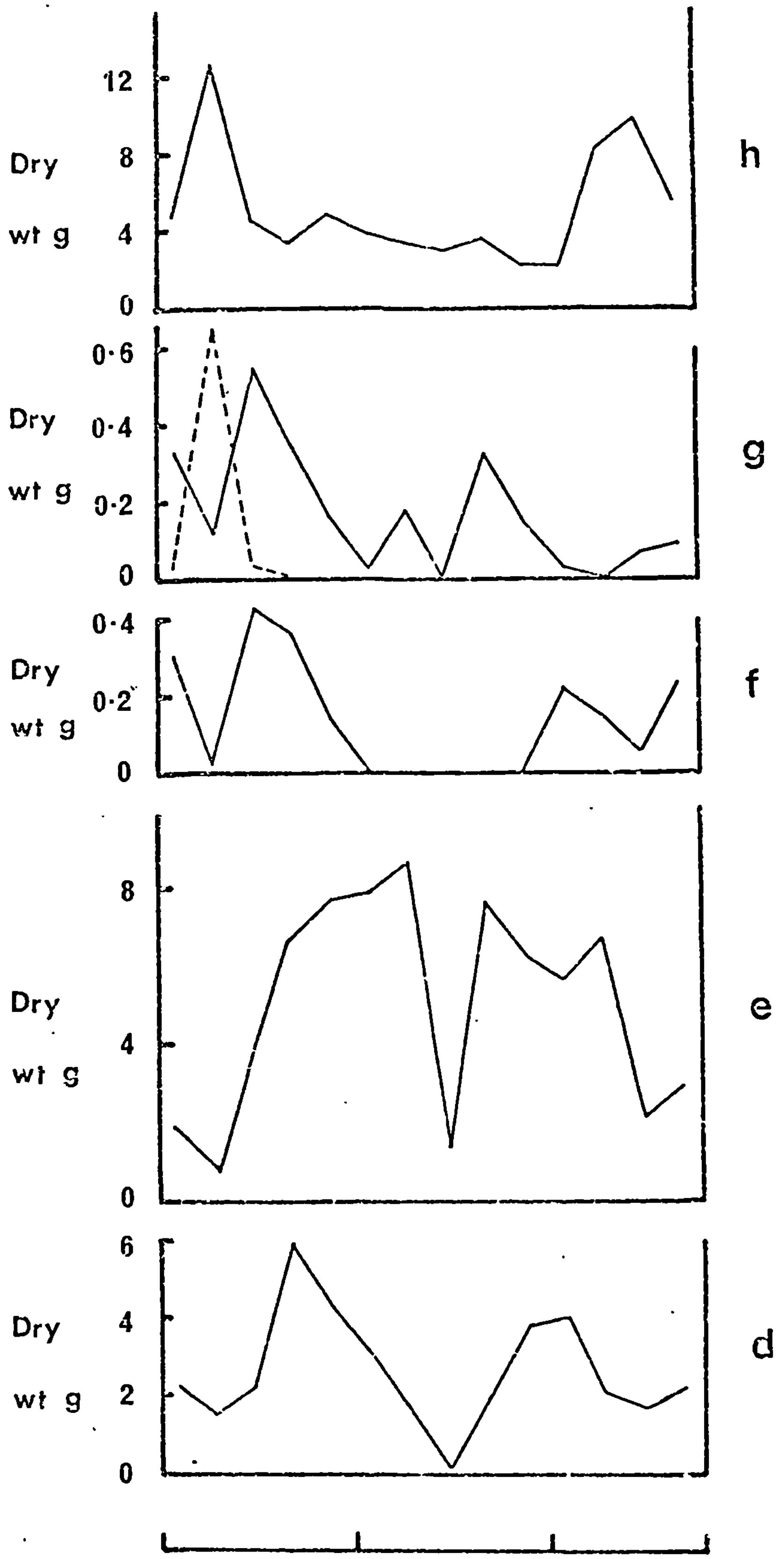
o) ——— species number - - - diversity index

p) Total biomass

q) Percentage resistant species



2
Dry
1
wt g
0
c
3
Dry
2
wt g
1
0
b
0
10
20
20
Depth
in cm
10
15
40
10
60
a
0
125
250
cm



12
Dry
8
wt g
4
0
h
0·6
Dry
0·4
wt g
0·2
0
g
0·4
Dry
0·2
wt g
0
f
8
Dry
4
wt g
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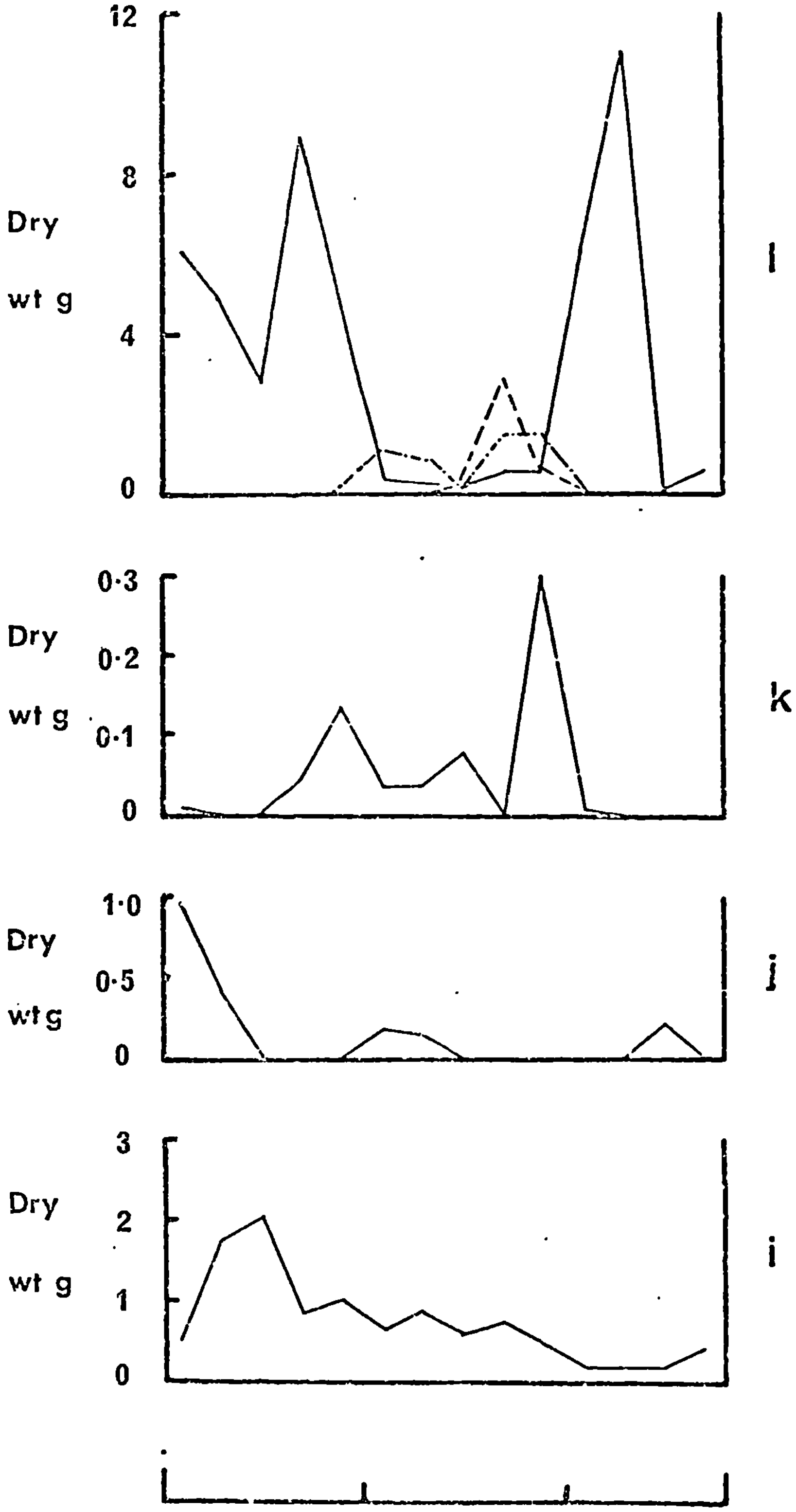
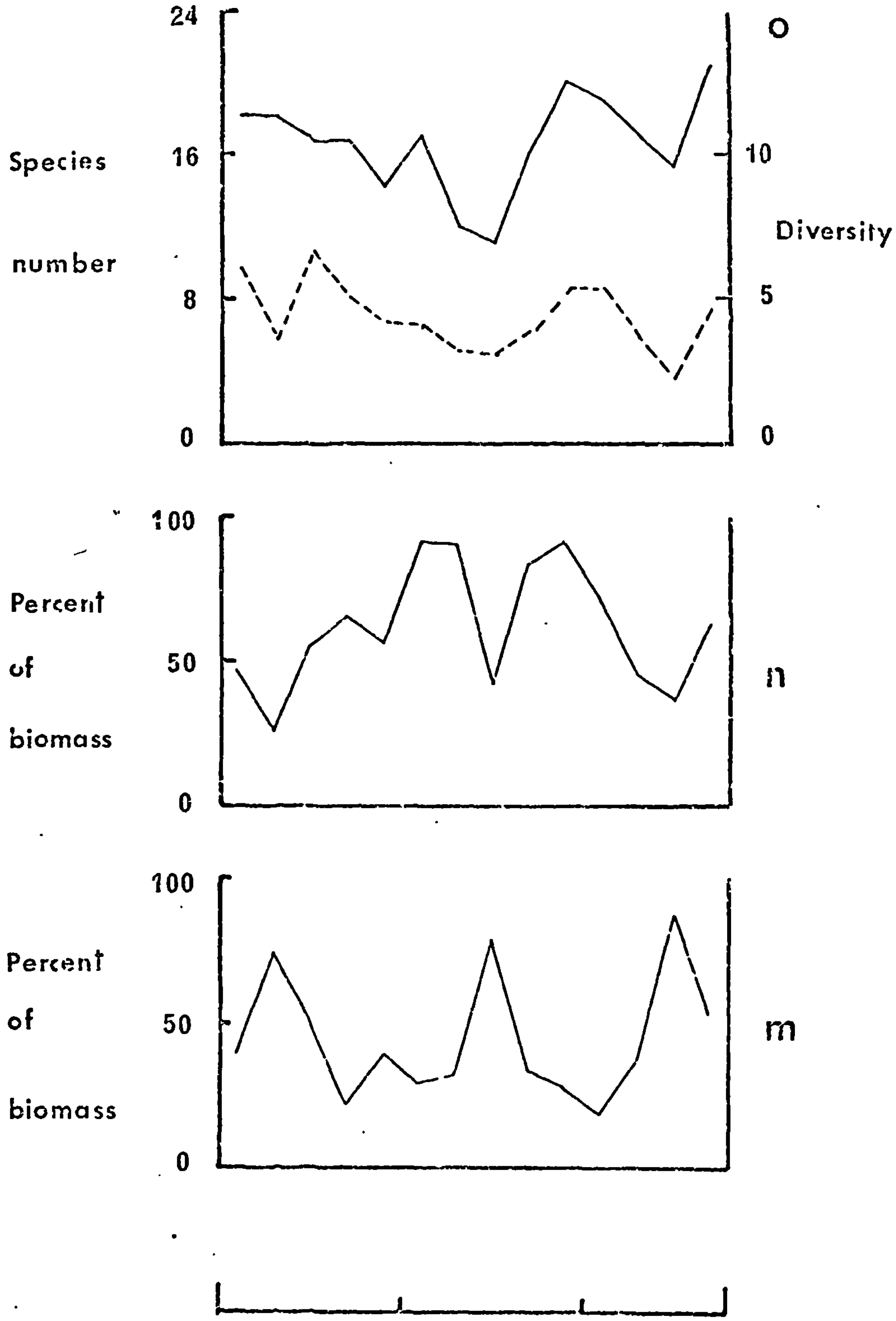
e
6
Dry
4
wt g
2
0
d



12
8
Dry
wt g
4
0
l
0·3
Dry
0·2
wt g
0·1
0
k
1·0
Dry
0·5
wt g
0
j
3
Dry
2
wt g
1
0
i



24
16
8
0
Species
number
10
5
0
Diversity
o
100
50
0
Percent
of
biomass
n
100
50
0
Percent
of
biomass
m

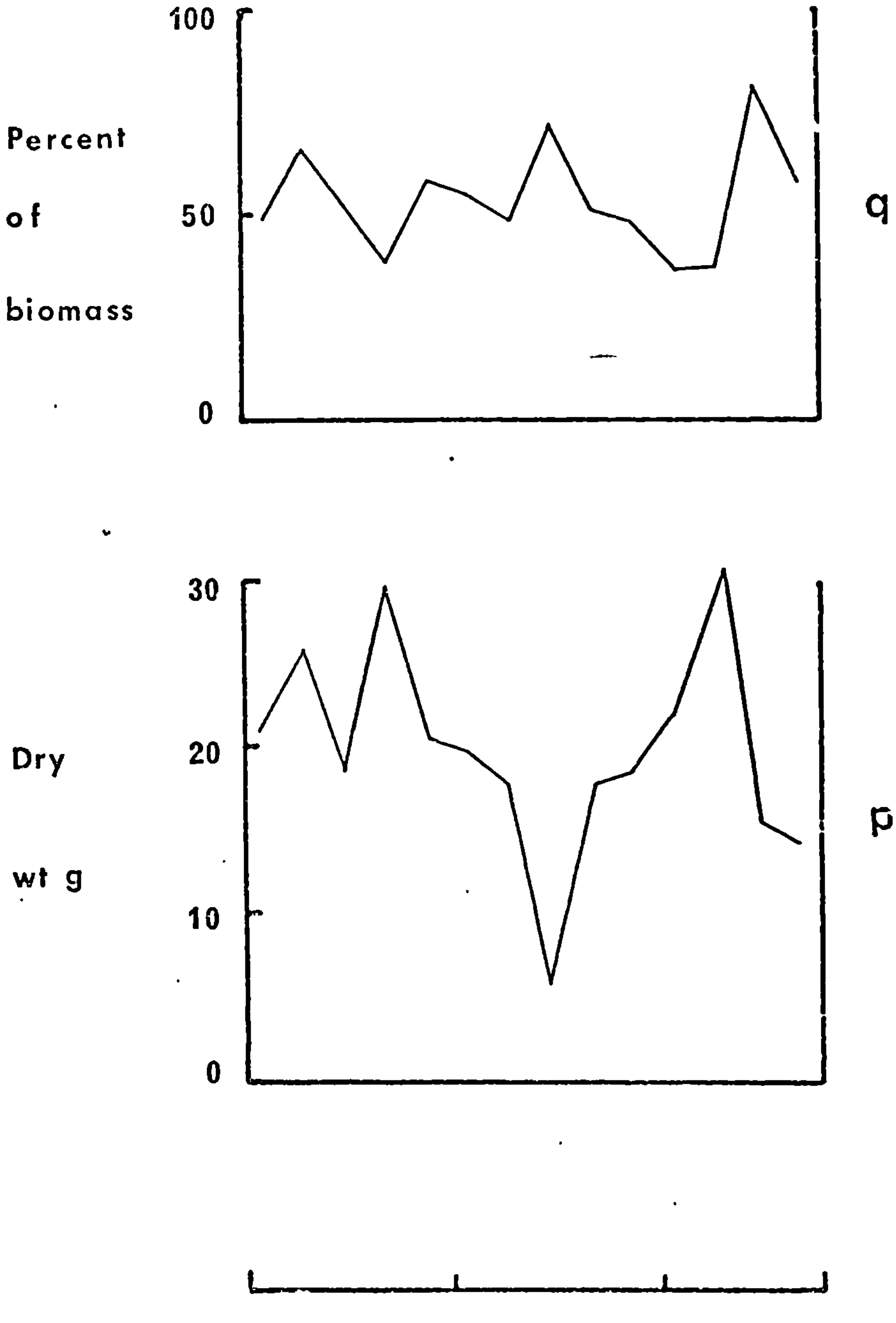

100
Percent
of
biomass
50
0
q
30
Dry
20
wt g
10
0
p

Fig.2-7

Transect III sheep and cattle track.

a) Surface profile and vertical contours of equal soil penetrationresistance. Number of hits for each 6 cm depth indicated by contours. Vertical scale exaggerated 25 times.

b) _Bellis perennis_

c) _Galium verum_

d) _Trifolium repens_

e) _Luzula campestris_

f) ---- _Carex flacca_ - - - _Carex arenaria_

g) _Festuca rubra_

h) _Poa pratensis_

i) _Agrostis tenuis_

j) ---- _Pseudoscleropodium purum_ - - - _Rhytidiadelphus squarrosus_

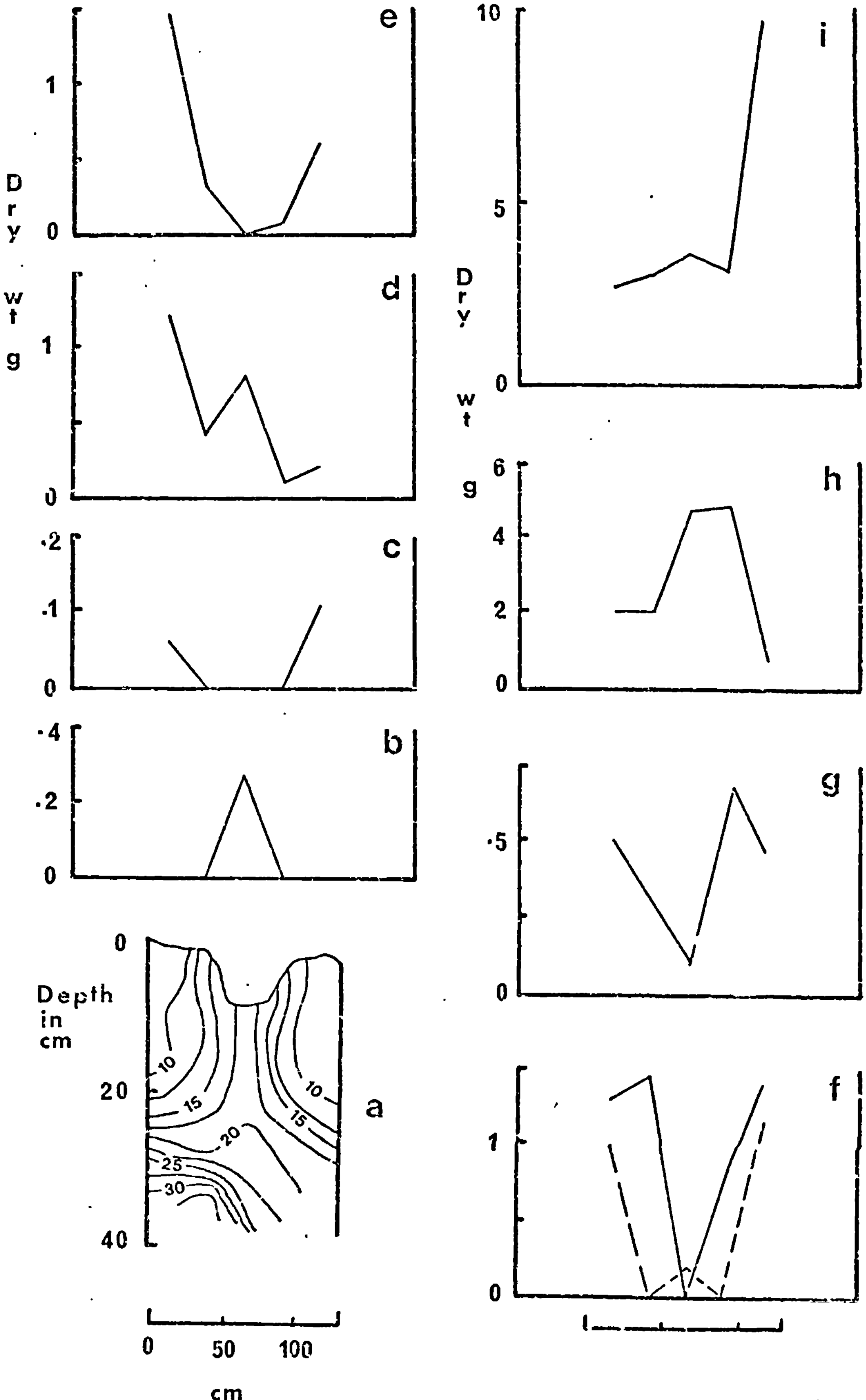
k) Percentage monocotyledonous species

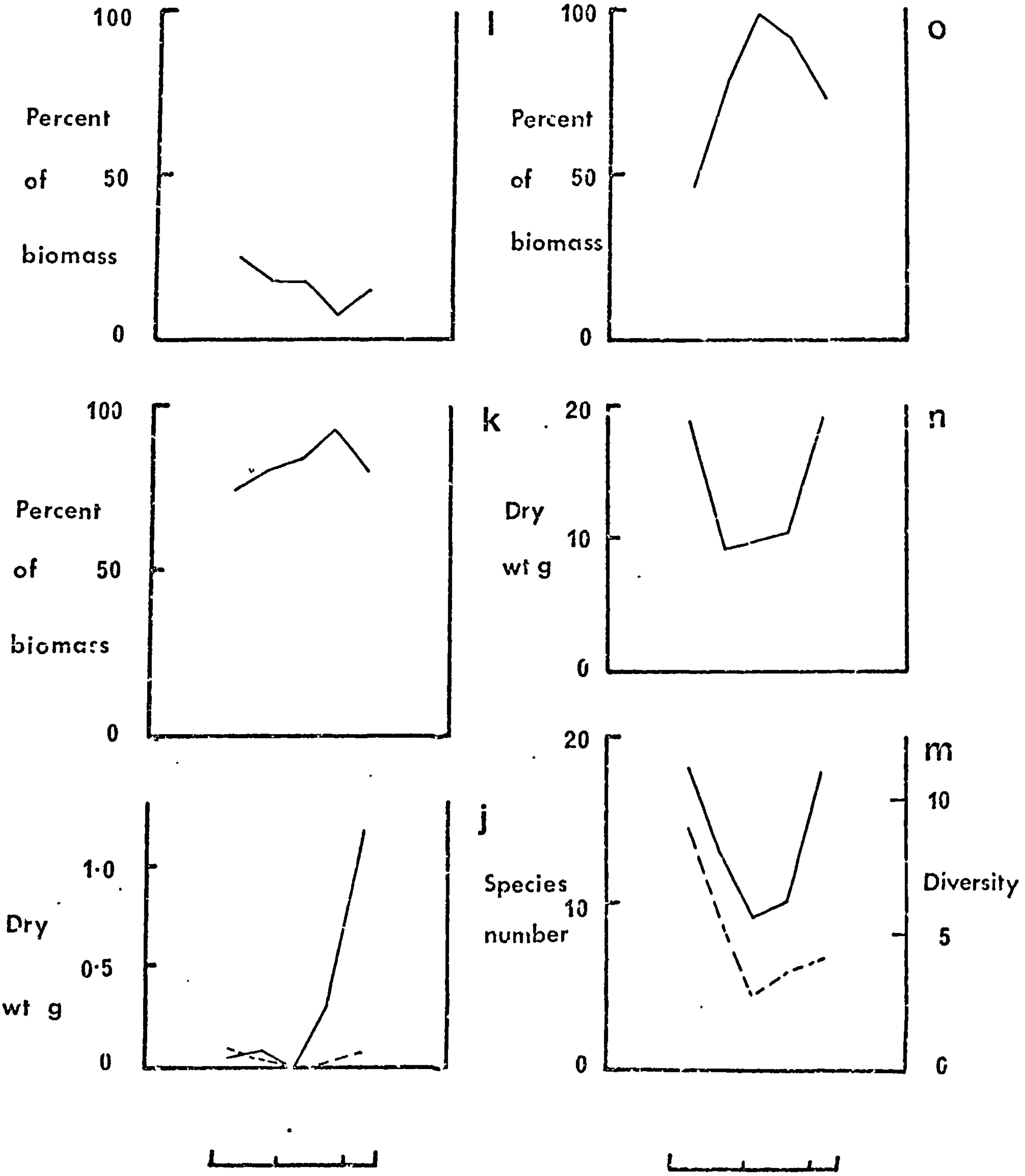
l) Percentage dicotyledonous species

m) ---- species number - - - diversity index

n) Total biomass

o) Percentage resistant species


e
d
c
b
a
i
h
g
f
Dry wt g
Depth in cm
10
15
20
25
30
0
20
40
0 50 100
cm
1
0
·2
·1
·4
10
5
6
4
2
·5



l
100
Percent
of 50
biomass
0
o
100
Percent
of 50
biomass
0
k
100
Percent
of 50
biomass
0
n
20
Dry
10
wt g
0
j
1·0
Dry
0·5
wt g
0
m
20
Species
10
number
0
10
Diversity
5
0

shown by Bayfield (1971) and Goldsmith et al (1970). The deep vertical sided cattle track (Fig.2-7) is of the type described as typical by Bates (1951).

The general distribution of compressed zones as shown by the penetrometer readings was similar at all three sites with the maximum reading beneath the most impressed area of track at a depth of 12-18 cm, except under the animal track where the reading was distorted by a clay layer. The surface layers may have been moved by the horizontal torque forces exerted by feet (see Harper et al 1961) and wheels (Freitag 1968) thus preventing maximum compaction being retained at these levels this effect was also noted by Arndt & Rose (1966). Below 18 cm depth the soil on sites I and II became less compacted with increasing depth to the lowest level measured.

The maximum readings were 38.5, 23.7 and 33.0 on transects I, II and III respectively, the footpath only reaching two thirds of the compaction under the car track (L.P.I. 1.59, 1.38 and 1.52 respectively). The lateral spread of compaction beneath the soil is particularly evident at transect I (Fig.2-5) and suggests that the influence on deep rooting plants may be wider than the apparent width of the track. This effect was not obvious at the other two sites.

The total biomass of the above ground part of the vegetation is reduced in the centre of all transects and at the extreme end of I and II (Figs.2-5n and 2-6p). The reduction in the centre may be predicted from casual observation, the peaks in the marginal areas agree with observations made by Randerson (1969).

When distribution of individual species is examined two principal forms are observed, a unimodal one with the peak in the centre of wear (or bimodal on transect I), and a bimodal one with the peaks at the side of the paths (or trimodal on transect I). The former distribution is shown by <u>Brachythecium albicans</u> on transect I (Fig.2-5h), <u>Agrostis tenuis</u> and most monocotyledonous species and the sum of resistant species on III (Fig.2-7i, k and o). The latter is shown by most dicotyledonous species, <u>Poa pratensis</u>, <u>Camptothecium lutescens</u> and <u>Festuca rubra</u> on II (Figs.2-6n, i, e and h) and by rosette plants on I (Fig.2-5j). Resistant species and monocotyledonous species show an unexpected trimodal distribution on transect II (Figs.2-6q and m) which suggests that they are not so successful under moderate levels of trampling. It is probable that they succeed in the competition for light away from the path by virtue of their taller growth; moderate trampling breaks the taller structure but it is not sufficient to damage the dicotyledonous species. Towards the centre where the trampling is greater the protected apices and intercalary meristems again give the monocotyledonous species an advantage.

Diversity which gives an indication of the evenness of the community (Hill 1973b) and species number show a generally similar bimodal distribution except on transect I (Fig.2-5m) where diversity is relatively uniform but reaches the highest point in the centre. This indicates that as the number of species have been reduced by wear, so the total biomass has been shared more equally between them, possibly due to a reduction of the interference between species. This could be interpreted as a more efficient use of the resources remaining available to the plants. Crocker (1953) considers that heavy grazing creates vacant ecological niches which are occupied by less palatable species either from within the community or from outside; trampling appears to have a similar effect. But if the occupying species is from within the community then an existing niche has been expanded in area at the expense of others rather than a new one created and the trampling has imposed uniformity on the environment. This could produce a less diverse community and may be the condition created by extreme wear in the centre of the ruts and on the path. The fact that both species number and diversity have been reduced by trampling, except diversity at the edges and centre of transect I, is contrary to the expectations of both Westhoff (1967) and van der Maarel (1971) who consider that moderate trampling may increase species diversity, but this may be due to grazing having an effect on the whole area similar to that of light trampling.

There was generally a better correlation between plants and soil penetration resistance at 6-12 cm depth than any other level, so this depth will be used in the following discussion. (It is not thought that this relationship is directly causal with most species as many have their roots only in the surface layers). The percentage of dicotyledons and monocotyledons best summarises this relationship, and is illustrated in Figs.2-8a and b. In the left hand ~~lower~~ part of the curve dicotyledons increase and monocotyledons decrease with increasing penetration resistance, but this relationship is reversed above a penetration resistance of 15 ~~10.5~~.

A similar relationship emerges for transect II (Figs.2-8d and e) but transect III (Figs.2-8g and h) has insufficient points to show a clear pattern; there is apparently more treading damage at lower soil penetration resistance. Percentage resistant species show a

Fig.2-8

Percentages of monocotyledonous species, dicotyledonous species and resistant species plotted against soil penetration resistance between 6 and 12 cm depth. from each of the three transects.

Transect I with the greatest range of soil penetration resistance.

a) Monocotyledonous species

b) Dicotyledonous species

c) Resistant species

Transect II with relatively low penetration resistance.

d) Monocotyledonous species

e) Dicotyledonous species

f) Resistant species

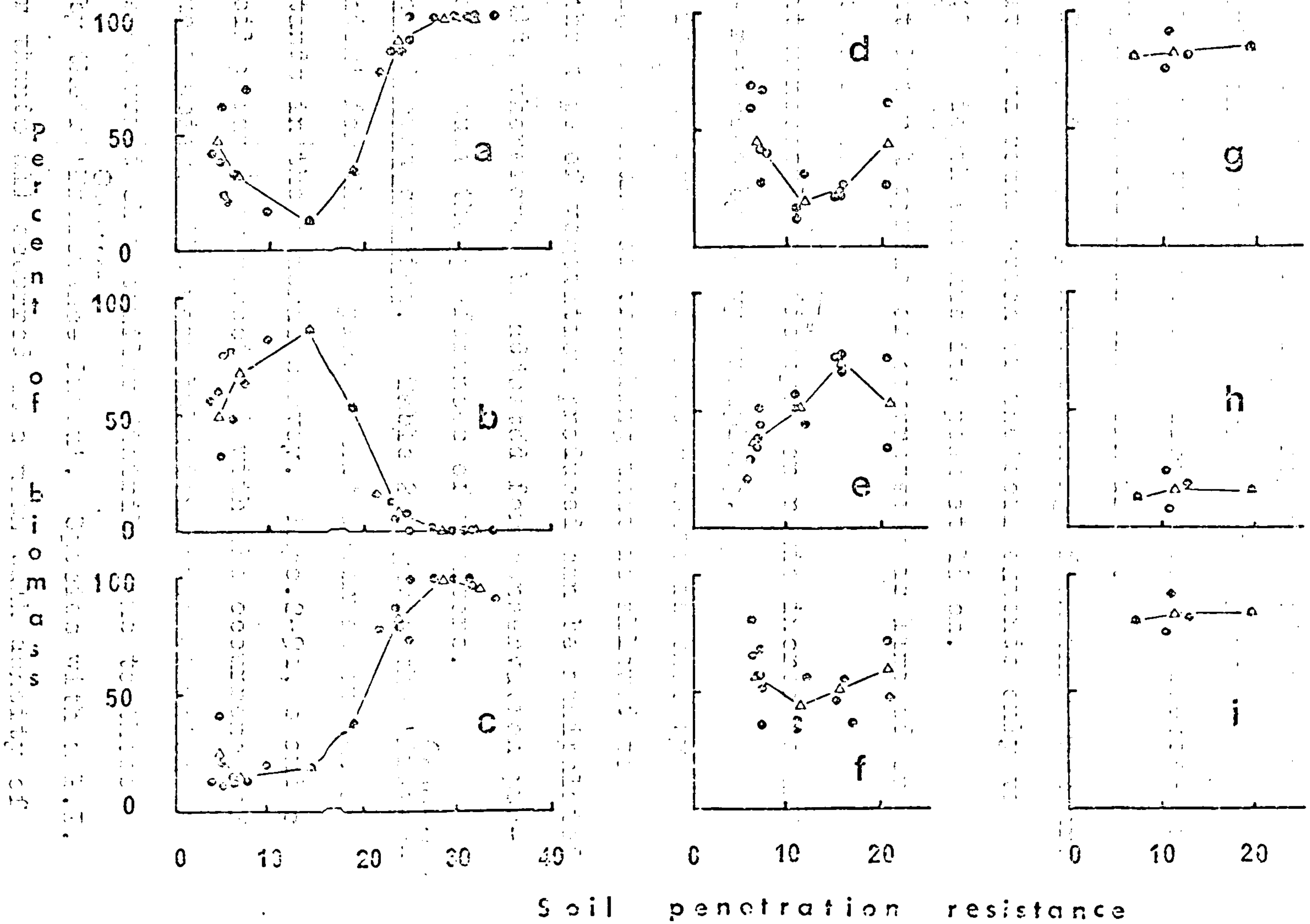
Transect III with intermediate penetration resistance.

g) Monocotyledonous species

h) Dicotyledonous species

i) Resistant species

△ mean of all occurrences in each group of 10 penetrometer impacts


Percent of biomass
100
50
0
a
b
c
d
e
f
g
h
i
0
10
20
30
40
Soil penetration resistance

2-3

level ~~lag~~ phase and then a steep increase with increasing hardness (Figs2-8c, f and i). They may differ from monocotyledonous species in having a low representation in unworn vegetation and from dicotyledonous species in their high proportion in the worn areas.

The principal points to emerge from this work are:

1. That high compression of the soil extends only to about 40 cm depth and has its peak at 18 cm.
2. That lateral spread of compression is limited but that it does occur.
3. That monocotyledon/dicotyledon ratio increases and then is reversed by heavy trampling.

The implication of these results is that by changing the amount of trampling that is allowed to occur the type of vegetation produced can be manipulated and could, therefore, be adjusted for conservation purposes or to suit the preferences of visitors.

Data on selected species. Table 2-6 gives the 'Occurrence ~~Preference~~ Index' for the 30 species that occurred in ten or more stands in the general survey. Figs.2-9a, b and c give soil parameters associated with the occurrence of the same species: the mean bulk densities at which species occurred show similar distributions to those given by their 'Occurrence ~~Preference~~ Index'. Species with a O.I. greater than 08 all occurred at a mean bulk density of

TABLE 2-6

Occurrence ~~PREFERENCE~~ INDEX OF SPECIES COMMON IN SURVEY

Species	No. of occurrences in each stand group A	B	C	D	E	Calculation of Occurrence ~~preference~~ index: $\frac{2xA+B+D}{2xA+B+C+D+E}$	=	$-0.18 \div 0.65$	=P.I.
Bellis perennis	5	8	3	7	5	25/33	0.83	0.65	1.0
Poa pratensis	8	7	4	9	3	32/39	0.82	0.64	1.0
Juncus articulatus	4	5	3	3	2	16/21	0.76	0.58	0.9
Potentilla anserina	3	4	3	1	1	11/15	0.73	0.55	0.9
Brachythecium albicans	2	3	1	3	4	10/15	0.67	0.49	0.8
Taraxacum laevigatum	3	1	1	4	4	11/16	0.69	0.51	0.8
Agrostis tenuis	2	4	4	3	3	11/18	0.61	0.43	0.7
Carex flacca	3	4	6	5	4	15/25	0.60	0.42	0.7
Festuca rubra	7	7	7	10	9	31/47	0.66	0.48	0.7
Galium verum	4	4	6	6	6	18/30	0.60	0.42	0.7
Taraxacum officinale	2	5	4	3	4	12/20	0.60	0.42	0.7
Trifolium repens	2	7	5	5	5	16/26	0.61	0.43	0.7
Agrostis stolonifera	2	6	7	5	6	15/28	0.54	0.36	0.6
Leontodon autumnalis	2	4	5	2	3	10/18	0.55	0.37	0.6
Leontodon taraxacoides	3	7	8	10	9	23/40	0.57	0.39	0.6
Thymus drucei	2	5	6	7	6	16/28	0.57	0.39	0.6
Tortula ruraliformis	1	3	2	3	4	8/14	0.57	0.39	0.6
Anthoxanthum odoratum	1	2	2	3	5	7/14	0.50	0.32	0.5
Camptothecium lutescens	1	1	3	4	5	7/15	0.47	0.29	0.5
Carex arenaria	3	4	8	9	9	19/36	0.53	0.35	0.5
Lotus corniculatus	1	4	6	5	5	11/22	0.50	0.32	0.5
Ammophila arenaria	2	2	6	6	8	12/26	0.46	0.28	0.4
Luzula campestris	0	1	3	4	4	5/12	0.42	0.24	0.4
Potentilla reptans	2	1	5	1	3	6/14	0.43	0.25	0.4
Senecio jacobaea	0	4	3	1	4	5/12	0.42	0.24	0.4
Viola canina	1	2	7	6	7	10/24	0.42	0.24	0.4
Poa subcaerulea	0	3	7	4	5	7/19	0.37	0.19	0.3
Prunella vulgaris	0	2	5	3	4	5/14	0.36	0.18	0.3
Viola tricolor	0	1	3	2	4	3/10	0.30	0.12	0.2
Linum catharticum	0	0	3	2	6	2/11	0.18	0.00	0.0

Fig.2-9

Soil data for each of the common species.

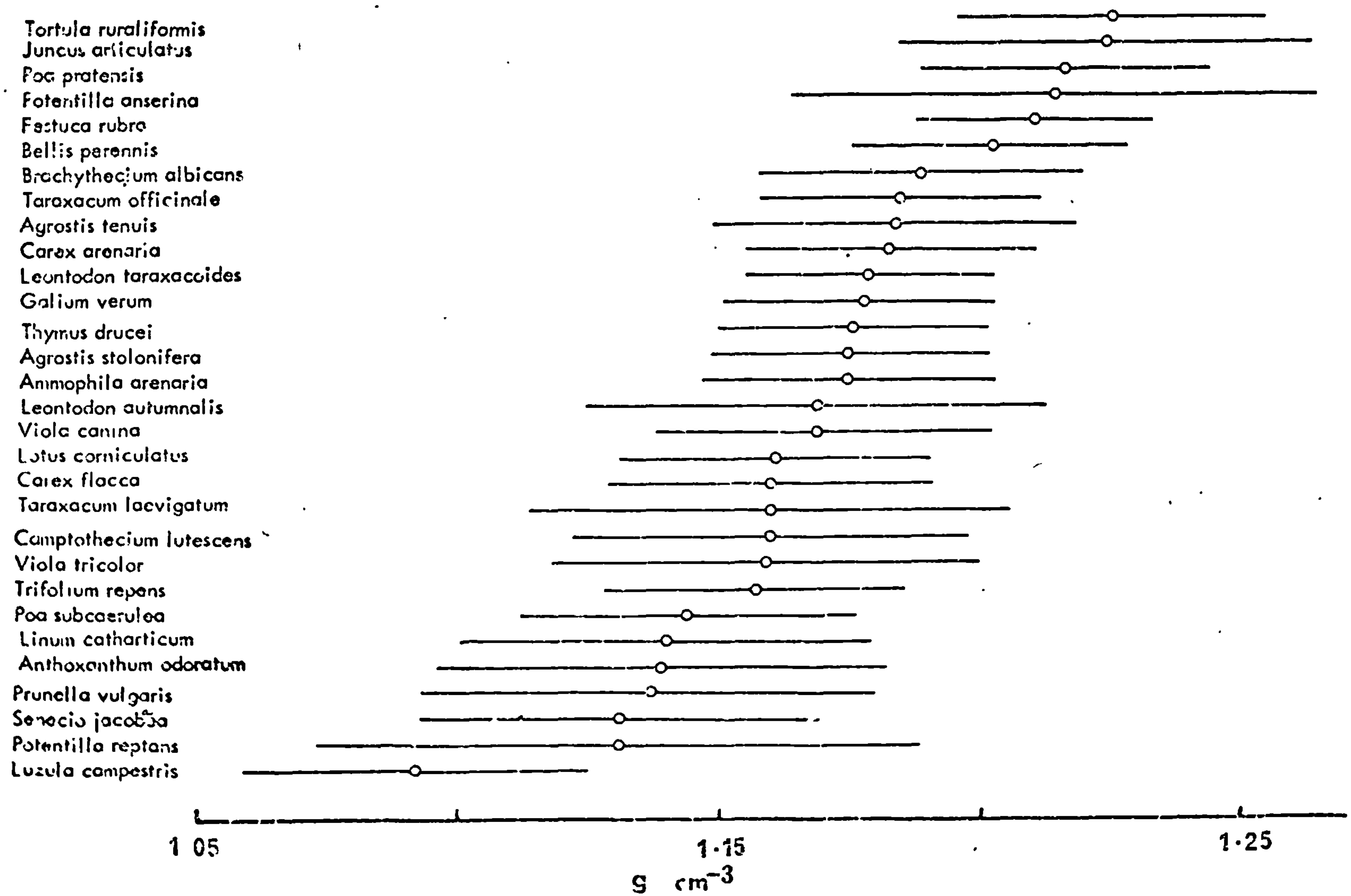
a) Soil bulk density g.cm^{-3}

b) Log soil penetration resistance

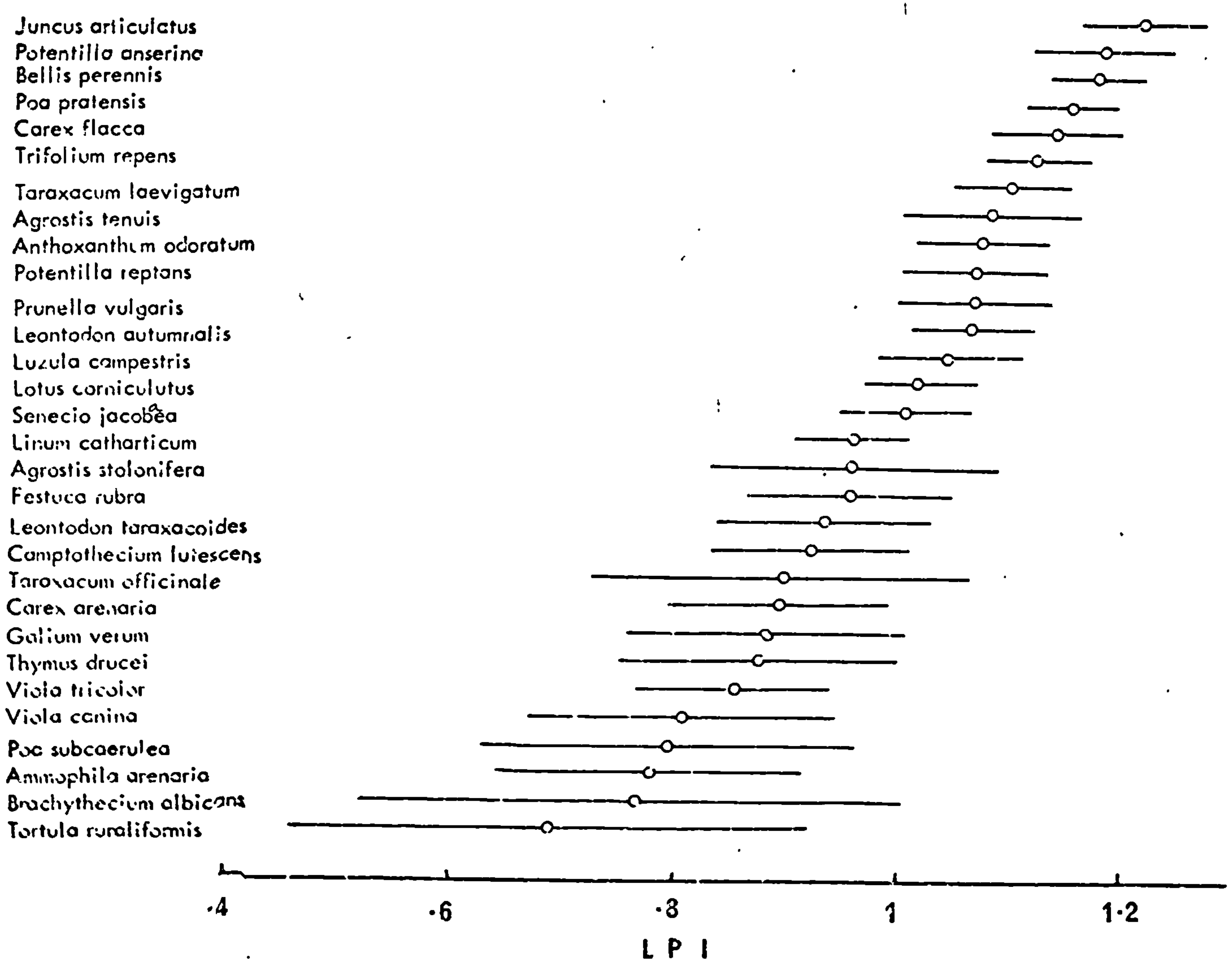
c) Percentage volumetric soil water content

♁ Mean

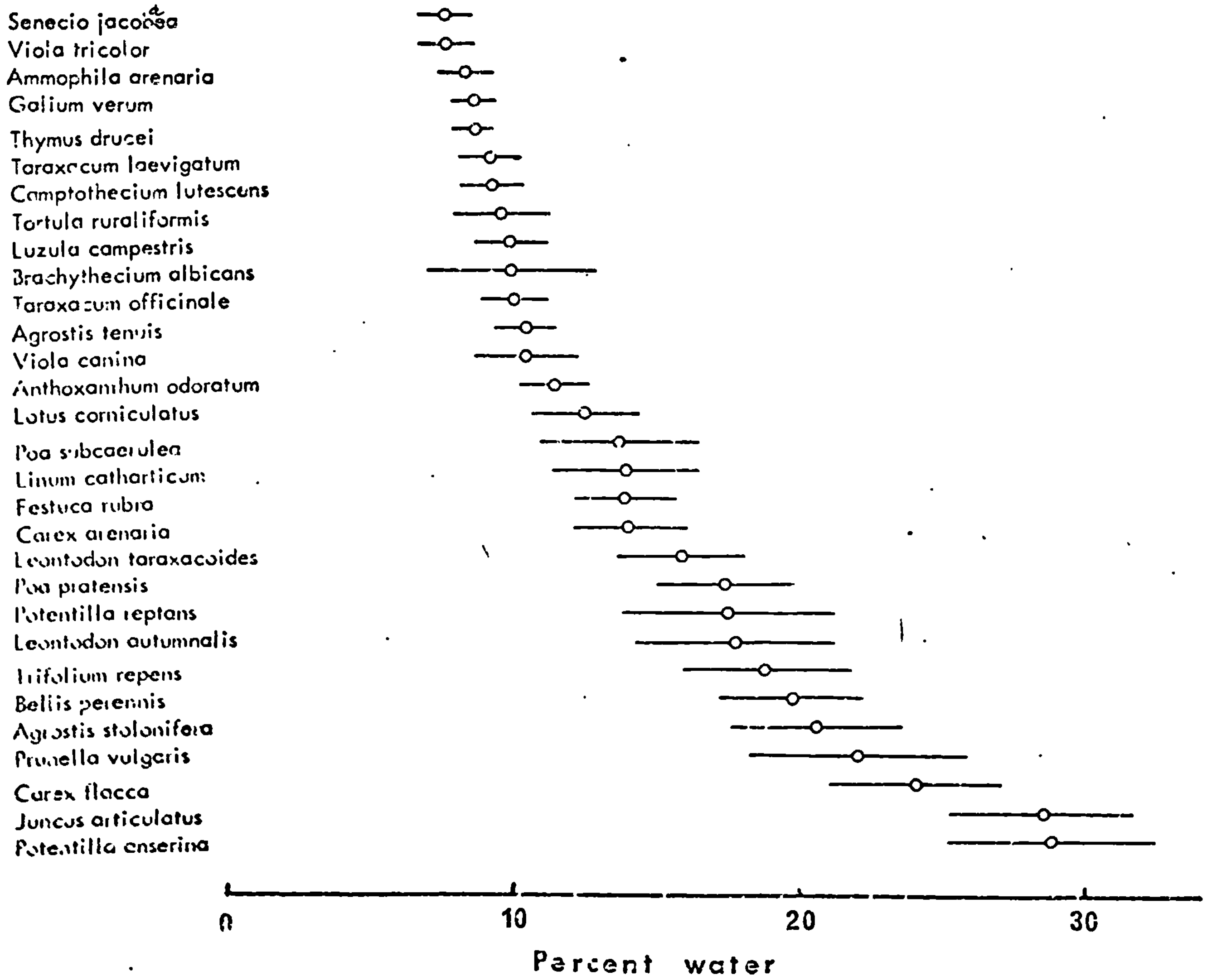
——— 2 standard errors


Tortula ruraliformis
Juncus articulatus
Poa pratensis
Potentilla anserina
Festuca rubra
Bellis perennis
Brachythecium albicans
Taraxacum officinale
Agrostis tenuis
Carex arenaria
Leontodon taraxacoides
Galium verum
Thymus drucei
Agrostis stolonifera
Ammophila arenaria
Leontodon autumnalis
Viola canina
Lotus corniculatus
Carex flacca
Taraxacum laevigatum
Camptothecium lutescens
Viola tricolor
Trifolium repens
Poa subcaerulea
Linum catharticum
Anthoxanthum odoratum
Prunella vulgaris
Senecio jacobaea
Potentilla reptans
Luzula campestris
1 05
1·15
1·25
g cm^{-3}

2 – 9a



Juncus articulatus
Potentilla anserina
Bellis perennis
Poa pratensis
Carex flacca
Trifolium repens
Taraxacum laevigatum
Agrostis tenuis
Anthoxanthum odoratum
Potentilla reptans
Prunella vulgaris
Leontodon autumnalis
Luzula campestris
Lotus corniculatus
Senecio jacobaea
Linum catharticum
Agrostis stolonifera
Festuca rubra
Leontodon taraxacoides
Camptothecium lutescens
Taraxacum officinale
Carex arenaria
Galium verum
Thymus drucei
Viola tricolor
Viola canina
Poa subcaerulea
Ammophila arenaria
Brachythecium albicans
Tortula ruraliformis
·4
·6
·8
1
1·2
L P I



Senecio jacobaea
Viola tricolor
Ammophila arenaria
Galium verum
Thymus drucei
Taraxacum laevigatum
Camptothecium lutescens
Tortula ruraliformis
Luzula campestris
Brachythecium albicans
Taraxacum officinale
Agrostis tenuis
Viola canina
Anthoxanthum odoratum
Lotus corniculatus
Poa subcaerulea
Linum catharticum
Festuca rubra
Carex arenaria
Leontodon taraxacoides
Poa pratensis
Potentilla reptans
Leontodon autumnalis
Trifolium repens
Bellis perennis
Agrostis stolonifera
Prunella vulgaris
Carex flacca
Juncus articulatus
Potentilla anserina
0
10
20
30
Percent water

2 - 9c

over 1.2 $g.cm^{-3}$ and it is noticeable that these species occurred in wet areas with a mean water content above 15%. This suggests that watering may well be a technique that would encourage the growth of these species. The correlation may be directly caused by increased water content allowing faster plant growth or by such indirect causes as reduction in soil movement. The soil penetration resistance means tended to be a combination of the bulk density and water content; this is probably because both factors affect penetrometer readings.

GENERAL DISCUSSION

The general survey emphasised the importance of trampling as an environmental factor. The phenomena of increasing soil bulk density and penetration resistance showed a similar distribution in relation to the vegetation as that found by Bayfield (1971) and Streeter (1971). The resistant species had mostly been described as such by Bates (1935 and 1938a) and more recently LaPage (1967). *Taraxacum laevigatum* and the moss *Brachythecium albicans* have not previously been noted as path species.

The tendency for trampling to produce more mesic conditions should be interpreted with some caution; a few measurements of soil conductivities suggested that in dry areas there are more nutrients available in the intermediately worn areas than on the path or in taller dune vegetation. This is apparently contrary to Goldsmith *et al* (1970) but may be due to leaching effects in the sandy soil. The correlation of resistant species with higher moisture contents is, however, fairly evident and suggests that the maintenance of a higher water table under a path (or directing a path to a higher water table) may be a good management technique for the drier dune slacks. The addition of nutrients is considered in a later paper; it should be borne in mind, however, that this particular dune system is very calcareous and, as Westhoff (1967) points out, an acid system is much more liable to trampling damage.

The transect data shed an interesting light on two related aspects of the consequences of trampling. The relationship between species number and a diversity index that considers the standing crop of these species suggests that the initial effect of trampling may be to reduce interference between plants or simply reduces the dominant species. Some species may, however, have a higher turnover and, in fact, be utilising more of the resources than standing crop measurements suggest. The discussion in Harper (1971) of species relationships in a hypothetical mixed community illustrates this type of interaction and the dominant species in this case are the monocotyledons. The related aspect is the increase in the percentage of aesthetically pleasing dicotyledonous species with moderate amounts of trampling. From the point of view of managing these sand dune pastures for recreation, total exclosure and prevention of all wear on some areas may be as detrimental as the destruction of all the vegetation.

The main generalisation that can be made from the autecological information is the common occurrence of tussock forms on paths and tracks. The tussock form has the following advantageous features :

1. Most tillers or shoots leave the ground at an angle.
2. The closely spaced inner shoots or tillers cushion each other when under pressure, and the meristems are less likely to be damaged. (Brougham *et al* (1960) have shown that grazing acts as a selection agent for higher tiller numbers in *Lolium perenne* x *L. multiflorum*).
3. The root mass beneath the tussock has a high elasticity and this cushions the shoots when compressed from above.
4. The short rhizomatous connections facilitate the transport of assimilates to young or damaged shoots (Nyahoza 1971).

When the species considered resistant by other workers are examined a large number are found to be tussock formers and Lock (1972) found that this form was resistant to grazing and trampling by hippopotamuses.

Westhoff (1967) comments that the vegetation characteristic of ecotones is also found on paths and that a path is itself a special kind of ecotone with a sharp gradient of wear from the centre to the edges. This hypothesis is rather hard to test as paths have a tendency to follow a vegetational boundary and the question becomes a semantic one of 'are all paths ecotones or all all ecotones paths?' The idea, however, is worth noting especially when reading phytosociological literature and may well prove useful in practice.

Throughout this study, which was carried out in the field from June to October 1970, there has been no mention of the age of the tracks and paths. A set of aerial photographs taken in 1960 shows very few routes within the dune system and the majority of the sites are probably less than ten years old (Paper 1, Figs.1a and b). There is, therefore, a possibility that conditions are not yet stable and this should be considered when comparisons are made with other dune systems.

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A P P E N D I X 1

Subjective Group

	A										B										C										D										E									
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Species																																																		
Equisetum variegatum																		+				+				+		+				+								+		+					+			
Equisetum palustre																															+										+									
Equisetum arvense																+						+				+	+		+																					
Ranunculus bulbosus																			+					+				+			+		+	+																
Ranunculus flammula																						+																												
Ranunculus repens																						+																												
Viola canina										+			+						+		+	+	+	+		+		+		+	+		+	+	+	+			+		+		+	+	+	+	+		+	
Viola tricolor																			+		+		+	+							+								+		+		+		+	+				
Polygala vulgaris																			+					+	+				+								+	+	+						+		+			
Cerastium holosteoides																								+	+																									
Cerastium atrovirens													+										+							+	+			+				+					+		+	+				
Sagina nodosa				+										+												+		+																			+		
Cf. Honkenya peploides																																														+				
Arenaria leptoclades																							+																				+			+				
Linum catharticum																							+		+			+						+						+		+	+		+		+	+		+
Erodium glutinosum																				+																														
Ononis repens				+		+								+		+								+		+								+		+									+					
Trifolium dubium																							+										+					+	+				+							
Trifolium repens		+					+				+			+	+		+	+	+	+		+		+	+		+	+					+	+	+		+			+		+	+		+		+			+
Trifolium arvense																			+				+		+				+	+			+						+											
Anthyllis vulneraria																											+		+																					
Lotus corniculatus										+	+		+		+				+		+		+	+			+	+		+	+		+	+			+			+			+	+			+	+		+
Lotus pedunculatus																																		+																
Rubus fruticosus																												+	+																					
Potentilla anserina						+	+	+				+				+	+	+				+					+	+				+										+								+
Potentilla reptans				+		+										+						+		+		+	+	+						+							+			+			+			
Sedum anglicum																							+							+						+										+				
Hydrocotyle vulgaris																		+				+					+	+														+						+		
Euphorbia portlandica																																														+				
Euphorbia paralias																																														+				
Rumex acetosella																																		+										+						
Salix repens																												+				+						+		+		+					+	+		+
Anagallis tenella																						+																		+		+								
Anagallis arvensis														+																				+																
Centaurium erythraea											+																																							
Centaurium littorale																								+								+								+		+				+				+
Gentianella amarella																																																		+
Veronica officinalis																								+									+	+										+			+			
Veronica chamaedrys																								+																				+	+					
Euphrasia [illegible]																			+					+																+		+					+	+		+
Mentha aquatica																											+																							
Thymus drucei	+				+						+		+		+				+	+	+		+	+	+				+	+	+		+	+	+		+		+	+	+		+	+	+		+		+	
Armeria vulgaris												+		+								+		+			+	+	+			+		+						+			+				+	+		+
Plantago major								+						+		+										+																								
Plantago lanceolata											+			+							+			+																										
Plantago coronopus														+		+												+									+													+
Galium verum			+	+	+				+		+		+		+				+		+		+	+	+				+	+	+		+	+	+		+		+		+		+	+	+		+		+	
Galium palustre																											+																							
Senecio jacobaea											+		+		+				+		+			+	+						+										+		+		+		+			
Bellis perennis	+	+		+			+			+	+	+	+	+	+		+	+	+			+	+					+			+	+	+		+		+	+		+		+			+		+	+		+
Cirsium arvense																					+																				+						+			
Hypochoeris radicata																																																+		
Leontodon autumnalis			+			+										+	+	+	+			+			+	+	+	+						+			+				+						+	+		
Leontodon taraxacoides	+				+		+				+	+	+		+	+	+		+		+	+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+
Cf. Sonchus oleraceus				+							+		+		+	+															+		+		+		+						+							+
Hieracium pilosella																			+																														
Crepis vesicaria																									+			+																+					
Crepis capillaris														+				+		+	+		+		+									+					+								+			
Crepis sp.																									+																								
Taraxacum officinale			+	+							+			+	+			+	+		+		+	+	+								+		+					+	+		+		+				+	
Taraxacum laevigatum				+	+				+				+								+										+		+		+		+						+	+	+		+			
Veronica spp																															+																			

A P P E N D I X 1 (Continued)

Subjective Group

Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Subjective Group	A										B										C										D										E									
Species																																																		
Juncus bufonius													+		+								+																															
Juncus articulatus		+				+	+	+				+		+		+	+	+				+						+	+				+						+		+			+								+
Luzula campestris											+										+			+	+								+	+	+		+							+	+	+		+			
Eleocharis quinqueflora													+						+										+																								
Eleocharis multicaulis																							+																													
Isolepis setacea													+																																									
Carex flacca		+		+			+					+		+			+	+			+	+		+			+	+	+			+		+			+	+		+		+					+	+		+
Carex nigra													+						+			+	+										+										+								
Carex arenaria	+								+	+	+							+	+	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+
Bromus mollis															+					+					+					+	+																					
Festuca ovina																					+					+				+					+								+	+				
Festuca rubra	+	+	+	+	+				+	+	+		+	+	+		+		+	+	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Vulpia membranacea																																														+				
Poa annua					+											+																	+	+																		
Poa pratensis	+	+	+	+	+		+	+	+				+	+	+		+	+	+	+		+		+	+		+				+	+	+	+	+		+	+	+	+			+	+			+			
Poa subcaerulea											+							+		+	+	+			+		+	+	+	+	+		+	+	+							+	+	+	+					+	
Catapodium marinum																																														+				
Cynosurus cristatus														+																																				
Koeleria cristata															+				+									+																					
Aira caryophyllea																								+																									
Aira praecox													+									+	+																					+				
Holcus lanatus																													+				+						+		+		+					+	+		
Anthoxanthum odoratum	+									+									+	+			+									+	+	+								+	+	+		+			+
Ammophila arenaria	+				+												+				+		+		+	+	+				+	+	+			+	+	+	+		+		+	+	+	+	+	+	+		+	
Agrostis canina																																																		+
Agrostis tenuis	+			+						+		+	+						+	+		+	+						+	+		+		+								+	+	+					
Agrostis stolonifera		+					+					+			+	+	+	+	+			+	+		+	+	+	+	+			+	+	+				+		+	+	+					+	+	+	+
Phleum arenarium																																				+			+						+				
Sieglingia decumbens					+											+																																			
Ditrichum flexicaule																														+																			
Ceratodon purpurius														+																																			
Dicranum scoparium																									+									+										+						
Tortula ruraliformis								+		+			+						+	+			+							+	+				+		+			+					+		+	+	
Bryum pseudotriquetrum																											+															+						+		
Bryum argenteum																				+																												+	+
Climacium dendroides																					+												+										+							
Thuidium abietinum																							+																		+									
Thuidium philiberti											+										+												+								+									
Cratoneuron filicinum																																																		+
Amblystegium serpens																														+																			
Acrocladium cuspidatum								+				+									+					+																									
Camptothecium lutescens										+	+										+		+							+				+		+		+			+	+		+		+	+	+			
Brachythecium albicans						+			+			+			+				+								+						+		+		+		+					+				+	+			+	
Brachythecium glareosum																											+		+												+									
Brachythecium rutabulum								+						+			+			+						+	+																		+					
Pseudoscleropodium purum															+								+	+																			+						
Hypnum cupressiforme														+										+										+									+		+					
Rhytidiadelphus triquetrus																								+										+										+	+					
Rhytidiadelphus squarrosus																																		+										+	+					
Preissia quadrata																																								+										
Riccardia sinuata																																										+						+		
Riccardia pinguis													+																											+			+				+				+
Pellia endiviifolia																				+																						+									
Leiocolea badensis																																								+										
Lophocolea bidentata																																			+									+					
Frullania tamarisci																								+																									
Cladonia furcata																				+				+	+						+				+										+	+					
Cladonia rangiferina																								+																									
Evernia prunastri																																								+										
Peltigera canina											+																					+																	
Cladonia spp.																								+								+																	

APPENDIX 2

Autecological discussion of selected species

Linum catharticum L.   L.P.I. 0.96, B.D. 1.14 $g.cm^{-3}$, D.I. 0.0, % H_2O 13.8.

This was the only annual to occur in any quantity during the survey and the reason is probably that other dune annuals all grow earlier in the year and the dead remains would be easily destroyed by treading. Westhoff (1967) describes this as a species typical of ecotones and, in fact, tracks unused in winter often have large numbers of annuals growing on them, probably because they provide small areas of open ground suitable for the germination and establishment of seeds. The presence of this species also agrees with the calcareous nature of these dunes.

Trifolium repens L.   L.P.I. 1.12, B.D. 1.16 $g.cm^{-3}$, D.I. 0.7, % H_2O 18.6.

This was able to survive treading much better than wear by cars. This is shown in Table 2-4. Harper (1969) gives data indicating that hard spring grazing favoured this species and moderate trampling must involve some of the effects of grazing. Many workers have noted an increase with treading including LaPage (1967), Gillham (1956), Davies (1938), Westhoff (1967) and Bates (1935) who comments 'except on dry sandy soils';

this agrees with its absence from drier transect I. However, his observations were made largely on acid soils. He also suggests that it is intolerant of low light conditions in high swards; this appears to be a general dicotyledonous feature. Bates (1934) observed that treading reduces leaf size and suggests that this is due to a reduction of root system and consequent limitation of water supply. Whisler et al (1965) state that even slight soil compaction reduces the nitrates produced in the soil and this could account for the success of *Trifolium repens* with its associated nitrifying bacteria. Streeter (1971), however, found that the level of soil nitrogen was increased by moderate trampling. Gilchrist (1906) (cf. Harper 1971) noted that increasing phosphorus also increased the quantity of *Trifolium repens* in a sward and Streeter (1971) recorded an increase in this element with moderate trampling, so this provides an alternative or additional hypothesis to explain its presence. Snaydon (1962) found an association with high Ca^{++} and pH values, which are also present at Aberffraw. However, Bates (1934) also found that lower pH restricted root growth and Goldsmith et al (1970) found a tendency to lower pH in trodden areas. The final situation is clearly the result of a complex of factors that may produce favourable conditions under moderate trampling but adverse effects become dominant as pressure of use increases. It can, therefore, be considered a vegetative coloniser.

<u>Potentilla anserina L.</u> L.P.I. 1.18, B.D. 1.22 g.cm^{-3}, D.I. 0.9, % H_2O 28.7.

Occurs on tracks as small rosettes but stolons do not appear to survive. This plant is also one that Westhoff (1967) considers as typical of ecotones but Bates (1935) states 'it does not, however, tolerate much treading'.

<u>Potentilla reptans L.</u> L.P.I. 1.07, B.D. 1.13 g.cm^{-3}, D.I. 0.4, % H_2O 17.2.

The main difference between this species and its congenor above is its much lower P.I. The main morphological difference appears to be the longer leaf petiole and the folded young leaflets of <u>P. anserina</u>.

<u>Thymus drucei Ronn</u> L.P.I. 0.88, B.D. 1.18 g.cm^{-3}, D.I. 0.6, % H_2O 8.3.

This species occurred on footpaths where the leaves may be stripped from the branches; it does not survive so well on tracks. This may be due to the softer soil surface in the drier areas where <u>Thymus</u> occurs cushioning the branches from compression damage but not from the greater horizontal torque forces produced by motor cars. Streeter (1971) noted its disappearance under high visitor pressure at Box Hill. Piggott (1955) states that it is favoured by grazing as tall grasses are removed and it is avoided by sheep, possibly because of its high phenol content. Thomas' (1951) data shows a reduction in <u>Thymus</u> when the minimum vegetation height was over 10 cm. Watt (1940) found that it was almost eliminated in his Breckland sheep exclosures, and Willis (1963) found that the increase in grasses following NPK fertiliser additions to the slacks in Braunton Burrows eliminated this species. The bimodal distribution on transects I and II agrees with these data; interference from 'natural' vegetation may be reducing the amount of <u>Thymus</u> while it is also reduced in the worn areas; it thrives only when competition for light is reduced and trampling pressures are not extreme and can also be classed as a vegetative coloniser of paths and tracks.

<u>Prunella vulgaris L.</u> L.P.I. 1.07, B.D. 1.14 $g.cm^{-3}$, D.I. 0.3, % H_2O 21.9.

This plant does not appear on car tracks and has a low resistance to treading. Observation indicates that the upright rectangular Labiate stem is especially liable to breakage, and this may be the only reason for the low resistance to wear. This species usually fruits during June, before the major wear by holiday makers and there is some possibility that its phenology could allow it to survive on tracks.

Senecio jacobaea L. L.P.I. 1.01, B.D. 1.13 $g.cm^{-3}$, D.I. 0.4, % H_2O 7.2.

Bellis perennis L. L.P.I. 1.18, B.D. 1.20 $g.cm^{-3}$, D.I. 1.0, % H_2O 19.6.

These two species are considered together because they have a ~~very~~ somewhat similar habit in their first year but Bellis occurs much more frequently on paths. The differences between the two should indicate the essential characteristics required for wear resistance. The following are the principal morphological differences :

1. The leaf of Bellis has a smoother surface and edge and is less liable to damage by crushing.
2. The leaf of Bellis is smaller and less energy is lost by leaf detachment.
3. The leaf of Bellis has an apparently higher tensile strength and the cuticle is apparently thicker.
4. The leaf of Bellis is angled closer to the ground.
5. Bellis can reproduce vegetatively by many lateral buds, whereas Senecio can only produce a restricted number of units by separation of multiple crowns. It can, however, reproduce from root buds.
6. Senecio flower is on a longer stem and it may put more energy into flowering than Bellis.

7. *Bellis* can produce a flower very quickly.

Harper & Wood (1957) state that trampling does not kill *Senecio* or hinder its establishment as many are found on paths as in 'natural' vegetation. These data may differ from their observations either because Harper & Wood's (1957) paths were only subject to light trampling or because of soil differences. The fact that *Senecio* does not occur at high altitudes in the north of Britain and that it occurs on drier dune soils than *Bellis* may point to these factors causing the differences between the species rather than trampling *per se*. *Bellis* appears to colonise paths by seeding but has intrinsic resistance to trampling.

Taraxacum officinale Weber L.P.I. 0.90, B.D. 1.19 $g.cm^{-3}$, P.I. 0.7, % H_2O 8.8.

Taraxacum laevigatum (Willd.) DC

L.P.I. 1.10, B.D. 1.16 $g.cm^{-3}$, P.I. 0.8, % H_2O 8.8.

These species showed a high resistance especially to cars. *T. laevigatum* has a ~~one unit~~ 0.1 higher P.I. than *T. officinale* and differs from it by having dissected leaves; a similar difference occurs between *Potentilla anserina* and *P. reptans*. The leaves are also more appressed to the soil. *T. laevigatum* is a species that is restricted to lowland areas in Britain and is associated with high summer temperatures. If this is a causal correlation then the fact that tracks tend to have higher summer maximum temperatures (see Paper 5) may well affect its distribution at Aberffraw.

Juncus articulatus Ehrh. L.P.I. 1.22, B.D. 1.23 g.cm^{-3}, D.I. 0.9, % H_2O 28.3.

This species has the following features that may contribute to high resistance to wear :

1. Occurs in dwarf form.
2. The semi-prostrate habit of this form likely to prevent damage by bending the base of the stem.
3. Apex of stem protected until near flowering.
4. Leaf meristem not apical.
5. Cylindrical leaf with lignified epidermis prevents damage under compression.

LaPage (1967) also found a gradual increase of Juncus (species not determined) as trampling increased.

Carex flacca Schreb. L.P.I. 0.90, B.D. 1.18 g.cm^{-3}, D.I. 0.5, % H_2O 23.9.

Carex arenaria L.P.I. 0.89, B.D. 1.18 g.cm^{-3}, D.I. 0.5, % H_2O 12.8.

Bellamy et al (1971) found that Carex species were important in natural regeneration of worn areas of Arctic tundra. But LaPage (1967) found that an unspecified species was eliminated by trampling but most authors have found this genus resistant. Chappell et al

(1971) show an increase of *C. flacca* in areas subject to intermediate levels of pressure.

The principal morphological differences between these two *Carex* species are the single shoots of *C. arenaria* and the slightly tufted habitat of *C. flacca* and the fact that *C. flacca* often emerges from the ground at an angle, whereas those of *C. arenaria* ~~is~~ are usually upright. It is likely that this latter fact accounts for the difference in P.I. Excavation has shown that there is a tendency for the rhizomes of *C. flacca* to be killed under heavily used car tracks whereas *C. arenaria's* is often rather deeper and may escape injury.

Festuca rubra L. L.P.I. 0.96, B.D. 1.2 $g.cm^{-3}$, D.I. 0.7, % H_2O 13.6.

This species occurred as frequently on tracks and paths as *Poa pratensis* but has a lower P.I. as it is more common in 'natural vegetation' than the *Poa*. The resistance of this species to wear seems to be rated differently by different authors. LaPage (1967) found that a Fescue (cf unstated species) disappeared from a camp ground over a period of time. Davis (1938) found that *Festuca* decreased as a road was approached (and presumably treading increased). Bates (1935) found *F. ovina* in nearly all footpath floras he examined but he later stated (Bates 1938b) that it does not recover so well from injury as *Poa* or *Trifolium*. Hubbard (1968) considered that *F. rubra* is a species which is found in most types of fine lawn and Gillham (1956) found that it was among those species that occurred most frequently on paths in the Pembrokeshire islands. Morrish & Harrison (1948) also placed it in the group of species with highest resistance to vehicular traffic. The amount of wear to which the species had been exposed is not stated except by Morrish & Harrison (1948) and the type of soil involved is not always clear. LaPage's (1967) observations of increasing *Juncus* and *Poa* suggest that the soil was relatively moist and this may be the reason for the reduction of *Festuca*. There is sufficient evidence to suggest that this species should be included in seed mixtures sown for regeneration of drier areas.

Poa pratensis L. L.P.I. 1.15, B.D. 1.22 $g.cm^{-3}$,
D.I. 1.0, % H_2O 17.1.

Poa subcaerulea Sm. L.P.I. 0.80, B.D. 1.14 $g.cm^{-3}$,
D.I. 0.3, % H_2O 13.4.

The common appearance of *P. pratensis* on paths and tracks was very obvious during this survey and has been noted by many authors including LaPage (1967), Bates (1935), Klecka (1937) and Edmond (1963). Davies (1938) found *P. annua* on paths and *P. pratensis* mainly near hedgerows.

The speed of growth may play an important part in the survival of this species. The principal difference between the two Poa species is that P. subcaerulea is not tufted and the specimens observed off the path were all quite large individuals with long internodes. This may mean that to produce sufficient leaf area to survive P. subcaerulea may have to grow taller and is, therefore, more liable to be killed by trampling than P. pratensis.

Mosses

Tortula ruraliformis (Besch.) Dix.

L.P.I. 0.68, B.D. 1.23 $g.cm^{-3}$, P.I. 0.6, % H_2O 9.2.

Camptothecium lutescens (Hedw.) Brid.

L.P.I. 0.93, B.D. 1.16 $g.cm^{-3}$, P.I. 0.5, % H_2O 8.9.

Brachythecium albicans (Hedw.) B. & S.

L.P.I. 0.77, B.D. 1.19 $g.cm^{-3}$, P.I. 0.8, % H_2O 9.6.

All records of these species were in fairly dry stands with high bulk density but low hardness. These data suggests that they were colonising dry, unstable but compressed soil; this suggests that their ability to colonise may account for their presence. The high P.I. of Brachythecium albicans may be due to its pleurocarpous habit but if this is so then the lower figure for the closely related Camptothecium lutescens needs explanation.

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PAPER 3

THE EFFECT OF CONTROLLED LEVELS OF TRAMPLING AND DRIVING ON SAND DUNE PASTURE

THE EFFECTS OF CONTROLLED LEVELS OF TRAMPLING AND DRIVING ON SAND DUNE PASTURE

INTRODUCTION

The previous papers in this series have described existing car track and footpath vegetation in the sand dune system at Aberffraw, Anglesey. The creation of tracks and paths can be considered to take place in two stages (Burden & Randerson 1972). First, the existing vegetation is damaged and only the trampling resistant species survive; soil changes also start at this time. Secondly, over a longer period the species that are favoured by path conditions colonise the new route or increase in number and a dynamic equilibrium between vegetation, soils and level of trampling may be reached.

Previous studies of the effects of trampling, as distinct from grazing and trampling combined, can be divided into two main groups on the basis of the processes described above. The first group comprise those where existing situations have been examined and an estimate of past wear may have been made, using parameters such as soil bulk density or penetrability. (The work of Bates 1935, Davies 1938, Streeter 1971, Chappell 1972 and the first two papers in this series fall into this category). The other group consists of studies of the effects of known levels of wear applied under control of, or at least measured by, the experimenter. This type can be sub-divided into three categories: experiments carried out using an artificial method of wear on plants grown under controlled conditions, experiments where either the method of applying wear or the vegetation was 'natural', and experiments in which both these factors were 'natural'. A brief account of each of these groups will give a picture of this field of research.

Simulated trampling in greenhouse conditions falls into the first category. Bayfield (1971b) used Phleum pratense and an artificial trampler and found an initial increase of growth up to 10 impacts; and at higher intensities of wear there tended to be a straight line relationship between reduction in tillers and leaves per plant, dry weight of shoot and the log of the number of impacts. The regression calculated from graphs in Bayfield (1971b) using

$$y = a + b(\mathrm{Log}_e x)$$

where y is percentage survival and x is the number of impacts gave b = -6.4. The regression coefficient of percentage cover or estimates of a similar nature on the number of impacts, or vehicle or walker passages provides a possible index of vulnerability for comparison of different habitats or methods of wear. The larger the negative figure the more vulnerable the vegetation is to the type of wear being applied. The results given in Table 3-1 summarise the data presented in the papers discussed here. Comparisons can be made between the tramplers of Wagar (1964) and Bayfield (1971b) and between the various tracked vehicles used by Bellamy _et al_ (1971). But the action of the different methods of imposing wear was not the same and comparisons between them should be avoided.

The second category includes work by Wagar (1964) who applied wear by means of a trampler to 'natural' vegetation that had already been subject to trampling and found that the log of the dry weight of surviving vegetation and the dry weight of the surviving vegetation expressed as a percentage of the adjacent control plots was related to the log of the number of impacts. The technique of expressing the results as a percentage of the adjacent control plots was considered successful by Wagar (1964), although Cieslinski & Wagar (1970) found that direct measurements gave better results on a wider survey. Wagar (1964) found that the dry weight of the surviving vegetation decreased to about 50% of the original level at about 20 impacts of the trampler per week for 6 weeks and remained at this level up to 35

TABLE 3-1

REGRESSION ANALYSIS OF PREVIOUS DATA

$$y = a + bx$$

y = percent cover, x = number of passages or trampler impacts.

Source of Data	b	a
Wagar (1964) Trampler in field	-2.0	31.9
Bayfield (1971) Trampler in greenhouse	-6.4	77.1
Morrish & Harrison (1948)		
Car 1,520 kg	-3.6	55.9
Truck 18,182 kg	-2.4	62.5
Bellamy et al (1971) Vehicle with conventional tracks and grouser bars. 3,864 kg		
Vegetation types A1	-9.9	30.2
Wet A2a	-8.5	41.9
B3	-6.5	71.7
A2	-8.4	61.3
A4	-7.6	58.7
A3	-8.3	42.7
C1	-6.9	67.0
B4	-8.0	57.2
B2	-7.5	59.6
B1	-7.9	45.9
C3	-6.6	69.2
Dry C2	-6.9	68.4
Different weight tracked vehicles		
54,545 kg	-9.3	41.4
20,909 kg	-7.9	61.6
6,100 kg	-7.1	66.4
4,090 kg	-7.0	68.2
Vehicle with pliable rollers		
9,090 kg	-5.1	73.8
7,727 kg	-5.6	72.4

impacts per week. Calculation based on the data given in Wagar (1964) gives b = -2.0. The difference between this and the results of Bayfield (1971b) using *Phleum pratense* could be due to the nature of the tramp or the plant material. Morrish & Harrison (1948) tested various species for survival in the field and *Poa pratensis* and *Festuca rubra* were among the most wear resistant. They compared the effects of a car weighing 1,520 kg and a truck weighing 18,182 kg on 'light silt loam' plots containing various mixtures of grasses and clovers. The regression of the mean of the percentage surviving cover of all types of vegetation on the number of vehicle runs given in their paper gives b = -3.6 and -2.4 for the car and truck respectively.

The results of various intensities of walking on a wet *Calluna*-*Trichophorum* heath community in the Cairngorms are presented by Bayfield (1971b). The calculated slope of the regression of surviving cover on the log of the number of passages is -4.5. Bellamy *et al* (1971) carried out experiments with tracked and wheeled vehicles on arctic tundra. They showed that the degree of wetness is an important factor affecting the vulnerability of this type of vegetation. Higher moisture levels in a poorly structured silt loam also lead to increased vegetation damage when trampled by sheep (Edmond 1962).

Regressions calculated on the data of Bellamy _et al_ (1971) gave a range of coefficients from -6.6 in the dry areas to -9.9 in the more vulnerable wet site (Table 3-1). Their data for tracked vehicles gave a nearly straight line relationship between the regression coefficient and the weight of the vehicle. Pliable rollers give a clear advantage to these vehicles producing a coefficient of less than -6 in the same habitat.

The work reported in this paper is an investigation of the effects of subjecting a relatively untrampled area of sand dune pasture to wear by walking and by a vehicle for a limited period of time; recovery after a rest period of six months was also considered. Statements can be made about the initial response of the components of this semi-natural vegetation to the effect of vehicles and walking and their relative ability to recover from injury but not about the long term changes that occur in path formation. This is considered to extend the various kinds of artificial trampler experiment to the field situation, e.g. Wagar (1964), Cieslinski & Wagar (1970) and Bayfield (1971b). Since no quantitative field data for this habitat existed the design was that of a pilot experiment giving a wide range of treatments with a limited amount of labour. Comparisons were made between the effects of vehicles and walking, frequency and intensity of wear, summer and winter wear and summer and winter recovery periods. These results and those of other workers are also considered in relation to management of recreation areas.

MATERIALS AND METHODS

Eight plots were selected in a dry sand dune pasture area of the Aberffraw dune system (Site 6, Fig.1-1c). The site of each plot was chosen for visual similarity and so that they were all on a similar level. (See Table 3-2). It was also necessary to choose a position where the vehicle could complete a circular course without getting stuck! Separate treatments were randomly allocated to each of the 8 plots. They were carried out at intervals of 1, 2, 4 and 8 weeks over a period of 20 weeks, in the winter from November 1970 to April 1971 and in the summer from April 1971 to September 1971. Table 3-3 gives the code letter for each plot. Measurements were made immediately after treatment and after a period of recovery: the winter-worn plots in May and October 1971 and the summer-worn plots in October 1971 and May 1972.

Table 3-3 Plot Code Letters

	Time of Treatment							
	Winter				Summer			
Week intervals	1	2	4	8*	1	2	4	8*
Code letter	A	B	C	D	E	F	G	H

In subsequent discussion 'a' is used to denote autumn measurement and 's' is used to denote spring measurement.

* These plots received three treatments during the 20 week period.

TABLE 3-2

HEIGHT OF EXPERIMENTAL PLOTS

Plot	Mean height above lowest plot	Height range
A	0.08 m	0.23 m
B	0.12 m	0.25 m
C	0.21 m	0.24 m
D	0.29 m	0.29 m
E	0.40 m	0.20 m
F	0.37 m	0.22 m
G	0.18 m	0.23 m
H	0.00 m	0.13 m

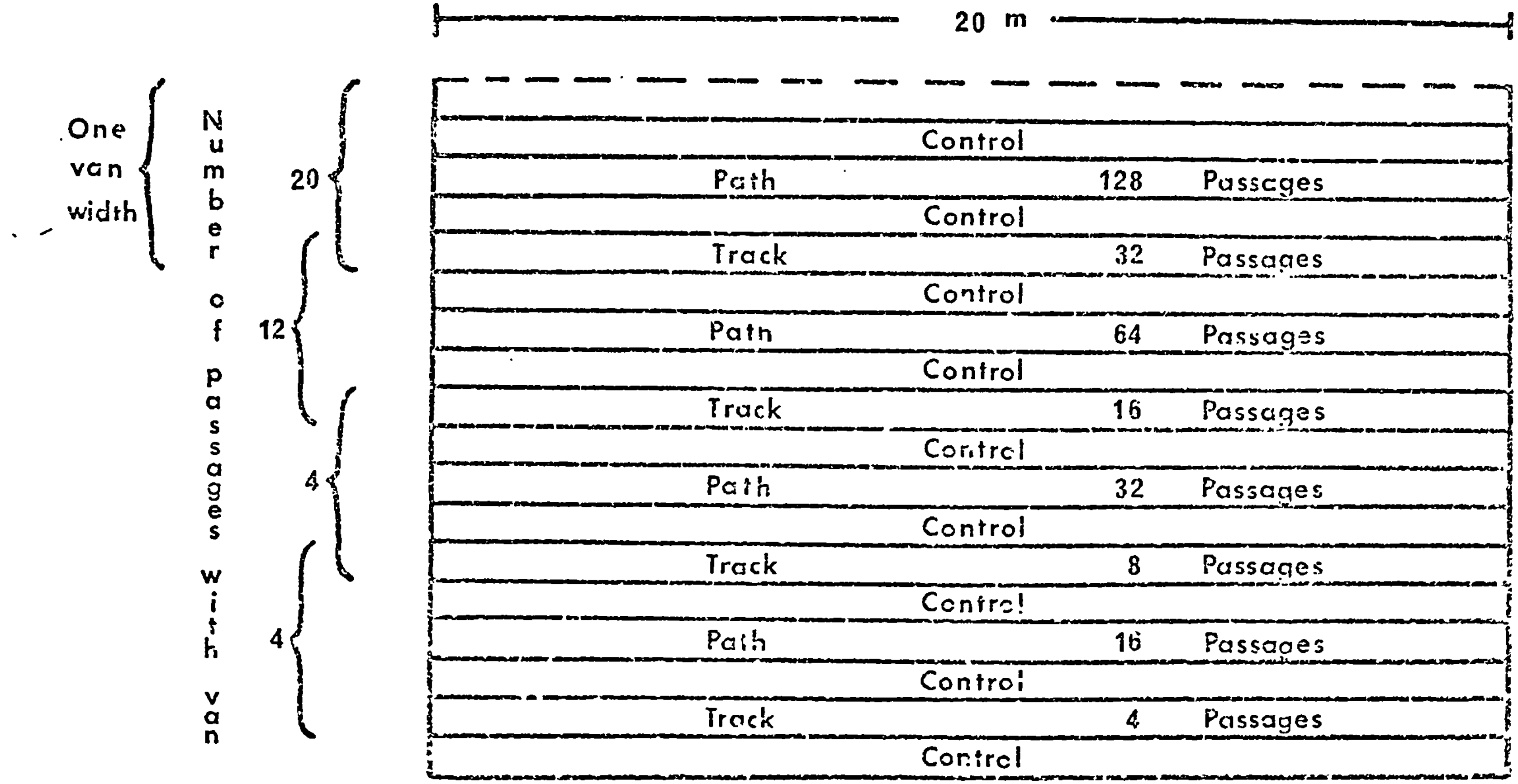
The plots were divided into 20 m strips of alternate treatments and controls (Fig.3-1). By using one plot for each frequency and season of treatment and by grading the intensity across the plot a single wheel track could be used for each intensity, thus reducing the area damaged. Driving intensities were 4, 8, 16 and 32 passages and walking intensities were 16, 32, 64 and 128 passages on each occasion. One half of each intensity was carried out in one direction of travel and the other half in the opposite direction.

The vehicle used was a 'Bedford 6 cwt.' van. The actual weight including the driver was 760 kg. The tyres were normal cross ply (i.e. not low pressure radial ply). All wear was applied at about 8 k.p.h. (5 m.p.h.) in bottom gear and care was taken to see that the wheels were kept to the narrow tracks so that the wear was always on the same plants. To extrapolate to the normal track width the amount of wear must be divided by a factor of 2. The walking was divided equally between two adults weighing 57 kg and 80 kg; walking boots with Vebrum soles were worn. The path was 20 to 25 cm wide, narrower than a normal 45 cm single file track (Huxley 1970).

The effects of these treatments on the vegetation were measured by point quadrats, 3 mm in diameter which

Fig.3-1

The layout of the experimental plots.


20 m
One van width
Number of passages with van
20
12
4
4
Control
Path 128 Passages
Control
Track 32 Passages
Control
Path 64 Passages
Control
Track 16 Passages
Control
Path 32 Passages
Control
Track 8 Passages
Control
Path 16 Passages
Control
Track 4 Passages
Control

were marked by grooves and different coloured paint every centimetre so that the height of each contact could also be recorded. One hundred points were recorded on each 20 m control strip and two hundred on each 20 m treatment strip. The species of plant was recorded for each top contact unless that part of the plant was completely dead, in which case it was classed as litter. The raw data are ~~is~~ given in Appendix 1. The soil penetration resistance was recorded by impact penetrometer to a depth of 6 cm (see Paper 1 for method); ten readings were made on each control strip and 20 on each treatment strip. Measurement of the plot height was carried out with a levelling telescope and staff in the normal way; the level was recorded in each control strip at 0, 5, 10, 15 and 20 m along the plot.

The analysis of the results was carried out in two ways. In the first, the records from the path or track were expressed as a percentage of the sum of the two adjacent control strips; this is termed relative cover or relative diversity etc. This was done to overcome the problem of confusing the block differences with the effect of different treatments. An assessment was also made of the variation between plots.

The analysis was carried out by computer using the 'Superfoot' programme written for this purpose, see

Appendix 3-2. The percentage values from this calculation were then subjected to analysis of variance. The sums of squares from third and fourth order interactions were used to make up the residual sum of squares. A complication was introduced by the fact that the sum of the number of passages was not the same for each frequency and thus frequency effects could be confused with the effect of intensity. For this reason the interactions involving frequency were not included in the residual sum of squares and the frequency effects were only considered for those parameters where the interaction between intensity and frequcncy was also significant. The frequency effects were also plotted from higher order interactions with intensity so that all the frequency points had the same total number of passages.

The second approach was to sum the adjacent control plot records in pairs so that eight groups were produced. These were then used as stands in principal components ordinations for comparison with the treated strips and for an examination of the differences between all eight plots at the different seasons.

RESULTS

Assessment of plot variation. The plots can be divided into two groups on the basis of mean height (Table 3-2). Those less than 0.20 m above the mean height of the lowest plot were A, B, G and H (the lowest of all) and the rest above 0.20 m. The height ranges of each plot were all between 0.20 m and 0.29 m except plot H with a range of 0.13 m. It is this plot, therefore, that can be separated from the rest on the basis of comparative height.

The Principal Components Ordination of the control groups from all measurements are shown in Fig.3-2. The plots that stand out from the rest are Ha, Hs and Ga. It is possible to interpret axis I as stand difference and axis II as the result of seasonal change; if this is correct then only Ha and Hs were markedly different from the rest. When the plots measured in the spring and autumn were ordinated separately (Figs.3-3a and 3-3b), plots G and H appeared to be different from the rest in the spring, although the differences within the plots were in all cases greater than the differences between them (Fig.3-3b). In the autumn the distance between stands within each plot except F was also greater than the distance between plots.

Fig.3-2

Ordination of all control stands at both seasons at which they were measured. Lines surround all stands from one plot measured at one season.

Plot group codes :

	Time of Treatment							
	Winter				Summer			
Week intervals	1	2	4	8	1	2	4	8
Code letter	A	B	C	D	E	F	G	H

a autumn measurement, s spring measurement

Axis I appears to be associated with plot differences and axis II with seasonal change, spring records towards the positive end and autumn records towards the negative end.

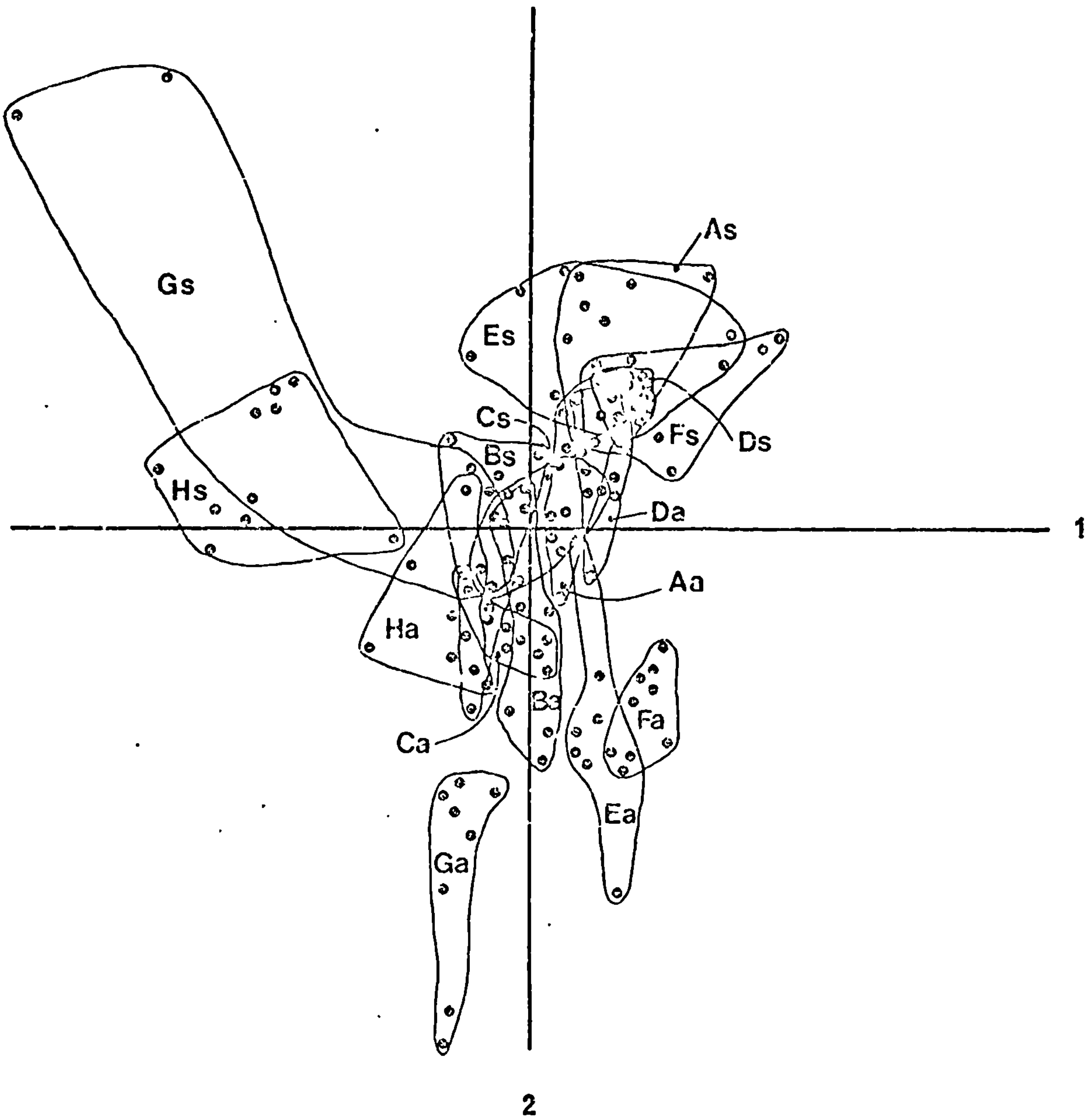

As
Gs
Es
Cs
Fs
Ds
Bs
Hs
Da
1
Aa
Ha
Ba
Fa
Ca
Ea
Ga
2

Fig.3-3

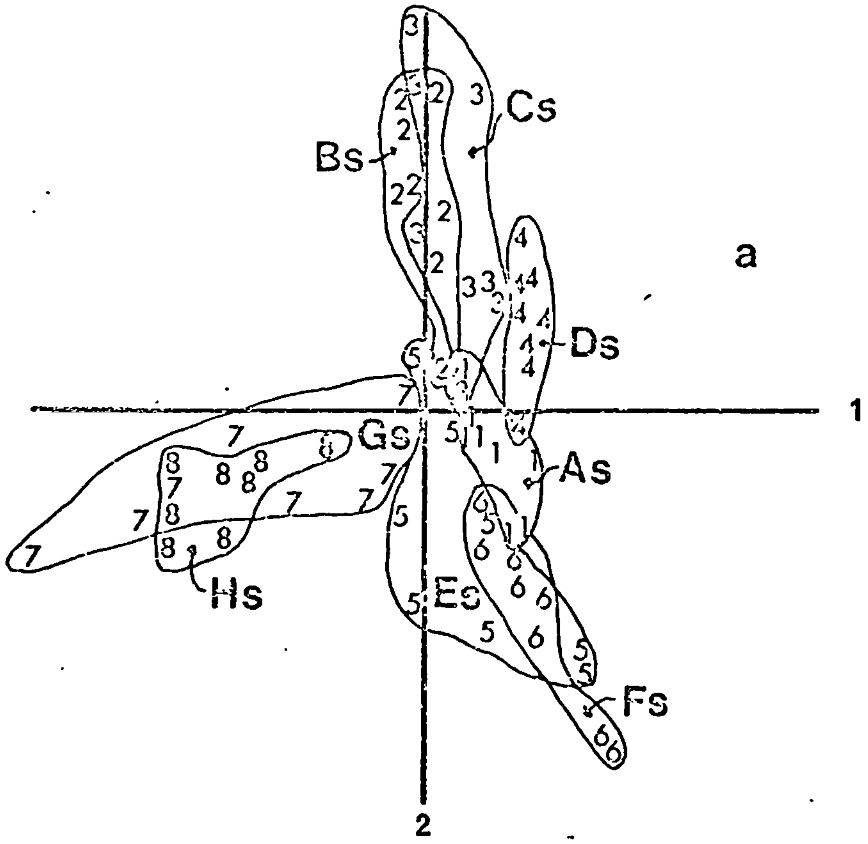
Ordination of control stands at different seasons.

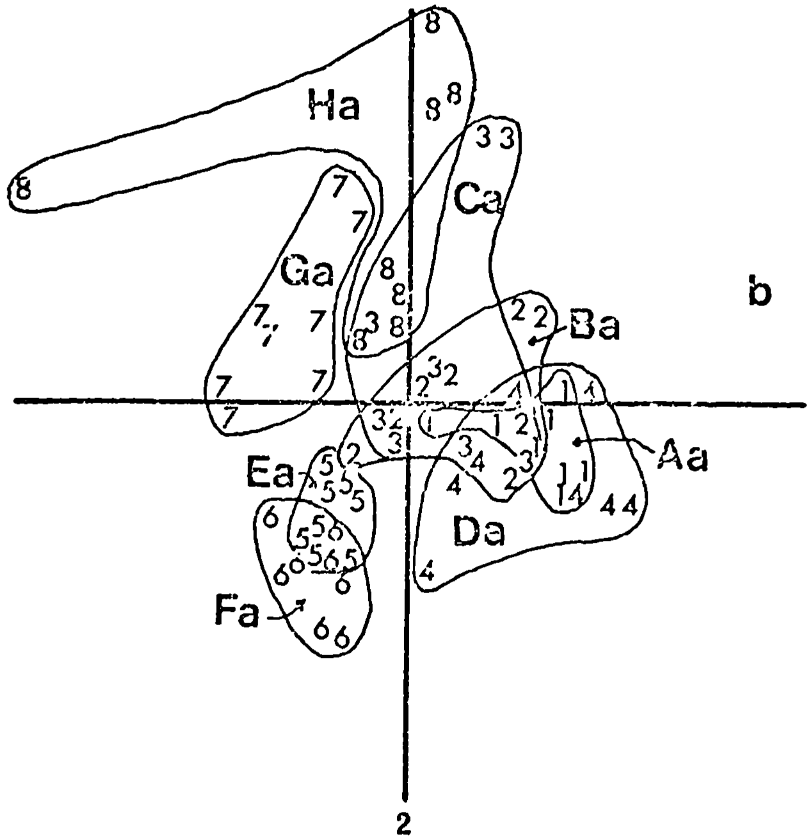
3-3a spring records

3-3b autumn records

Plot groups coded as for Fig.3-2 and code numbers used for each point:-

Code letter	A	B	C	D	E	F	G	H
Code number	1	2	3	4	5	6	7	8


Cs
Bs
Ds
As
Gs
Hs
Es
Fs
a
1
2


Ha
Ca
Ga
Ba
Aa
Ea
Da
Fa
b
1
2

When the autumn and spring records of plots which received treatment at the same season were ordinated (Figs.3-4a and 3-4b) the internal differences of the plots recorded in the spring were greater than the differences between plots except plot H. The internal difference was reduced in the autumn but the plots drew together so that it was still greater than the distance between them. When the spring and autumn records of the four plots of each treatment were ordinated separately, Fa and Fs and Hs were the only ones with a greater distance from some of the other plots than their internal differences.

The approach used here showed that the floristic differences between the eight plots were less than the differences within the plots. Plot H was a possible exception and since it was also the lowest plot this should be borne in mind when considering the results.

<u>Results of the treatments.</u> The cover data were divided into ~~four~~ 3 groups, the effect of a vehicle on the vegetation (Fig.3-5a), the effect of walking on the vegetation (Fig.3-5b), and the recovery after these treatments (Figs.3-6a and 6b). The wear in terms of total number of passages had a direct relationship with relative cover, the vehicle despressing the percentage to below 10 and walking to below 30. There was no

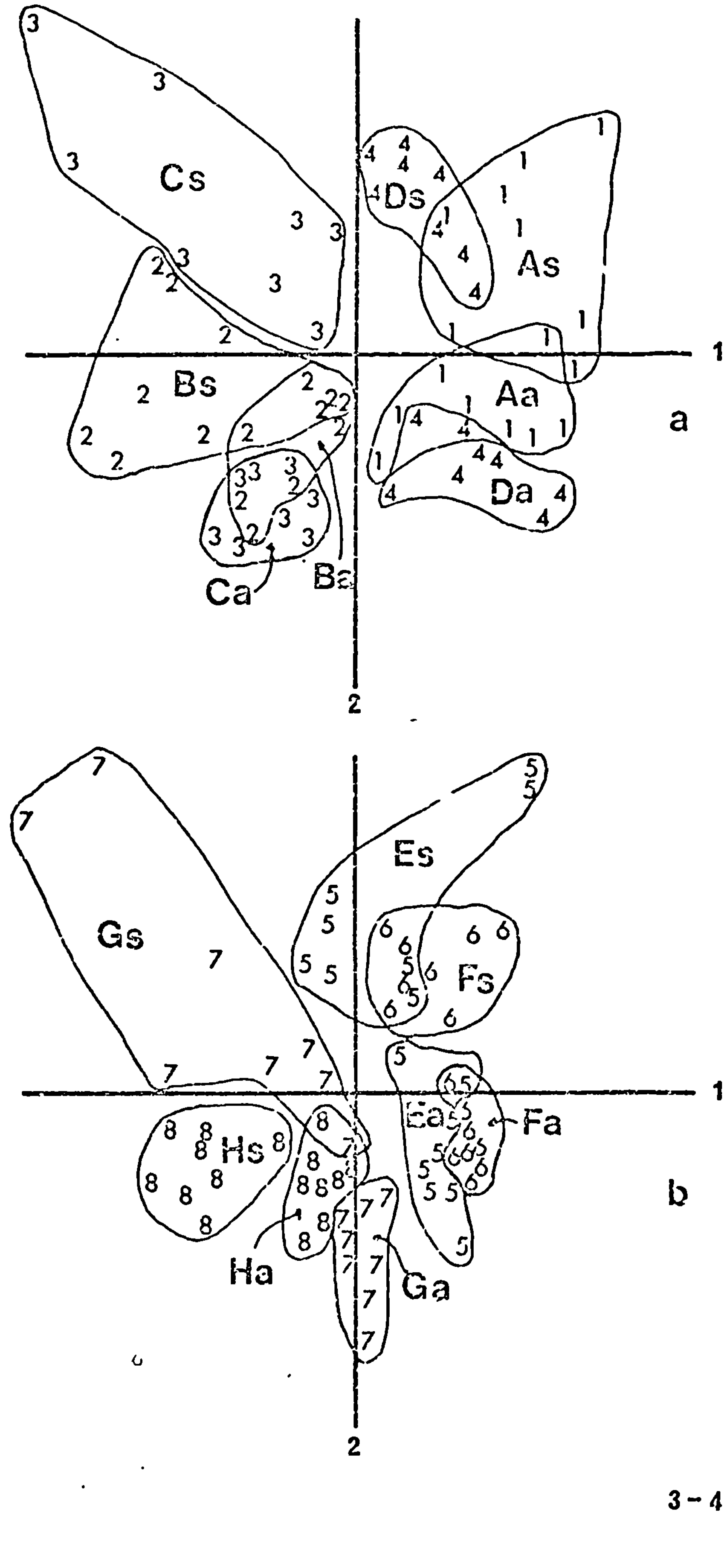
Fig.3-4

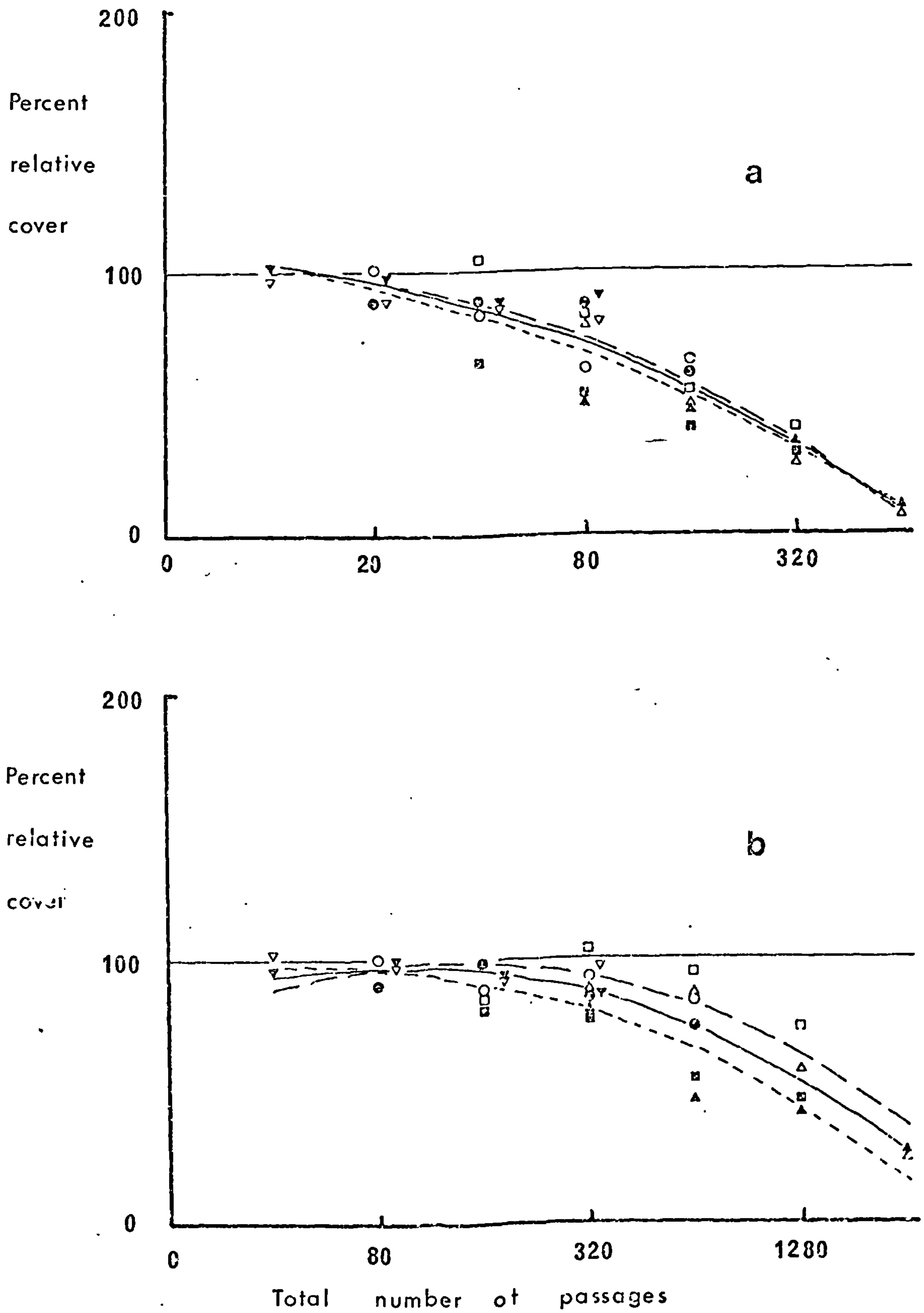
Ordination of control stands according to treatment received.

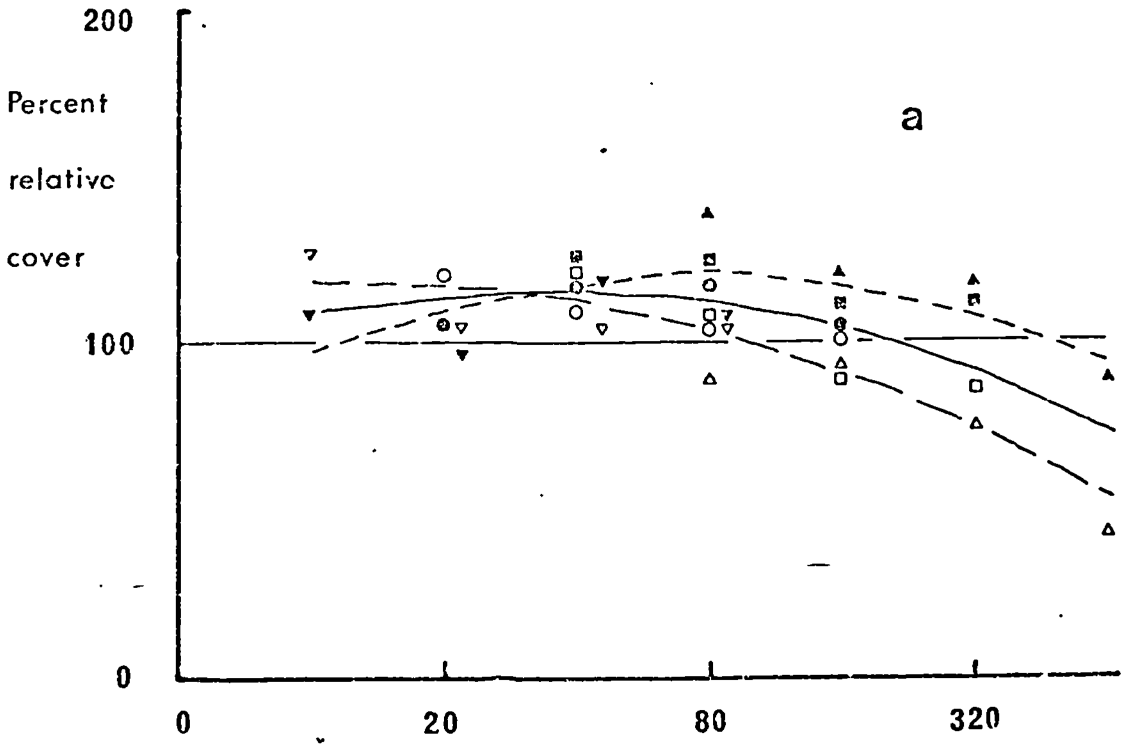
3-4a Plots treated in the winter

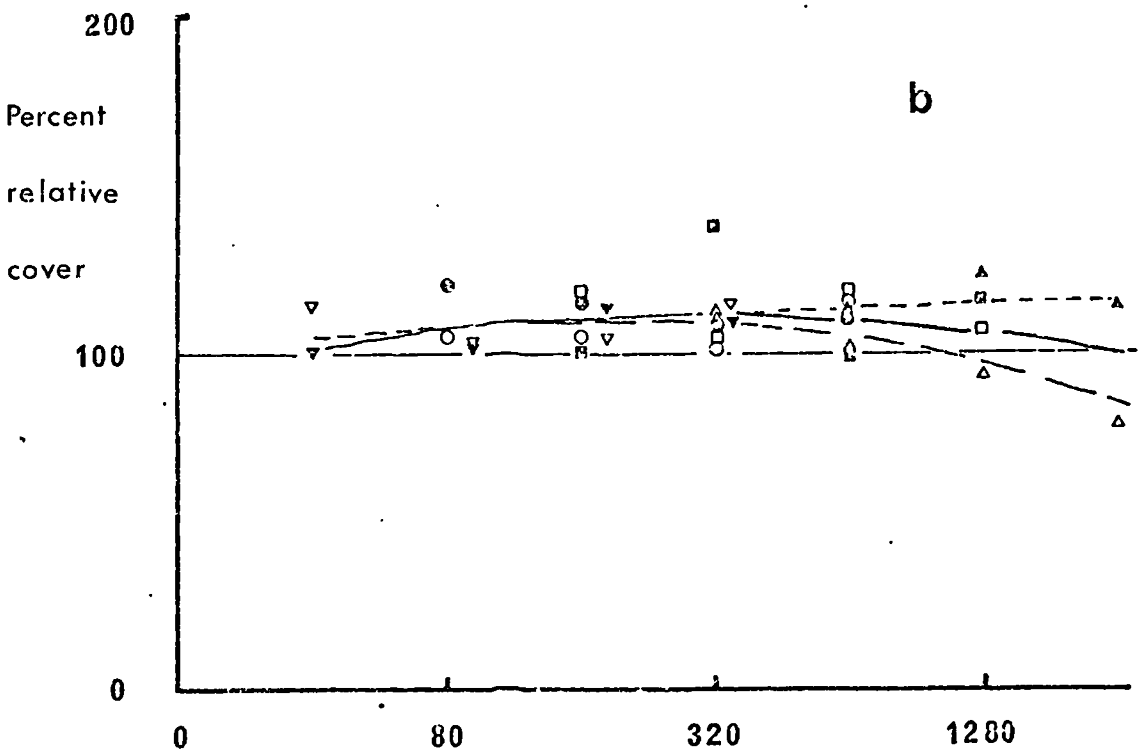
3-4b Plots treated in the summer

Plot groups coded as for Fig.3-3


Cs
Ds
As
Bs
Aa
Da
Ca
Ba
1
2
a
Es
Gs
Fs
Hs
Ea
Fa
Ha
Ga
1
2
b


200
Percent
relative
cover
a
100
0
0
20
80
320
200
Percent
relative
cover
b
100
0
0
80
320
1280
Total number of passages


200
Percent
relative
cover
100
0
a
0
20
80
320


200
Percent
relative
cover
100
0
b
0
80
320
1280

marked seasonal difference in the effect of vehicles, but walking at the highest total number of passages did twice the amount of damage in winter, leaving 17% relative cover compared with 37% in summer. The frequency effect caused some dispersion in the data. The analysis of variance suggested that frequency may be statistically significant but consideration of Fig.3-7a showed that it was minimal compared with the effect of intensity.

The recovery of the vegetation was, as expected, rather better during the summer period and the mean recovery on the footpath reached 100% relative cover at all intensities, whereas over 200 passages on the tyre tracks it was less than 100%. The significance of the analysis of variance results are given in Table 3-4 and the data on the main effects in Table 3-5.

Intensity. The main group of statistically significant parameters had nearly linear relationships with the log of intensity (Fig.3-7b). These include total relative cover of live plants, monocotyledons, *Festuca rubra* and the relative mean of log height. The first three parameters started from about 100% at the lowest level of intensity while height was already reduced by 50%. Each time intensity was doubled these parameters all dropped by 5 to 7% except *Festuca rubra* which averaged ig.3-7

Graphs of various aspects of the treatments

3-7a The effects of frequency and intensity on relative cover

3-7b The effect of different intensities on various parameters

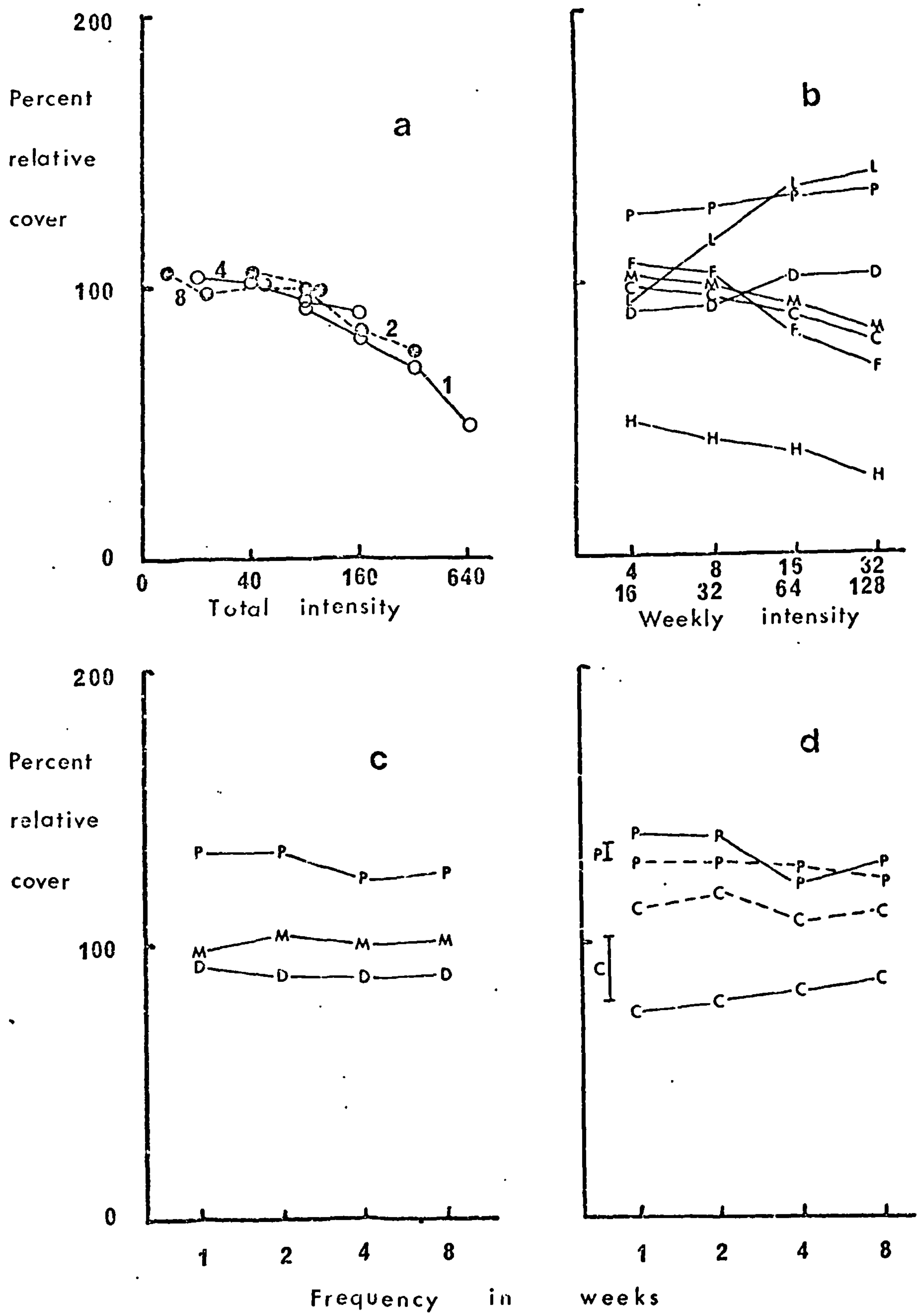
3-7c The effect of different frequencies on various parameters

3-7d, e, f and g The relationship between frequency and wear vs wear followed by recovery

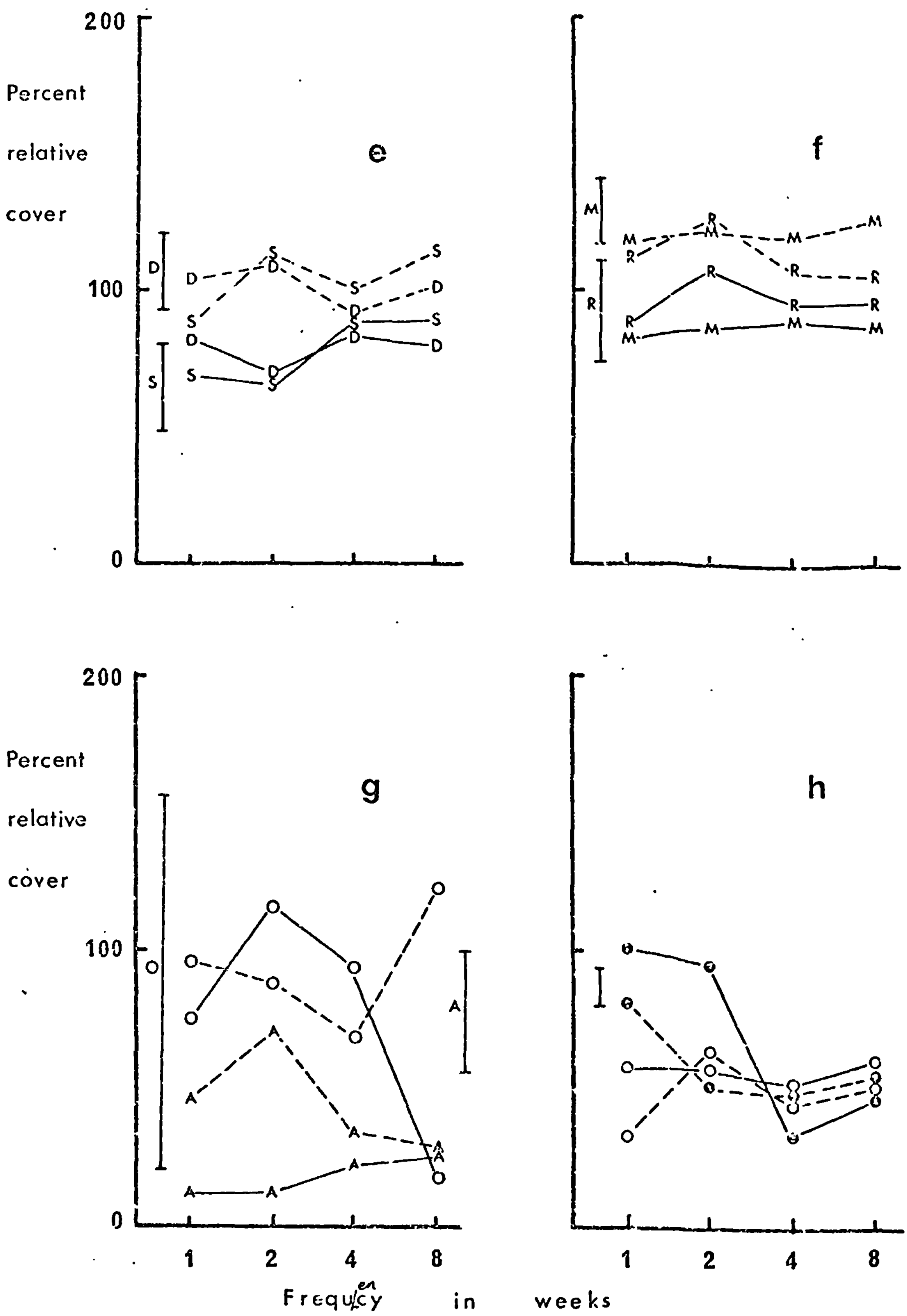
3-7h, i and j The relationship between frequency, wear vs wear followed by recovery and season of treatment. h, penetration resistance, i, total cover, j, diversity.

3-7a
F8 eight week intervals
F4 four week intervals
F2 two week intervals
F1 one week intervals

A *Carex arenaria*
C total cover
D diversity
F *Festuca rubra*
H vegetation height
L litter
M monocotyledonous species
O *Anthoxanthum odoratum*
P penetration resistance
R resistant species
S species number
● winter treatment Figs. h, i and j only
○ summer treatment Figs. h, i and j only
——— wear
- - - wear followed by recovery
I least significant difference. P <0.05.



Percent relative cover
200
100
0
a
4
8
2
1
0
40
160
640
Total intensity
b
P
L
F
M
C
D
H
4
8
16
32
16
32
64
128
Weekly intensity
c
d
P
M
D
C
1
2
4
8
Frequency in weeks


200
Percent
relative
cover
e
f
100
0
200
Percent
relative
cover
g
h
100
0
1
2
4
8
1
2
4
8
Frequency in weeks

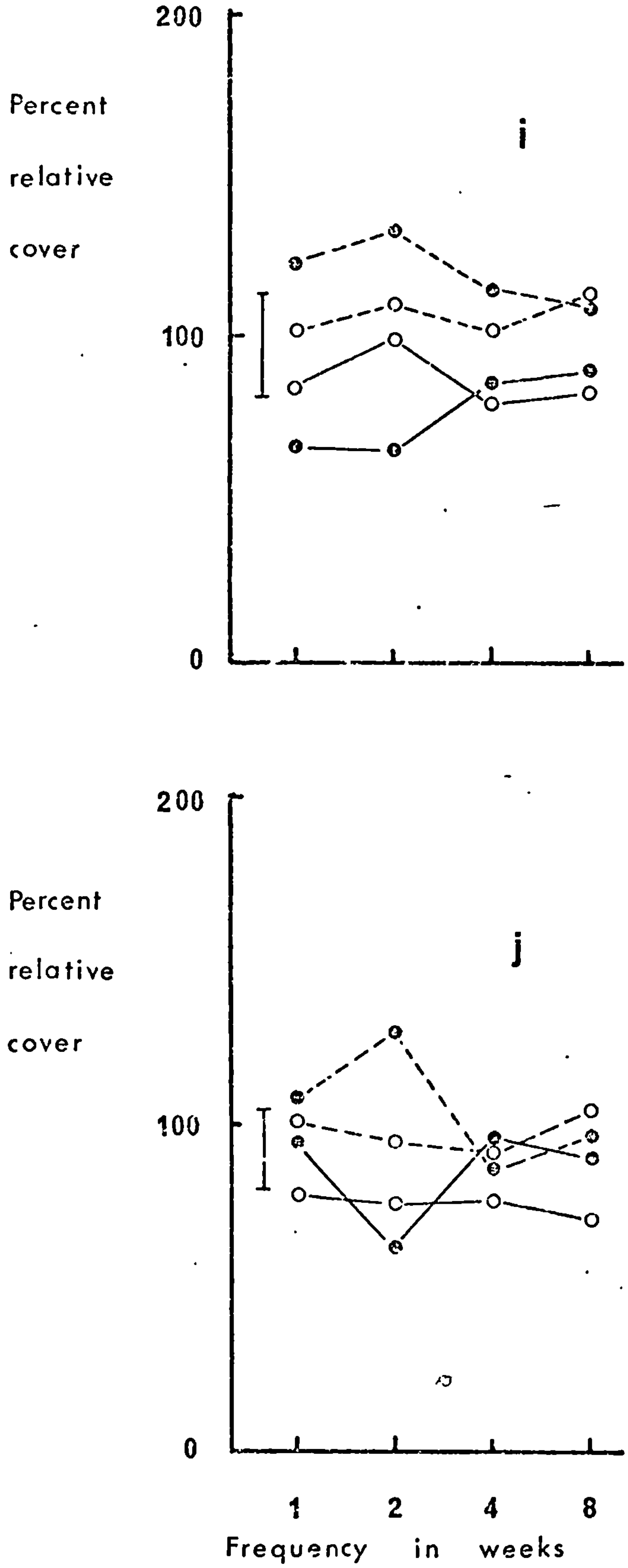

200
Percent
relative
cover
i
100
0
200
Percent
relative
cover
j
100
0
1
2
4
8
Frequency in weeks

TABLE 3-4

ANALYSIS OF VARIANCE : SIGNIFICANCE OF MAIN EFFECTS AND 1st ORDER INTERACTIONS

	Log soil penetrability	Mean of log height	Cover of live plants	Species number	Inverted Simpsons diversity index	Litter	Cover monocotyledonous species	Cover dicotyledonous species	Resistant species	*Thymus drucei*	*Festuca rubra*	*Anthoxanthum odoratum*
I	xx	xx	x	NS	x	x	xx	NS	NS	NS	xx	NS
F	xxx	xxx	xx	x	xx	x	xxx	NS	x	NS	xx	NS
R	xx	xx	xxx	xx	xxx	xx	xx	xx	xx	NS	xx	NS
M	xxx	xx	x	NS	NS	NS	x	NS	NS	x	x	NS
T	xx	xx	NS	NS	xx	NS	NS	x	NS	NS	NS	x
IF	x	NS	NS	NS	x	NS	x	NS	NS	NS	NS	NS
IR	NS	NS	NS	NS	xx	NS	x	NS	NS	NS	NS	NS
IM	NS	NS	NS	NS	x	NS	x	NS	NS	NS	NS	NS
IT	x	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
FR	xx	NS	x	NS	x	x	xx	NS	x	NS	NS	NS
FM	x	NS	NS	NS	x	NS	x	NS	NS	NS	NS	NS
FT	xx	x	NS	NS	x	NS	x	NS	NS	NS	NS	NS
RM	x	NS	NS	NS	x	NS	NS	NS	NS	NS	NS	NS
RT	xx	NS	x	NS	x	NS	x	x	x	x	NS	xx
MT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

I intensity
F frequency
R wear vs wear and recovery
M method of wear
T season of wear

x $P < 0.05$
xx $P < 0.01$
xxx $P < 0.001$
NS Not significant

TABLE 3-5

TREATMENT RESULTS : MAIN EFFECTS

	Log soil penetra-bility	Mean of log height	Cover of live plants	Species number	Inverted Simpsons diversity index	Litter	Cover monocotyle-donous species	Cover dicotyledon-ous species	Resistant species	Thymus drucei	Festuca rubra	Anthoxanthum odoratum
I = Intensity Significance%	xx	xx	x	NS	x	x	xx	NS	NS	NS	xx	NS
4, 16 passages	123	50	101	95	91	100	102	105	107	101	107	176
8, 32 passages	126	43	95	96	94	114	97	103	106	87	101	170
16, 64 passages	129	38	87	93	102	131	89	92	90	77	80	165
32,128 passages	133	29	79	84	102	138	80	88	91	46	68	147
L.S.D. 5%	1.7	4.4	8.2	11.5	5.7	23.6	5.0	44.2	13.3	53.6	13.3	47.6
F = Frequency Significance*	xxx	xxx	xx	x	xx	x	xxx	NS	x	NS	xx	NS
1 o	134	36	94	79	93	113	97	78	97	95	87	185
2 o	134	34	99	89	90	105	105	57	113	45	104	201
4 o	123	44	95	94	88	111	99	98	103	95	105	181
8 o	125	45	98	102	90	101	102	95	99	73	103	169
L.S.D. 5% +	7.9	3.7	8.5	12.5	15.5	27.9	10.5	45.9	22.7	56	15.7	48.5
R Significance	xx	xx	xxx	xx	xxx	xxx	xx	xx	xx	NS	xx	NS
Wear	130	35	73	79	87	155	77	59	83	60	79	163
Recovery	126	45	108	105	107	86	107	136	114	96	99	166
M Significance	xxx	xx	x	NS	NS	NS	x	NS	NS	x	x	NS
Van	133	36	86	89	98	126	89	84	94	52	82	164
Walking	123	44	95	35	97	115	95	111	103	104	96	165
T Significance	xx	xx	NS	NS	xx	NS	NS	x	NS	NS	NS	x
Summer	130	45	91	95	103	117	91	120	101	93	85	136
Winter	126	35	90	89	91	125	94	75	96	63	93	193
L.S.D. 5%	1.2	3.1	5.8	8.1	4.1	16.7	3.5	31.2	9.4	37.9	9.4	33.7

* Calculated by analysis of variance, therefore confounded with intensity.
+ Based on number of observations, not confounded with intensity.
o From equal passage means of F x I table, not confounded with intensity.

a drop of 13%. Soil penetration resistance and inverted Simpson's diversity index both showed a gradual increase of approximately 3% with every doubling of intensity to reach maxima of 132% and 102% respectively. Litter rose 13% over this range ending at 138% relative cover at the highest intensity. Anthoxanthum odoratum reached 176% relative cover at the lowest intensity and even at the highest number of passages it was still 147%, but these figures are not statistically significant (Table 3-5).

Frequency. The effect of the frequencies which have a significant interaction with intensity are shown in Fig.3-7c and Table 3-5. Relative penetrability decreased by 8% at the longer intervals but relative diversity and relative cover of monocotyledonous species remained almost unchanged.

Wear vs 'wear followed by recovery'. For the purpose of the analysis of variance, these treatments were considered as two levels of a single factor. They were statistically significant for all the parameters given except Anthoxanthum odoratum and Thymus drucei. The reduction by wear and the percentage of the controls that they reached on recovery is given in Tables 3-5 and 3-6; the actual amount of recovery (i.e. the difference between the first two measurements) is also

TABLE 3-6

WEAR VS WEAR FOLLOWED BY RECOVERY

Wear		Wear followed by recovery		The amount of recovery = difference between col.1 & 2	
% relative measure-ment		% relative measure-ment		% relative measure-ment	
193	Poa pratensis(NS)	258	Carex flacca(NS)	+159	Carex flacca
163	Anthoxanthum odoratum(NS)	166	Anthoxanthum odoratum(NS)	+ 77	Dicotyledonous species
155	Litter	139	Agrostis tenuis(NS)	+ 65	Agrostis tenuis
130	Penetrometer readings	137	Poa pratensis(NS)	+ 44	Carex arenaria
+		136	Dicotyledonous species	+ 36	Thymus drucei
−					
99	Carex flacca(NS)	126	Penetrometer readings	+ 35	Cover of live plants
87	Diversity index	114	Resistant species	+ 31	Resistant species
33	Resistant species	110	Cover of live plants	+ 30	Monocotyledonous species
79	Species number	107	Monocotyledonous species	+ 28	Ammophila arenaria
79	Festuca rubra	107	Diversity index	+ 26	Species number
77	Monocotyledonous species	105	Species number	+ 20	Diversity index
		+			
		−			
74	Agrostis tenuis(NS)	99	Festuca rubra	+ 20	Festuca rubra
73	Cover of live plants	96	Thymus drucei(NS)	+ 10	Height of vegetation
60	Thymus drucei(NS)	86	Litter	+ 3	Anthoxanthum odoratum
59	Dicotyledonous species	85	Carex arenaria	− 4	Penetrometer readings
41	Carex arenaria	45	Height of vegetation	− 58	Poa pratensis
35	Height of vegetation	40	Ammophila arenaria	− 69	Litter
12	Ammophila arenaria				

given in Table 3-6.

The relative height of the vegetation, 35%, and relative cover of Ammophila arenaria, 12%, were the parameters most affected by trampling and driving, followed by the relative cover of dicotyledons, 59%, and Carex arenaria, 41%. Relative diversity, relative cover of the group of resistant species and Carex flacca (N.S.) were only slightly reduced. Penetrability and litter both increased and there were extremely large increases of Poa pratensis, 195% (N.S.) and Anthoxanthum odoratum, 163% (N.S.).

Most of the measured parameters had returned to between 80% and 120% of the level of the controls after a six month recovery period, but the relative mean height of the vegetation and relative cover of Ammophila arenaria were slow to recover, remaining at 45% and 40% respectively. Anthoxanthum odoratum stayed at a high relative cover of 166% (N.S.) and was only exceeded by Carex flacca at 258% (N.S.). The dicotyledonous species and Agrostis tenuis showed a considerable resilience, gaining 77% and 65% relative cover in the recovery period.

Method of treatment. For many of the parameters one passage of the vehicle or four passages of a walker had similar effects. Those parameters that showed a significant difference between these treatments were relative species number and relative cover of the resistant species and are given in Table 3-7. The relative cover of Festuca rubra and the dicotyledonous species were less reduced by walking than by the vehicle; Thymus drucei in particular showed a 52% difference, being more heavily damaged by the vehicle.

Season of treatment. The majority of parameters that showed statistically significant effects had a greater relative cover or number as a result of winter treatment followed by summer recovery. This was particularly true of the dicotyledons (45%) and of Thymus drucei (30% N.S.) (Table 3-8). Penetrability was, however, 4% greater after summer treatment and winter recovery which suggests that treatment at this time had less effect on the soil or that greater cover increased soil strength. Anthoxanthum odoratum was also favoured by this sequence ending with 57% greater relative cover. A 12% greater diversity index occurred after summer treatment and winter recovery, but the winter treatment and summer recovery had a 6% higher species number.

The interaction between frequency and wear vs 'wear followed by recovery'. This was the first order interaction involving frequency that had the highest number of significant parameters. The most striking feature was the group of reactions in which the recovery

TABLE 3-7

THE DIFFERENCE BETWEEN WEAR BY VAN (M1)
AND 4 x WALKING (M2)

+	52%	*Thymus drucei*
+	27%	Cover of dicotyledonous species
+	14%	*Festuca rubra*
+	9%	Cover of resistant species (NS)
+	8%	Log height of vegetation
+	9%	Cover of live plants
+	6%	Species number (NS)
+	6%	Cover of monocotyledonous species
-	10%	Log penetrometer readings

+ 'survive' better on footpath

- 'survive' better on van track

TABLE 3-8

THE DIFFERENCE BETWEEN WINTER TREATMENT AND SUMMER RECOVERY (T1) AND SUMMER TREATMENT AND WINTER RECOVERY (T2)

+	57%	*Anthoxanthum odoratum*
+	8%	*Festuca rubra* (NS)
-	4%	Log penetrometer readings
-	10%	Height of vegetation
-	12%	Diversity Index
-	30%	*Thymus drucei* (NS)
-	45%	Cover of dicotyledonous species

+ recover better in winter

\- recover better in summer

graph tended to present a mirror image of the graph of wear (Figs.3-7d, e, f and g). At short intervals the relative cover tended to be depressed more by wear than at the longer intervals, but the recovery after wear was greater at the lower intervals, the recovery graph thus being a 'mirror image' of the effect of wear.

It was notable that the resistant *Anthoxanthum odoratum* (Fig.3-7g) fell into this category along with both measures of diversity (Fig.3-7e) and relative cover of *Carex arenaria* (Fig.3-7g). The species reactions are included because of their biological interest, although they were not statistically significant. All parameters except relative cover of *Anthoxanthum odoratum* at the shortest intervals, and relative penetrometer readings were depressed more at the low intervals (high frequency) than at the lower frequencies.

The interaction between wear vs 'wear followed by recovery' and season of treatment. Wear in the summer depressed relative diversity and relative cover of dicotyledonous species more than wear in winter (Table 3-9). All the other statistically significant parameters were depressed to a lower level by winter treatment. It was notable that the relative cover of *Poa pratensis* and of *Anthoxanthum odoratum* was 154% and 100% respectively after winter treatment, but after

TABLE 3-9

DATA ON THE INTERACTION BETWEEN WEAR AND RECOVERY AND SEASON

T1 winter treatment, summer recovery R1 zero recovery (wear effect)
T2 summer treatment, winter recovery R2 After 6 months' recovery

	R1	R2	Diff.	R1	R2	Diff.	R1	R2	Diff.	R1	R2	Diff.	R1	R2	Diff.
T1	134	126	-8	69	113	+44	97	110	+13	73	108	+35	63	176	+113
T2	126	125	-1	77	102	+25	78	105	+26	82	105	+23	54	95	+41
Diff.	-8	-1		+8	-11		-19	-5		+9	-3		-9	-81	
LSD	1.7			8.1			5.7			5.0			44.2		
	Log penetrability			Cover of live plants			Diversity index			Cover of monocotyledonous species			Cover of dicotyledonous species		
T1	77	124	+47	53	133	+80	70	99	+29	154	152	-2	100	172	+72
T2	88	105	+17	67	59	-8	87	100	+13	236	122	-114	225	160	-66
Diff.	+11	-19		+14	-74		+17	+1		+82	-30		+126	-12	
LSD	13.3			53.6			13.3			86.0			47.6		
	Resistant species			_Thymus drucei_			_Festuca rubra_			_Poa pratensis_			_Anthoxanthum odoratum_		

summer wear the figures reached 236% and 225% respectively.

Recovery was generally greater during the summer after winter treatment; this was especially true of dicotyledonous species, which reached a relative cover of 176% compared with 95% in the winter. _Poa pratensis_ and _Anthoxanthum odoratum_ were both depressed during recovery periods but to a greater extent after winter recovery than after the summer recovery period.

The interaction between frequency, wear vs 'wear followed by recovery' and season of treatment. The overall effect of frequency was that the other treatments usually showed greater effects at the shorter intervals. Figs.3-7h, i and j showed the more interesting parameters. This interaction was particularly evident in the penetrometer readings where the winter treatment was 20% above the summer treatment at one week intervals, but they were within 5% of each other at 8 week intervals. The relative cover records and relative diversity showed a 60% difference between winter treatment and summer recovery at 2 week treatment intervals, but after summer treatment and winter recovery the differences were below 20%; this seasonal effect was reduced at the longer intervals.

<u>Multivariate analysis</u>. This analysis was used as a summary of the floristic changes brought about by the various treatments. The records made immediately after treatment generally showed the higher intensity treatments further away from the area on the ordination occupied by their controls than the low intensity treatments (Figs.3-8a and b). The areas occupied by controls from the same plots are surrounded by a line on the ordinations. The effect of the van appeared greater than that of walking, although the most extreme stands were from paths in both cases. The analysis on the data collected after the recovery periods showed that the high total intensity plots did not return to the same areas as the controls after summer recovery (Fig.3-9a), whereas after winter recovery it was the least worn plots that were still outside the control areas (Fig.3-9b). Observation of the heavily worn plots a year after these measurements were made suggested that the flora had changed; although they had a full cover they were still conspicuous as lines of species differentiated from the control strips. Finally, the wear effects during the winter appeared to 'push' most of the stands along the same axis as that on which the greatest spread of the controls occurred, while after summer treatment the worn plots 'moved' in a different direction from their controls.

Fig.3-8

Ordination of control and worn stands immediately after treatment. Plot codes as for Fig.3-3.

3-8a After winter treatments

3-8b After summer treatments

(8), eight week intervals between treatments

(4), four week intervals between treatments

(2), two week intervals between treatments

(1), one week intervals between treatments

○ ◐ footpath stands

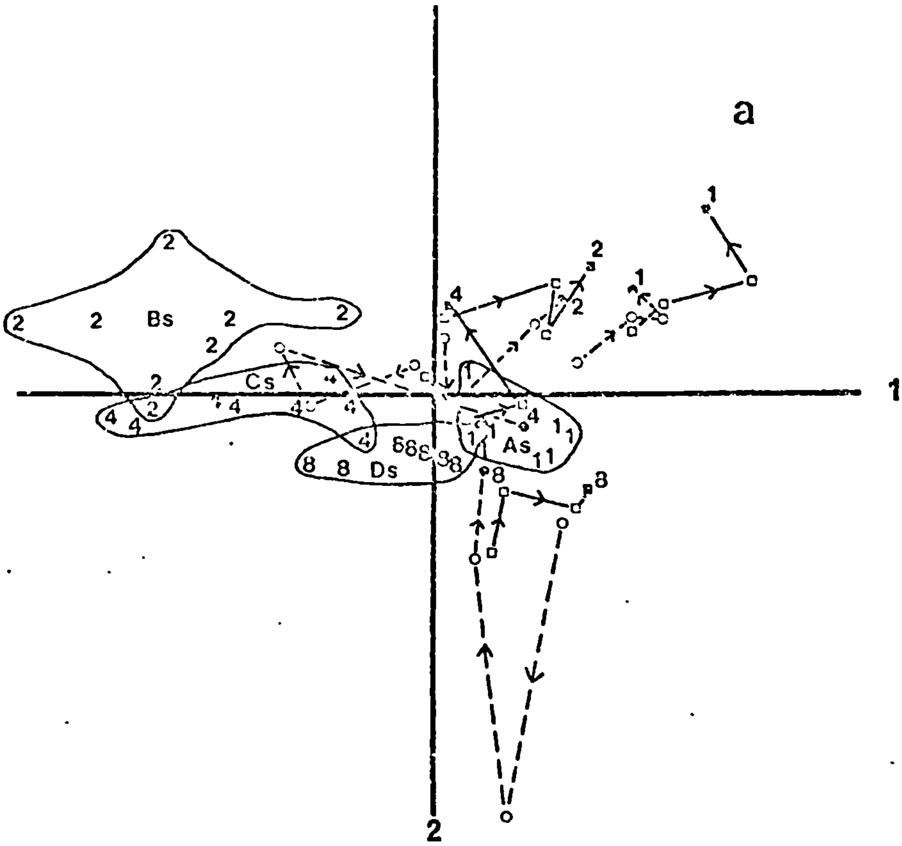
□ ◪ car track stands

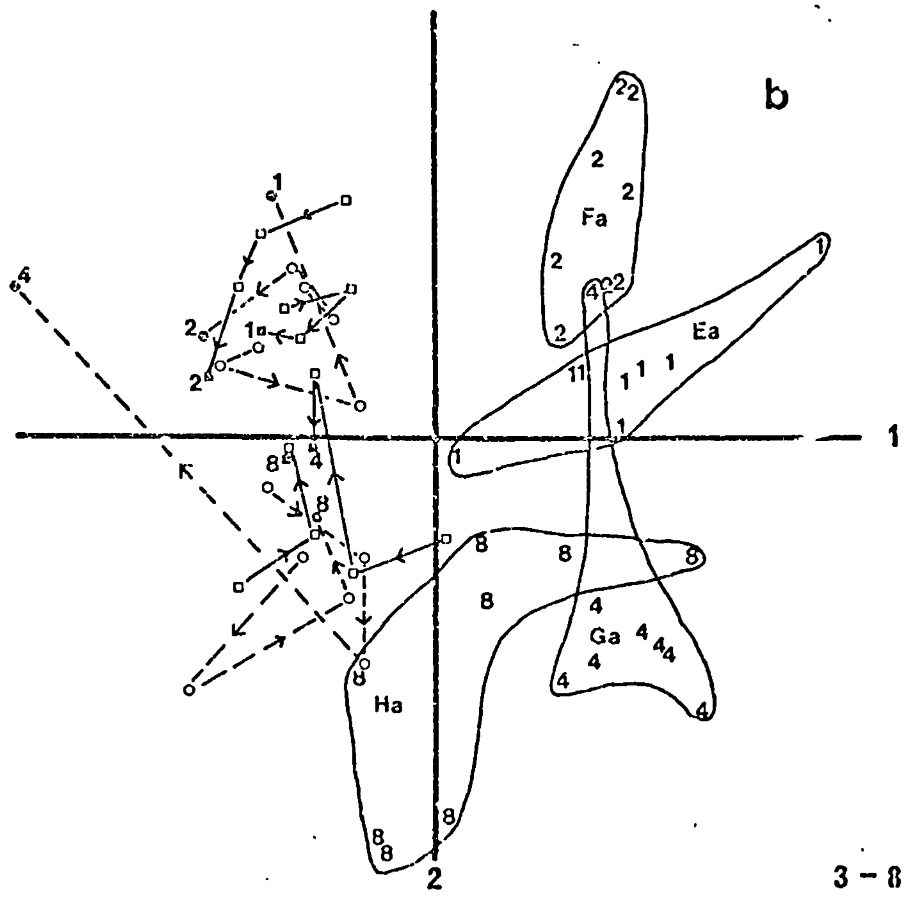
● ■ stands with greatest wear. Adjacent numbers give treatment interval.

—>— lines connect worn stands; arrows point in direction of greatest wear.

——— tracks

- - - - footpaths





3 – 8

Fig.3-9

Ordination of control and worn stands after recovery periods.

3-9a Recovery after winter treatment

3-9b Recovery after summer treatment

(8), eight week intervals between treatments

(4), four week intervals between treatments

(2), two week intervals between treatments

(1), one week intervals between treatments

○ ◍ footpath stands

□ ▣ car track stands

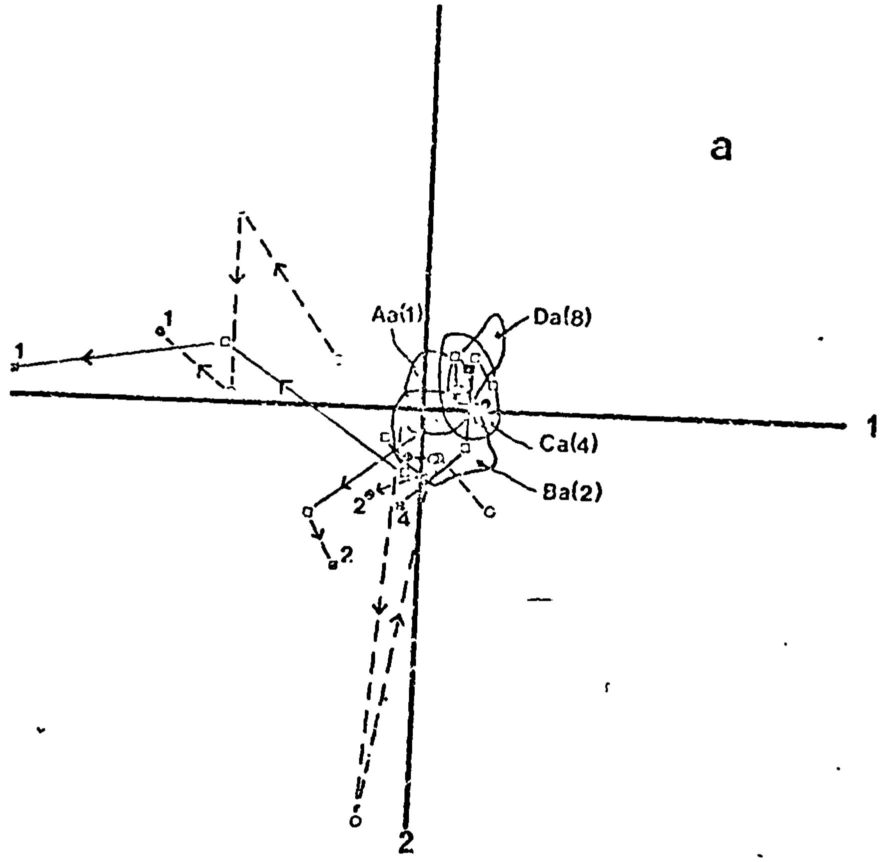
▣ ◍ stands with greatest wear. Adjacent numbers give treatment interval.

—>— lines connect worn stands; arrows point in direction of greatest wear.

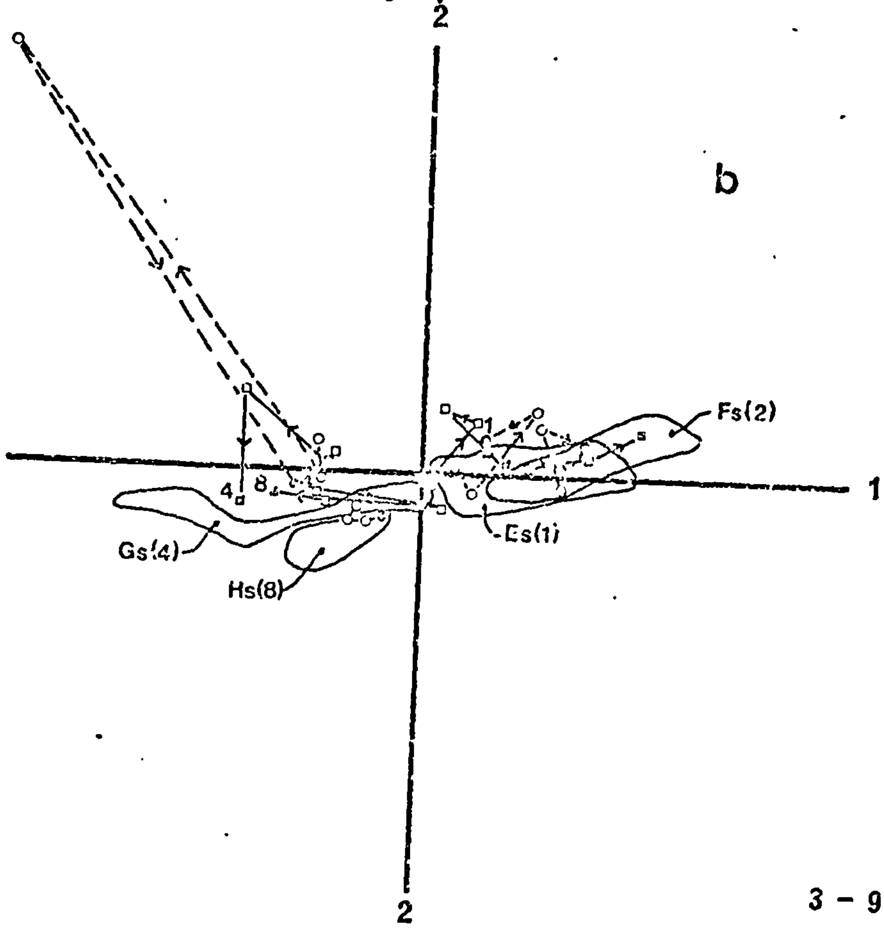
——— tracks

- - - - footpaths

a



b



DISCUSSION

The main practical problem that had to be overcome in the design of this experiment was how to arrange all the treatments when the use of a vehicle imposed a large plot size. Repeated passages required a circular course and although the plots to be measured were only 20 m long each circuit was approximately 40 m by 30 m. Replications of all treatments would have involved the use of an unacceptable amount of land, and while achieving statistical respectability, the improvement might have been offset by a wider range of environmental variation. Thus each plot received a different treatment but the results were expressed as percentages of the internal controls to reduce the variation due to plot differences.

This does not, however, remove the possibility of different blocks having varying ecological conditions and thus causing differing responses by the various plant species.

The principal ecological consideration was to discover how trampling interacts with the composition of plant communities and in what way it related to the biology of the individual species. A number of community measures were considered, and diversity, total cover and the mean height of the vegetation gave a fairly comprehensive picture. The greater relative diversity produced by the high intensity wear and recovery suggested that a dominant species was removed or reduced and that it had not regained its position at the time recovery measurements were taken. The increase of *Poa pratensis* and *Anthoxanthum odoratum* under the influence of wear (Table 3-6) also suggested the removal of a limiting factor and that wear ~~only~~ became limiting only for these species at high total intensities. Their decrease during recovery also supported this hypothesis. The normal limiting factor may have been light, which was reduced by the combined effect of *Festuca rubra* (which generally made up 20-30% of the cover of the controls) and plant litter which contributed 30-40% of the cover. The fact that diversity maintained a higher level under summer recovery conditions after winter treatment also suggested that it may be maintained by growth of previously repressed species (Fig.3-7j). The processes may have been similar to the winter overgrazing and summer rest period stated by Jones (1933) to give a high 'floristic richness'. The high diversity after a six month recovery period could also imply that the path edges of high diversity (see Chapter 2) may not be the result of a low intensity use but of a lateral movement of the position of the main path. Cover measurements indicated that recovery was complete in many cases but the low mean height of the 'recovered' vegetation showed that there was still some adjustment to be made before conditions were similar to the controls.

The ordination results (Figs.8 and 9) suggested that the stands subjected to high levels of wear in the winter and intermediate intensity in the summer may have undergone a long term change, perhaps due to the effect of compaction on soils. They also indicated that the controls had become more uniform during the recovery periods or that the worn stands still outside the control plot areas on the ordination were more differentiated from the controls after recovery. However, similarity in the ordinations does not imply a return to original conditions so much as the potential to do so after a further period of growth.

The growth rate of vegetation under pressure is also likely to be important. In general, the recovery curves are mirror images of the wear curves and this indicates that the greater the damage, the greater is the potential for repair. (Figs.3-7d, e, f and g). The recovery was generally better for all species during the summer period, but it is noticeable that dicotyledonous species showed the greatest increase of all the parameters during the summer and winter recovery periods

TABLE 3-10

RELATIVE GROUND PRESSURES

	area cm^{-2}	wt. kg.	$g.cm^{-2}$
Sheep*	85	80	941
Cattle*	300	440	1,467
Cars 1600 cc Estate			
Soft ground			
Tyre pressure 22 psi	1,376	1,289	936
Tyre pressure 32 psi	1,332	1,289	968
Hard ground			
Tyre pressure 22 psi	924	1,289	1,406
Tyre pressure 32 psi	800	1,289	1,611
Bedford Van			
Tyre pressure 32 psi			
Hard ground	624	760	1,218
Soft ground	1,024	760	742
Man	388	80	206
Woman	356	57	160

* Derived from Spedding (1971)

A comparison of ground distribution between a walker and the small van.

Man. One pace, 70 cm. Path width, 25 cm.
Therefore, area per pace is 1,750 cm^{-2}.
Average weight is 69 kg.
Average weight per passage per cm^{-2} of path
69,000/1,750 = 39 $g.cm^{-2}$.

Van. This does not leave the ground so the pressure is 2 x 1,030 per cm^{-2} of track.

Therefore, the weight ratio is 2,060 : 39 = 53 : 1 per unit length of path or track per passage.

in spite of being the most affected by wear, except Thymus drucei alone which is 10% below the mean for dicotyledonous species. The increase during recovery of Carex flacca and Agrostis tenuis may also have been due to a high growth rate relative to other sand dune species. The great increase of Poa pratensis and Anthoxanthum odoratum during the periods of wear suggests that these species may also have a high growth rate combined with an intrinsic resistance to damage.

The degree of mechanical damage suffered by a plant may depend to some extent on its turgidity. Edmond (1962) and Bellamy et al (1971) (Table 3-11) have shown that vegetation is more susceptible to damage the greater the level of soil moisture. This may account for the fact that treatment in winter tends to have a more damaging effect except to the relative cover of the dicotyledonous species. In sand dune pasture the soil moisture content during summer may often be below that required to maintain the plants in a fully turgid condition. The effect of downward compaction partially depends on the weight per unit area of the compacting 'body', and the data for the conditions of this experiment and some other examples are given in Table 3-10. This is also discussed in Paper 1 of this series. One effect of compaction on the moist soils in the winter treatment was to incorporate the litter into the surface humus on the highest intensity car rut; this must increase the nitrogen demand by the bacteria and consequently reduce the amount available to higher plants. There was, however, a noticeable increase of Carex flacca in this rut during the recovery period. Willis & Yemm (1961) found that the treatment of turves from damp dune slacks with nitrogen only, caused a large increase in Carex flacca but NPK stimulated grasses. This suggests that the litter may have been broken down by soil organisms quite quickly and that extra nitrogen was available in that particular rut during the recovery period while it was water logged. The long term change postulated to have occurred as a result of the higher intensity winter treatments (Fig.3-9a) may be due to the incorporation of litter and the greater degree of compaction as a result of wear at this season (Fig.3-7h). This type of long term effect cannot be considered as a simple inhibition of a successional sequence as it may lead to a different edaphic climax. The different direction of displacement of the wear plots in relation to the controls at the two seasons (Figs.3-8a and b) of wear also indicated that the consequences of trampling may not be the same in the summer and winter.

The management recommendations that can be made from these data are all based on the supposition that the wear will occur in the manner described for this experiment. In fact, there will be much more erratic use of these areas with high maxima at peak holiday periods; there is, therefore, a need for further experiments using frequency and intensity models based on surveys of the temporal distribution of visitors.

Management for a specific species composition or diversity requires a very careful regulation of light wear in terms of spatial and temporal distributions. If, however, the aim is to preserve a 100% cover of vegetation and the recovery periods are similar to this experiment, then the number of people or cars that can be allowed are as given in Table 3-11. These are for a sand dune pasture vegetation that has not had time to adapt to trampling; in field situations an adapted path will probably withstand a higher intensity of use. The width of a path or car track is normally 1.5 to 4 times the 25 cm single file track used in this experiment (Bayfield 1971a, Huxley 1970) so a more realistic figure will be obtained by multiplying the data in Table 3-11 by 4. At this level of wear the vegetation may change but it will not be destroyed; the more vulnerable fore dunes would, however, need some protection to prevent

TABLE 3-11

MAXIMUM NUMBER OF PASSAGES IN 20 WEEKS
TO ALLOW 100% RECOVERY OF COVER

	Car	Walking
Summer wear and winter recovery	80 (With 2 week rest periods)	1,280 (With 2 week rest periods)
Winter wear and summer recovery	320 (With 1 week rest periods)	2,560 + (With 1 week rest periods)

erosion. These figures suggested that the light van or car was between 8 and 16 times more damaging to the vegetation than one person walking. A figure of 7.55 times has been derived from the mean of the wear data (~~e.g.~~ i.e. 1412/187 = 755 Table 3-12).

Vanden Berg & Gill (1962) have shown that a low pressure tyre will impose a lower ground pressure over a larger area than a conventional tyre; the more common use of low pressure radial types in the future should, therefore, reduce the amount of damage caused by cars. Cohron (1971) points out that compaction is reduced by higher vehicle speeds but since this would cause greater lateral stresses on vegetation when cornering and greater compaction on the rebound after passing over bumps, this is not recommended. Soil erosion on sand dune tracks can often be observed at the top of small bumps where the downward force exerted by moving cars is increased.

The frequency suggested in Table 3-11 is based on the data in Figs.3-6a and b. While frequency of use is statistically significant for many parameters given in the analysis of variance examination of the data suggests that its importance is mainly at low levels of use and, therefore, only of management interest where it is desired to maintain the original composition of the vegetation.

The need to compare the vulnerability of different vegetation types to the effects of vehicles and trampling was pointed out by Bayfield (1971b). A crude comparison can be made by regressing the percentage cover of vegetation left after wear (y) on the $\log_e$ of the number of passages (x) and using the coefficient b from the equation

$$y = a + bx$$

as a vulnerability index; this method was used to construct Table I. The higher the absolute value of the figure, the more vulnerable the vegetation. Some results of this technique were given in the Introduction. An alternative is to use the more realistic curvilinear regression equation

$$y = ax^2 + bx + c$$

derived from trampling data to predict x at 50% cover. Thus the equation becomes

$$x = \frac{-b \pm \sqrt{b^2 - 4a(c-50)}}{2a}$$

The 50% point is more useful in management and avoids extrapolation beyond the range of most experiments (Table 3-12, Col.2). The data used in this table were converted to a percentage basis from cover and biomass parameters where necessary.

TABLE 3-12

Source of data	No.of passages at y = 50%	No.of passages / weight correction factor	7.55 x Col. 3 *
Liddle			
Driving winter	171	193	1,457
Driving summer	203	229	1,729
Walking winter	1,061	-	1,061
Walking summer	1,828	-	1,828
Mean Driving	187	211	1,593
Mean Walking	1,412	-	1,412
Morrish & Harrison (1948)			
Car	154	193	1,457
Truck	140	340	2,567
Wagar (1964)			
Trampler	23	-	-
Bayfield (1971b)			
Trampler	27	-	-
Bellamy _et al_ (1971)			
Wet A1	13	19	151
A2a	0.63	1	8
B3	11	16	128
A2	12	18	144
A4	12	18	121
A3	0.49	1	8
C1	20	30	234
B4	8	12	98
B2	17	25	204
B1	12	18	144
C3	25	37	295
Dry C2	23	34	272
Soft rollers	51	96	725
	38	68	513

* The relative vulnerability of habitats in number of walking passages to reduce cover to 50%.

An adjustment can then be made according to the weight of the vehicle and the type of wear. The earlier calculations (Table 3-10) suggest that this is reasonable. The data in Bellamy et al (1971) show a relationship between vegetation damage and $\log_e$ of the weight of the vehicle and the parameters of this regression can be used to calculate an empirical correction factor. (Fig.3-10 and Table 3-13). The amount of damage caused to the vegetation was expressed on a scale 0.0 for bare ground to 1.0 for 100% cover and regressed on the weight of the vehicle. The resulting quadratic

$$y = -0.0081186\ W^2 - 0.0036036\ W + 1.362002$$

where W = the $\log_e$ of the weight of the vehicle and y = the amount of damage was used to calculate correction factors (theoretically to zero weight) by which the number of passages to reach 50% cover derived from the first equation was divided (Table 3-12, Col.3). A final adjustment by multiplying by 7.55 derived from the data presented in this paper, was used to give a comparative figure between walking and vehicle effects (Col.4). However, this should be treated with great caution as the mechanisms of damage are different.

The data in Table 12 suggest that the cultivated plots used by Morrish & Harrison (1948) in Michigan, U.S.A. may have been more resistant than Aberffraw sand

Fig.3-10

Calculation of vehicle weight correction factor from data of Bellamy <u>et al</u> (1971).

Y Axis: correction factor (surviving vegetation cover expressed from 0.0 to 1.0)

X Axis: vehicle weight

W = Log_e vehicle weight in lb.

- - - Calculation of correction factor for 8,500 lb. vehicle (= 0.67).

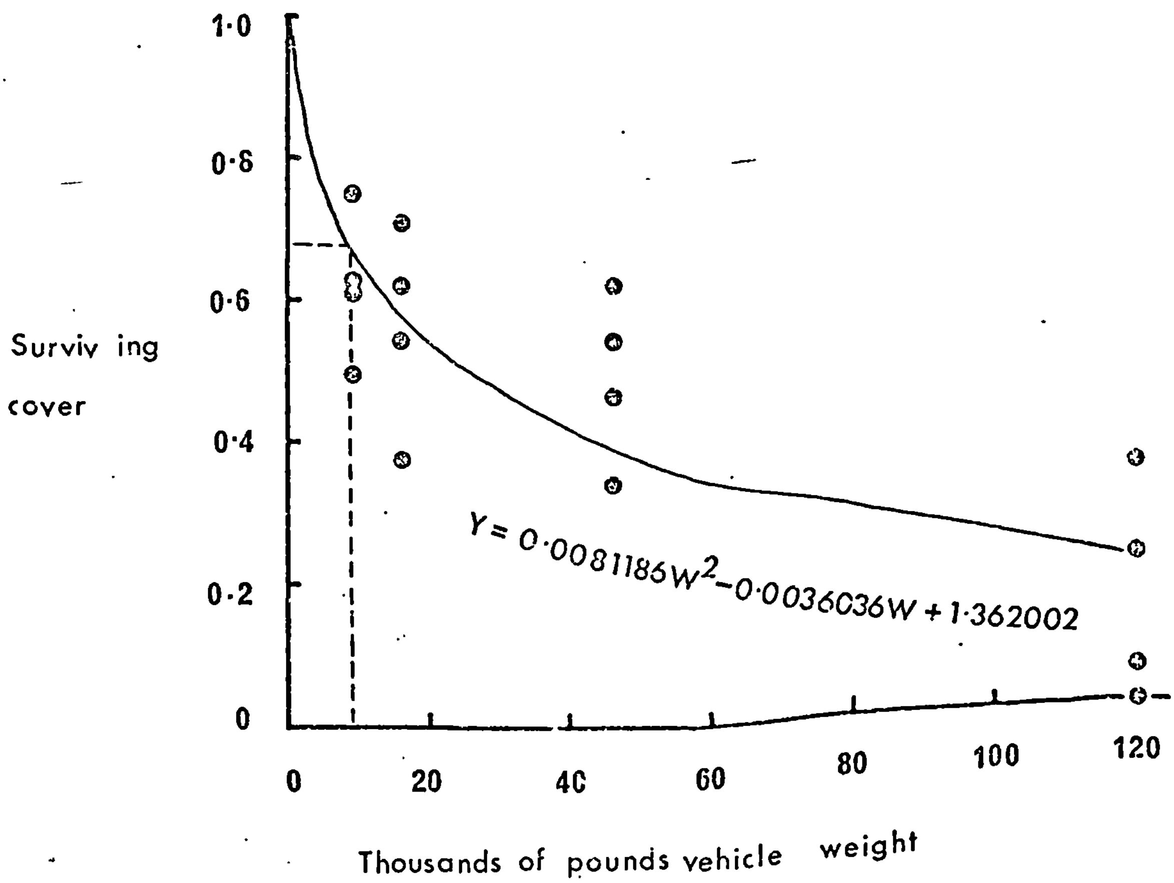

1·0
0·8
0·6
0·4
0·2
0
Surviv ing
cover
Y= 0·0081186W²–0·0036036W + 1·362002
0
20
40
60
80
100
120
Thousands of pounds vehicle weight

TABLE 3-13

VEHICLE WEIGHT CORRECTION FACTORS

Vehicle	Weight kg	Weight lb	Correction Factor
Liddle			
grey van	760	1,672	0.88
Morrish & Harrison (1948)			
car	1,520	3,300	0.80
truck	18,182	40,000	0.41
Bellamy *et al* (1971)			
Vehicle used for different vegetation types	3,864	8,500	0.67
Vehicles with soft rollers	7,727 9,090	17,000 20,000	0.56 0.53

dune pasture. The Alaskan muskeg is more vulnerable to the effect of vehicles, but since the effect of tracks and wheels is probably different a direct comparison cannot be made. The comparison of the effects of Wagar's trampler in a field situation in Michigan (Wagar 1964) and Bayfield's trampler on Phleum pratense grown in greenhouse conditions (Bayfield 1971b) show a remarkable similarity.

This approach to classifying vegetation according to its vulnerability will improve as more trampling data becomes available, but as these experiments are extremely labour intensive there will always be a need for the use of results from various experimental techniques and I would suggest that the method presented here is a more practical approach to the problem than that of Cieslinski & Wagar (1970) which does not allow the use of information from various sources.

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APPENDIX 1

WINTER TREATED PLOTS MEASURED IN THE SPRING (WS)

Plot	A								B								C								D							
Frequency	1 week interval								2 weeks interval								4 weeks interval								8 weeks interval							
Numbers of passages	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	6	16	4	128	32	64	16	32	8	16	4
Species																																
Litter	107	35	128	119	128	130	105	138	130	146	120	137	93	126	91	115	99	109	90	88	61	86	82	89	63	60	54	61	45	53	69	63
Bare ground	51	150	7	30	1	4			12	12	3	7	2	5			1	6						1								
Ranunculus bulbosus																												1	2			
Viola canina																																
Viola tricolor																																
Polygala vulgaris		1																														
Cerastium cf. semidecandrum																																
Cerastium atrovirens																					1											
Linum catharticum																																
Ononis repens																																
Trifolium dubium																	1															
Trifolium repens				1						1	2	4	1	2	2	1		2	1	2					1	1	2	1	2	1		
Trifolium arvense																																
Anthyllis vulneraria																																
Lotus corniculatus					1		1		1		1	1	1				4	1	2	6	9	4	2	2	7	9	6	7	10	4	6	5
Potentilla reptans					1	1						1						1	1	2		1	3	1								
Myosotis ramosissima																																
Veronica officinalis																																
Thymus drucei			5		6	1	9		4		9	1	10	4	15	9	6	3	10	6	12	4	21	7	8	3	15	2	11	11	8	4
Prunella vulgaris																																
Galium verum							1						3				4	1	4		2	4	1	3	2	1	3	2	5	2	2	5
Senecio jacobaea									2		2	1	3	1	1	7		3	3	2	1		1	1	3	2	4	4	2	3		3
Bellis perennis																																
Carlina vulgaris																																
Cirsium arvense																																
Leontodon hispidus																									3	1	3					
Leontodon taraxacoides									2		1			1	1				1		1	1		2					1			
Crepis spp. indet.																1		1														
Taraxacum officinale							2										3	4	6	4	6	2	1	1	4	1	1	1	1	1		
Taraxacum laevigatum							1										2									1	2	1	2	1	1	
Luzula campestris	2		2	1	1	2	1	2	2	1	1	4	3	2	3	1		2	1	1		2	2	1		6	3		5	2	5	6
Carex flacca	8	13	10	15	11	9	9	8	1	4	2	5	4	7	8	3			1	2	3	4	1	5	4	15	10	11	13	18	16	8
Carex arenaria	3	1	1	1	3	3	2	3	1	5	4	4	9	1	8	4	7	10	8	7	8	13	9	7	4	4	3	3	5	5	7	6
Festuca rubra	11		21	7	14	18	47	29	14	5	35	13	46	38	49	40	41	27	36	35	64	48	49	48	57	60	59	42	43	52	53	65
Festuca ovina																																
Poa pratensis	4		5	6	5	10	6	8	8	12	4	3	5	5	3	5	5	7	5	8	4	3	3	5	6	8	3	9	5	3	6	2
Arrhenatherum elatius																																
Aira caryophyllea																			3		1			1								
Anthoxanthum odoratum	13		17	15	28	21	10	5	18	14	10	13	8	9	15	9	26	23	25	29	20	20	20	20	34	25	24	47	33	38	18	24
Ammophila arenaria							1	1	1			1				1			3		1		2	2	1	1	1		1		3	2
Agrostis tenuis	1		3	2	1	1	4	6	3		4	5	7		2	4	1			7	4	7	2	4	3	2	7	7	10	4	4	5
Agrostis stolonifera			1	3																1												
Thuidium spp. indet													1		1																	
Climacium dendroides															1								1					1	2	2	1	1
Camptothecium lutescens																																
Pseudoscleropodium purum																					1											
Hypnum cupressiforme																													2		1	1
Cladonia spp. indet																																
Peltigera canina							1		1		2			1							1	1										

APPENDIX 1 CONTINUED

WINTER CONTROL PLOTS MEASURED IN THE SPRING (WS)

Plot	A									B									C									D								
Frequency	1 week interval									2 weeks interval									4 weeks interval									8 weeks interval								
Control strip number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Species																																				
Litter	20	25	16	26	21	27	35	49	31	38	41	31	28	35	33	31	36	37	37	31	29	42	28	32	39	31	45	23	20	25	21	23	21	30	34	33
Bare ground																																				
Ranunculus bulbosus																																				
Viole canina															1															1						
Viola tricolor																																				
Polygala vulgaris																																				
Cerastium cf. semidecandrum																																				
Cerastium atrovirens																						1			1							1				
Linum catharticum																																				
Ononis repens																																				
Trifolium dubium																																				
Trifolium repens			2	1			1			1	1	2	2	2	2		2	1		1	2					2				1				1	1	
Trifolium arvense																																				
Anthyllis vulneraria																																				
Lotus corniculatus	6	2	1		1	1			2	1		1	1					1	2	3	4	3	4	2			5	4	1	4	1	6	2		2	2
Potentilla reptans		2	1				1		1													1		1												
Myosotis ramosissima										1								1																		
Veronica officinalis																																				
Thymus drucei	2	7	12	5	2	2	8	5	5	12	3	12	7	12	14	7	8	5	8	12	19	13	7	8	6	8	9	5	4	7	6	2	8	4	2	1
Prunella vulgaris																																				
Galium verum	2		2	1	1	1	1							1	1	1			1		4	1			1	1	1	1			1	1		3	1	
Senecio jacobea							1				1		2	2	1	1	1	2	3	2	1	1	2			3	2			1	2		1	3	2	1
Bellis perennis																																		1		
Carlina vulgaris																																				
Cirsium arvense																																				
Leontodon hispidus																																				
Leontodon taraxacoides	2		1					1		3			1	2	1	1					1	1	1								1	1				2
Crepis spp. indet.										1	1																									
Taraxacum officinale												1					1		1	2	4	1	4	1				1	1	1	1		2	2		
Taraxacum laevigatum				1			2							1					1							1										
Luzula campestris	1	2	1		1		2	1		3	2		2	1					1			4		1		2		2	1	2		1	1	2	3	2
Carex flacca	6	3	4	3	4	6	5	4	8			1		3	4	2	4	1		1			1	4	2	1	3	6	5	6	3	2	7	5	8	5
Carex arenaria	2	3	2	3	5	3	1	6	7	4	5	4	10	7	10	7	3	7	8	8	8	5	9	6	14	4	3	7	2	2	9	6	6	5	1	2
Festuca rubra	33	38	30	28	37	43	28	26	31	23	32	30	29	22	20	27	25	37	19	22	19	15	31	28	20	25	16	27	32	28	30	31	26	25	27	28
Festuca ovina																																				
Poa pratensis	12	5	2		6	1	2	1	2	1	6	4	1	1	3	1	3		4				2		1	3	1		2	3	2	2	6	2	3	4
Arrhenatherum elatius																																				
Aira caryophyllea										2			1			2						1														
Anthoxanthum odoratum	12	9	23	29	20	14	7	4	9	5	5	7	12	4	4	2	7	2	12	10	5	7	10	12	9	12	6	11	24	11	19	23	12	12	12	9
Ammophila arenaria							1			4	1	3	2	3	3	13	6	6	1	5	3	4		3	7	3	7	7	5	2	1		4	4	1	8
Agrostis tenuis	1	4	3	2	2	2	4	1	3	1	1	3	1	3	2	2	1			2			1	3		4	2	6	2	5	2	1	4	1	2	2
Agrostis stolonifera				1																																
Thuidium spp. indet.	1							1						1	1		3			1															1	
Climacium dendroides																																				
Camptothecium lutescens									1		1	1	1			3			2											1						
Pseudoscleropodium purum																																				
Hypnum cupressiforme	1							1																												
Cladonia spp. indet.																															1					
Peltigera canina																																				

APPENDIX 1 CONTINUED

WINTER TREATED PLOTS MEASURED IN THE AUTUMN (WA)

Plot	A								B								C								D							
Frequency	1 week interval								2 weeks interval								4 weeks interval								8 weeks interval							
Numbers of passages	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4
Species																																
Litter	42	60	30	34	54	47	61	42	59	55	65	59	47	50	61	50	59	58	56	55	67	73	75	80	55	56	51	56	53	71	80	77
Bare ground		17		1					3	5	1	1		1																		
Ranunculus bulbosus					1																											
Viola canina																																1
Viola tricolor											1																					
Polygala vulgaris																																
Cerastium cf. semidecandrum																																
Cerastium atrovirens																																
Cerastium spp.																										1						1
Linum catharticum																																
Ononis repens																																
Trifolium dubium																																
Trifolium repens		4	3	1			1	4	1	4	1	5	3	1		1	1	4					2	1	1		1	1	1			
Trifolium arvense																																
Anthyllis vulneraria																																
Lotus corniculatus	6	11	3		2			1	2	4		2				2	1	2	1		2	1				2	3	1	2	1		
Potentilla reptans	2			3	1	1			1	1		1																				
Myosotis ramosissima																																
Veronica officinalis																																
Thymus drucei	5	3	10	3	10	4	7	12	28	15	9	12	13	15	18	3	20	19	19	15	12	7	13	12	6	2	4	3	13	9	8	8
Prunella vulgaris																																
Galium verum	8	12	6	6	2		4	1	6	4	5	7	4	3	2	1	3	5	1	1	2	1				1			1			1
Senecio jacobaea		1		1		3				9	1	4	2	2		4	1	3		3	1		2			1		1				
Bellis perennis																																
Carlina vulgaris																							1									
Cirsium arvense																																
Leontodon hispidus																																
Leontodon taraxacoides	3	4	2			2	1		2	3	1	2	4	3	3	1	5	3	1	2	1		2		1	2	1	1	1			1
Crepis spp. (indet.)										1									1	1	1		1						1			
Taraxacum officinale						1												2	1								1					
Taraxacum laevigatum													1																			
Luzula campestris	2	2	2				2	2	1	1	1	2	2	1	2		1	2	2	1			1		1			1	1	2	2	1
Carex flacca	11	47	8	25	6	8	13	7		6	6	9	5	5	8	6					1	3		2	6	7	8	8	8	12	9	10
Carex arenaria	9	5	4	10	4	11	6	9	12	11	4	13	14	14	17	24	15	11	24	15	21	14	26	17	4	10	5	9	4	3	6	8
Festuca rubra	23	2	47	27	59	59	58	65	49	30	61	36	71	68	53	76	51	51	56	65	57	57	42	57	56	62	60	51	52	55	53	54
Poa pratensis	3	4	4	13	1	11	2	12	2	15	7	4	2	9	3	7	5	7	2	3	2		2	3	6	5	5	9	8	6	11	6
Arrhenatherum elatius																																
Aira caryophyllea																																
Anthoxanthum odoratum	83	21	69	66	48	44	35	31	31	31	23	36	17	17	24	19	32	27	31	30	23	22	23	18	51	44	32	43	34	40	19	24
Ammophila arenaria	1	4			2		2	4			5	2	6	5	8	5	5	1	5	3	2	1	4	5		3	7	2	4	1	5	6
Agrostis tenuis	2		7	8	6	8	6	10	2	4	7	4	6	4		1	1	3		4	5	11	4	4	2	3	7	5	5		2	2
Agrostis stolonifera			1		3																											
Grass A			3									1														1						
Tortula ruraliformis													1																			
Climacium dendroides																																
Thuidium spp. (indet.)									1		1		1														1	1			1	
Camptothecium lutescens		3	1			1				1	1		1	1	1			1		2	3		1	1	1						2	
Pseudoscleropodium purum					1									1				1									1	1	2		2	
Hypnum cupressiforme																																
Rhodobryum roseum																																
Lophocolea bidentata																																
Peltigera canina																																

APPENDIX 1 CONTINUED

WINTER CONTROL PLOTS MEASURED IN THE AUTUMN (WA)

Plot	A									B									C									D								
Frequency	1 week interval									2 weeks interval									4 weeks interval									8 weeks interval								
Control strip number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Species																																				
Litter	32	30	32	30	31	40	33	39	47	41	42	33	33	41	48	32	32	49	40	35	32	37	40	45	47	49	37	38	31	37	40	38	28	40	42	46
Bare ground																																				
Ranunculus bulbosus																																				
Viola canina								1																												
Viola tricolor																					1															
Polygala vulgaris																																				
Cerastium cf. semidecandrum																																				
Cerastium atrovirens																																				
Linum catharticum																																				
Ononis repens																																				
Trifolium dubium																																				
Trifolium repens											1	1			1							1												1		
Trifolium arvense																																				
Anthyllis vulneraria																																				
Lotus corniculatus			1					1	2										1		1		1		2											
Potentilla reptans		1											1																							
Veronica officinalis																																				
Thymus drucei	2	3	5	1	2		2	4		11	8	8	5	4	10	7	6	3	3	11	9	6	7	3	5	5	4	1	3	4	1	7	5	1	3	
Prunella vulgaris																																				
Galium verum			1	2	1		2	1				3	1	1	1	2	1	1				1	1										1			
Senecio jacobaea		1		1										1			1					1			1									1		
Bellis perennis																																				
Carlina vulgaris																																				
Cirsium arvense																																				
Leontodon hispidus																																				
Leontodon taraxacoides													2	1	2	2	1		3									1								
Crepis spp. indet.										1	1										1															
Taraxacum officinale				1															1		1															
Taraxacum laevigatum																																				
Luzula campestris			1		2		2				1	1	1	1	1					1	1					1		3			2			1	1	
Carex flacca	2		1	4	2		6	1	2	1	1	2					2					1	2	1			1	2		1	3	2	4	4	8	3
Carex arenaria	4	4	10	4	8	7	7	10	8	7	5	5	10	4	2	5	10	5	7	5	10	9	15	13	11	16	9	3	6	4	4	3	5	5	4	3
Festuca rubra	42	32	23	35	27	30	32	26	28	25	26	34	29	32	29	32	35	22	23	29	23	26	24	23	17	18	28	32	35	29	25	26	24	23	25	20
Poa pratensis	1	3	1	3	4	3	2	2		2	3	3	2	1	1	2		3		2	2	2			2	1	2		5	2	4	3	6	2		3
Arrhenatherum elatius																																				
Aira caryophyllea																																				
Anthoxanthum odoratum	14	21	23	15	17	13	7	7	7	10	8	5	11	5	3	6	4	2	12	7	9	11	9	5	12	7	8	12	10	15	10	17	22	13	8	12
Ammophila arenaria	2	1		1		4	3	4	3	2	2	3	2	6	1	11	9	14	8	9	7	4		7	2	2	10	6	6	2	4		4	5	6	13
Agrostis tenuis	1	3	1	3	6	2	3	3	3		1	1	1	2	1		1			1	2			3	1	1	1		4	4	4	3		3	2	
Agrostis stolonifera						1																														
Grass A		1										1																								
Tortula ruraliformis																																				
Climacium dendroides																																				
Thuidium spp. indet.							1				1		1						2									1			1				1	
Camptothecium lutescens			1					1										1			1	1	1									1				
Pseudoscleropodium purum																												1		2	1		1			
Hypnum cupressiforme																																				
Rhodobryum roseum																																				
Peltigera canina													1			1																				

APPENDIX 1 CONTINUED

SUMMER TREATED PLOTS MEASURED IN THE AUTUMN (3A)

Plot	E								F								G								H							
Frequency	1 week interval								2 weeks interval								4 weeks interval								8 weeks interval							
Numbers of passages	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4
Species																																
Litter	144	171	108	145	86	133	66	89	95	142	63	123	56	84	74	59	73	99	79	112	68	87	76	76	83	114	86	95	75	81	69	74
Bare ground	13	16	5	10		2					1						1	4			1				1							
Ranunculus bulbosus																																
Viola canina																	1	1														
Viola tricolor																																
Polygalg vulgaris									1																							
Cerastium cf. semidecandrum																													1			
Cerastium atrovirens																																
Linum catharticum																													1		1	
Ononis repens																																
Trifolium dubium					2		1																								1	4
Trifolium repens			1				1									1	5			1		3		4		1	1	2				1
Trifolium arvense																	1						1									
Anthyllis vulneraria			1																													
Lotus corniculatus								1					1		1	3	2				1				1	1	2					
Potentilla reptans	1						1										1	1	2	1	1	1										
Veronica officinalis																																
Thymus drucei			3		[illegible]		4	1	1		2		2		4		17		34	2	23	7	13	11	20	2	27	15	25	16	12	23
Prunella vulgaris																	1															
Galium verum					1		3				1								2		4		7	2		1	2		4	4	8	7
Senecio jacobea													1				1	1		1	1		1	1								
Bellis perennis																																
Carlina vulgaris																		1														
Cirgium arvense																																
Leontodon hispidus																																
Leontodon taraxacoides			1				1	1			1		2		1		2	2	3	5	3		3	3	2		1	1			1	3
Crepis spp. indet.																		1				2										
Taraxacum officinale				1	1						1	1								1	1	1										
Taraxacum laevigatum																																
Luzula campestris			1							1					1	1	1	1			1	1			1	2	2	2	1	2	2	1
Carex flacca	6	3	2	7	3	9	5	5	9		3	3	11	4	14	3	2	3	1	3	1	1		1	3	4	4	2	5	3	7	7
Carex arenaria	3	3	4	2	7	1	5	6	4		10	1	7	1	4	4	18	16	11	12	21	10	20	10	7	4	2	6	10	4	7	10
Festuca rubra	14	1	44	5	51	20	56	37	49	9	63	25	63	50	58	61	37	31	37	25	47	43	44	52	45	46	43	32	44	60	44	38
Poa pratensis	8	4	7	11	11	5	7	13	11	25	14	15	17	30	15	26	2			1	3	2	3	4	10	3	6	7	4	9	5	4
Arrhenatherum elatius																																
Aira caryophyllea																																
Anthoxanthum odoratum	10	2	23	19	32	25	48	43	30	17	39	32	39	29	22	41	33	39	28	35	18	39	24	32	25	20	18	33	27	21	43	27
Ammophila arenaria						1				5	2		1	2	3	1	1				2		6	2			1	2				
Agrostis tenuis	1						2	4							3				1		2	1	2	2	1	1	2	3				1
Agrostis stolonifera																			1													
Phleum arenarium																																
Grass A																										1	2					
Thuidium spp. indet.																									1							
Camptothecium lutescens																			1		2	2					1		2			
Pseudoscleropodium purum																																
Hypnum cupressiforme																																
Cladonia spp. indet.																																
Peltigera canina																																

APPENDIX 1 CONTINUED

SUMMER CONTROL PLOTS MEASURED IN THE AUTUMN (SA)

Plot	E									F									G									H								
Frequency	1 week interval									2 weeks interval									4 weeks interval									8 weeks interval								
Control strip number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Species																																				
Litter	16	24	22	31	25	42	22	29	32	32	27	30	27	32	30	31	24	41	30	22	33	38	22	28	37	39	39	44	36	42	38	41	32	34	37	36
Bare ground																																				
Ranunculus bulbosus																																				
Viola canina							1																			1										
Viola tricolor																																		1		
Polygala vulgaris																											1									
Cerastium cf. semidecandrum																																				
Cerastium atrovirens																																				
Linum catharticum																							3						1							
Ononis repens																	1																			
Trifolium dubium																																				2
Trifolium repens			1	1				1																			1			1					1	1
Trifolium arvense																																				
Anthyllis vulneraria			1																																	
Lotus corniculatus		3		1		1		1	2	1	2		2	1	1		4	1	4	2	1		1					2		1						2
Potentilla reptans	1							1					2																							
Veronica officinalis																																				
Thymus drucei	3	4	5	3	4	3			3	3	1		1	1	1		2		8	12	3	8	7	9	5	8	7	6	5	11	18	14	17	20	9	8
Prunella vulgaris																																				
Galium verum	3	2	1		2	1	2	3	1		2			1	1		1	1	2	5	4		5	2	5	1	8	7	4	6	4	3	1	4	5	1
Senecio jacobea			1	1	1		1	1		1	1				1					2						2		1						1		1
Bellis perennis																																				
Carlina vulgaris																																				
Cirsium arvense																																				
Leontodon hispidus																																				
Leontodon taraxacoides	1		3	1		1	2			4		4		3					2	2	1	1	3					1				1		1		1
Crepis spp. indet.									1															1												
Taraxacum officinale			1																																	
Taraxacum laevigatum																																				
Luzula campestris				1					1		1									1				1				1					1		3	1
Carex flacca	7	7	2	2	4	2	3	3	6	10	3	4	2	6	7	3	3	3	3	1	1	1	1		1			1	1	4	2	3	3	3	2	5
Carex arenaria	12	20	13	15	15	10	10	14	10	7	13	5	14	17	7	17	8	6	16	21	22	17	22	20	20	11	11	6	18	4	7	7	9	5	5	3
Festuca rubra	25	21	22	30	31	18	34	28	19	28	26	27	26	21	30	25	28	27	19	17	19	16	18	23	17	19	14	24	19	23	20	22	26	19	29	22
Poa pratensis	1		1	1	3	1	2	7	3	2	8	11	3	4	2	7	8	4			1		1			1	1	2	2		1	1		6		1
Arrhenatherum elatius																																				
Aira caryophyllea																																				
Anthoxanthum odoratum	4	5	11	3	3	6	7	7	12	6	4	7	8	1	9	4	8	11	5	11	5	11	4	6	4	6	6	4	10	7	5	7	9	5	3	16
Ammophila arenaria	22	12	14	7	10	15	13	3	9	5	13	11	13	13	11	13	13	6	10	3	7	7	13	10	10	11	10	1	1	1	2					
Agrostis tenuis	5	2	2	3	2		2	2	1	1	1	1	1						1	1	2						2		2		3	1				
Agrostis stolonifera																																				
Phleum arenarium																																	1			
Grass A																																				
Thuidium spp. indet.																																				
Camptothecium lutescens																					1				1	1							1	1		
Pseudoscleropodium purum													1																1							
Hypnum cupressiforme																																				
Cladonia spp. indet.																																				
Peltigera canina																						1														

APPENDIX .1 CONTINUED

SUMMER TREATED PLOTS MEASURED IN THE SPRING (SS)

Plot	E								F								G								H							
Frequency	1 week interval								2 weeks interval								4 weeks interval								8 weeks interval							
Numbers of passages	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4	128	32	64	16	32	8	16	4
Species																																
Litter	75	106	68	87	66	82	39	62	58	89	49	79	52	34	47	47	52	68	67	69	74	71	78	74	72	77	78	71	74	81	73	50
Bare ground	16	35	1	9	1	2						1					3	1										1				
Ranunculus bulbosus													1																			
Viola canina																				1												
Viola tricolor																																1
Polygala vulgaris																																
Cerastium cf. semidecandrum																																
Cerastium atrovirens	1	1						1							1			2														
Linum catharticum	1																															
Ononis repens																																
Trifolium dubium																			5	3	3	5		1				1	1		2	7
Trifolium repens	3	1	2	1	2		2	4									3	6	1	1		3	1	5			2		2	1		
Trifolium arvense																	2			2	3		1									
Lotus corniculatus	1	1	2	1	6		1	3	1		2		1	3	4	2	2		1		2	1	1		1	2	3	1				3
Potentilla reptans								1		1		1	1	2	3	3	1	5		2	3	2	1	1		1						
Sedum anglicum																			1													
Cynoglossum officinale																																
Myosotis ramosissima	1																	1	1	1				1		1	1					
Veronica officinalis																																
Veronica chamaedrys																			2													
Thymus drucei			2		7		7			1	2		1		4		14		17	1	16	4	7	6	16	6	25	10	18	23	17	21
Prunella vulgaris																										1						
Galium verum	2	2	2	8	1	4	1	7	3	1	2	2		1	3	2	3	3	1	1	4	3	11	2	7	5	8	4	5	4	3	6
Senecio jacobaea	1			3		1					1			1	1	1	1	3		1	1		1	2	1							
Bellis perennis				1																												
Carlina vulgaris																																
Cirsium arvense																																
Leontodon autumnalis																			2				2									
Leontodon hispidus																		2	1			1	1	3								
Leontodon taraxacoides	3	2	2	4		1	1	1	1		2		2				2		3	1		1	1	3	1	5	1	1	1		1	5
Hieracium pilosella		6	2																													
Crepis spp. (in det.)																	1	2					1					1	1			
Taraxacum officinale			2	1		1				2										1	1	1	1									
Taraxacum laevigatum	1		1	2		2							1				1		4	2	1							1				
Spp B																																
Spp C																			1													
Luzula campestris			1	1	2	1	2		1	1			1	2	2	1	1	2	3	1	2	2		3	2	2	2	3	4	2	7	2
Carex flacca	12	13	5	9	5	14	9	8	12	13	15	9	14	13	10	3	2	2	2	5		2		1	2	4	3	9	10	6	8	2
Carex arenaria	11	7	9	7	10	4	9	7	6	2	6	1	15	3	8	4	19	13	15	12	13	14	11	10	4	1	8	7	9	4	5	8
Festuca rubra	39	7	56	25	52	26	66	43	73	37	66	40	56	54	73	64	47	31	35	37	50	45	41	45	52	41	33	39	35	42	31	44
Poa pratensis	12	13	9	8	4	13	5	11	8	24	15	30	14	11	12	17	1	2	3		1	2	4	3	2	3	2	4	5	11	3	7
Arrhenatherum elatius																																
Aira praecox	1			3													2	11	1	1				1	2	9	2	4	7		3	7
Aira caryophyllea																																
Anthoxanthum odoratum	10	1	22	27	31	35	50	43	29	21	34	31	34	45	29	51	29	35	24	39	14	30	26	28	31	26	26	32	21	21	37	32
Ammophila arenaria	1	1	1		2	4	1			1	1	2	1	3	2	1		1	3	1	2	1	5	4			2					2
Agrostis tenuis	3	4	8	1	5	3	4	6	4	1	2	2	6	6		4	10	5	5	6	7	8	4	7	3	3	3	5	3	5	1	3
Agrostis stolonifera																																
Phleum bertolonii									2	1	1																1				1	
Phleum arenarium																																
Grass ?																																
Tortula ruraliformis																																
Climacium dendroides																			1									2				
Thuidium spp. (in det.)						2	2												1	1	1	1	1		1	1					2	
Camptothecium lutescens	2			1	2	2		3									4	5		5	2	3	1		3	3		2	3			
Pseudoscleropodium purum	4		4	1	1	2	1		2	5	2	2	1	2	1																	
Hypnum cupressiforme																																
Rhodobryum roseum																																
Rhytidiadelphus triquetrus			1																													
Cladonia spp. (in det.)																																
Peltigera canina																													1				

APPENDIX 1 CONTINUED

SUMMER CONTROL PLOTS MEASURED IN THE SPRING (SS)

Plot	E									F									G									H								
Frequency	1 week interval									2 weeks interval									4 weeks interval									8 weeks interval								
Control strip number	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Species																																				
Litter	29	24	30	32	31	41	35	23	23	37	32	39	31	34	28	37	34	33	34	39	32	35	39	40	42	42	53	45	44	40	43	34	43	44	44	37
Bare ground																																				
Ranunculus bulbosus																																				
Viola canina																											1									
Viola tricolor																						1							1							
Polygala vulgaris																																				
Cerastium cf. semidecandrum																																				
Cerastium atrovirens								1																												
Linum catharticum																																				
Ononis repens																																				
Trifolium dubium																															1	2			1	
Trifolium repens	1					2	1													1										2						
Trifolium arvense																																				
Lotus corniculatus	1		5	2	2	1	2	3	1	1	1		1	4	1	2			3	2	1			2					1	1	1			1	1	2
Potentilla reptans	1												1		1		1	2	1	1	1	1	1	2	1	1	2									
Cynoglossum officinale												1																								
Myosotis ramosissima																					1															
Veronica officinalis																																				
Veronica chamaedrys						1															1															
Thymus drucei	4	1	4			2	1	3	6	3	2		1		4	1	3	1	7	3	5	8	5	5	6	5	7	11	10	16	9	9	14	[illegible]	10	10
Prunella vulgaris																																				
Galium verum α	1	1		3	2	2		5	3	3				1	1	1	1	2	1	2	8	5	4	2		4	1	5	4	3	4	2	5	7	3	4
Senecio jacobaea		1	1								1	1			1		1			1						1										
Bellis perennis																																				
Carlina vulgaris																																		1		
Cirsium arvense																																				
Leontodon hispidus																			3	1												1				
Leontodon taraxacoides	1								1	1											1							1								
Hieracium pilosella			2																																	
Crepis spp. in def.		1			1										1				1	1	1		1													
Taraxacum officinale			1																																	
Taraxacum laevigatum													1									1		1												
Spp B												1																								
Luzula campestris	1	1				1		4	2	2					2	1		2		1		1		1		2	1	1		1				1	3	2
Carex flacca	2	2	4	2	4	2	2	1	6	6	1	3	3	1	2	2	5	1			2				2			1			6	2	1	1	4	3
Carex arenaria	11	6	5	5	7	5	3	2	5	3	4	2	5	6	8	7	1		16	7	9	17	14	15	9	12	1	5	5	4	6	7	1	3	4	1
Festuca rubra	30	35	25	38	29	18	33	31	32	27	40	32	35	32	26	28	21	25	19	18	15	22	20	24	16	16	17	21	21	22	25	18	18	18	18	19
Poa pratensis	6	4	3	4	3	2	2	6	4	3	5	10	5	4	6	9	14	10					2	4	2	1	3	4				3	2	2	1	2
Arrhenatherum elatius																																				
Aira praecox																						1							2				1	1	1	1
Aira caryophyllea																																				
Anthoxanthum odoratum	4	7	8	5	10	11	10	18	13	11	7	7	11	12	13	6	10	13	8	13	12	10	5	5	10	9	4	4	6	9	13	15	10	8	8	14
Ammophila arenaria	1	3	3	5	6	5	7	1			4	3	5	4	2	6	5	5	1		1	2	3	5	6	4	8					1				1
Agrostis tenuis	3	3	1	2	3	5	1	1	2	1	1		1		4		1		2	2	4	2	3	2	5	3	1	1	3	1		1	2	3	2	
Agrostis stolonifera			1																																	
Phleum bertolonii									1	1	1			1							1				1											
Phleum arenarium																																				
Grass A																																				
Tortula ruraliformis																					1															
Climacium dendroides																													1			1				1
Thuidium spp. in def.							1		1											1		2											1	1		1
Camptothecium lutescens				1		1	1												4	1	3	1	3	2				1	1	1	2	3	1	1		1
Pseudoscleropodium purum	2	1	4	1	1	1				1	1	1		1			3										1									
Hypnum cupressiforme																																				
Rhodobryum roseum																																				
Rhytidiadelphus triquetrus					1																															
Cladonia spp. in def.																																				
Peltigera canina																													1			1				1

APPENDIX 2

COMPUTER PROGRAMME 'SUPERFOOT'

```
&ALGOL;L;

SUPERFOOT;
"BEGIN" "INTEGER" K,I,J,P,Q ;
"REAL"BNB,SSD,.,II,DIFF,R,SB;.
"ARRAY"A[1:4,1:8],B[1:4,1:9],
                      Y,  X[1:20], TT, SD[1:4,1:8], A2[1:4,1:17];
"PROCEDURE"TEE(A,B,TT);
"ARRAY"A,B,TT;
"BEGIN" "INTEGER" I,J;
"REAL"BSUM,BSS,SD,MN;
"FOR"I:=1"STEP"1"UNTIL"4"DO"
"BEGIN"BSUM:=BSS:=0;
"FOR"J:=1"STEP"1"UNTIL"9"DO"
"BEGIN"BSUM:=BSUM+B[I,J];
BSS:=BSS+B[I,J]*B[I,J];
"END";
SD:=SQRT((BSS-BSUM*BSUM/9)/8);
MN:=BSUM/9;
"FOR"J:=1"STEP"1"UNTIL"8"DO"
TT[I,J]:=ABS((A[I,J]/2)-MN)/(0.784174*SD);
"END";
"END"TEE;
"FOR"I:=1"STEP"1 "UNTILL"4 "DO"
"FOR"J:=1"STEP"1"UNTILL"8"DO"
"READ" A[I,J];
"FOR"I:=1"STEP"1"UNTILL"4"DO"
"FOR"J:=1"STEP"1"UNTILL"9"DO"
"READ" B[I,J];
TEE(A,B,TT);
"FOR"I:=1"STEP"1"UNTILL"4"DO"
"BEGIN"
"FOR"J:=1"STEP"1"UNTILL"17"DO"
A2[I,J]:="IF"(J"DIV"2)*2=J
"THEN"A[I,(J+1)"DIV"2]
"ELSE"B[I,(J+1)"DIV"2];
"END";
"BEGIN" "ARRAY"                   P[1:4,1:4], D[1:4,1:4],
CP[1:4,1:4], CD[1:4,1:4],  S[1:4,1:8];
"INTE" "ARRAY" TITLE[1:100];
"INTEGER" I,J1,J2,J,M;
"PROCEDURE"  PCENT( A2,P,S,I,J1,J2);
"VALUE" I,J1,J2;
"ARRAY"  A2,P,S;
"INTEGER" I,J1,J2;
"BEGIN" "REAL" Q;
Q:=(A2[I,J1-1]+A2[I,J1+1]);
"IF" Q=0 "THEN" "BEGIN" P[I,J2]:=-1; "PRINT" '*';
"GOTO" OUT; "END";
P[I,J2]:=A2[I,J1]*100/(A2[I,J1-1]+A2[I,J1+1]);
OUT:
S[I,J2]:=(A2[I,J1-1]+A2[I,J1+1]); "END" PCENT;
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"BEGIN" "FOR" J1:=2 "STEP" 4 "UNTIL" 14 "DO"
PCENT(A2,P,CP,I,J1,(J1+2) "DIV" 4);
"FOR" J1:=4 "STEP" 4 "UNTIL" 16 "DO"
PCENT(A2,D,CD,I,J1,J1 "DIV" 4);
"END";
              "PRINT" ''P''; M:=1; INSTRING (TITLE,M); M:=1;
OUTSTRING(TITLE,M);
"PRINT" ''L' PLOT TOTALS 'L'';
"FOR" J:=1 "STEP" 1 "UNTIL" 17 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"PRINT" SAMELINE, ALIGNED(3,3), A2[I,J];
"END";
```

```
"PRINT"''L3' PATH TREATMENT TOTALS';
"FOR"J:=2"STEP"4"UNTIL"17"DO"
"BEGIN" "PRINT"''L'';
"FOR"I:=1"STEP"1"UNTIL"4"DO"
"PRINT"SAMELINE,ALIGNED(4,0), A2[I,J];
"END";
"PRINT" ''L3' PATH ADJACENT CONTROL  SUMS ';
"FOR" J:=1 "STEP" 1 "UNTIL" 4 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"PRINT" SAMELINE,DIGITS(4), ENTIER(CP[I,J]);
"END";
"PRINT"''L3'PATH  PERCENTAGE OF CONTROL  MATRIX';
"FOR" J:=1 "STEP" 1 "UNTIL" 4 "DO"
"BEGIN" "PRINT" ''L'';
"FOR"  I:=1 "STEP" 1 "UNTIL"  4 "DO"
"PRINT" SAMELINE, DIGITS(4), ENTIER(P[I,J]);
"END";
"PRINT"''L3' PATH T VALUES';
"FOR"J:=1"STEP"2"UNTIL"8"DO"
"BEGIN" "PRINT"''L'';
"FOR"I:=1"STEP"1"UNTIL"4"DO"
"PRINT" SAMELINE, ALIGNED(4,3),TT[I,J];
"END";
"PRINT" ''L3' PATH T TEST MATRIX';
"FOR" J:=1 "STEP" 2 "UNTIL" 8 "DO
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"IF"TT[I,J]"GE"3.355 "THEN" "PRINT"SAMELINE,'  0.01 ' "ELSE"
"IF" TT[I,J] "GE"2.306 "THEN" "PRINT" SAMELINE,'  0.05 ' "ELSE"
"IF"TT[I,J]"GE"1.860 "THEN" "PRINT" SAMELINE,'  0.1  '"ELSE"
"PRINT"SAMELINE,'  NS   '      ;
"END";
"PRINT" ''F'';  M:=1;INSTRING(TITLE,M);  M:=1;
OUTSTRING(TITLE,M);
"PRINT" ''L' PLOT TOTALS 'L'';
"FOR" J:=1 "STEP" 1 "UNTIL" 17 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"PRINT" SAMELINE, ALIGNED(3,3), A2[I,J];
"END";
"PRINT"''L3' DRIVING TREATMENT TOTALS';
"FOR"J:=4"STEP"4"UNTIL"17"DO"
"BEGIN" "PRINT"''L'';
"FOR"I:=1"STEP"1"UNTIL"4"DO"
"PRINT"SAMELINE,ALIGNED(4,0), A2[I,J];
"END";
"PRINT"''L3' DRIVING  ADJACENT CONTROL  SUMS';
"FOR" J:=1 "STEP" 1 "UNTIL" 4 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"PRINT" SAMELINE, DIGITS(4), ENTIER(CD[I,J]);
"END";
"PRINT"''L3' DRIVING PERCENTAGE OF CONTROL   MATRIX ';
"FOR" J:=1 "STEP" 1 "UNTIL" 4 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"PRINT" SAMELINE, DIGITS(4), ENTIER(D[I,J]);
"END";
"PRINT"''L3' DRIVING T VALUES';
"FOR"J:=2"STEP"2"UNTIL"8"DO"
"BEGIN" "PRINT"''L'';
"FOR"I:=1"STEP"1"UNTIL"4"DO"
"PRINT"SAMELINE,ALIGNED(4,3),TT[I,J];
"END";
"PRINT" ''L3' DRIVING T TEST MATRIX';
"FOR" J:=2 "STEP" 2 "UNTIL" 8 "DO"
"BEGIN" "PRINT" ''L'';
"FOR" I:=1 "STEP" 1 "UNTIL" 4 "DO"
"IF"TT[I,J]"GE"3.355 "THEN" "PRINT"SAMELINE,'  0.01 ' "ELSE"
"IF" TT[I,J] "GE"2.306 "THEN" "PRINT" SAMELINE,'  0.05 ' "ELSE"
"IF"TT[I,J]"GE"1.860 "THEN" "PRINT" SAMELINE,'  0.1  '"ELSE"
"PRINT"SAMELINE,'  NS   '      ;
"END";
"END";
"END"  PROGRAM;
```

'SUPERPOOT' PRINT OUT

SPECIES NUMBER S/A

PLOT TOTALS

9.000	11.000	10.000	12.000
13.000	12.000	17.000	17.000
9.000	11.000	12.000	10.000
7.000	9.000	16.000	17.000
14.000	8.000	12.000	9.000
16.000	15.000	16.000	21.000
13.000	11.000	7.000	9.000
10.000	10.000	17.000	17.000
10.000	10.000	11.000	9.000
16.000	17.000	23.000	17.000
10.000	10.000	8.000	9.000
10.000	9.000	19.000	16.000
12.000	6.000	8.000	11.000
18.000	18.000	18.000	17.000
12.000	10.000	10.000	8.000
15.000	14.000	20.000	21.000
12.000	8 000	10.000	13.000

DRIVING TREATMENT TOTALS

7	9	16	17
10	10	17	17
10	9	19	16
15	14	20	21

DRIVING ADJACENT CONTROL SUMS

23	19	24	19
23	21	18	18
22	16	16	20
24	16	20	21

DRIVING PERCENTAGE OF CONTROL MATRIX

30	47	66	89
43	47	94	94
45	56	118	80
62	77	100	100

DRIVING T VALUES

5.510	3.024	1.268	1.153
4.441	3.257	0.912	1.153
4.440	3.624	0.198	1.538
2.655	1.791	0.159	0.384

DRIVING T TEST MATRIX

0.01	0.01	NS	NS
0.01	0.05	NS	NS
0.01	0.01	NS	NS
0.05	NS	NS	NS

SPECIES NUMBER S/A

PLOT TOTALS

9.000	11.000	10.000	12.000
13.000	12.000	17.000	17.000
9.000	11.000	12.000	10.000
7.000	9.000	16.000	17.000
14.000	8.000	12.000	9.000
16.000	15.000	16.000	21.000
13.000	11.000	7.000	9.000
10.000	10.000	17.000	17.000
10.000	10.000	11.000	9.000
16.000	17.000	23.000	17.000
10.000	10.000	8.000	9.000
10.000	9.000	19.000	16.000
12.000	6.000	8.000	11.000
18.000	18.000	18.000	17.000
12.000	10.000	10.000	8.000
15.000	14.000	20.000	21.000
12.000	8.000	10.000	13.000

PATH TREATMENT TOTALS

13	12	17	17
16	15	16	24
16	17	23	17
18	18	18	17

PATH ADJACENT CONTROL SUMS

18	22	22	22
27	19	19	18
20	20	19	18
24	16	18	19

PATH PERCENTAGE OF CONTROL MATRIX

72	54	77	77
59	78	84	116
80	85	121	94
75	112	100	89

PATH T VALUES

3.369	2.524	0.912	1.153
2.299	1.425	1.268	0.384
2.299	0.692	1.229	1.153
1.586	0.326	0.555	1.153

PATH T TEST MATRIX

0.01	0.05	NS	NS
0.1	NS	NS	NS
0.1	NS	NS	NS
NS	NS	NS	NS

PAPER 4

THE EFFECT OF CULTURAL TREATMENTS ON THE REGENERATION OF SOIL STRUCTURE AND VEGETATION OF COMPACTED SAND DUNE PASTURE

THE EFFECT OF CULTURAL TREATMENTS ON THE REGENERATION OF SOIL STRUCTURE AND VEGETATION OF COMPACTED SAND DUNE PASTURE

INTRODUCTION

In previous papers in this series the changes that occurred in vegetation and soils as a result of trampling and the passage of vehicles were considered. The present paper is a report on the regeneration of worn areas. The effect of trampling results in a plagio climax (Tansley 1949), and the effect of the removal of this force will be to initiate a subsere which should lead to the re-establishment of the original succession. The various factors that may affect this process must be considered if it is to be understood and manipulated.

Previous work on the regeneration of soil structure after compression has largely dealt with agricultural situations. Among the natural forces that may alleviate compaction in soils swelling and shrinking as a result of wetting and drying are normally important but in sandy soils with low clay content this has little effect. Freezing and thawing can have a major effect on bulk density; ice formation and consequent frost heaving is more likely to occur in compacted than in uncompacted soils, as the thermal diffusivity is increased and the removal of vegetation exposes the soil to greater extremes of temperature (cf. Paper 5) (Larson & Allmaras 1971).

The beneficial effect of soil animals on the fertility of the soil has been well known since Darwin (1881) reported on the activities of earthworms. They can counteract soil consolidation by voiding earth on top of the ground and creating tunnels below the surface. Barley (1961) quotes data from Stöckli showing that these tunnels may make up to 5% of the soil volume and earthworms can significantly improve the yield of certain crops on puddled clay soils (Hopp & Slater 1949). Plant roots can also affect soil structure, at first causing compaction and then an increase in permeability after decay of the dead root material (Barley 1954). It is a reasonable hypothesis that for any given soil type there is a bulk density which is in equilibrium with the environmental conditions; if some external agency causes the soil to beoome more or less compacted, then the environmental forces will work to restore equilibrium conditions (compare Larson & Allmaras 1971).

The effect of tillage of bare ground on subsequent vegetation operates via the effect on germination and establishment of seed present in the soil. Over 40 million seeds per acre were found under a lowland

Agrostis-*Fescue* grass turf (Champness & Morris 1948) and viable seeds were recovered from soil under 58 year old pastures by Brenchley (1918); the deeper the seeds were buried the greater was their viability. The soil is, therefore, likely to hold sufficient seeds to regenerate a vegetation cover if they can be induced to germinate.

In compacted soils dormancy is likely to be enforced by decrease in aeration and consequent rise in CO_2/O_2 ratio and by reduced water flow (Crocker & Barton 1953). The increased temperature fluctuation when compared with vegetated soils could, however, stimulate germination (Warington 1936). Crocker & Barton (1953) also state that *Poa* seeds do not require light to break dormancy except when fresh and this may partly account for the success of *Poa pratensis* on paths, but unfortunately the authors do not state to which *Poa* species they are referring. These data all suggest that deep digging should produce a large number of seedlings even on an old path. However, the survival of weed species in Duval's experiment (Toole & Brown 1946) and the results of Chepil (1946) both suggest that sandy soils will have fewer dormant seeds than soils with a high clay content. Since the sandy tracks often have a smooth soil surface the effect of the increase of the surface micro-topographic variance brought about by tillage on the germination of different species (Harper *et al* 1965) is also likely to be important. But as Thurston (1960) points out light soils may dry out after tillage and prevent germination.

The practice of seeding to prevent soil erosion has become commonplace in recent years. Various species were sown at 700 m in the Cairngorm of which *Lolium spp*, *Festuca rubra*, *F. rubra spp. commutata*, *Poa annua*, *Phleum pratense* (S50) and *Agrostis tenuis* were most successful and acted as a nurse crop for the slower growing natural species. (Bayfield, Pers. comm. 1973). In sand dunes *Ammophila arenaria* has long been planted but the modern technique of hydraulic seeding combined with a fertiliser and temporary soil binder such as straw mulch has been used with some success. At Camber Sands the Kent River Authority has sown a mixture of *Dactylis glomerata*, *Festuca rubra*, *Plantago lanceolata* and *Lotus corniculatus* at the rate of 4.13 $g.m^{-2}$ on to a straw mulch. This had previously been disc harrowed into the sand and a slow release NPK fertiliser was added every two months. The area was enclosed to allow recovery and when vegetation was established a 'Flymo' was used to create a short turf. (Midmer, pers. comm. 1970).

Thurston (1969) reported that plots of high pH and nitrogen content in the Rothamsted park grass experiment were dominated by a few fast-growing grasses. Ca, N, P and K were added to species-poor acidic hill grassland and produced a vegetation similar to lowland pasture, but the plots left open to sheep grazing changed very little as the sheep selectively grazed the lowland species (Milton 1940). Where the soil is already at a high pH the addition of nitrogen and phosphorus can lead to an increase of grasses especially *Festuca* species (Jeffery 1971). At Braunton Burrows where the soil pH was generally above 8, Willis (1963) found that the addition of nitrogen and phosphorus created an initial increase in species richness attributable mainly to dicotyledonous species which were later eliminated by grasses, especially *Festuca rubra* in the dry dune pasture plots. Finally, Kemper *et al* (1971) comment that the addition of fertilisers can overcome the disadvantages of moderate compaction providing the soil moisture conditions are adequate for plant growth.

The following work falls into two sections, one dealing with the effect of vegetation on the soil regeneration and the second with the effect of manipulation of soil characteristics on the vegetation.

The work on soils presented in this paper was undertaken to establish the manner and the rate at which the soils would decompress, and also to estimate the relative contributions of plant growth and other natural agencies. The study of the vegetation was concerned with the effects of tillage, seeding and fertilisers on regeneration of cover, species number, diversity and other parameters.

MATERIALS AND METHODS

Soil Experiment 1

The worn areas used to study the short term effects of driving and walking on sand dune pasture were used for this experiment (see Paper 1). The decompression was estimated from monthly penetrometer readings of the worn sites, the last measurement of the wear experiment being used for the first estimate in this series. Subsequent readings were made in sixteen separate positions arranged systematically in the worn areas to avoid measurement of soil disturbed by a previous reading. Standard errors were calculated for each point on the diagrams and the monthly totals were analysed by regression of soil penetration resistance on time.

Soil Experiment 2

A length of the linking car track used 40 times every week in the wear experiment from November 1970 to April 1971 and then abandoned was selected for this experiment. Six 1 m^{-2} plots spaced 0.5 m apart were marked out: these were treated as three blocks of two treatments each a control plot and one which was treated with 45 gm of 'Boots Path Weed Control' containing 25% Simazine, in 9.1 litres of water. This weedkiller is a photosynthetic inhibitor and does not, ~~therefore,~~

directly harm the soil animals. The treatments were randomly positioned.

The recovery of these plots was measured by 16 penetrometer readings in each plot, all to a depth of 6 cm, before the treatment with weedkiller and at eight-week intervals for one year. The means and standard errors were calculated for the treated and the control plots. The results are presented as the differences between the means.

Vegetation Experiment 1

The site of this experiment was a track in the Aberffraw sand dune system which had been worn down to bare earth but the organic soil crust was still intact. Plate 4-1. The surrounding vegetation was visually homogeneous but grazed continuously by cattle and sheep to approximately 5 cm high. There was a slight slope giving an extreme difference in height of 44 cm between the opposite ends of the treated area and a shallow drainage ditch approached the track at right angles at one point; no treatments were carried out within 10 m of this position. Shallow ditches were dug across the track at intervals to prevent further wear by vehicles.

The treatments were arranged as a 2 by 2 by 3 factorial with one extra treatment (Table 4-1). There were five replicates laid out as five blocks along the

Photo 4-1

Vegetation experiment 1. Sand dune track before treatment carried out.

Note the ruts devoid of any surface vegetation.

A secondary track can be seen on the left of the one which received treatment.

Photo 4-2

Vegetation experiment 2. Turves at start of greenhouse treatment.

A Control
B 'Dug'
C Fertilised with 'Fisons 41'
D 'Dug' and fertilised

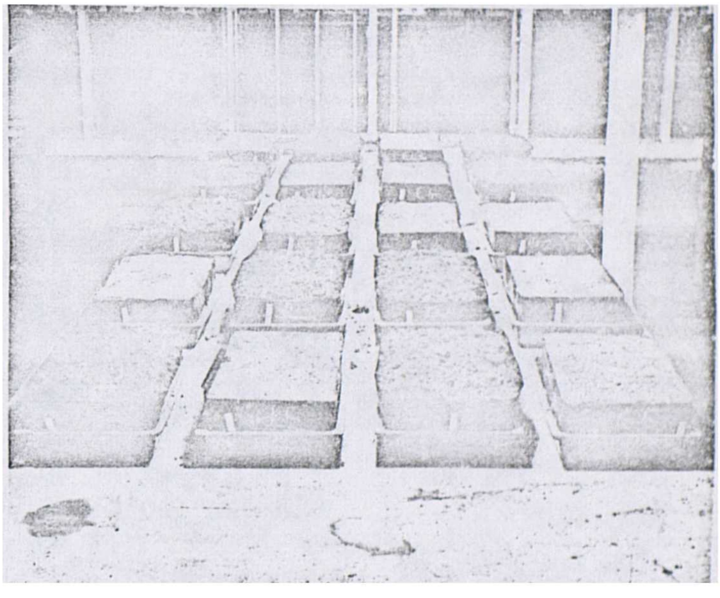


TABLE 4-1

VEGETATION EXPERIMENT 1

TABLE OF TREATMENTS

Main effects	1st order interactions	2nd order interaction
Dig & straw	Dig & seed	Dig & seed + fertiliser
Seed	Dig & fertiliser	
Fertiliser 2 'levels', NPK & NPKM	Seed & fertiliser	
Dig *		

Seed — *Festuca rubra* and *Poa pratensis*

NPK — Nitrogen, Phosphorus and Potassium

NPKM — Nitrogen, Phosphorus, Potassium and Micornutrients

* — Not included in analysis of variance

track and the plots were randomised within each block. Both wheel ruts were utilised and the individual plots were 25 cm by 1 m with a space of 1 m between each plot. The first treatment was digging to 15 cm depth with the addition of 302 $g.m^{-2}$ of chopped straw to prevent wind erosion. The second treatment was a seed mixture of one part of Festuca rubra to 0.283 parts of Poa pratensis by weight: this ratio was based on a difference of percentage of laboratory germination rate of 1 : 0.77 and in seed weight of 1 : 0.23.

The seed was sown at a rate of 9.48 $g.m^{-2}$ ($\frac{1}{4}$ oz/yd^2) and spread over the surface of the undug plots, but when combined with digging the soil was lightly raked and pressed down with the back of a spade after seeding.

The third treatment consisted of 'Fisons 41' and 'Vitax Q4' fertilisers. They both contain similar amounts of nitrogen and phosphorus (as P_2O_5) but they contained 1.8 and 0.9 parts respectively of Potassium (as K_2O); the 'Vitax Q4' also contained chelated micronutrients listed in Appendix 1. The nitrogen was principally present as available ammonium nitrogen 4 parts and nitrate nitrogen 1 part in the 'Fisons 41', whereas it was present as slow release 'nitroform' in the 'Vitax Q4'. The 'Fisons 41' was applied at the rate of 50 $g.m^{-2}$ (40 units of N per acre) in May and July of 1971 and

1972 and the 'Vitax Q4' was applied once at the rate of 190 $g.m^{-2}$ (80 units of N per acre) in the June of each year. There was an annual total of 10 $g.m^{-2}$ of nitrogen and of phosphorus on each plot but there was 18.1 $g.m^{-2}$ and 8.4 $g.^{-2}$ of potassium on the 'Fisons 41' and 'Vitax Q4' plots respectively. The final treatment was digging without the addition of straw; this was not in the factorial system.

The cover of each species was recorded in October 1971 and 1972 and May 1972, one hundred points being measured in each plot giving a total 500 points for each treatment. Each calculated parameter and each species that occurred frequently was considered by analysis of variance. The means of all occurrences on each treatment at each time of recording were also used as 'stand data' for ordinations to give a summary of the results. The primary data are presented in Appendix 2.

Vegetation Experiment 2

This was carried out on 'turves' in a heated greenhouse. They were dug from areas of track on which there was no surface vegetation, situated in a dry to slightly moist slack with a similar flora to the site of Experiment 1. The 'turves' were 21 cm by 34 cm and 10 cm thick; they were placed in seed trays and the sides were covered in black polythene (Plate4-2).

The experimental design was that of a 2 by 2 factorial with five replicates. The blocks were randomly arranged along the bench and the 'plots' were randomised across the bench within each block. The first treatment was digging to 10 cm depth, the second was one application of 'Fisons 41' at the rate of 100 $g.m^{-2}$ (or 80 units of N per acre) a rate similar to that used annually in Experiment 1. The 'turves' were watered regularly every morning. The experiment was started in February 1971 and continued for a period of 62 weeks and cover measurements using one hundred points on each 'turf' were made approximately every eight weeks.

The assessment was carried out by analysis of variance and by ordination in a similar manner to the previous experiment. In addition an ordination was carried out with all the stands from both experiments. A degree of caution must be used interproting this ordination as the plots in Experiment 1 are 3.5 times the area of the 'turves'. The primary data are presented in Appendix 3.

RESULTS

Soil Experiment 1

Fig.4-1 shows that decompression does occur, apparently starting as soon as traffic is removed. The rate in the foot areas b = -0.087 is slightly higher than the car site, b = -0.061. If the decompression rate is constant, the trodden area will have returned to its original soil penetration resistance by mid-October, after treatment in the previous May. The car area will reach the original soil penetration resistance by March, 11 months after treatment.

The upper layers composed of compressed vegetation also had the greatest soil penetration resistance immediately after treatment and decompressed most rapidly. Fig.4-2.

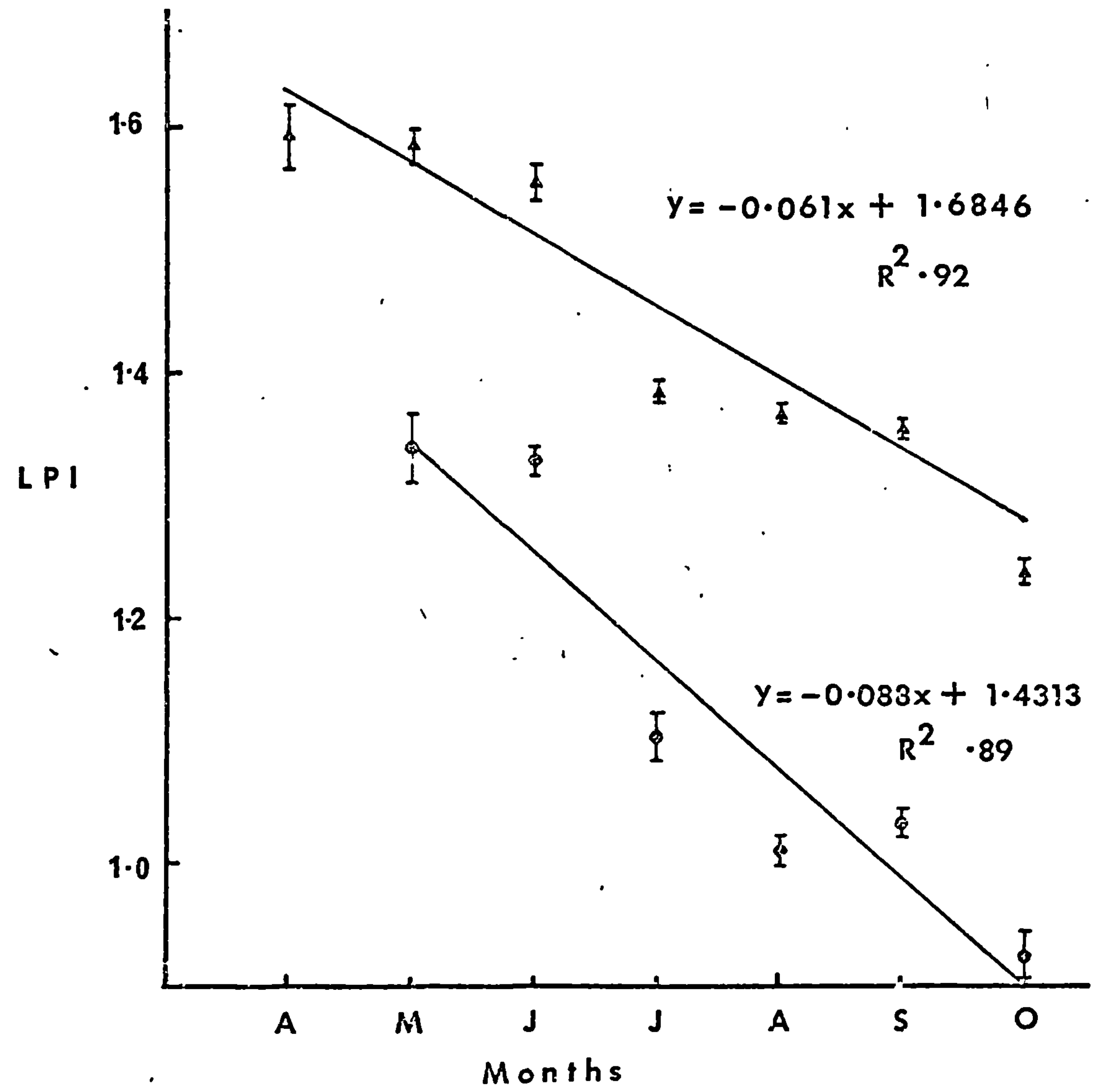
Soil Experiment 2

There was a statistically significant difference between the penetrability of the control and the treated plots except at the first reading made before treatment was carried out. Fig.4-3. The amount of difference fluctuated but tended to increase throughout the year. The treated plots had lower penetrability than the untreated ones, especially at a depth of 2 cm, Fig.4-4, but the lower layers again showed an initial increase in soil strength after the compacting forces were removed.

Fig.4-1

Natural decompression of soil. The change in soil penetration resistance with increasing recovery time.

- ▲ car
- ● walking
- I 2 standard errors



y= −0·061x + 1·6846
R2 ·92
y= −0·083x + 1·4313
R2 ·89
1·6
1·4
1·2
1·0
LPI
A
M
J
J
A
S
O
Months

4 – 1

Fig. 4-2

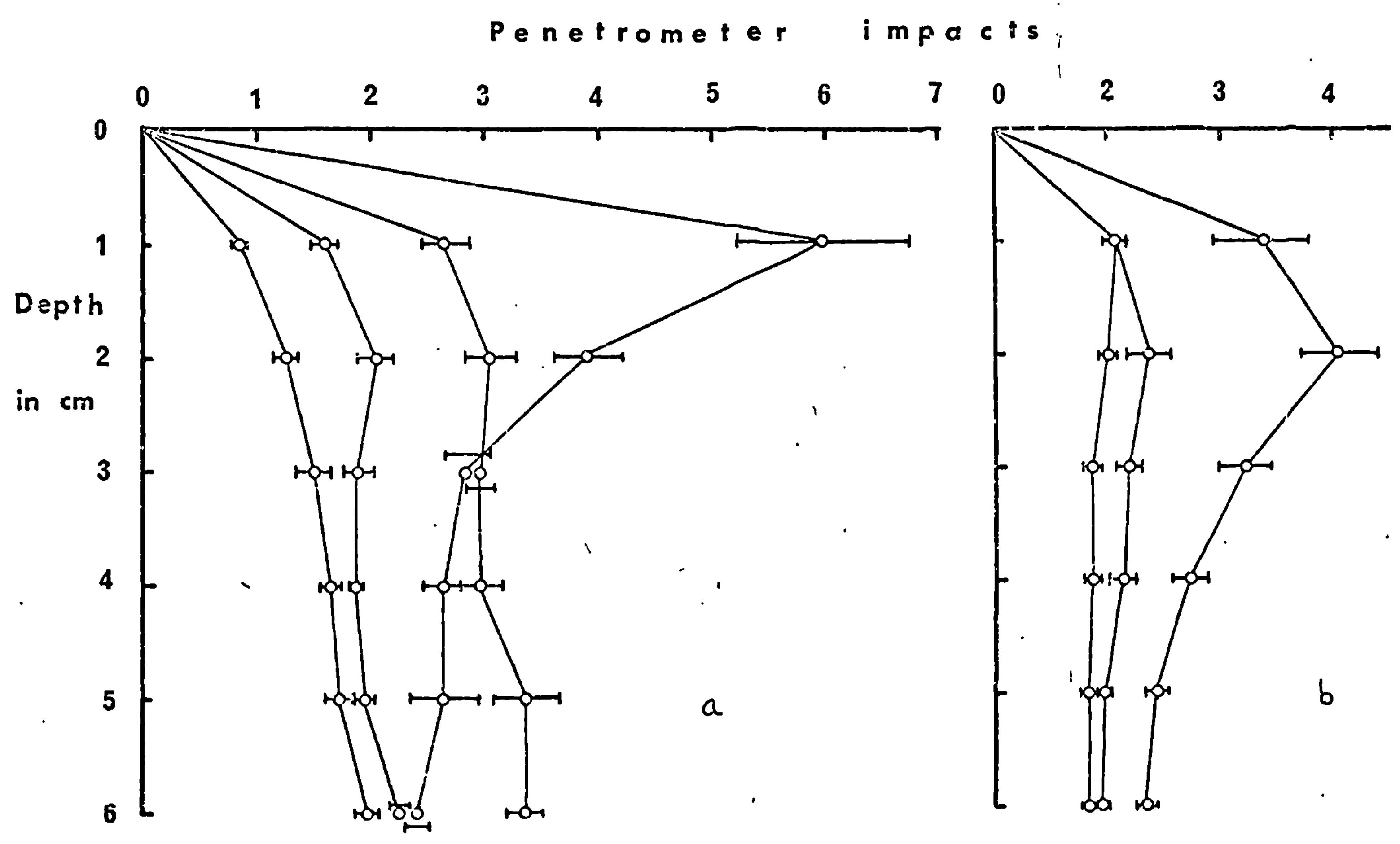
Natural decompression of soil. Changes of soil penetration resistance for each cm to a depth of 6 cm at two monthly intervals over the experimental recovery period.

a) car track

b) footpath

o mean

⊢⊣ 2 standard errors



4 – 2

Fig.4-3

The increase in soil penetration resistance of the control plots minus the soil penetration resistance of the plots treated with weedkiller.

O difference in soil penetration resistance

I two standard errors

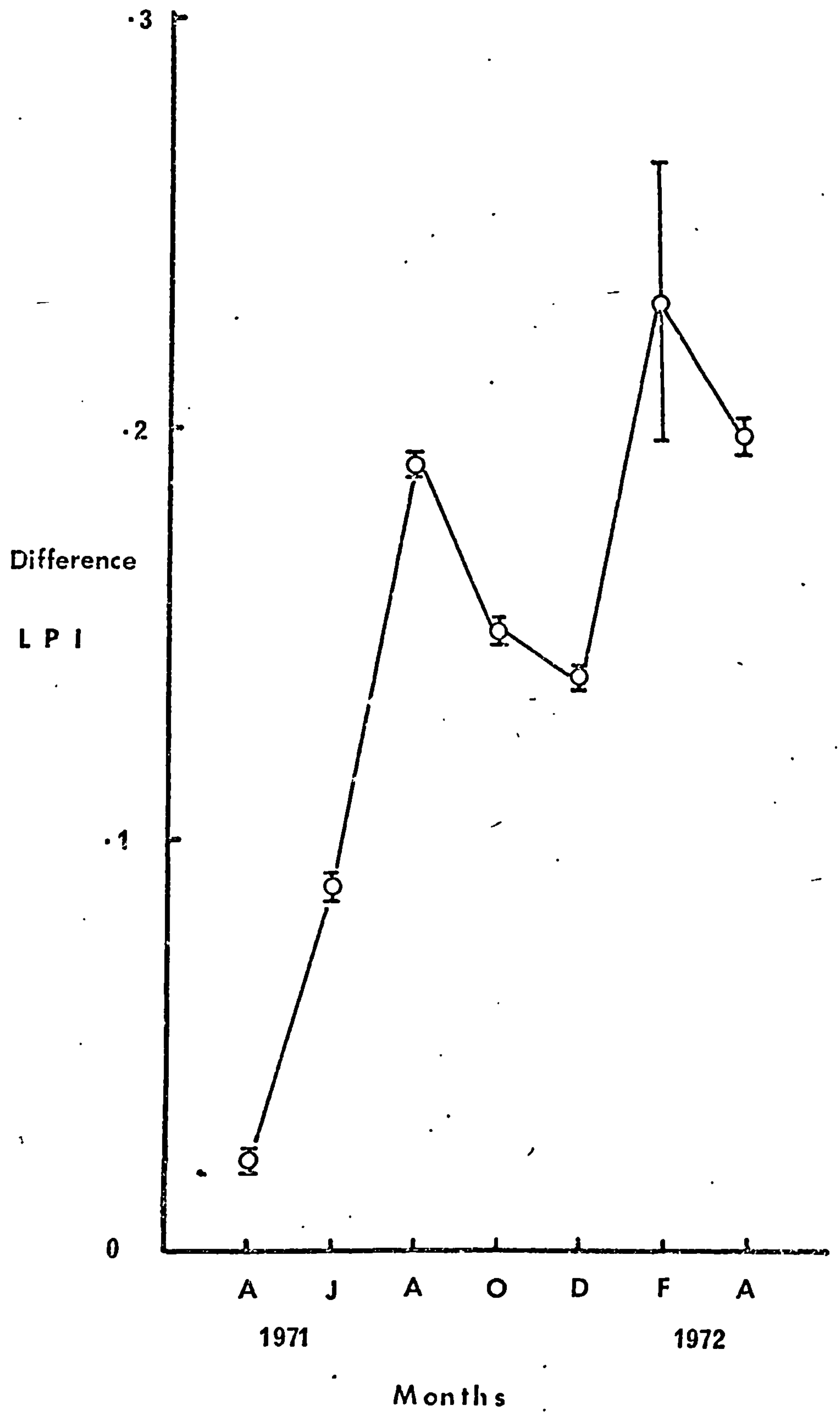

·3
·2
·1
0
Difference
L P I
A
J
A
O
D
F
A
1971
1972
Months

Fig.4-4

Soil penetration resistance of the treated and control plots at four monthly intervals from April 1971 to April 1972. Soil penetration resistance shown for each cm depth.

a) April 1971

b) August 1971

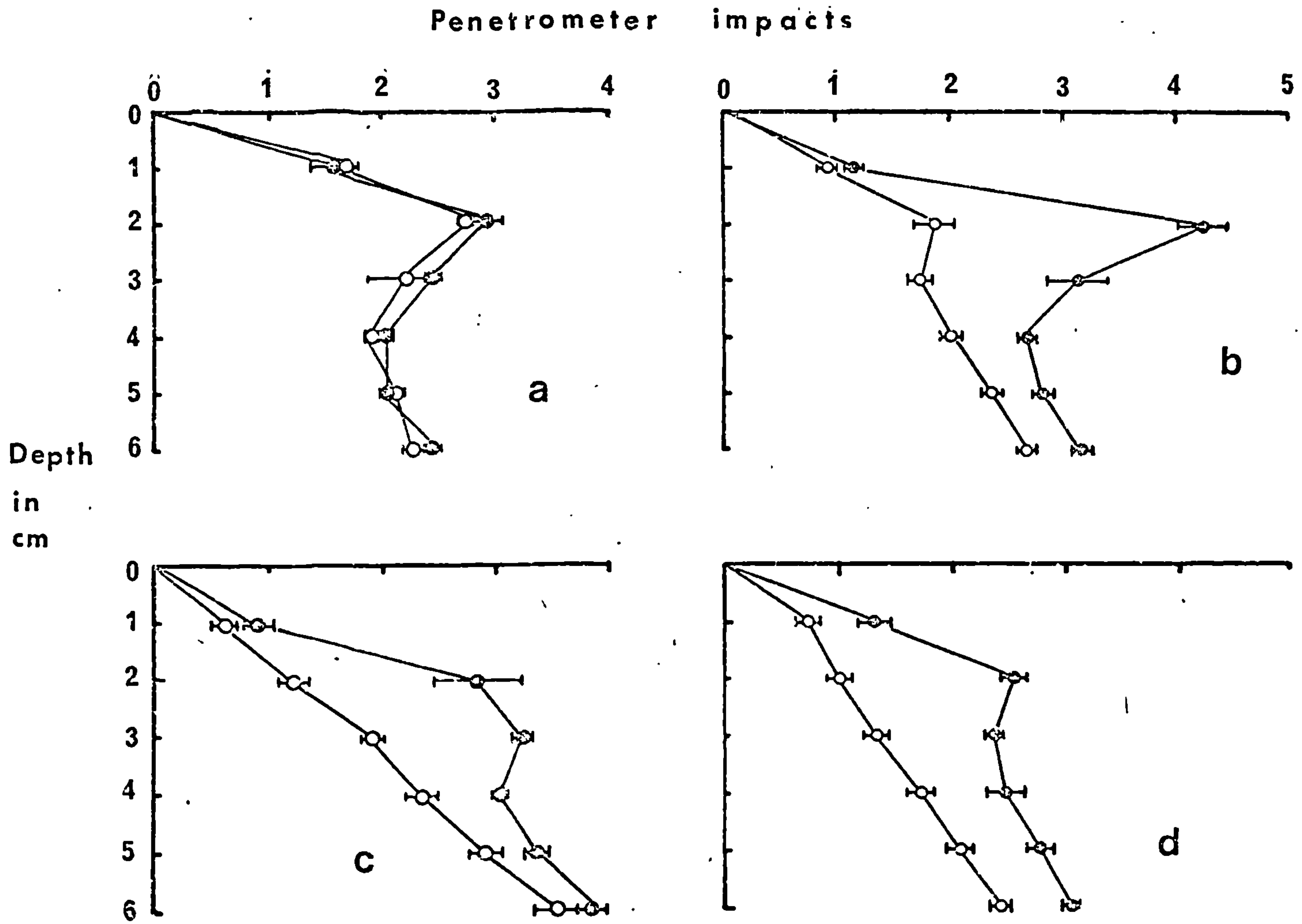
c) December 1971

d) April 1972

● mean of control plots

○ mean of plots treated with weedkiller

⊢⊣ two standard errors



4 – 4

Vegetation Experiment 1

The effects of the various treatments are summarised in the analysis of variance (Tables 4-3a and b). Generally, seed and fertiliser gave positive results, and the effect of digging and straw was not statistically significant. Digging alone and the interaction between digging plus straw and fertiliser tended to depress the results below that expected from the addition of the main effects while most of the other interactions were not statistically significant.

The percentage cover increased steadily on all treatments throughout the two seasons, reaching 48% on the control plots, Fig.4-5. The seeded and fertilised plots reached 92% cover ('Fisons 41') and 95% ('Vitax Q4'), while those only receiving fertiliser reached 81% and 84% respectively. Digging alone reduced cover to 44% but with straw it produced 73%; however, this treatment also reduced the combined seeding and fertiliser treatments to 87% and 90% cover. The control plots were one year behind the seeded and 'Vitax Q4' treatment, see Fig.4-5.

The mean species number was 5.8 on the controls at the end of the period and the highest final measurement was 7.6 on the plots treated with 'Fisons 41' fertiliser, Fig.4-6a, b, c and d. The seeded and

TABLE 4-2a

RESULTS OF ANALYSIS OF VARIANCE. VEGETATION EXPERIMENT 1.

		Main effects				1st order interactions			2nd order interactions
		Dig ≠ only	Dig & straw	Seed	Ferti-liser	Dig & straw + seed	Dig & straw + ferti-liser	Seed + ferti-liser	Dig & straw + seed + fertiliser
Total cover	1*	NS	NS	xxx	NS	NS	x	NS	NS
	2	xxx	NS	xxx	xx	NS	xxx	NS	NS
	3	NS	NS	xxx	xxx	NS	x	NS	NS
Inverted Simpsons diversity index	1	NS	NS	NS	NS	NS	NS	NS	NS
	2	NS	NS	NS	NS	NS	NS	x	NS
	3	xx	NS	NS	NS	NS	NS	NS	x
Species number	1	NS	NS	NS	NS	NS	NS	NS	NS
	2	NS	NS	x	xx	NS	x	NS	NS
	3	NS	NS	NS	xx	NS	NS	NS	NS
Resistant species	1	NS	NS	xxx	NS	NS	NS	x	NS
	2	x	x	xxx	NS	NS	NS	NS	NS
	3	NS	NS	x	NS	NS	NS	NS	NS
Annuals	1	NS	NS	NS	NS	NS	NS	NS	NS
	2	NS	NS	NS	x	NS	NS	NS	NS
	3	NS	NS	NS	NS	NS	NS	NS	NS
Perennials	1	NS	NS	xxx	NS	NS	x	NS	NS
	2	xx	NS	xxx	xxx	NS	xxx	NS	NS
	3	NS	NS	NS	xxx	NS	NS	NS	NS
Festuca rubra	1	NS	NS	xxx	NS	NS	NS	NS	NS
	2	NS	NS	xxx	NS	NS	NS	NS	NS
	3	NS	NS	x	NS	NS	NS	NS	NS
Poa pratensis	1	NS	NS	NS	x	NS	NS	NS	NS
	2	xxx	NS	NS	xxx	x	NS	NS	NS
	3	xxx	NS	NS	xx	x	NS	NS	NS

* 1st, 2nd and 3rd readings. ≠ Based on T tests of difference from controls.
x $P < 0.05$, xx $P < 0.01$, xxx $P < 0.001$.

TABLE 4-2b

RESULTS OF FIELD PLOT TREATMENTS. VEGETATION EXPERIMENT 1

		Control	Dig only	Dig & straw	Seed	Fertiliser 'Fisons 41'	Fertiliser 'Vitax Q4'	Dig & straw & seed	Dig & straw 'Fisons 41'	Dig & straw 'Vitax Q4'	Seed 'Fisons 41'	Seed 'Vitax Q4'	Dig & straw seed 'Fisons 41'	Dig & straw seed 'Vitax Q4'
Total % cover	1*	13.6	24.2	25.8	27.4	21	39.8	48.4	26.4	27.2	44.2	47	38.4	38.8
	2	20.6	42.2	56.4	39.2	43	65.2	66.4	53	45.8	64	77.2	64.4	64.2
	3	48.4	44	72.6	62.4	81.4	83.4	80.6	84.4	78.2	92.4	95.4	89.6	87
Inverted Simpsons Diversity Index	1	3.28	2.2	2.62	2.68	3.64	2.1	1.92	3.84	2.78	3.2	3.14	2.5	3.22
	2	3.08	3.42	4.42	2.76	4.2	3.36	2.4	3.84	3.02	4.26	4.3	2.86	4.2
	3	4.67	3.1	2.84	3.22	4.57	3.47	3.56	4.17	5.02	3.87	4.38	4	3.71
Species number	1	4	3.4	4.4	4.4	5.2	4.6	4.2	5.8	4	6.8	5	3.6	5
	2	4.2	5.6	6.4	4.4	7.8	5.6	5.8	5.8	5.6	8.4	9.2	6.8	7.4
	3	5.8	5.6	5	5.6	7.6	6.8	5.4	6.8	7.6	7.6	7.4	6.2	6.4
Resistant species % cover	1	5.4	6.4	5.8	21.8	7.8	22.8	44	13.6	13	30.8	27.8	28.6	25.2
	2	2.8	11.6	10	14.6	7.2	15.2	25.8	15.6	13.2	24.6	23.6	24.6	23
	3	6.6	12.6	9.2	14.4	10.6	22.2	15.8	16.8	12.8	27.0	18.8	17.4	14.8
Annuals % cover	1	2.0	0	2.2	2.6	1	4	0.2	6	2.8	3	5	2.8	3.8
	2	1.4	3	3.2	3.6	3.2	2.8	2	9.4	3	5.4	10	9.4	8.6
	3	0.4	0.8	1.4	3.0	0.8	0.4	1.6	3.2	3.8	1.6	1.2	3.4	2
Perennials % cover	1	11.6	24.2	23.6	24.8	20	35.8	48.4	20.4	24.4	41.2	42	35.6	35
	2	9	18.8	16.2	16.8	25	33.2	31	21.4	20.6	33.6	35.2	24.4	25.4
	3	23.2	27	21.8	22.2	39	34.6	26.4	37.4	29.4	45.4	36	32.2	29.4
Festuca rubra % cover	1	3.0	3.2	0.4	16.8	2.4	5.8	29.8	3	2	21.4	14.6	19.6	15.6
	2	0.8	3.2	1.8	10.8	3.2	5.6	19.4	1.8	1.6	15.2	8.4	15.6	11.6
	3	5.2	6	4.6	12.4	5.8	17.6	11	10	4.4	20.2	11.4	12.8	10.2
Poa pratensis % cover	1	1.0	3.2	2.2	3.2	1.2	13.8	13.2	4.8	8.6	6.6	9.8	6.2	7.0
	2	1.2	7.2	3.6	2	1,2	7.2	5.4	5	9.4	6.6	8.6	2.8	5.4
	3	0.4	6.6	2.4	2	1.8	3.4	3.2	5.4	6.2	6.4	6.8	4.6	4.2
Realised diversity at last reading		0.62	0.55	0.57	0.58	0.51	0.51	0.66	0.61	0.66	0.50	0.59	0.66	0.58

* 1st, 2nd and 3rd readings.

Fig.4-5

Vegetation experiment 1. Total cover.

a) and b) Single treatments (main effects).

c) and d) Combined treatments (interactions).

- control
- dug
- dug plus straw
- seed
- 'Fisons 41' fertiliser
- 'Vitax Q4' fertiliser
- dug plus straw and seed
- dug plus straw and 'Fisons 41' fertiliser
- dug plus straw and 'Vitax Q4' fertiliser
- seed and 'Fisons 41' fertiliser
- seed and 'Vitax Q4' fertiliser
- dug plus straw, seed and 'Fisons 41' fertiliser
- dug plus straw, seed and 'Vitax Q4' fertiliser

lines connecting dug plots

lines connecting undug plots

two standard errors

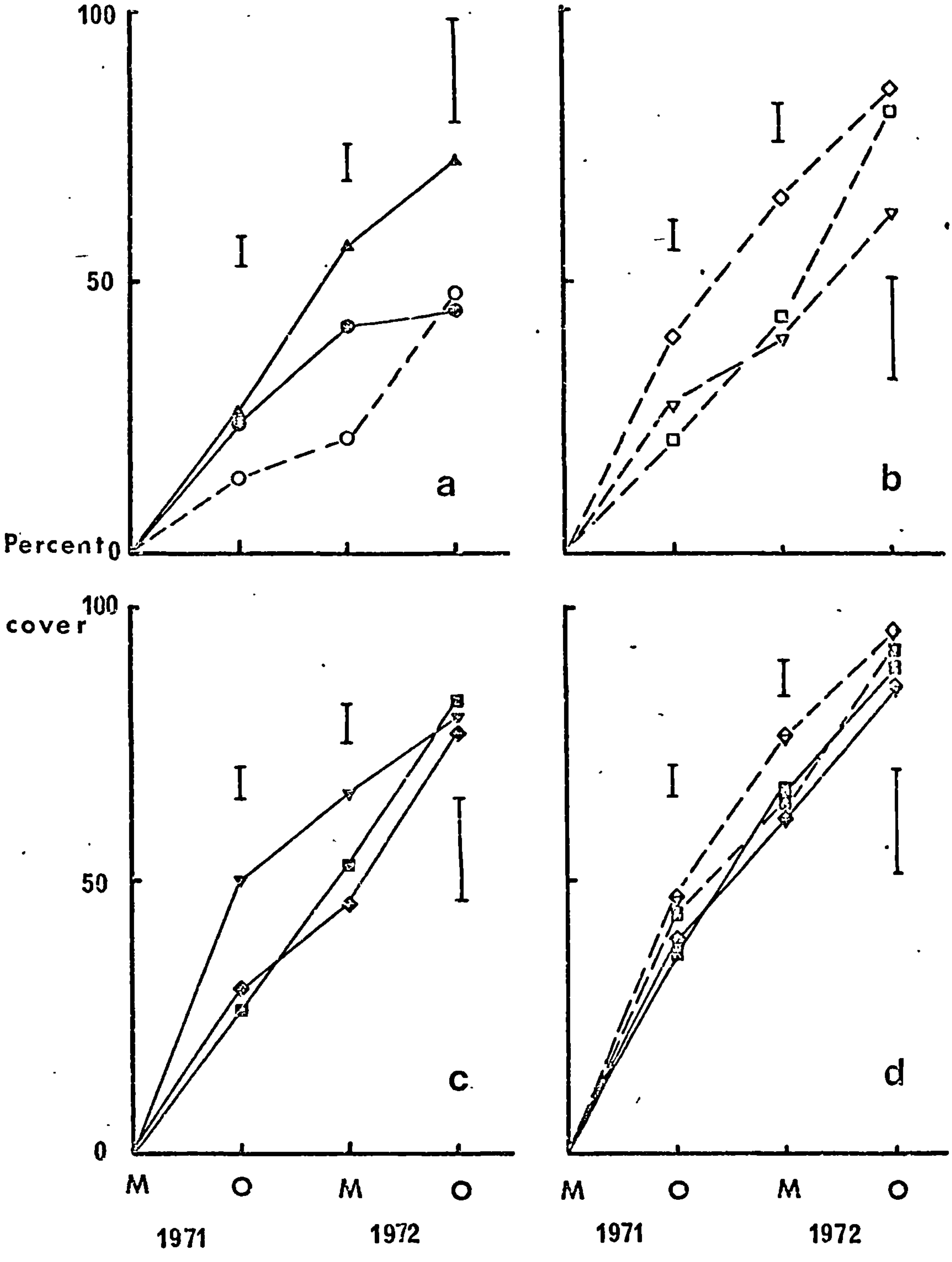

100
50
Percent 0
cover
100
50
0
a
b
c
d
M
O
M
O
M
O
M
O
1971
1972
1971
1972

Fig. 4-6

Vegetation Experiment 1.

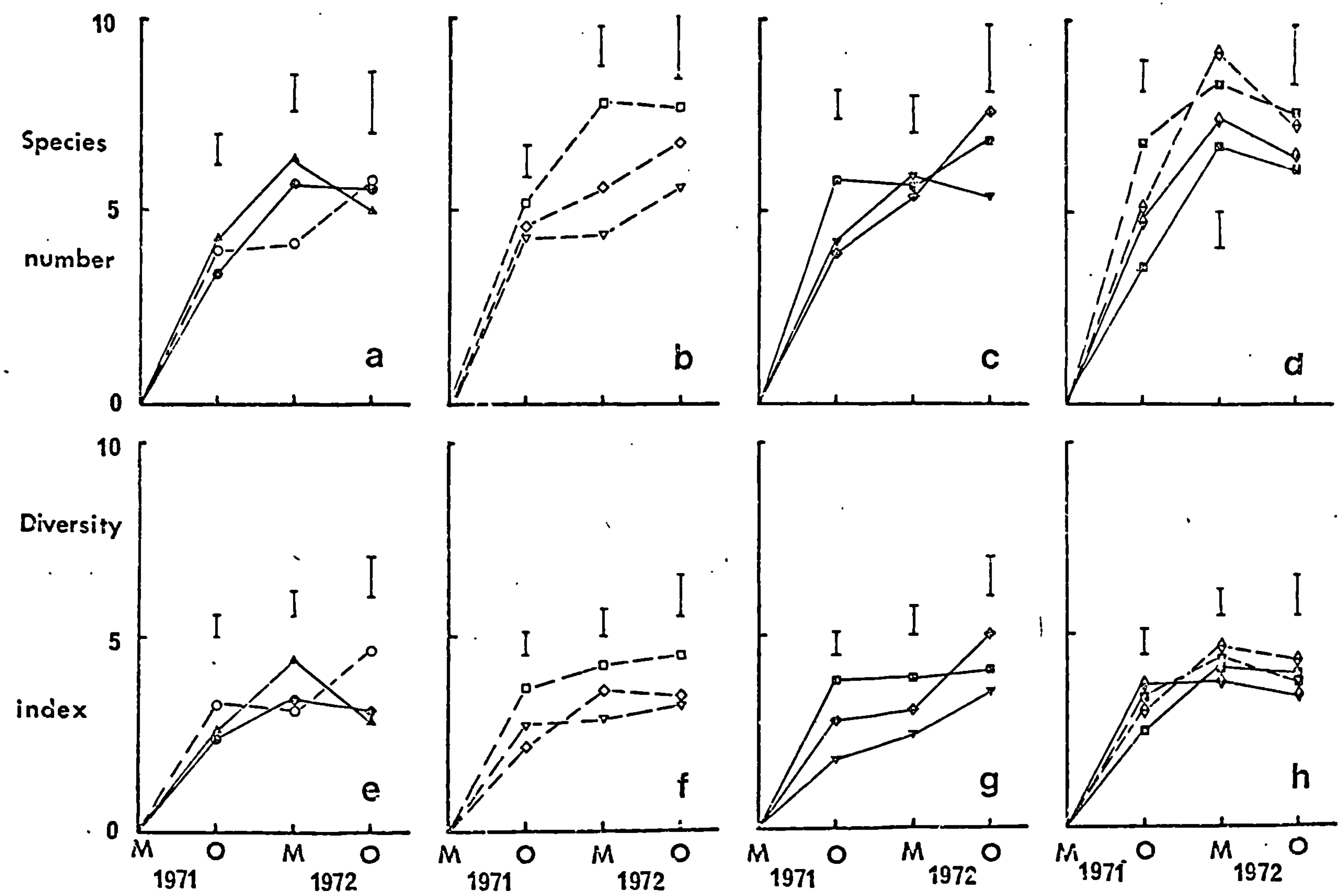
a, b, c and d) Species number.

e, f, g and h) Inverted Simpsons diversity index.

a, b, e and f) Single treatments (Main effects).

c, d, g and h) Combined treatments (Interactions).

- ○ control
- ◉ dug
- ▲ dug plus straw
- ▽ seed
- □ 'Fisons 41' fertiliser
- ◇ 'Vitax Q4' fertiliser
- ▼ dug plus straw and seed
- ◘ dug plus straw and 'Fisons 41' fertiliser
- ◈ dug plus straw and 'Vitax Q4' fertiliser
- ⊠ seed and 'Fisons 41' fertiliser
- ◊ seed and 'Vitax Q4' fertiliser
- ◙ dug plus straw, seed and 'Fisons 41' fertiliser
- ◊ dug plus straw, seed and 'Vitax Q4' fertiliser
- ——— lines connecting dug plots
- — — — lines connecting undug plots
- I two standard errors



4 - 6

fertilised plots reached 8.4 and 9.2 at the second reading for 'Fisons 41' and 'Vitax Q4' respectively, but these plots fell to 6.2 and 6.4 at the last reading. The diversity indices were all between 2.84 (dig and straw) and 5.02 (dig and straw and 'Vitax Q4') at the last reading. Fig.4-6e, f, g and h. The control was relatively high at 4.67 and the realised diversity of these plots was 0.82; the others were all between 0.51 and 0.66 (see Table 4-2b). The maximum possible realised diversity is 1.0 and in this case all species present would have an equal share of the cover.

The cover of annual species reached 10% on the seed with 'Vitax Q4' plots in the spring of the second year and declined to below 4% on all plots by the second October, Fig.4-7a, b, c and d. The perennial species reached between 35% and 42% on all seeded fertilised plots in the first October while the controls were at 12%, Fig.4-7e, f, g and h. By the second spring there was a drop in all plots but in the following October a general rise was again recorded with the controls reaching 23% and the plots treated with seed and 'Fisons 41' reaching 45%. The resistant species reached their highest level (up to 44%) at the first readings on the seeded and fertilised plots and then declined, see Table 4-2b. <u>Poa pratensis</u> also showed a similar pattern

Fig.4-7

Vegetation Experiment 1.

a, b, c and d) Percentage cover of annual species.

e, f, g and h) Percentage cover of perennial species.

a, b, e and f) Single treatments (Main effects).

c, d, g and h) Combined treatments (Interactions).

○ control

dug

▲ dug plus straw

▽ seed

□ 'Fisons 41' fertiliser

◇ 'Vitax Q4' fertiliser

▼ dug plus straw and seed

dug plus straw and 'Fisons 41' fertiliser

dug plus straw and 'Vitax Q4' fertiliser

seed and 'Fisons 41' fertiliser

seed and 'Vitax Q4' fertiliser

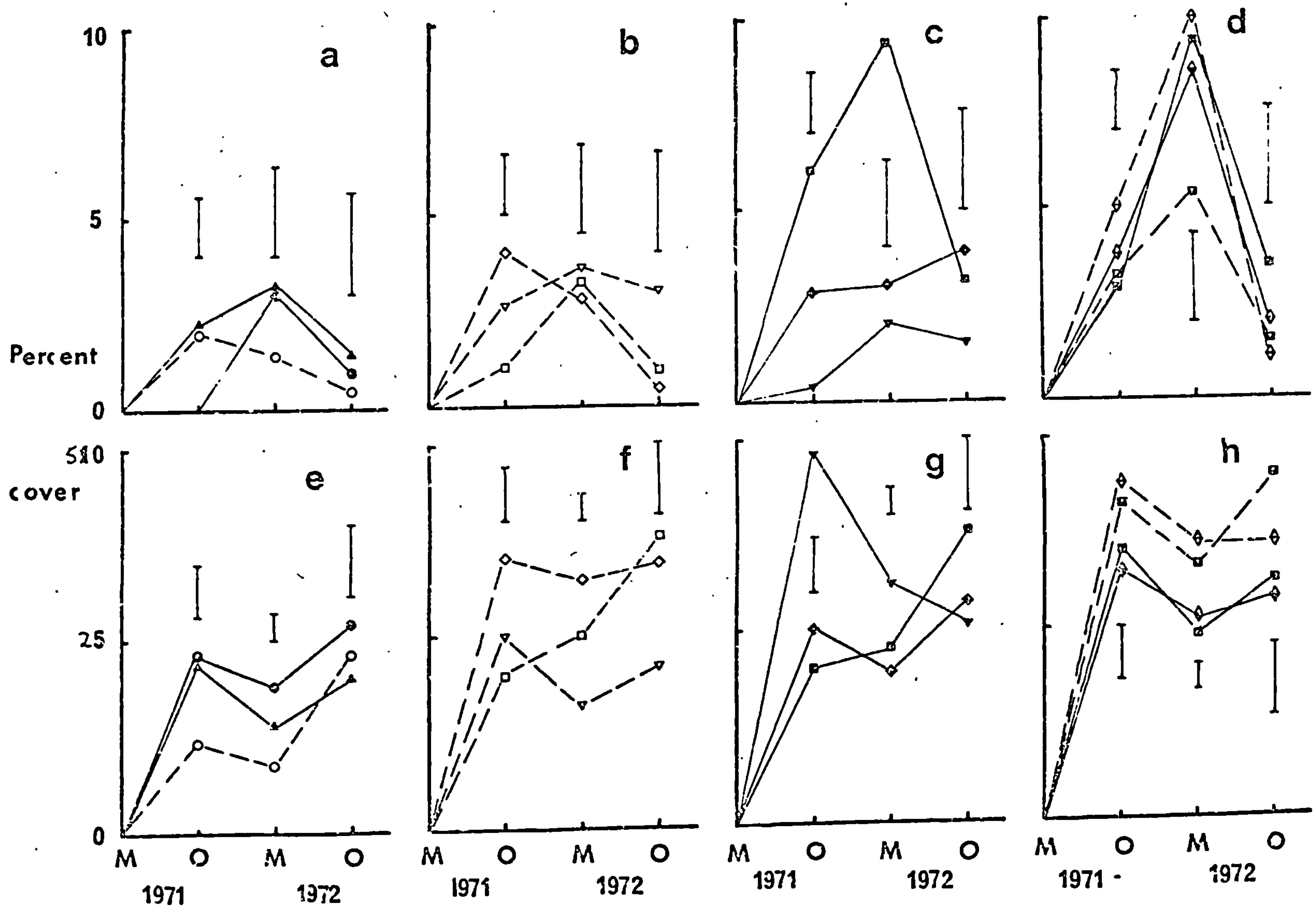
dug plus straw, seed and 'Fisons 41' fertiliser

dug plus straw, seed and 'Vitax Q4' fertiliser

lines connecting dug plots

lines connecting undug plots

two standard errors



10
5
0
Percent
510
cover
25
0
a
b
c
d
e
f
g
h
M
O
M
O
1971
1972

with fertilisers and seeding reaching 14%, Table 4-2b. Digging without the addition of straw produced the highest level of *Poa pratensis* at the final reading (6.6%); the cover of *Festuca rubra* was about four times that of *Poa pratensis*.

The multivariate summary, Fig.4-8, has responded mainly to the number of species in the various stands. Axis 1 tends to run from high content of annuals at the minus end to a high content of perennials at the positive end; the major stand movement which is associated with seasonal change runs partially parallel to axis 2.

The soil data from this experiment (Table 4-3) show that there was no statistically significant erosion effect but the data suggest that digging tends to lower the level by about 1 cm. Fertilisers caused a lowering of pH from 7.3 to 7.2 while digging resulted in a slight increase in alkalinity (0.1). Fertilisers also caused a slight but significant (5%) increase of 4 umho in conductivity. A few samples of soil from some of the plots in October 1972 were analysed for their chemical content (Appendix 4). There was a 59% higher nitrogen content in the controls (0.064%) than in the dug plus straw and fertilised plots (0.038%). The position was reversed for P, K and Na: the adjacent short turf had nutrient levels similar to the dug plus

Fig.4-8

Ordination of field plot vegetation records at three points in time; lines connect similar treatments at different points in time.

○ control

⊕ dug

▲ dug plus straw

▽ seed

□ 'Fisons 41' fertiliser

◇ 'Vitax Q4' fertiliser

▼ dug plus straw and seed

⊠ dug plus straw and 'Fisons 41' fertiliser

◈ dug plus straw and 'Vitax Q4' fertiliser

⊠ seed and 'Fisons 41' fertiliser

◇ seed and 'Vitax Q4' fertiliser

⊠ dug plus straw, seed and 'Fisons 41' fertiliser

◈ dug plus straw, seed and 'Vitax Q4' fertiliser

——— lines connecting dug plots

- - - - lines connecting undug plots

I two standard errors

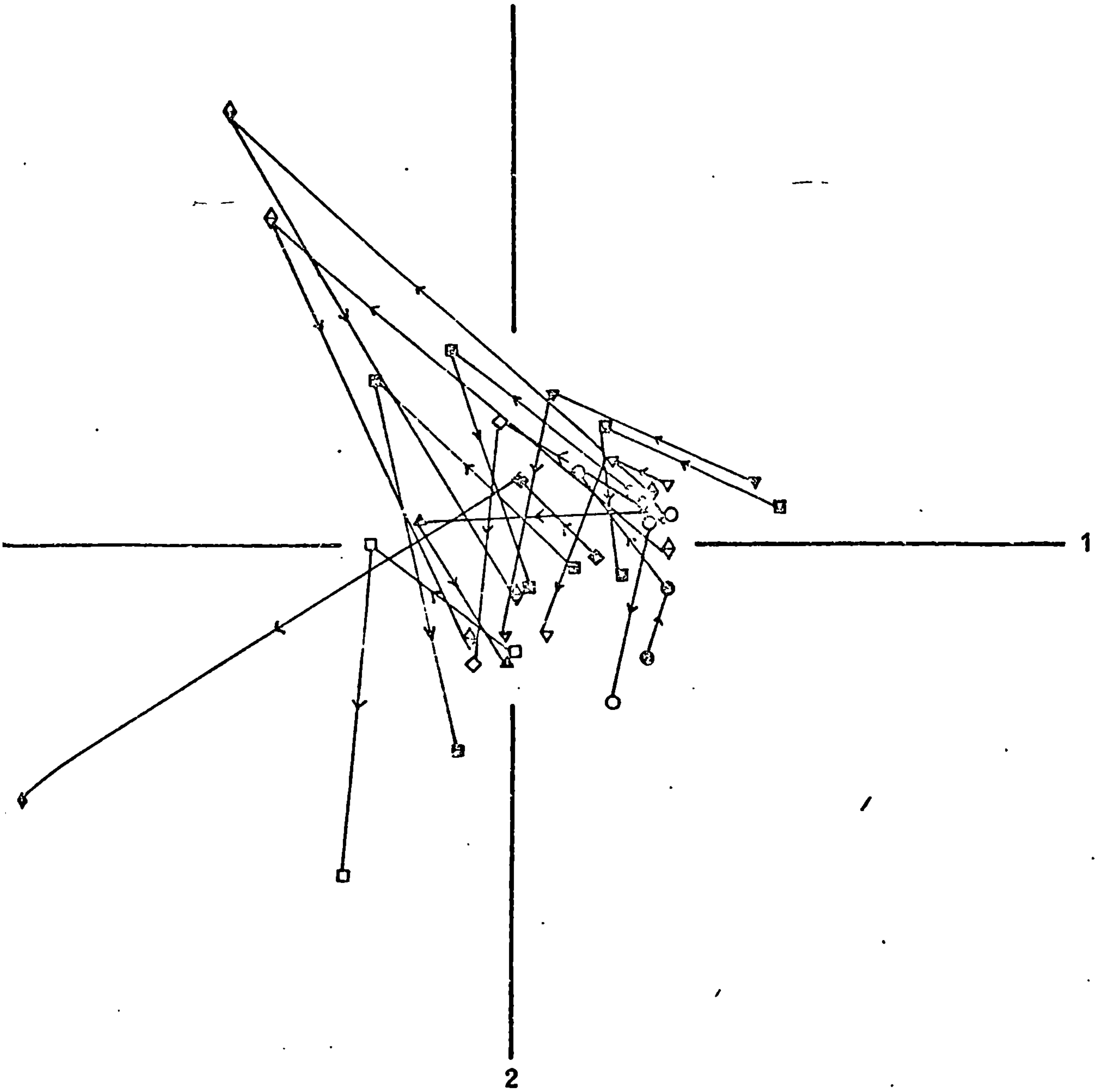

1
2

TABLE 4-3

SOIL ANALYSIS

FIELD PLOTS AT THE END OF THE EXPERIMENT

Treatment	Erosion depth below sides of rut mm	Soil pH	Soil conductivity μ mho 1:1 vol. soil + distilled water
Control	71	7.3	41
'Fisons 41'	82	7.2	43
'Vitax Q4'	64	7.1	58
Seed	80	7.3	42
Seed + 'Fisons 41'	62	7.1	36
Seed + 'Vitax Q4'	73	7.3	49
Dig & straw	74	7.4	51
Dig & straw + 'Fisons 41'	82	7.3	39
Dig & straw + 'Vitax Q4'	99	7.2	48
Dig & straw + seed	73	7.2	48
Dig & straw + seed + 'Fisons 41'	75	7.3	40
Dig & straw + seed + 'Vitax Q4'	73	7.2	50
Dig	86	7.4	42
Adjacent short turf	0	7.2	48

The only statistically significant treatment was the main effect of fertiliser on conductivity $P < 0.05$.

straw and fertilised plots.

Vegetation Experiment 2

The total cover on all turves was over 90% by the end of the fifty sixth week of this experiment, Fig.4-9a; the data and significance values from the analysis of variance are given in Table 4-4. The untreated control turves were six to eight weeks behind the rest and only reached 90% cover after 50 weeks, the highest initial cover occurring on the turves that had been 'dug' and fertilised.

The mean species number was over seven on the unfertilised turves at the end of the experiment, Fig. 4-9b. In the first 30 weeks the dug turves had a mean of up to two more species than the controls but this difference was slightly reversed by the end of the experiment. The diversity index was initially suppressed to below 2 by fertiliser but the undug turves rose towards the end of the period, the controls reaching an index of 3.7 (Fig.4-9c), equal to 0.53 of the potential diversity (species number). The fertilised turves had reached 0.7, the dug 0.44 and the turves receiving both treatments 0.53 of their potential diversities.

The cover of trampling resistant species was higher on the controls and lower on the dug turves throughout the whole period, Fig.4-9d. The measurement

Fig.4-9

Vegetation Experiment 2.

a) Total cover

b) Species number

c) Inverted Simpsons Diversity Index

d) Percentage cover trampling resistant species

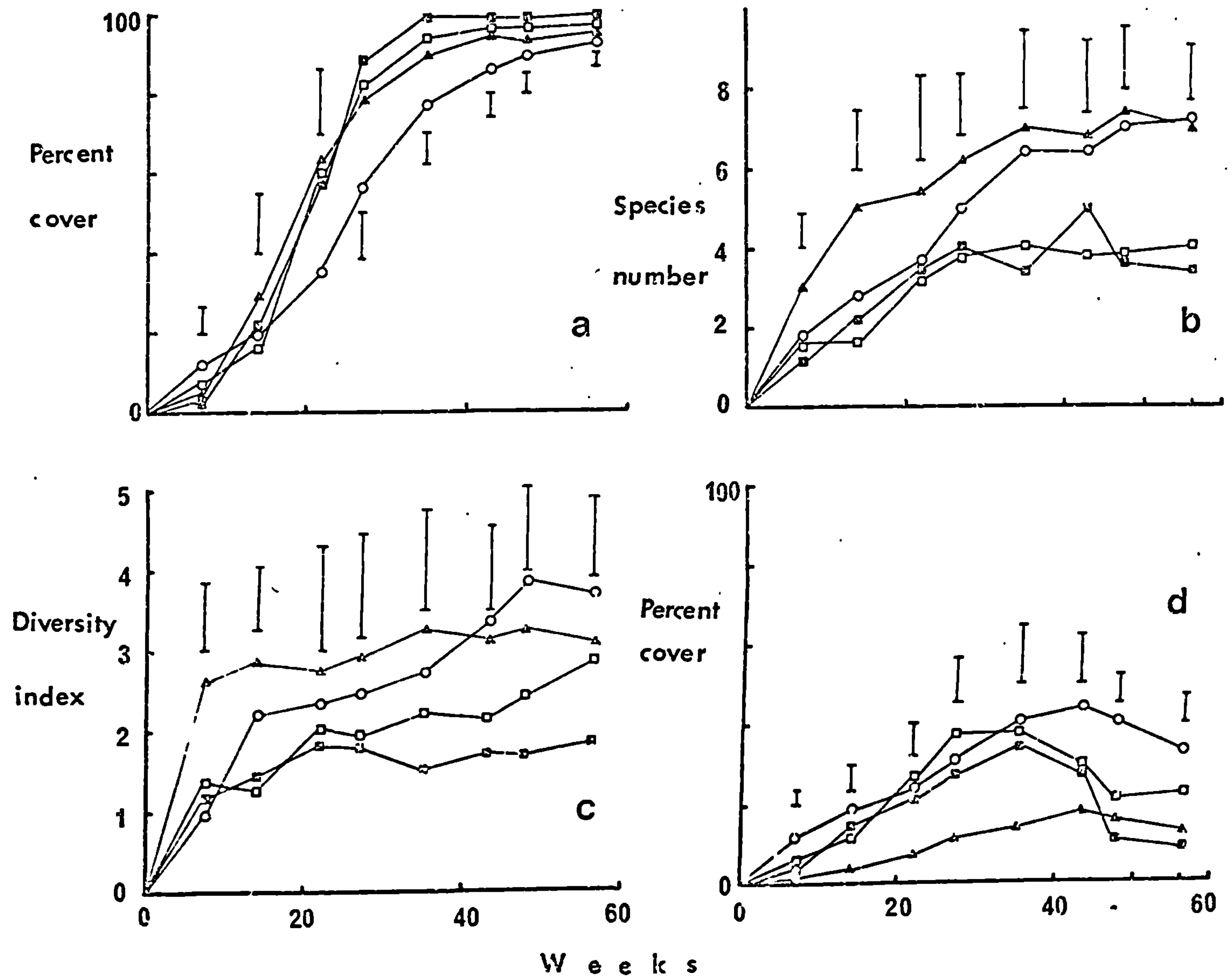
○ control

▲ dug

□ 'Fisons 41' fertiliser

⊠ dug and 'Fisons 41' fertiliser

I two standard errors


Percent cover
Species number
Diversity index
Percent cover
a
b
c
d
100
0
8
6
4
2
0
5
4
3
2
1
0
100
0
0
20
40
60
W e e k s

4-9

TABLE 4-4

RESULTS OF VEGETATION EXPERIMENT 2, TURVES IN GREENHOUSE

Week No.		7	14	22	27	35	43	48	56
Total % cover	C	11.6	19.6	34.8	56.2	75.4	85.6	89.2	93.8
	H	4.2	28.6	63.4	78.8*	89.4**	94.6*	93.4*	94.6*
	F	4.8	16.4	60	82.2*	93.2*	96.6	97.4	98.6
	HF	4	21.6	57.6	88.4	98.6	99.4	99.4	99.6
Inverted Simpsons Diversity Index	C	0.94	2.18	2.34	2.46	2.72	3.34	3.88	3.68
	H	2.6	2.88*	2.76	2.92	3.24	3.12*	3.26*	3.12
	F	1.32	1.28	2.02	1.92	2.2	2.16	2.44	2.88
	HF	1.16*	1.44	1.82	1.82	1.52	1.72	1.7	1.86
Species Number	C	1.4	2.8	3.6	5	6.4	6.4	7.0	7.2
	H	3	5*	5.4	6.2*	7**	6.8*	7.4*	7***
	F	1.4	1.6	3.4	3.8	4	3.8	3.8	4
	HF	1.2	2.2	3.4	4	3.4	5.0	3.6	3.4
Resistant Species % cover	C	11.4	18.8	24.2	31.4	40.4	44.2	41.4	33.2
	H	0.8	6.4	7.2	11.4	14.6	18.2	16.8	13.4
	F	4	11	25	38.8	38	29.8	21.2*	22.4*
	HF	3.6	13	20.4	27.6	34	28	10.4	9.8
Annuals % cover	C	0.6	2	8.2	17.8	28.4	34.4	30.2	28.8
	H	1.2	7.2	11*	13.8**	17.4**	20.8*	21.2	17
	F	0.4	3	16.4	38.2	47.8	49.8	41.8	41.4
	HF	3.2	0.4*	45.6	74.2	90.6	73	52	42.8
Perennials % cover	C	11	17.6	26.6	38	47	48.8	49	40.4
	H	3	21.4	52.4	65*	72*	66.2**	58.8**	52.2***
	F	4.4	13.4	43.6	44	45.4	39.6	35.6	30.2
	HF	0.8	21.2	12**	14.2*	8*	10.2*	10.8*	8.6*

C control. H harrow (dig). F fertiliser.

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

at week 35 marks the point where the annuals and perennials start to decrease although total cover continues to increase due to the increase of litter, Fig.4-10a and 10b. The multivariate summary of the turves, Fig.4-11a, also shows a change in direction of the controls and the harrowed plots at week 35 when between 75% and 99% cover was reached.

Measurements of pH and conductivity (Table 4-5) of the turf soil showed that fertiliser has a significant (5%) effect in lowering the pH and a statistically non-significant raising of conductivity. These results are similar to the changes measured in the field plots.

Fig.4-10

Vegetation Experiment 2.

a) Percentage cover of Annual species

b) Percentage cover of Perennial species

○ control

▲ dug

□ 'Fisons 41' fertiliser

▣ dug and 'Fisons 41' fertiliser

I two standard errors

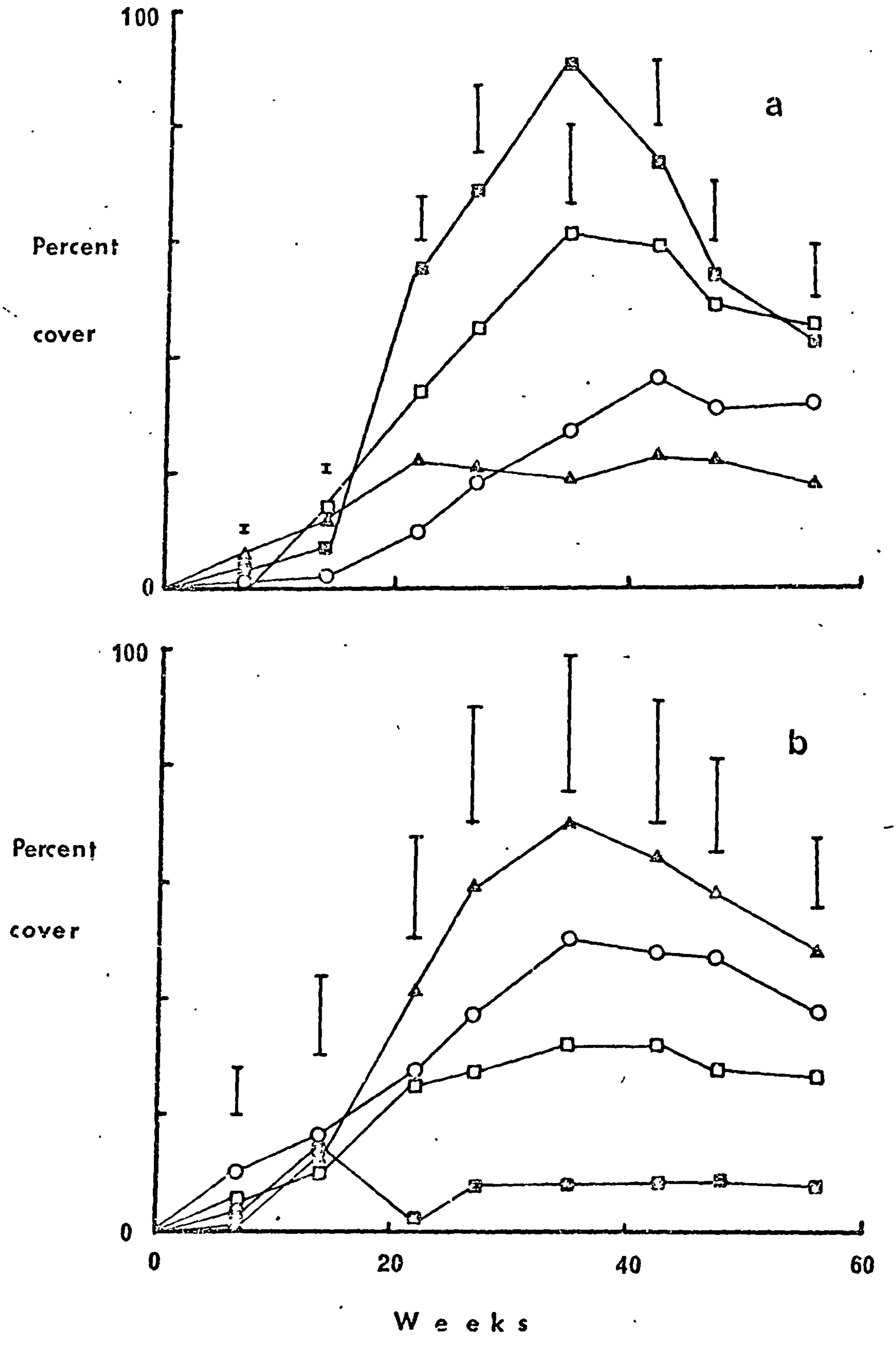

100
a
Percent
cover
0
100
b
Percent
cover
0
0
20
40
60
Weeks

Fig.4-11

a) Vegetation Experiment 2. Ordination of vegetation records at eight points in time.

○ control

▲ dug

□ 'Fisons 41' fertiliser

⊠ dug and 'Fisons 41' fertiliser

Figures adjacent to plots give time in weeks for control and dug treatments only.

Lines connect similar treatments at different points in time.

b) Vegetation Experiments 1 and 2. Ordination of vegetation records from Experiment 1 at two points in time and Experiment 2 at eight points in time.

○ control turves

▲ dug turves

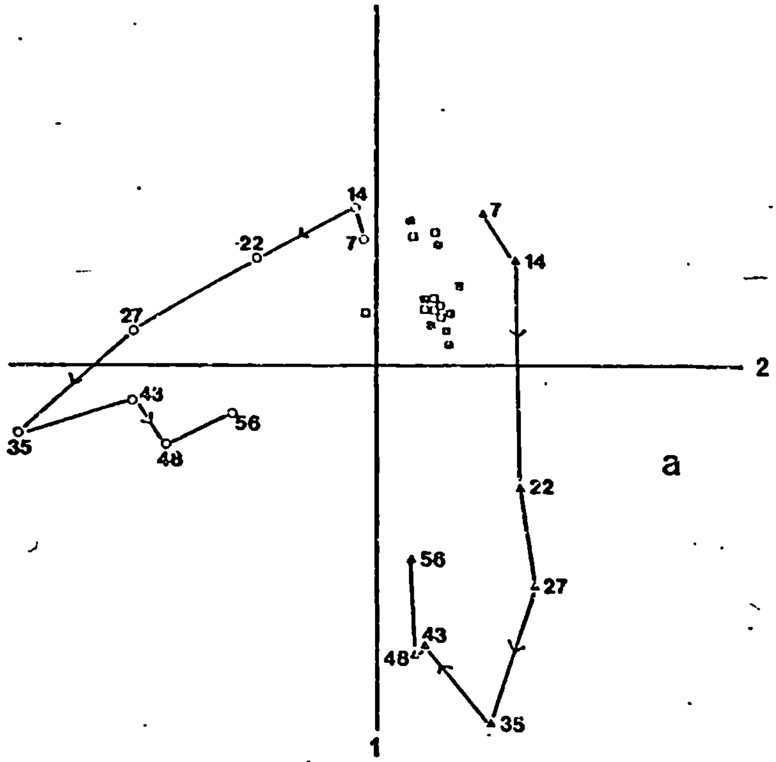
◊ dug plus straw, seed and 'Vitax Q4' fertiliser. Field plots.

◊ ~~dug plus straw~~ seed and 'Vitax Q4' fertiliser. Field plots.

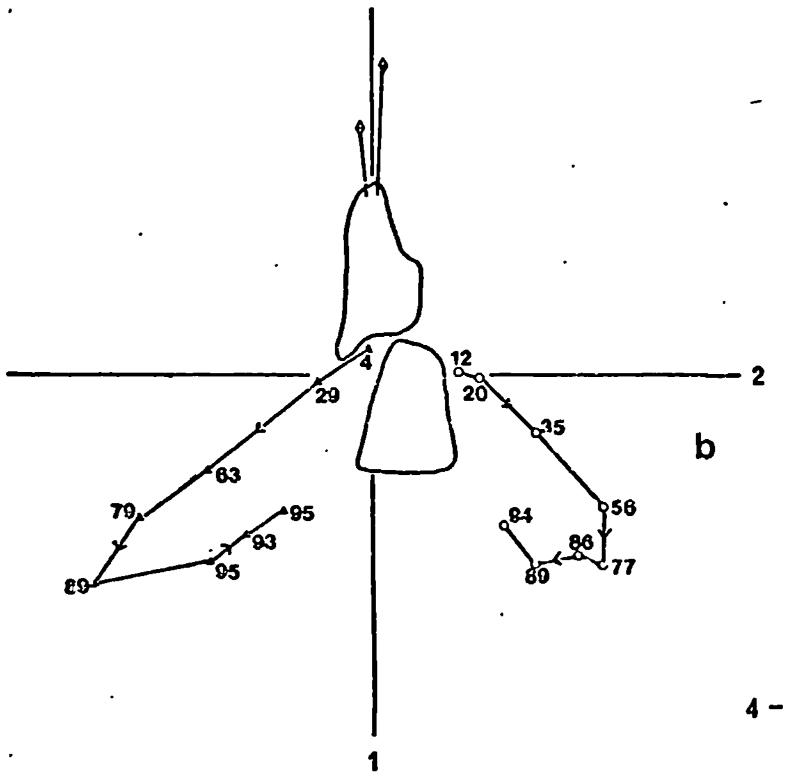
Plots occurring in the two main groups not presented individually.

Figures adjacent to points give percentage cover for the control and dug turves.

Lines connect similar treatments at different points in time.



14
7
22
27
35
43
48
56
7
14
22
27
35
43
48
56
2
1
a



4
29
63
79
89
95
93
95
12
20
35
56
77
86
89
84
2
1
b

TABLE 4-5

ANALYSIS OF VARIANCE OF TURVES pH AND CONDUCTIVITY

	Control	Dig	Fertiliser	Dig and Fertiliser
pH	7.28	7.48	7.12	7.34
Significance	NS	NS	*	NS
Conductivity µmho	113	115	140	101
Significance	NS	NS	NS	NS

* $P < 0.05$

DISCUSSION

Soil Experiments

The vertical distribution of soil penetration resistance after compaction in Fig.4-2 supports the hypothesis that short term wear creates a more resistant surface layer than that produced by normal conditions. The results of the second experiment showed that the growth of plants retarded decompression of soil, at least for the first year. These same data also showed a 'transmission' of soil penetration resistance to the lower levels suggesting that even after 20 weeks of wear the compaction forces were not in equilibrium throughout the soil profile. The plants raised the last penetrometer reading of Experiment 2 from 0.95 to 1.15; at this point they were 21% more penetration resistant than the unvegetated plots, Table 4-6. Since this area did not have a compacted layer of surface vegetation the peak of hardness at 2 cm depth, Fig.4-4, must be due to a factor associated with live plants. This could either be increased compaction caused by plant roots or higher soil water content associated with the increasing plant cover.

Larson & Allmaras (1971) suggest that soil animals and plant roots exert forces that may compact the soil near their path, although the long-term effect

TABLE 4-6

SOIL EXPERIMENT 2

MEAN LOG PENETROMETER READINGS

Month		April	June	August	October	December	February	April
Treatment								
Untreated control plots	$\bar{x}$	1.125	1.166	1.223	1.158	1.227	1.100	1.156
	SE	0.013	0.006	0.013	0.014	0.005	0.009	0.012
Plots treated with 'Simazine'	$\bar{x}$	1.102	1.077	1.033	1.007	1.089	0.870	0.959
	SE	0.012	0.023	0.018	0.025	0.020	0.033	0.025

of biological activity is to decrease compaction. They also point out that freezing and thawing and wetting and drying create stresses in the soil which may alleviate soil compaction, although they consider that these factors do not have a great effect in sandy soils. The actual penetrometer readings were extremely erratic, Table 4-6, but the large decrease in soil strength between December and February of 0.127 on the untreated plots and 0.219 on the treated plots when most of the 39.3 annual ground frosts occur at Valley, four miles away, does suggest that frost heaving may be an important factor in the regeneration of compressed soil. This will be especially evident where vegetation is removed and the soil is exposed to greater extremes of temperature (also see Chappell _et al_ 1971). A further cause of decompression in the Simazine treated soils may have the decay of the roots of plants that had been killed (Barley 1954).

Since the management aim when manipulating regeneration is some form of plant cover, this indicates that soil strength has drawbacks as a parameter by which to judge the recovery of worn areas.

Vegetation Experiments

The aim of Experiments 1 and 2 was to use the accelerated growth rate in the greenhouse as a means of predicting the effects of the treatments in the field. Willis & Yemm (1961) and Willis (1963) successfully used a similar technique. These turves were used after 35 weeks of regeneration to predict changes that would occur after the second reading of the field plots; this is the time at which the sequence of the successional process on the turves apparently reaches a critical point, as can be seen in the ordination, Fig.4-11a. This may possibly be due to a leaching of nutrients from the soils under the rather plentiful supply of water in the greenhouse, and the plants may also have started to compete with each other for the available resources.

Total cover was used to estimate the relative positions in the successional sequence. The comparable field treatments at this period had 20% cover on the controls, 41% on digging and on 'Fisons 41' separately and 53% for those treatments combined, Fig.4-5. The equivalent time for the same cover on the turves was 14, 17, 18 and 21 weeks respectively, Fig.4-9a. Taking these positions in time on the various other parameters of the turf experiment the predictions for the field plots were as given in Table 4-7, which also gives the changes that actually occurred. The predictions for diversity index, species number and cover are fairly good but more detailed parameters such as annuals and perennials

TABLE 4-7

PREDICTED AND ACTUAL CHANGES IN FIELD PLOTS

	Fig. No.	Control	Digging	Fertiliser	Dig & Fertiliser
Diversity Index	4-6b 4-2	STEADY RISE steady rise	SLIGHT RISE slight fall	STEADY RISE slight rise	CONSTANT v.slight rise
Species number	4-6c 4-3	LARGE RISE steady rise	SLIGHT RISE constant	RISE slight fall	RISE steady rise
Total cover	4-6a	V.SLIGHT RISE v.slight rise	FAST RISE steady rise	FAST RISE fast rise	FAST RISE fast rise
Annuals	4-6d	STEADY RISE steady fall	SLIGHT RISE steep fall	FAST RISE steep fall	V.FAST RISE v.steep fall
Perennials	4-6e	STEADY RISE steady rise	V.FAST RISE steady rise	STEADY RISE steady rise	CONSTANT steady rise

UPPER CASE indicates prediction

lower case indicates actual changes

were rather poor. This suggests that predictions of general measurements are reasonable but detailed predictions would be unreliable.

The rate of cover regeneration in the field plots was relatively high. Beardsley & Wagar (1971) used 13.5 $g.m^{-2}$ of slow release nitrogen and seeding treatments and only reached 40% cover after four years in an area that was still exposed to trampling, while 40% was achieved by Herrington & Beardsley (1970) in one year, but they used nitrogen at the rate of 35.4 $g.m^{-2}$ and seed and watering treatments combined.

The events in the field plots may be explained by postulating that Festuca rubra and Poa pratensis at first acted as a nurse crop for other species giving high diversity (4.3) and species number (8.4 and 9.2) at the second reading when combined with fertiliser. This effect had decreased by a third reading to diversities of 3.9 and 4.4 and species numbers of 7.6 and 7.4, probably because the seeded species interfered with the less vigorous members of the community. This is partially substantiated by the fact that the cover of annual species (Fig.4-7a, b, c and d) reached a maximum of 10% at the second reading and then sharply declined to below 4% at the third reading, whereas the cover of the perennials (Fig.4-7e, f, g and h) was still between

21% and 39%. A part of this decline was, however, due to the steadily increasing cover of litter to between 20% and 60%.

The ordination of the field plot data, Fig.4-8, showed a great deal of movement between readings which suggested that none of the stands had reached a stable condition and further changes may be expected. The ordination of turf stands, together with the first two field plot mensurations, Fig.4-11b, indicated that the processes taking place were rather different and extrapolations from turves to field plots should be treated with caution. The control and dug turves still show the same pattern of movement as when ordinated alone but the field plots are bunched closely together, fertiliser treatments tending to have a 'restrictive' effect except for the seed plus fertiliser with and without digging treatments. The ordination including the third reading of the field plots produced similar results on axes 1 and 2 except that the most extreme field plots were the final controls. Axis 3, Fig.4-12, however, bunches the more 'adventurous' turf plots along one line and puts the second reading of the field plots mentioned above at the extreme positions. This appears to be a critical phase in the succession of these plots; the cover at this stage was 76% and 63% respectively.

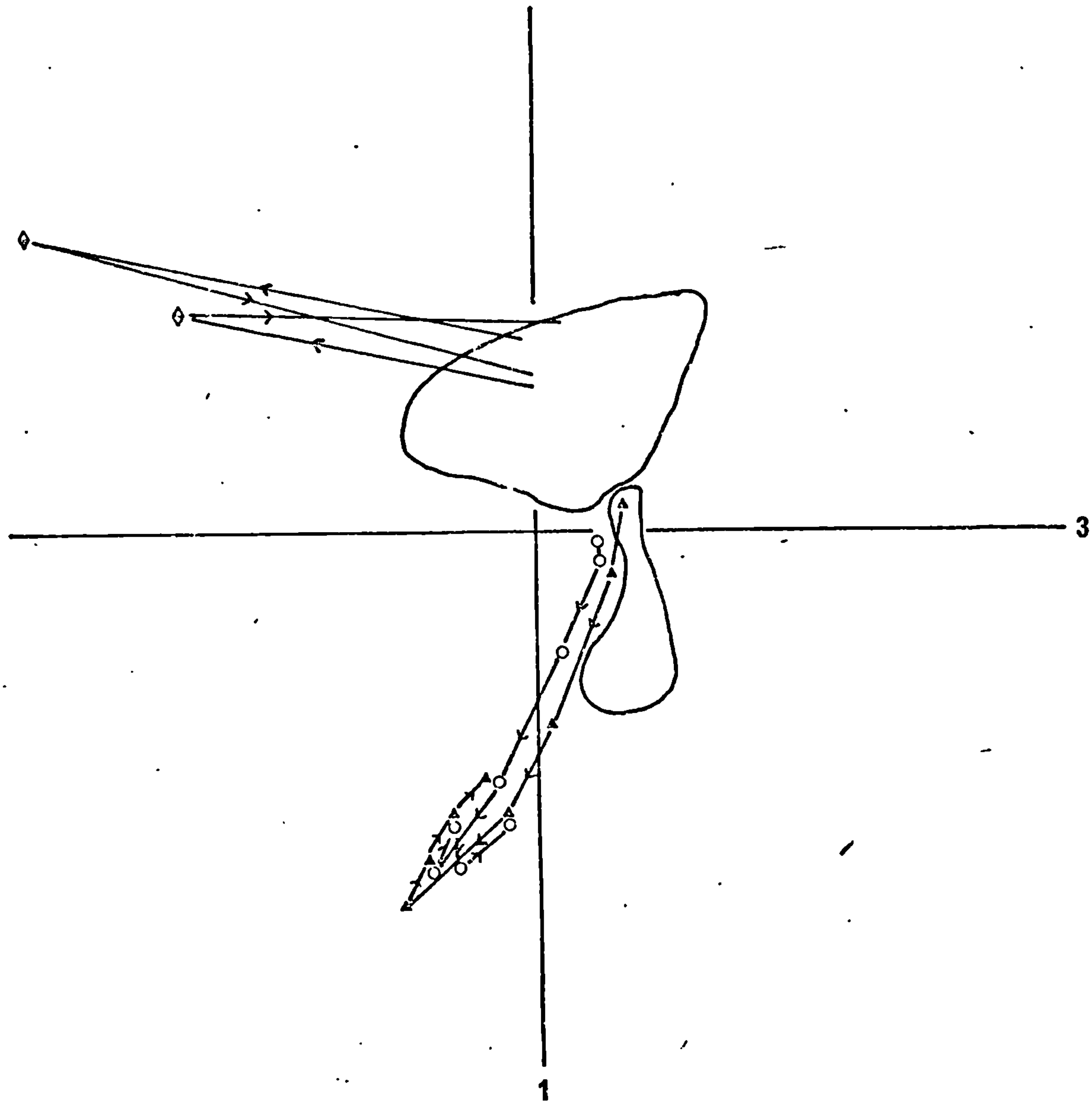
Fig.4-12

Vegetation Experiments 1 and 2. Ordination of the three field plot records and eight turf vegetation records together.

- O control turves
- ▲ dug turves
- ◈ dug plus straw, seed and 'Vitax Q4' fertiliser
- ◇ ~~dug plus straw and~~ seed and 'Vitax Q4' fertiliser

Plots occurring in the two main groups not presented individually.

Lines connect similar treatments at different points in time.


3
1

But it should be noted that in Fig.4-12 all the field plots were further away from the central grouping at the second reading. There is still a clear separation of turves and field plots.

Further predictions from the turves suggested that the diversity index will rise on the controls and the fertilised plots followed by a fall in the controls, the other treatments remaining constant. Species number will be nearly double on the unfertilised plots and all treated plots will reach a 100% cover before the controls.

GENERAL DISCUSSION

The ecological problems will be considered first and the management implications are set out at the end of this discussion.

The differences between turves and field plots may be demonstrated by the fact that the natural regeneration on the controls in the field was primarily by _Agrostis stolonifera_ followed by _Festuca rubra_, while the first major species on the control turves was _Plantago coronopus_ followed by _Isolepis setacea_, _Juncus articulatus_, _Poa annua_ and _Agrostis stolonifera_ (see Appendices 2 and 3). A number of _Festuca rubra_ seedlings were observed on the turves but they all failed to become established. The species content of the field plots appear closest to the secondary succession described by Hewitt (1970) which included _Festuca rubra_ among the first colonisers, followed by _Agrostis stolonifera_ in the damper areas. The species list of the turves suggested a damper habitat such as the damp pasture 'S5' of Willis _et al_ (1959). This may be the result of increased water supply in the greenhouse and indicates a possible cause of the differences between turves and field plots in the ordinations. On the areas treated with fertiliser alone, _Festuca_ and _Poa_ made up 10% of the vegetation on the 'Fisons 41' plots and 25%

on the 'Vitax Q4' plots. The latter treatment produced results closest to those on plots treated with micro-nutrients by Willis (1963) and this suggests that these may be limiting plant growth at Aberffraw.

There was an initial phase of colonisation of the turves by annual species followed by a reaction phase which may have been the result of the interaction between plants as the peak in the cover of annuals coincided with the time when the total cover was approaching 90%. The annuals may be excluded by the increased soil compaction caused by plants as shown in Soil Experiment 2. Alternative explanations are the leaching out of nutrients or the completion of the life span of the individual plants. The field plots were prepared at the end of April 1971 and since many dune annuals had germinated previously a faster initial growth and greater cover might have been achieved if the treatments had been carried out earlier in the year.

Tillage increased the cover of the field plots and turves but reduced it when combined with other treatments in the field. The establishment of annuals was also reduced by digging in the field (Fig.4-7a, b, c and d) but was initially stimulated and then depressed by tillage on the turves. Fig.4-10a. The possible advantage of increased surface microtopographic variance may have been offset by a drying out of the surface layers especially in the field (cf. Thurston 1960). But the seedlings that had been able to penetrate the surface of the untilled plots may have found a better water supply and so been able to survive (see Paper 1). Digging had no effect on the perennials in the field (Fig.4-7e, f, g and h) except when combined with fertiliser when there was a negative interaction producing less cover than would be expected from the addition of the main effects. Digging of the turves had a positive effect on the perennials (Fig.4-10a) but the interaction with fertiliser was again negative. Tillage of the top one or two centimetres may be the best compromise as it would provide a greater surface micro-topographic variance and, therefore, a greater range of species would germinate (cf. Harper *et al* 1965). This would also remove a high compaction layer if it was present but still leave an improved water supply within 'reach' of the seedlings.

The difference in establishment between *Poa pratensis* (2%) and *Festuca rubra* (12.4%) in the field is interesting, particularly as care was taken to sow potentially equivalent numbers. The first reading in October 1971 showed similar cover of the two species when the plots were dug but where no seed was sown;

this indicated that either the test conditions did not coincide with those in the field, or that the sown seed was different from that occurring naturally. If the latter hypothesis is true, then the *Poa* strain is not so well adapted as the *Festuca* to the field conditions and this may be a reflection of the fact that the *Poa* seed was only 23% of the weight of the *Festuca*. There is a tendency for the *Festuca* to increase its lead on the dug plots so the *Poa* may also be suffering from water shortage; naturally occurring *Poa* was found to prefer slightly wetter stands than the *Festuca*, see Paper 2. A nutrient shortage may also have affected the ratio of occurrence of these grasses as fertiliser had a positive effect on *Poa* but not on *Festuca*. Grazing by sheep and cattle is a factor which may well have affected all the field results particularly as sheep are selective and could have grazed the *Poa* and similar 'lowland' species preferentially (Milton 1940).

Both fertilisers caused an increase of *ca* 32% in the amount of cover and number of species present on the field plots, especially in conjunction with seeding (*ca* + 2 spp.); diversity was apparently unaffected. The realised diversity tended to be suppressed by the fertilisers alone which suggested that only a few species were able to spread as a result of the additional nutrients. The two fertiliser treatments produced similar effects on the main parameters. If the fertiliser treatments are discontinued then a change of the proportions of the various species may be expected, especially on the dug plots from which the nutrients may leach out quite quickly. The higher nitrogen level in the compact control plots (Appendix 4) is interesting and may well be the result of the mobile nitrogen being leached from the dug plots or locked up in the greater vegetation cover on all the non-control plots.

The management recommendations for recovery of worn sand dune pastures depend on the future use of the areas. By the time of the third field reading it is already clear that the management aims, e.g. for cover or diversity, must be decided before regeneration techniques can be selected.

If regeneration of the natural vegetation is required the assumption that untreated plots will regenerate to a 'natural' state must be made as there was no 'natural' vegetation near the experimental plots; the treated plots can then be considered in relation to the controls. On the basis of species number, 'Fisons 41' with or without seed, or digging and straw with 'Vitax Q4' all produce 7.6 species. But on the turves

'Fisons 41' suppressed species number to 4 and the highest number at the last reading was 7.2 occurring on the controls. Diversity comes nearest the control level (4.67) on the 'Fisons 41' field plots (4.57), but the ordinations suggested that digging alone, digging plus straw or seeding produce a vegetation nearest to the controls. On the turves, fertiliser alone is best on this criteria. Since the cover is greater on the treated plots either digging plus straw or two applications of an N.P.K. quick release fertiliser is probably the best treatment for 'natural' regeneration.

If cover alone, irrespective of which plants are involved, is required then the application of a slow release fertiliser and seeding give the best results at 95% cover. The spring of 1973 is likely to show nearly one hundred percent cover on these plots, but this is not the same as a close knit resistant turf which would take at least one more growing season to form. If the requirement is for a high level of resistant species the fertiliser should be of N.P.K. quick release type and two applications should be made. However, while the fertiliser initially gave a good cover of resistant species on the turves (Table 4-4) it dropped below the level of the controls after week 35, so this recommendation may have to be qualified at a later date.

The best general treatment for cover, diversity and species number is probably seeding and 'Vitax Q4', but since this area of pasture is relatively near the water table, care would be needed in extending this conclusion to the drier areas of sand dunes. As discussed above, the compacted soil may have a number of advantages so a very superficial disturbance (or none at all if seed is sown cf. Harper 1957) is recommended where the organic crust is still intact. There was also a close source of seed and vegetative spread from plants near the track so it may not be necessary to draw on the seed bank in the compacted soil if sufficient time is allowed for recovery. Areas of ground that have been probed by birds seeking a winter supply of food have been observed in the dune areas (Mr. R.W. Arthur, pers comm.); so the required amount of tillage and the preservation of the birds might be obtained by spreading the appropriate food on compacted areas of track during periods of bad weather and if the food is mixed with Festuca or Poa seed perhaps the whole operation can be carried out with minimum labour costs.

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APPENDIX 1

FERTILISER DETAILS

	Ratios		
	N	P	K
'Fisons 41'	1.0	1.0	1.8
'Vitax Q4'	1.0	0.9	0.92

Additional Elements Present

'Fisons 41' — Calcium sulphate and chloride in small quantities

'Vitax Q4' — Chelated micronutrients

Manganese	30 ppm
Iron	60 ppm
Zinc	43 ppm
Copper	30 ppm
Boron	16 ppm
Molybdenum	0.4 ppm
Magnesium	~~2 ppm~~ 1.75 %

APPENDIX 2

VEGETATION EXPERIMENT 1

MEAN OCCURRENCES FOR EACH TREATMENT

	October 1971													May 1972					
	A	B	C	D	E	F	CD	CE	CF	DE	DF	CDE	CDF	A	B	C	D	E	F
Erophila verna															0.2	0.2		1.2	1.2
Viola tricolor			1.2					1.2	0.4							1.2		0.6	
Cerastium atrovirens									0.2	0.2	0.2				1.6	0.6	0.2	0.6	0.2
Sagina nodosa					0.4						0.4								
Arenaria serpyllifolia						0.2		0.2							1.6	0.4	0.6	0.6	0.2
Linum catharticum			0.2				0.2												
Erodium glutinosum															0.8				
Trifolium repens			0.6		0.8		0.2		0.4					0.2		1.0		1.2	
Trifolium arvense																			
Lotus corniculatus																			
Potentilla reptans	0.4	2.6	0.2	1.4	3.6	0.4	0.2	1.4	1.6	2.8	6.4	0.2	4.2		0.6	0.4	0.8	1.0	
Sedum anglicum														0.2					
Anagallis arvensis									0.6	1.2									
Centaurium littorale										0.4									
Centaurium spp.	1.2			0.8	0.2	1.4		0.2	0.2	0.2	1.6			0.8	0.4		1.2	0.2	0.2
Veronica chamaedrys																			
Thymus drucei	0.2	1						0.2						0.8	1.4				
Prunella vulgaris																			
Plantago major					1													0.2	
Plantago lanceolata			1.6		1.4		0.2	1.2								1.2		0.4	
Galium verum	0.6									0.2	0.4				0.4				
Senecio jacobaea													0.2				0.4		
Senecio vulgaris																			
Bellis perennis																			
Leontodon autumnalis																			
Leontodon taraxacoides								0.8										0.2	
Crepis spp.													0.6						
Taraxacum officinale				0.2									0.4						
Taraxacum laevigatum																			
Juncus articulatus					0.2	0.2												0.2	
Carex arenaria	1.4	1.2	0.8		1.6	1.6		1.8	1.8	1.8	3.4	0.2	0.6		0.6	0.4		2.0	1.6
Carex flacca						0.2	0.6	0.2		0.6									
Carex hirta																			
Festuca rubra	3	3.2	0.4	16.8	2.4	5.8	29.8	3	2	21.4	14.6	19.6	15.6	0.8	3.2	1.5	10.8	3.2	5.6
Lolium perenne																			
Poa annua	0.8		0.8	1.6	0.8	2.4		4.4	2.0	2.2	3.2	2.8	2.6	0.6		1.2	1.8	0.6	1.0
Poa pratensis	1	3.2	2.2	3.2	1.2	13.8	13.2	4.8	8.6	6.6	9.9	6.2	7	1.2	7.2	3.6	2.0	1.2	7.2
Holcus mollis	0.2	1.8		0.8	2.2		0.2	1.0		1.8	0.8		0.4						
Anthoxanthum odoratum														0.8	2.0	0.4	0.4	1.8	0.2
Agrostis tenuis			0.2			0.4									0.8	1.2		0.2	1.4
Agrostis stolonifera	2.8	9.2	17.6	2.6	5.2	13.0	3.8	6.0	9.8	4.8	6.0	9.4	7.4	2.8	2.2	5.6	0.4	5.4	6.4
Bryum rubens														2.2			1.8	7.4	8.8
Climacium dendroides																0.2			
Camptothecium lutescens																			
Litter														11.6	18.4	37	18.8	14.8	29.2
Bare ground	86	76	74	73	79	60	52	74	73	56	53	62	61	78	58.6	43.6	60.2	57	35.8

A Control. B Dug. C Dug plus straw. D Seeded. E Fertiliser ('Fisons 41'). F Fertiliser ('Vitax Q4').

APPENDIX 2 continued

VEGETATION EXPERIMENT 1

MEAN OCCURRENCES FOR EACH TREATMENT

	May 1972							October 1972						October 1972						
	CD	CE	CF	DE	DF	CDE	CDF	A	B	C	D	E	F	CD	CE	CF	DE	DF	CDE	CDF
Erophila verna	0.6	1.6	1.0	0.6	1.6	1.0	1.8													
Viola tricolor			0.2		0.2				0.2	0.8		0.2	0.2	0.2		0.6		0.2		0.2
Cerastium atrovirens	0.6	1.4		0.8	1.2	1.8	3.0													
Sagina nodosa								0.4		0.4	0.6	0.4	0.4		0.2	1.0		0.4		0.2
Arenaria serpyllifolia	0.6	1.4	0.8	0.6	1.8	1.6	1.2					0.2	0.2	0.4	0.2	1.6	0.2	0.2	1.2	0.4
Linum catharticum																				
Erodium glutinosum									0.4						0.8					
Trifolium repens			0.6									0.4				1.4				
Trifolium arvense															2.6					
Lotus corniculatus													0.2				0.4			
Potentilla reptans		1.0	0.8	0.4	2.2	0.2	0.4	2.2	2.4		2.2	3.0			1.4	2.0	0.8	1.8	1.2	1.6
Sedum anglicum																				
Anagallis arvensis														0.4		0.2				
Centaurium littorale				0.8							0.2						1.0			
Centaurium spp.	0.2		0.2	0.6	1.0															
Veronica chamaedrys	0.2				0.2															
Thymus drucei		0.2		0.2			0.2	2.4	2.4		0.2	0.2	0.6			0.4	0.2		0.6	
Prunella vulgaris							0.4									0.4				
Plantago major												0.2								
Plantago lanceolata		1.6						0.2		2.0		2.0		1.2	0.8					
Galium verum				0.2	0.2			0.8												
Senecio jacobaea	0.2			0.2	0.2	0.4	0.6	0.4	0.2	0.6	2.4	0.4		0.8	0.2	1.0	0.2	0.8	1.6	1.0
Senecio vulgaris							0.2													
Bellis perennis	0.2	0.6			0.2					0.2			0.6	0.4		0.6		0.2		
Leontodon autumnalis									0.4											
Leontodon taraxacoides	0.2	0.2		0.2		0.4		0.6	0.4	0.2	0.8	1.2		2.4	1.6	0.6	1.2	0.2	1.6	1.0
Crepis spp.											0.2									
Taraxacum officinale					0.2		0.8									0.2	0.4	0.4		0.4
Taraxacum laevigatum					0.2															
Juncus articulatus					0.2							0.4	0.2		0.4					
Carex arenaria		1.2	0.8	1.6	1.6	0.8	0.4	1.0	0.6			4.0	2.8		5.0	2.6	2.4	2.2	2.2	1.2
Carex flacca	0.2	0.2		0.2									0.4							
Carex hirta														2.2			4.4			
Festuca rubra	19.4	1.8	1.6	15.2	8.8	15.6	11.6	5.2	6.0	4.6	12.4	5.8	17.6	11.0	10.0	4.4	20.2	11.4	12.8	10.2
Lolium perenne																0.2				
Poa annua	0.4	6.4	1.6	2.4	5.4	6.2	2.2				0.2				2.0	0.6	0.2		0.6	0.4
Poa pratensis	5.4	5.0	9.4	6.6	8.6	1.8	5.4	0.4	6.6	2.4	2.0	1.8	3.4	3.2	5.4	6.2	6.4	6.8	4.6	4.2
Holcus mollis			0.2				0.2													
Anthoxanthum odoratum	0.2		0.4	1.0	1.4	0.4	0.4	3.8	5.2	1.2	1.8	5.4	3.2	2.0	3.8	2.0	2.6	5.8	0.6	2.0
Agrostis tenuis	0.2				0.2		2.6								0.2			0.2		
Agrostis stolonifera	3.0	3.2	6.0	2.6	2.2	2.4	2.6	6.2	3.0	10.8	2.2	13.6	5.2	3.6	6.0	7.2	6.4	6.6	8.6	8.6
Phleum bertolonii												0.6								
Bryum rubens				4.8	8.0	0.2		1.2			2.2	4.8	5.[illegible]				2.6	1.8	0.4	
Climacium dendroides																				
Camptothecium lutescens								0.2										0.2		
Litter	33.4	22.2	22.2	25	32	30.6	30.2	23.4	28.2	49.4	35	36.8	43	52.6	43.8	45	42.8	56.2	53.6	55.6
Bare ground	35	53	54.2	36	22.4	36.6	35.8	51.6	44	27.4	37.6	18.6	16.6	19.4	15.6	21.8	7.6	4.6	10.4	13

APPENDIX 3

VEGETATION EXPERIMENT 2

MEAN OCCURRENCES FOR EACH TREATMENT

	Week 7				Week 14				Week 22				Week 27			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Equisetum variegatum						0.8				2				5		
Viola tricolor	0.2	0.4			0.4	2.2			0.8	2.2			0.2	2.6		
Sagina nodosa						2.8				11.6	3.8	0.2	1	16.4	3.2	1
Arenaria serpyllifolia																
~~Minuartia verna~~ Caryophyllaceae indet.																
Trifolium dubium													0.6			
Trifolium repens																
Anagallis tenella		0.4				3.8		2		11.4		0.6	0.6	12		5
Anagallis arvensis		1.2	0.2	0.2		6	2.8	6.2	0.6	11.8	16.8	10.2	2.6	10.4	17	5.2
Anagallis minima		0.8				1.2				0.2				0.4		
Centaurium littorale										0.6		0.4		0.8		1
Plantago major	0.4				2.2	0.8		0.4	1.6				0.6			
Plantago lanceolata	0.8				1.8	0.2			3.8				4.8	0.8		
Plantago coronopus	8.2		3.4	0.6	10.2		9.8	12.2	10		8.6	0.2	12.6		9.2	0.2
Bellis perennis	1.4				2				2				2.2			
Spp B										1		0.6	0.4	1.4	0.4	0.2
Spp C																
Juncus bufonius			0.2	0.6	0.2	1.4	1.8	0.4	0.8	3.8	3.8	10	1.8	3.8	9.6	26.6
Juncus articulatus			0.2		0.4			0.2	4.2	1.8	3.8		6.4	2.8	1	0.8
Isolepis setacea									5.6			14.8	12	0.6		20.4
Carex flacca					0.2	0.2			0.2	0.2			1.2	0.4		
Carex arenaria									0.6		0.8	0.2	1.6	0.4	2.4	1
Poa annua	0.6	0.4	0.2	2.6	1.8	4.6	1.2		1.8	5.8	12.6	20.2	2.6	7.4	23.2	25.6
Poa pratensis													0.6		0.4	
Poa subcaerulea									0.4				0.4			
Agrostis stolonifera		0.4	0.4		0.2	1.4	0.8		1.8	10.2	9.8		3.8	13.4	10.8	
Bare ground	88	96	95	96	80	71	84	78	65	37	40	42	44	21	18	12
Litter																

APPENDIX 3 continued

VEGETATION EXPERIMENT 2
MEAN OCCURRENCES FOR EACH TREATMENT

	Week 35				Week 43				Week 48				Week 56			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Equisetum variegatum	0.2	3.6			0.2	3.6				1.6			0.2	0.6		
Viola tricolor	0.2	1.8														
Sagina nodosa	1.4	22	6.2	0.6	3.6	18	6.2	1.4	4.6	17.6	6.4	0.6	6.6	11.4	3.8	0.6
Arenaria serpyllifolia	1.2	1		0.8	2	1.2		0.8	1.0	1			0.2	0.6		
~~Minuartia verna~~ caryophyllaceae in diet		0.2														
Trifolium dubium	1.2				1	0.2			0.8				0.2		1.2	
Trifolium repens										0.4				0.2		
Anagallis tenella	0.6	12	0.2	2.2	1	11.4	0.2	1.6	1.0	10	0.2	0.8	0.8	11.6		0.2
Anagallis arvensis	2.2	6.6	13.8	2.2	3	5.6	9.4	3.4	3.2	4.2	7.8	4	3.2	4.8	5.4	2.2
Anagallis minima																
Centaurium littorale		1.4		1		1.4		0.6		1		1.4		1.2		0.6
Plantago major	0.6				0.2											
Plantago lanceolata	3.6	2.2			3.4	1.6			3.2	1			2	0.8		
Plantago coronopus	15.6		7.6		11.4		3.8		9		3.8		5.6		4.2	
Bellis perennis	1.4				2.6				2.2				2.2			
Spp B	1.8	2.2	0.4	0.8	0.6	1.8		0.8	1.4	2.6		0.4	1.4	1.4	0.4	0.8
Spp C																
Juncus bufonius	1.4	3	18	27.2	4.6	0.8	25.4	22.4	5.2	2.2	27	13.4	6	3	26.6	10
Juncus articulatus	8.4	4	1	0.4	8.8	4	1.6	0.8	10	5.2	2.6	0.2	8.4	4.8	3.6	1.4
Isolepis setacea	16.8	0.4		27.2	13.2	6		21.2	9.8	7.2		26.6	9	7.8		23
Carex flacca	3.2	0.8			4	3			5.2	3			3.2	4.4	0.2	
Carex arenaria	2.6	1.6	6.8	2.6	3.8	1.4	6.6	4.4	5.8	2	5.8	5.2	5	2.2	6.6	4.2
Poa annua	5.4	7.6	29.4	33.6	13	9.4	24.4	27.2	11.6	7.4	14.8	10.2	11.8	3.2	13.2	8.4
Poa pratensis	3.4				0.6	0.2										
Poa subcaerulea	0.4				0.2											
Agrostis stolonifera	6.4	16.8	9.8		6	17.4	11.8		3.8	13.8	9		3.2	9.2	6.4	
Bare ground	23	11	7	1	14	5	3.4	0.6	10.8	6.6	2.5	0.6	6.2	5.4	1.4	0.4
Litter					2.4	7.6	7.2	16.8	10	13.4	20	35.6	24.6	27.4	27	48.2

PAPER 5

THE MICROCLIMATE OF SAND DUNE TRACKS

THE MICROCLIMATE OF SAND DUNE TRACKS

INTRODUCTION

The importance of change in microclimate caused by formation of tracks and its effect on the vegetation is at present unknown. The principal physical changes that occur when a track is created are the removal of the tall surface vegetation and the compaction of the soil. Previous workers have investigated the effect of such factors on the microclimate but not in the actual track situation.

The effect of vegetation removal has been considered in isolation by several workers. Whitman (1967) made the point that microclimate and plant cover are interdependent and Ellison (1960) draws attention to the fact that a reduction of standing herbage and mulch leads to a lighter, warmer and drier micro-environment as well as increasing water loss by evaporation. Vegetation cover has a damping effect on daily and annual temperature range and it also reduces the depth to which the thermal variations penetrate (Richardson 1958 and Willis <u>et al</u> 1959).

The surface temperature of a 'powdery mulch' can rise 20°C above that in tall crops and the latter may reradiate 46% of the solar radiation income compared incident radiation into the atmosphere. This effect was investigated by Ludwig & Harper (1958) and a dark soil colour was found to raise the maximum temperature by 5°C compared with a white soil surface and this mechanism may explain the high temperature of 63.5°C found under moss by Boerboom (1964). The surface angle in relation to incident radiation may also be significant on some sloping tracks; a change in angle of 2° from the horizontal alters the solar climate to the same extent as 140 miles of latitude at 42°N. (Sprague 1959).

The effect of soil compaction is to alter the relative amount of the soil components present in a given volume of soil. Since the principal components in this case all have different thermal properties, the thermal characteristics of the soil will alter as it is compressed.

Compaction of sandy soils increases the mass of sand in a given volume, and tends to increase the amount of water in dry areas and decrease it in wet ones (Fig. 1-10); the volume of air is decreased. An increase in the volume of sand at the expense of air will raise the conductivity of the soil as will the greater thermal contact between particles of sand in a compressed soil. Raising the water content at the expense of both sand

and air will considerably increase conductivity (λ). Both these factors will at first increase thermal diffusivity (k) but after an optimum point is reached the rise in specific heat (pc) will offset the increasing conductivity. The relationship between these is expressed by Lowry (1967) as follows :

$$k = \frac{\lambda}{pc}$$

The specific heat (pc) of the soils can be calculated from the relative sand (bulk density) and water contents assuming that all the solids are pure sand with a specific heat of 0.2. If the thermal diffusivity is estimated then the conductivity can also be calculated. Since bulk density is known to change as a result of path creation (see Paper 1), an associated change in the thermal climate of the path plants may be expected. An up-to-date and comprehensive account of this subject is given in Lowry (1967) and Munn (1966).

The aim of the first investigations, experiment 1a (summer) and 1b (winter), was to make a general survey of the microclimatic changes caused by the total effects involved in the creation of a path in 'natural vegetation'. The major emphasis was on temperature differences as this was considered likely to be the primary factor affecting plant growth. Theoretical considerations discussed above suggested that soil water content may be an important factor in the change in microclimate brought about by the creation of paths so in experiment 1a the micro climates of wet and dry areas were also compared.

The levels of the factors which are actually recorded at any one time will be strongly influenced by the seasonal and daily variations in climate as well as other environmental phenomena including the amount of clear sky, wind speed and the amount of precipitation. Comparisons between data recorded at different sites at the same time will, however, allow comparative statements to be made, although the interaction between site differences and variations in the weather must be considered.

Experiment 2 was a study of the relative effects of two components of path formation. Theoretical considerations suggest that the two principal factors affecting path microclimate are probably the removal of the tall vegetation and the changes in the thermal characteristics of the soil brought about by compaction. The aim of this experiment was to assess the relative importance of these two factors. This experiment was carried out in July.

The morphology of Festuca rubra from the areas used in experiment 1a is briefly described.

Photo 5-1

Experiment 1a,
Stand I.
The wet track stand.
Hygrograph with
cover in foreground,
soil thermometers
visible on rut with
anemometer beyond.

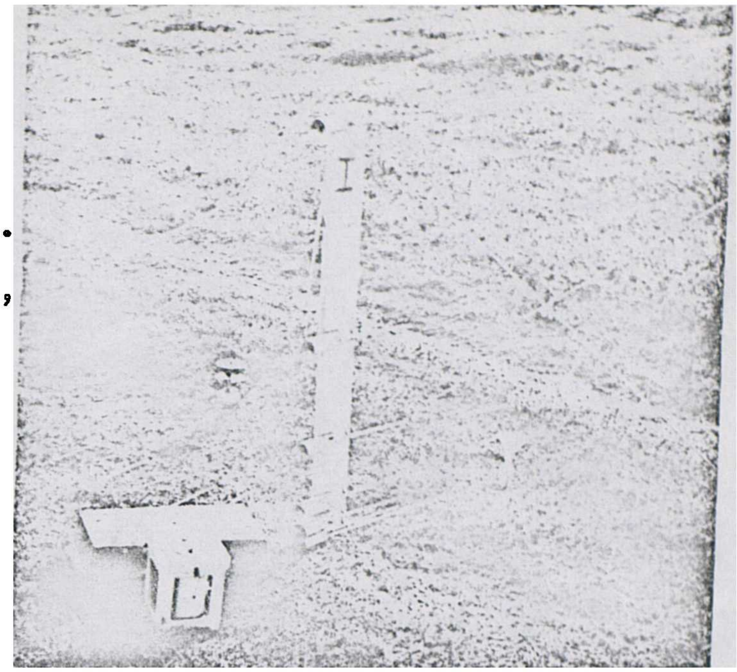


Photo 5-2

Experiment 1a,
Stand IV.
The dry 'natural
vegetation' stand
in tussock of
Ammophila arenaria.

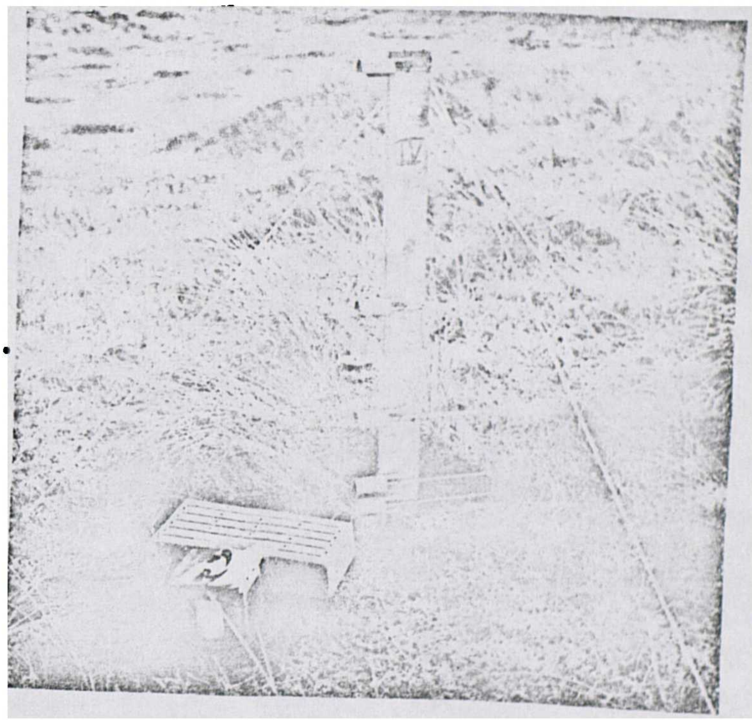


TABLE 5-1

VEGETATION IN $\frac{1}{2}$ m^{2} AT EXPERIMENTAL SITES: FEBRUARY 1972

Species	Domin ratings					
	Experiment 1a				Experiments 1b and 2	
	Wet area		Dry area			
	I	II	III	IV	I	II
Ranunculus acris		x				
Ranunculus flamula		x				
Cardamine pratensis		x				
Viola tricolor				x		
Cerastium atrovirens			1			1
Linum catharticum		x				
Trifolium repens		x				
Lotus corniculatus						x
Potentilla anserina		x				
Potentilla reptans	x					
Hydrocotyle vulgaris		x				
Salix repens		6				
Thymus drucei						2
Prunella vulgaris		x				
Galium verum			x			x
Bellis perennis	1		x			
Leontodon taraxacoides						x
Crepis spp.			x			
Taraxacum laevigatum					x	
Juncus articulatus	x					
Carex flacca	7	7				
Carex arenaria				x		
Festuca rubra			9	9	4	8
Poa annua	4					
Poa pratensis			x			
Poa pratensis spp. subcaerulea		1		x		x
Ammophila arenaria				6	x	5
Agrostis stolonifera	x	5				
Mibora minima						x

TABLE 5-1 continued

Species	Domin ratings					
	Experiment 1a				Experiments 1b and 2	
	Wet area		Dry area			
	I	II	III	IV	I	II
Tortula ruraliformis						1
Acrocladium cuspidatum		1				
Camptothecium lutescens				3		1
Brachythecium albicans			1			1
Moss *	x					
Lophocolea bidentata				1		

* Small relict too badly damaged to identify.

The vegetation was recorded by estimating Domin ratings in an area $\frac{1}{2}$ m^2. This was done in February 1972 and the deciduous <u>Salix repens</u> was without leaves. At the time of Experiment 1a it would have had a rating of 9 or 10.

Photo 5-3

Experiments 1b and 2.
Stand I on dry track.

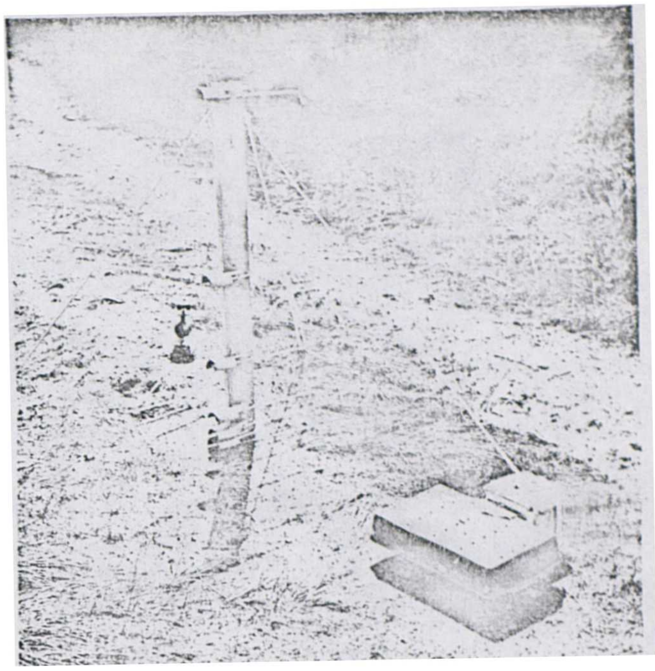
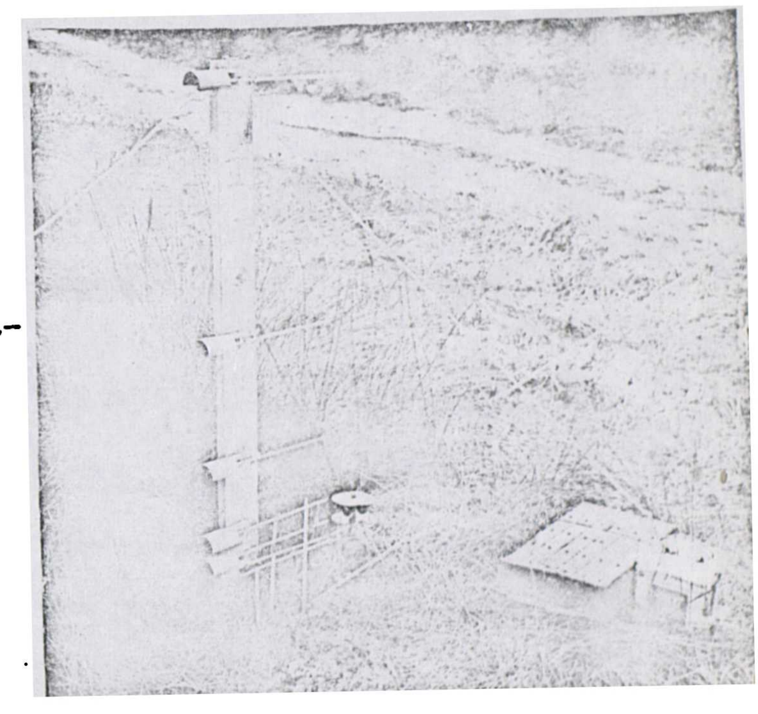


Photo 5-4

Experiments 1b and 2.
Stand II, dry 'natural vegetation'.

Note the soil temperatures were measured with standard thermometers in Experiment 2 when this picture was taken.



Temperature

The air temperature (^{o}C) was measured at the soil surface and 2, 5, 10, 25, 50 and 100 cm above it using standard mercury in glass thermometers. The bulbs were protected from radiation from earth and sky by enclosing each of them in a cylindrical screen of perforated zinc and they were protected from rain or snowfall by a half cylinder of plastic (see photos). The soil surface temperature was measured by placing a thermometer on the ground underneath the lowest screen.

Soil temperatures were measured by placing Cassella soil thermometers with 1.3 cm diameter bulbs at 2, 5, 10, 20 and 30 cm depths in holes made with an auger. The space between the thermometer stems and the sides of the holes were then filled with sand poured in from the top to prevent cold air flowing down to the bulbs. The thermometers were placed on the track in a line parallel to the side so that they would all be in a similar compaction zone. In the natural vegetation they were grouped in a circle with at least 8 cm between them, a layout that brought them as close together as possible without interfering with each other. All temperatures were recorded every hour during the 33 hour period.

Soil Thermal Characteristics

The specific heat estimation was based on the measured bulk density and the water content at 10 cm depth at each stand. The thermal diffusivity of the soils at the time of each experiment was estimated from the recorded temperatures. The heat equation used was given by Batschelet (1971) as :

$$\frac{dT}{dt} = k\frac{d^2T}{dz^2}$$

t = unit of time (a quarter of an hour in this case)

T = temperature C°

z = depth of soil 'unit' (1 cm in this case)

k = the arbitrarily chosen thermal diffusivity constant

The equation was used to calculate the heat flow through the soils between the 2 cm and 30 cm depth, starting with an estimated gradient which utilised the intermediate measurements at 5, 10 and 20 cm depth recorded at the start of the experiment. This was carried out by computer programme 'temp' Appendix 1 which was run for the 34 hour sequence using an arbitrarily chosen k value and the 2 and 30 cm depth records, estimating the temperatures at the intermediate depths. This was carried out for each site and for each 34 hour experiment.

These estimates were then checked against the temperature recorded at 5, 10 and 20 cm depths. Four instants in time were used, all based on the 10 cm depth records, one at the lowest night temperature and one at the highest temperature on the second day. The third was at the temperature half way between the highest first day record and the lowest night temperature and the fourth was half way between the latter point and the highest second day temperature. The difference between the estimated and the recorded temperatures were calculated and the k value that gave the lowest difference was considered to be the value for that particular soil.

Relative Humidity

This was continuously recorded on Cassella thermo hygrographs placed on the ground, one at each site. (plate 1). The hairs sensitive to humidity were between 7 and 10 cm above the ground so that the recording is an approximate mean for this layer of air. The machines were first calibrated under the same conditions when they recorded a maximum difference of 1.5%.

Light

This was recorded for all sites once an hour using a Weston Master exposure meter with an integrating 'cone' attached.

Wind

General air movement was measured linearly by a 12.7 cm cup anemometer placed on a stand 1.73 metres above the ground between the sites. The kilometres of wind were recorded every hour. Additionally for experiments 1a and 2 small anemometers with 2.1 cm diameter cups were placed 14.4 cm above ground level at each stand.

Precipitation

A small rain gauge consisting of 4 cm diameter funnel and collecting bottle was set up at each site. See photo 5-1.

Data from Valley Meteorological Station

The Meteorological Office at Valley is a 'Key Climatological Station' and the instrumentation is of the standard required for that status.

The weather was clear and sunny with high pressure areas centred over Southern England during each period of study. Experiment 1a was carried out on the 5th and 6th September 1971, Experiment 1b on the 22nd and 23rd February 1971 and Experiment 2 on the 7th and 8th July 1971.

RESULTS AND DISCUSSION

Comment on soil surface temperature measurements

The position of the surface thermometers was protected from direct radiation from the sun, but had the disadvantages that adjacent soil was not heated to the same extent as exposed soil, and radiation from the adjacent soil at night was restricted. Measured surface temperatures were, therefore, lower than true surface temperature during the day and may have been higher at night. The problems associated with measurement of the soil surface temperature are discussed by Munn (1966), Harrell & Richardson (1960) and Monteith & Szeicz (1962).

The effect of a path on microclimate

Experiment 1a

The soil strength readings and bulk densities, Table 5-2, showed differences between the wet and dry areas but the displacement of the track measurements from those of the adjacent undisturbed vegetation was similar in both cases. Thus, the assumption of similar wear at both positions appears to be justified. The differences in soil moisture are shown in Table 5-2. At 10 cm depth the wet sites have approximately three times the amount of soil moisture found in the dry soils. The presentation of the results follows those of Geiger

TABLE 5-2. EXPERIMENT 1a.

SOIL STRENGTH, BULK DENSITY AND WATER CONTENT

Soil Strength Log Penetrometer Impacts

	Site Numbers			
	I	II	III	IV
Depth cm 6	1.43	0.76	1.25	0.25
12	1.83	1.33	1.64	0.84
18	2.07	1.55	1.90	0.93
24	2.14	1.60	1.97	1.27
30	2.15	1.68	1.89	1.06

Soil Bulk Density $g.cm^{-3}$

Depth cm 6	1.21	0.82	1.41	0.99

Soil Water Content % Weight

Depth cm 10	15.7	19.4	5.9	4.9
20	14.7	14.8	5.1	3.7
30	14.3	11.7	6.2	6.1

N.B. The techniques used for estimating these parameter were described in Paper 1.

(1950) and Lowry (1967) (e.g. Fig.5-1). The vertical axis represents the height of the thermometer above or below ground and time is plotted on the horizontal axis. Thus a steep heat gradient at a particular level will be represented by closely spaced horizontal isotherms, e.g. just below ground level in Fig.5-1. A rapid change in time is represented by closely spaced vertical isotherms such as those occurring above ground after sunrise, on September 6th at 6.00 to 7.00 hours (Fig.5-1). The isotherms for air and soil temperatures are connected for ease of reading only: this is not meant to imply accuracy of the recorded surface temperatures.

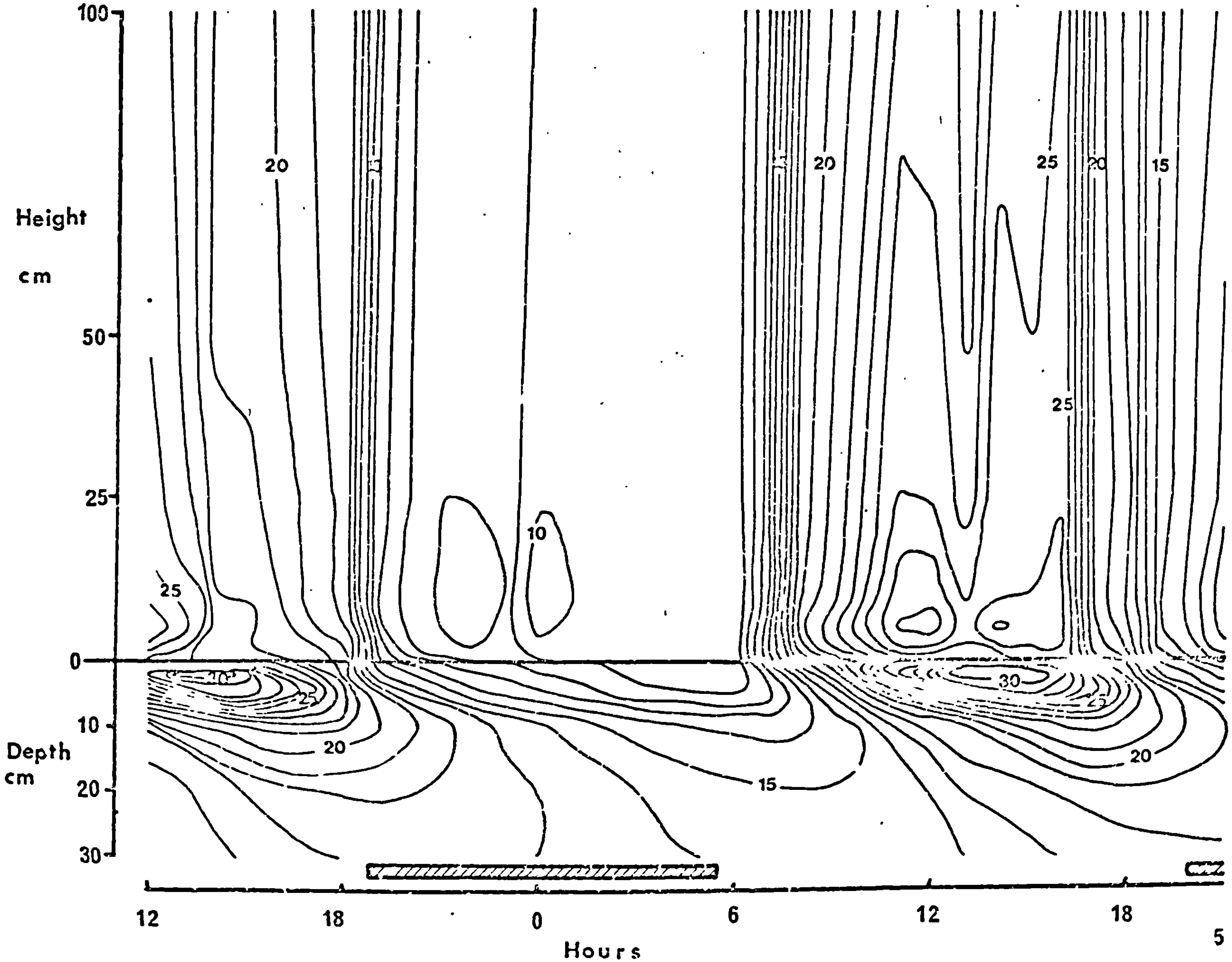
The main fact that became clear from this experiment is that the temperatures on the track are more extreme than in the adjacent vegetation. A comparison of the dry stands III and IV at 2 cm depth shows that the path was up to 12.4°C warmer during the day and 2.6°C cooler at night than the adjacent vegetation (Table 5-3). The mean temperatures for the three hours 1200 to 1500 hours and 2400 to 0300 hours illustrate these points and are presented in Fig.5-2. The differences were not so extreme in the wet area during the day (5.5°C) but only slightly less at night (1.5°C). The general relationship between path and vegetation air temperatures were similar to those found by

Fig.5-1

Experiment 1a. Stand III. Dry track temperatures.

Temperature changes in time are shown on the horizontal axis and with height above ground and depth below ground on the vertical axis. The ground level is shown by the horizontal line. The temperature is shown by isotherms for every degree C boundary except where they are very close together.

The period of darkness is indicated by the hatched line below the main diagram.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Hours

5 - 1

TABLE 5-3. EXPERIMENT 1a

SELECTED MAXIMUM AND MINIMUM SOIL TEMPERATURES, RELATIVE HUMIDITIES AND MAXIMUM WIND SPEEDS

N.B. The extreme measurements given here did not necessarily occur on all stands at the same time.

	Stand I	Stand II	Stand III	Stand IV	Site Position 1.73 m high	Valley Meteorological Station
Soil temperature at 2 cm depth						
Max.1200-1800	23.4	17.9	30.4	18.0	-	20.0*
Min.1800-0600	13.0	14.5	10.4	13.0	-	11.8*
Max.0600-1800	23.7	18.4	30.4	19.5	-	22.4*
Relative humidity %						
Min.1200-1800	54	56	49	54	-	61
Max.1800-0600	100	100	100	100	-	91
Min.0600-1800	43	47	43	43	-	62
Wind speed km/hr						
Max.1200-1800	2.6	0.5	3.1	0.0	7.3	11.1
Max.1800-0600	0.8	0.0	0.2	0.0	3.1	18.5
Max.0600-1800	5.0	0.8	3.8	0.1	12.3	20.4

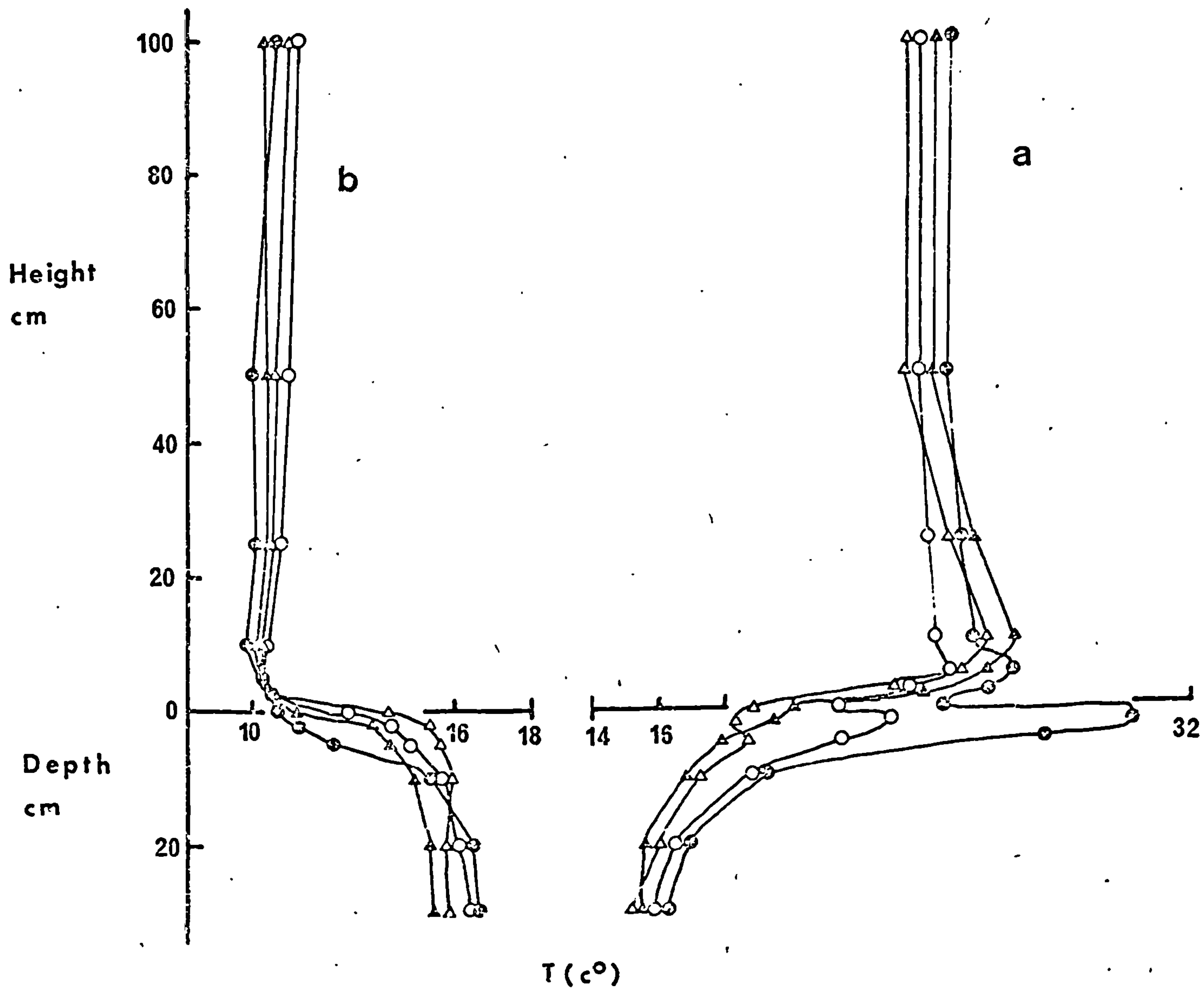
* Air temperature

Fig.5-2

Experiment 1a. Mean midday (1200 - 1500 hr) and midnight (0000 - 0300 hr) temperatures for all stands. Note the broken horizontal axis.

○	Stand I	Wet path
△	Stand II	Wet vegetation
●	Stand III	Dry path
▲	Stand IV	Dry vegetation

The effect of compaction can be seen by comparison of circles with triangles and of soil water by comparison of outline with solid figures.



5 - 2

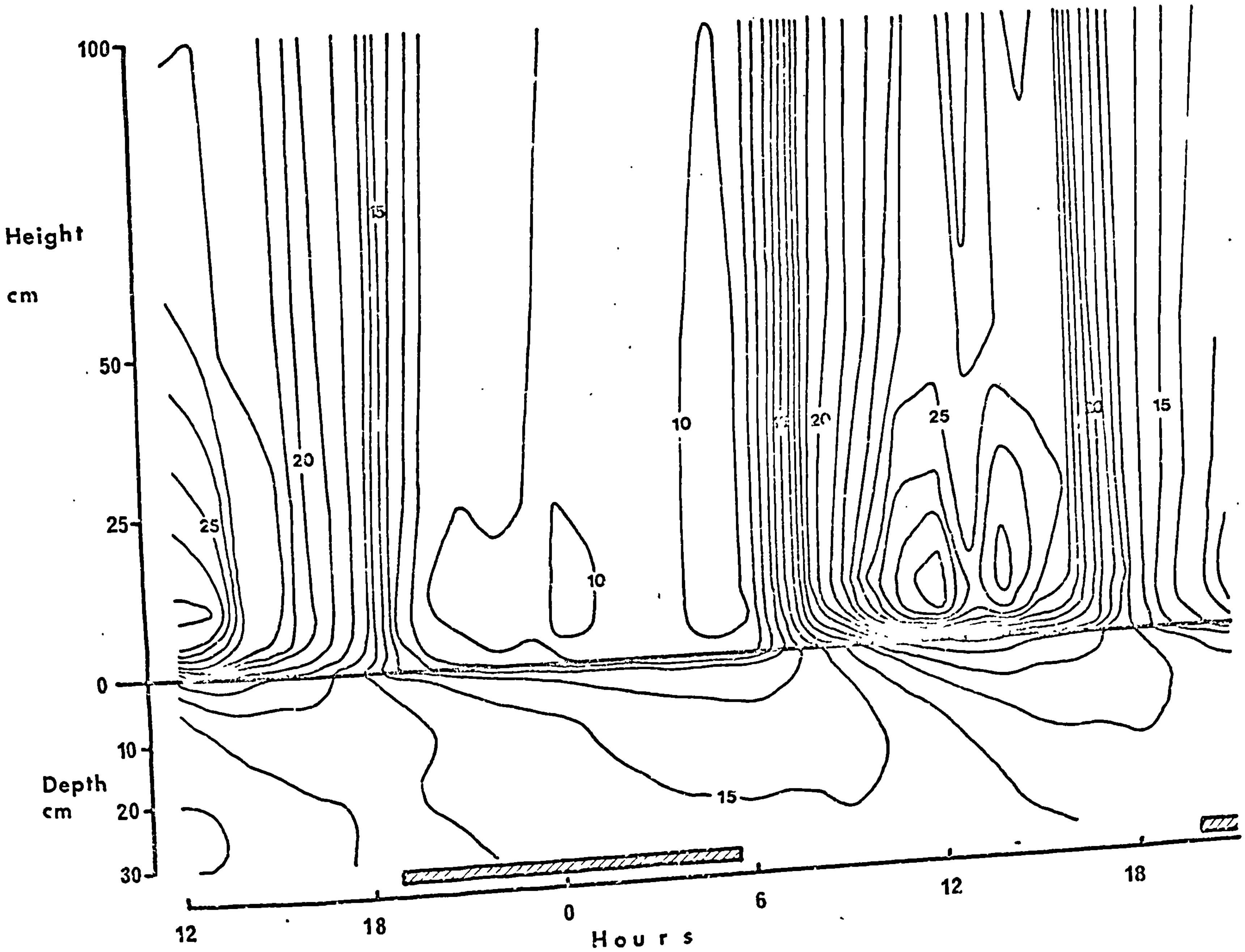
Kockenhauer (1934) between concrete and turf.

In the vegetation the main temperature gradient occurred above ground level, whereas it was below the soil surface on the path (Fig.5-1, stand III and Fig.5-3, stand IV). The differences between these two stands is shown in Fig.5-4. Wijk (1965) comments that the presence of dense vegetation shifts the effective 'soil' surface upwards and the upward displacement of the maximum temperature at stand IV conforms with his observation; these results are also similar to the temperature profiles in different vegetation densities measured by Barkley-Estrup (1971). One consequence of this displacement is that during the warmest part of the day the air above the path may be cooler than that in the vegetation; this is shown as a hatched area in Fig.5-4. However, after 1600 hours the relationship is reversed; a similar change was recorded by Boerboom (1964) in a dune wood.

The greater soil moisture at site I on the wet path (Table 5-2) had a considerable damping effect on the daily temperature range in the upper layers of soil when compared with the dry path, e.g. a reduction of 7^{o} at 2 cm depth, see Fig.5-5 and Table 5-3. The linear flow of wind at the path stands was up to 3 k.p.h. greater than that found in the vegetation and during

Fig.5-3

Experiment 1a. Stand IV. Dry natural vegetation.
The presentation is the same as in Fig.5-1.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12
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Hours

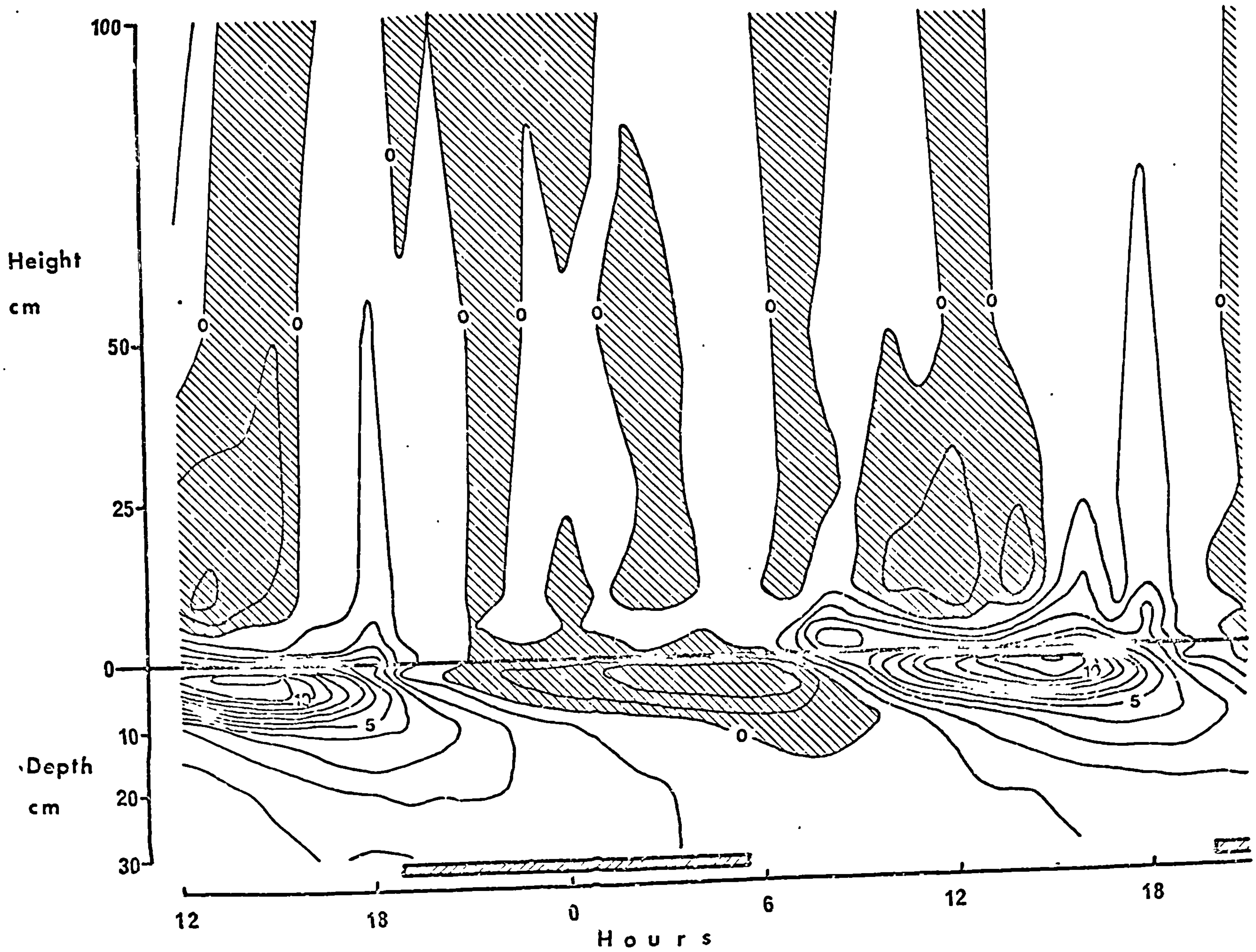
5 – 3

Fig.5-4

Experiment 1a. The difference between stands III and IV showing the effects on soil and air temperatures of a path in a dry area.

The presentation is the same as that in Fig.5-1 but the data presented are derived by subtracting the temperature of stand IV (dry vegetation) from that of stand III (dry path).

The hatched areas indicate times and heights where the path was colder than the vegetation.



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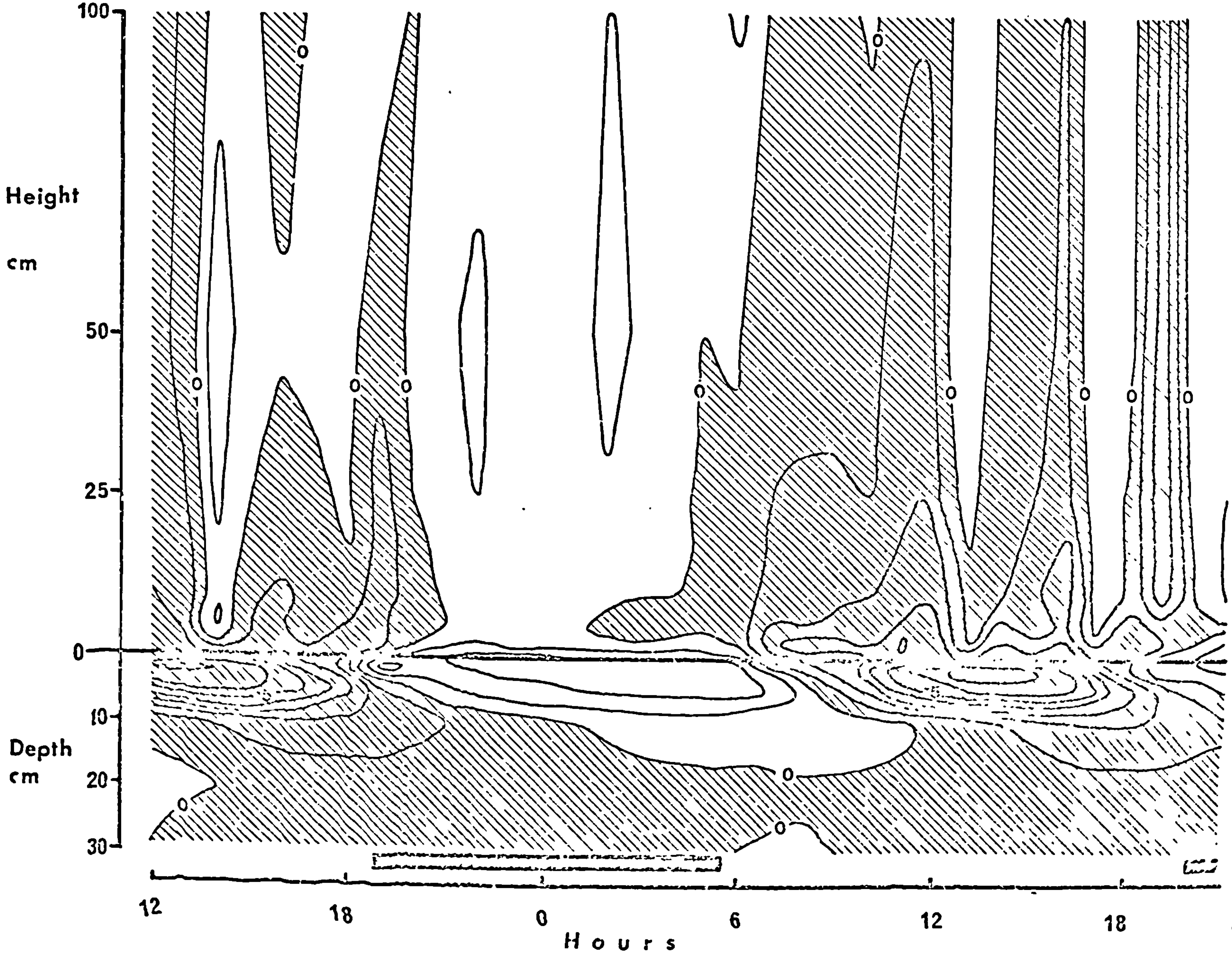

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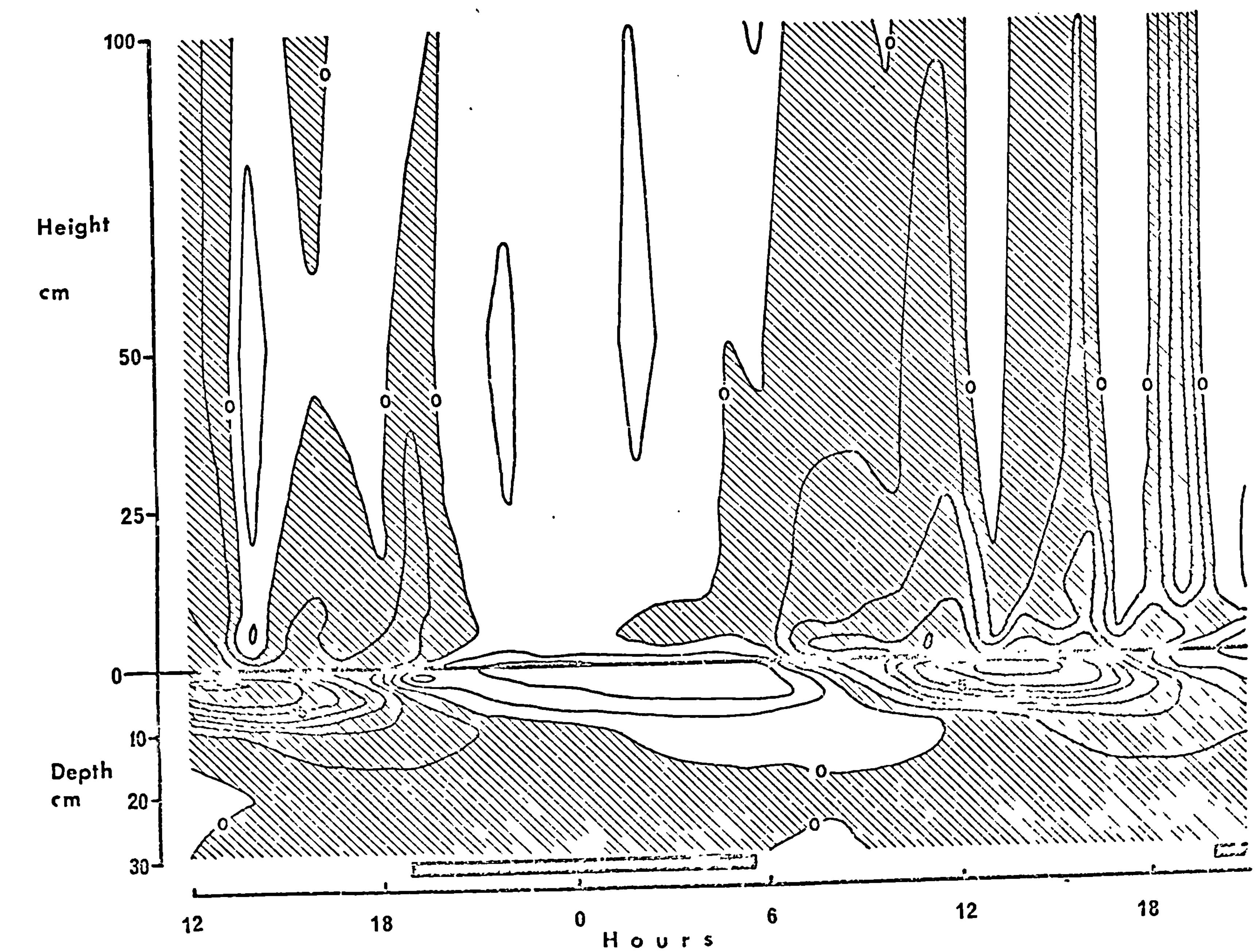


5 – 5

the periods of high incident radiation this could lower the air temperature at those sites (Table 5-3). Correspondingly, the lack of air movement in the vegetation may have been responsible for the greater development of the midday high temperature 'islands' between 5 and 20 cm above ground. The reduction of soil temperature range by vegetation has been shown by many workers, e.g. Wijk (1965) but the difference recorded here is probably extreme for this temperate environment, although not for the sand dune situation. The principal factor which caused this difference was the greater warming of the path surface by short wave radiation from the sun.

The thermal properties of the soils for all the experiments are given in Table 5-4. The estimated thermal diffusivities (k) for this experiment range from 0.025 ~~cal.deg.~~$^{\cancel{-1}}$cm.$^{2\,\cancel{-1}}$sec.$^{-1}$ to 0.0048 ~~cal.deg.~~$^{\cancel{-1}}$ cm.$^{2\,\cancel{-1}}$sec.$^{-1}$, all rather higher than the 0.004 ~~cal.deg.~~$^{\cancel{-1}}$ cm.$^{2\,\cancel{-1}}$sec.$^{-1}$ given by Lowry (1969) for wet sand but within a reasonable range. The estimates of thermal capacity (ρc) are similar to the range 0.31 to 0.35 cal.deg.$^{-1}$cm.$^{-1}$ calculated by Stoutjesdijke (1961) for dune sands. But the relationship between the maximum temperature and depth is not a linear one and this suggests that the thermal diffusivity varied down the soil profile so the estimates should be treated with caution. However, the

TABLE 5-4

THERMAL PROPERTIES OF SOILS

	ρc cal. deg.$^{-1}$ cm^{-1}	k cm.^{2} sec^{-1}	λ cal. deg.$^{-1}$ cm.$^{-1}$ sec^{-1}
Experiment 1a Summer			
Wet path Site I	0.4389	0.0077	0.0034
Wet vegetation Site II	0.3279	0.025	0.0082
Dry path Site III	0.3588	0.0048	0.0017
Dry vegetation Site IV	0.2455	0.0059	0.0015
Experiment 1b Winter			
Dry path Site I	-	0.1	-
Dry vegetation Site II	-	0.0064	-
Experiment 2 Summer			
Dry path Site I	0.3059	0.0036	0.0011
Dry vegetation Site II	0.2524	0.0033	0.0008
Cut dry vegetation Site III	0.2579	0.0031	0.0008

The thermal capacity (ρc) of the soil was calculated from bulk density and water content records, the thermal diffusivity (k) was estimated from soil temperature records and the thermal conductivity was calculated from ρc and k.

level of accuracy appears adequate for the purpose of making general statements about these soils.

The most obvious and expected effect associated with path creation was the increase in thermal capacity (ρc) of the compacted soils which was raised by about 30% (see Table 5-5). The thermal diffusivity was, however, reduced by compaction especially in the wet soils where conductivity was also reduced, but it was slightly increased at the dry sites. Since the value of k and the soil water content decreased as the consequence of compaction in the wet area, the 15% level of soil moisture appears to be towards the peak of thermal conductivity.

The effect of higher soil water content on both the paths and the vegetated stands was to raise the level of all the thermal constants (especially in the presence of plants) and to lower the maximum soil temperatures by 6.7°C and 1.1°C respectively. This was the consequence of the heat energy being dispersed more quickly through the wet soil and also the absorption of a greater amount of energy with less rise in actual temperature, thus ameliorating the extreme conditions found on paths.

The relative humidity was similar at all sites ranging from 49% to 56% on the first day, 100% at night

TABLE 5-5

THE DIFFERENCES BETWEEN THE THERMAL PROPERTIES OF VARIOUS SOILS CALCULATED TO SHOW THE EFFECTS OF SOME ENVIRONMENTAL FACTORS

Environmental Factors	pc cal.deg.$^{-1}$ cm^{-1}	k cm.^{2} sec^{-1}	λ cal.deg.$^{-1}$ cm.$^{-1}$ sec^{-1}
Experiment 1a			
Path effect in wet area			
Stand I minus stand II	+0.1110	-0.0173	-0.0048
Path effect in dry area			
Stand III minus stand IV	+0.1133	-0.0011	+0.0002
The effect of increased water content			
Path: stand I minus stand III	+0.0801	+0.0029	+0.0017
Natural vegetation: stand II minus stand IV	+0.0824	+0.0191	+0.0067
Experiment 2			
Dry path effect			
Stand I minus stand II	+0.0535	+0.0003	+0.0003
Effect of vegetation removal			
Stand III minus stand II	+0.0055	-0.0002	0
Effect of compaction of soil			
Stand I minus stand III	+0.048	+0.0005	+0.0003

and 43% to 47% on the second day. The wet areas, however, lagged approximately two hours behind the dry ones during the morning fall on the second day and stand II was one hour behind stand I in the early part of that fall.

The light readings were the same in the exposed portions of all sites.

No wind movement over 0.1 $km.hr^{-1}$ was recorded near the ground at stand IV and a maximum of only 0.8 $km.hr^{-1}$ was reached at stand II. Both path stands experienced over 2.5 $km.hr^{-1}$ on the first day and 3.8 $km.hr^{-1}$ on the second. The anemometer at 1.7 m height mid-way between the sites reached 7.3 $km.hr^{-1}$ on the first day and up to 12.3 $km.hr^{-1}$ on the second day. There was no air movement over 0.8 $km.hr^{-1}$ at ground level during the night. Sea breeze effects were noted at Valley on both days.

No measurable precipitation occurred during the time of the experiment.

Experiment 1b

This experiment was similar to the previous one, but only carried out in a dry area and during the winter (February 1971).

The diurnal variation of temperature was much less than that found during the summer but the path again showed greater extremes, Fig.5-6 and Table 5-6. One notable difference was that the deep path temperature at 30 om was lower than that under natural vegetation, whereas it was higher in summer.

The estimates of thermal diffusivity of the two stands are given in Table 5-4. That of the path stand is extremely high, partly a result of the method of estimation, but there is no doubt that it was much higher than the vegetated stand II. Unfortunately, the soil water content was not recorded so the other parameters cannot be calculated.

The relative humidity was about 64% over the path and 70% in the vegetation during the first day and 88% to 93% at night. The vegetated stand was up to 6% above the path except for the first four hours when the difference was 8% and for two hours after noon on the second day when the path stand was 3% higher than the vegetated one.

Wind speed was between 9 and 18 km.hr^{-1} from the S-SW throughout the experiment.

<u>A study of the relative effects of vegetation removal and soil compaction on the microclimate</u>

<u>Experiment 2</u>

Three stands were placed at the same site as that used for Experiment 1b, stand I was on the track

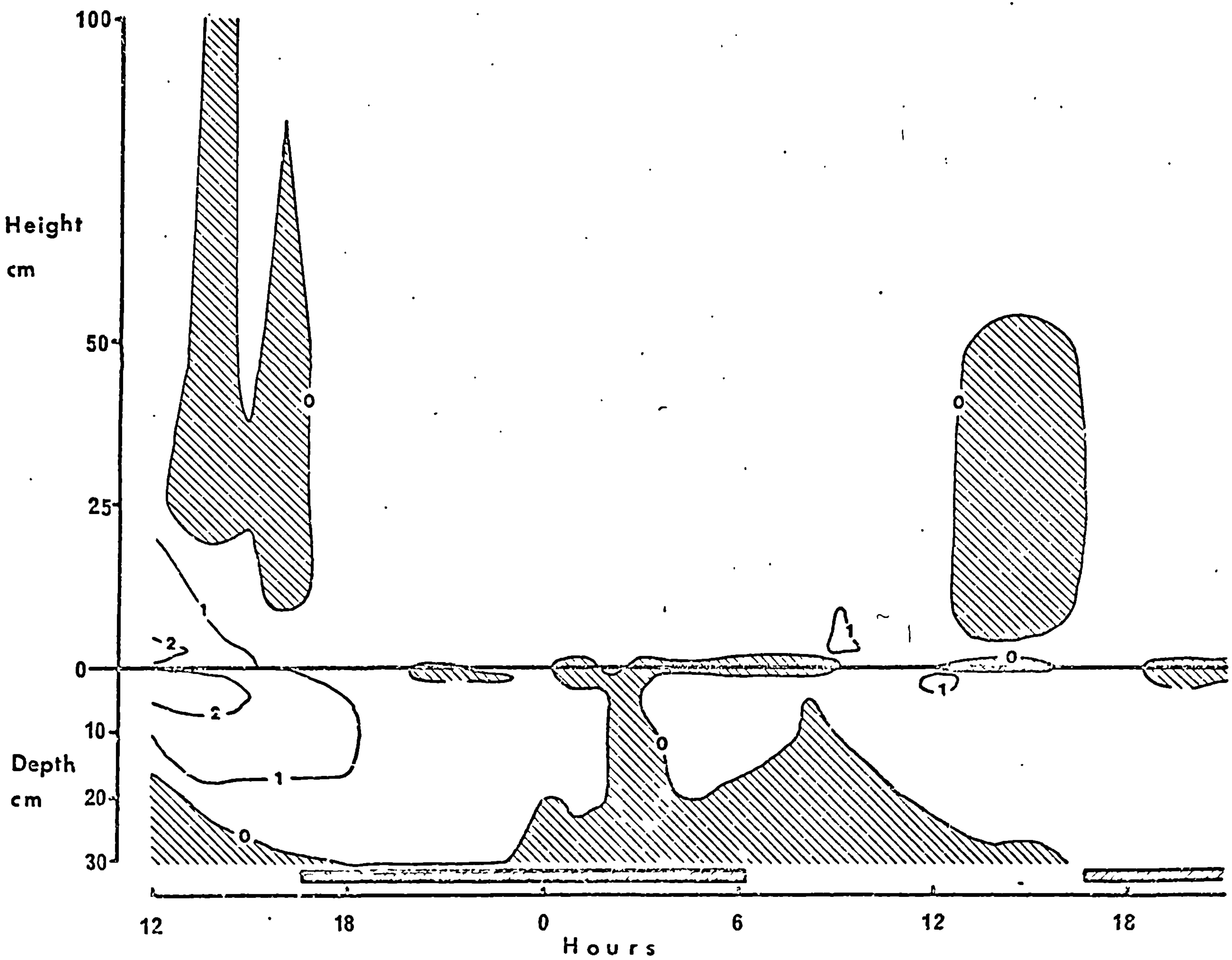
Fig.5-6

Experiment 1b. The difference between stands I and II showing the effects on soil and air temperatures of a path in a dry area during the winter.

The presentation is the same as in Fig.5-4.

The hatched areas indicate times and heights when the path was cooler than the vegetation.

Note the colder deep soil temperatures compared with the summer situation in Fig.5-4.



5 – 6

TABLE 5-6. EXPERIMENT 1b

SELECTED MAXIMUM AND MINIMUM SOIL TEMPERATURES, RELATIVE HUMIDITIES AND MAXIMUM WIND SPEEDS

N.B. The extreme measurements given here did not necessarily occur at all stands at the same time.

	Stand I	Stand II	Site position 1.73 m high	Valley Meteorological Station
Soil temperature at 2 cm depth				
Max. 1200-1800	8.0	6.1	-	8.6
Min. 1800-0600	5.0	5.2	-	6.1
Max. 0600-1800	8.4	7.5	-	8.8
Relative humidity %				
Min. 1200-1800	64	70	-	84.2
Max. 1800-0600	88	93	-	94.0
Min. 0600-1800	60	61	-	74.1
Wind speed km/hr				
Max. 1200-1800	-	-	12.4	26
Max. 1800-0600	-	-	16.1	37.1
Max. 0600-1800	-	-	17.7	37.1

showing the combined effects of vegetation removal and soil compression, stand II was in tall vegetation (photo 5-4) and stand III was in an adjacent area cleared of vegetation. A comparison of the results from stands I and III show the effect of soil compaction alone and a comparison of stands II and III demonstrates the effect of vegetation removal. The soil characteristics for this experiment are given in Table 5-7. Stands II and III are similar while I is more penetration resistant and has a higher bulk density and water content.

The effect of soil compaction was to lower the day time soil temperature by a maximum of 7°C and to raise it slightly at night (Fig.5-7). The day time air temperatures over the compacted soil were also generally cooler. This result was anticipated by Willis & Raney (1971) when they stated that a surfaco layer with a loose crumb structure, lighter texture and low water content will exhibit a greater amplitude in the daily temperature wave. The soil thermal characteristics are similar to the physical ones, Table 5-4, the path soil having a higher thermal diffusivity, capacity and conductivity than the other two stands (Table 5-5). These differences are then a summary of the effects of soil compaction which tended to ameliorate the conditions

TABLE 5-7. EXPERIMENT 2.

SOIL STRENGTH, BULK DENSITY AND WATER CONTENT

Soil Strength Log Penetrometer Impacts

		Site Numbers		
		I	II	III
Depth in cm	6	1.32	1.75	0.29
	12	1.86	0.46	0.64
	18	2.11	0.72	0.8
	24	2.28	0.74	0.84
	30	2.11	0.94	0.97

Soil Bulk Density $g.cm^{-3}$

To 6 cm depth	1.39	1.15	1.25

Soil Water Content % Weight

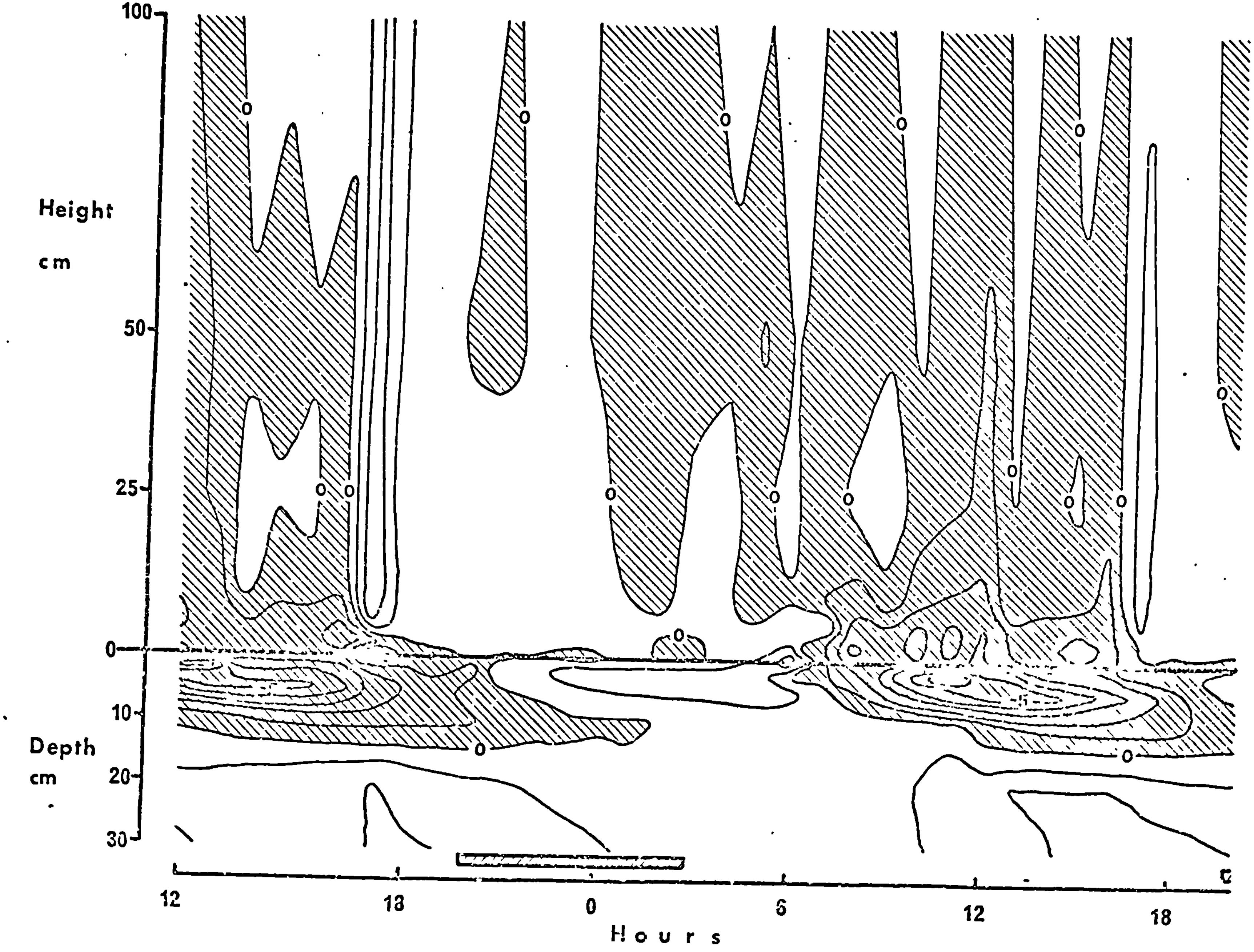
Depth in cm	0	0.2	0.9	0.2
	2	2.0	1.7	0.4
	5	3.3	1.2	0.5
	10	4.0	1.2	0.6
	20	4.4	1.5	1.0
	30	4.4	4.4	4.0

N.B. The techniques for estimating these parameters were described in Paper 1.

Fig.5-7

Experiment 2. The difference between stands I and III showing the effect on soil and air temperatures of soil compaction alone. The presentation is the same as in Fig.5-4.

The hatched areas indicate times and heights when the compressed soil was colder than the uncompressed soil.



5 – 7

found on bare soil away from the path.

The effect of vegetation removal alone was a great increase of up to 14°C in the soil temperatures during the day and a slight drop at night. The air temperatures were, however, generally cooler above a height of 5 cm. This can be seen from a comparison of stands II and III, Fig.5-8. The difference caused by vegetation removal was probably due to a greater absorption of the sun's radiation by the bare soil and a greater heat loss by long wave radiation from the soil at night. The displacement of the steep gradient from the soil to the air by the vegetation was again evident. The estimated heat diffusivity and specific heats of both sites were virtually the same (Table 5-5) so the thermal properties of the soil contribute very little to the observed differences.

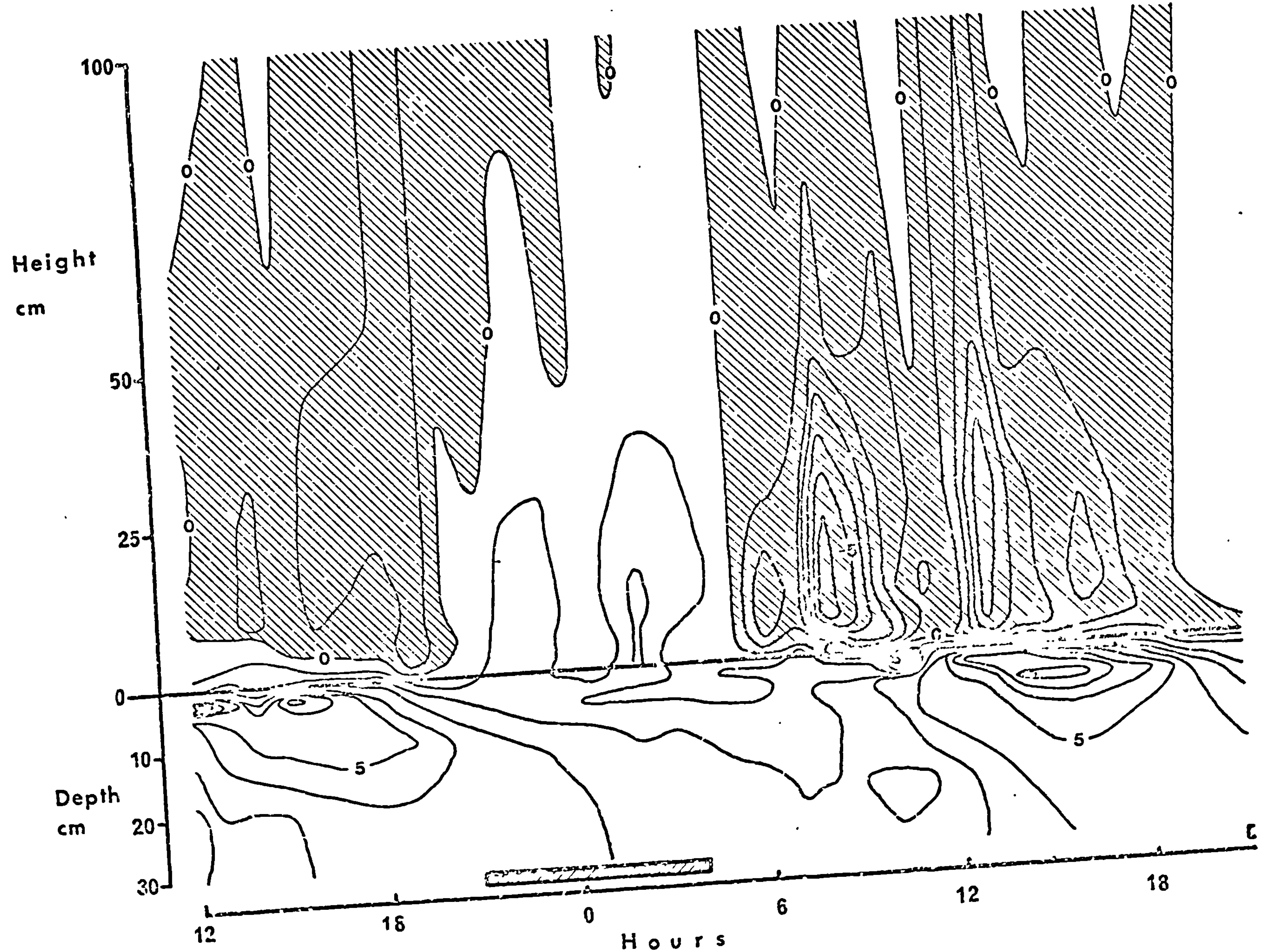
The combined effect of these two changes (Fig.5-8) was to raise the path soil temperature throughout the period; by up to 9°C during the day and 1°C at night. The air temperature over the path was up to 6°C colder than that over the long vegetation during the day and 2°C warmer at night.

The minimum relative humidity ranged from 34% to 47% on the first day, and the maximum from 91% to 100% at night; the following day the minimum was from 38%

Fig.5-8

Experiment 2. The difference between stands I and II showing the effect on soil and air temperatures of vegetation removal and soil compaction, i.e. of a path. The presentation is the same as in Fig.5-4.

The hatched areas indicate times and heights when the path was colder than the vegetation.

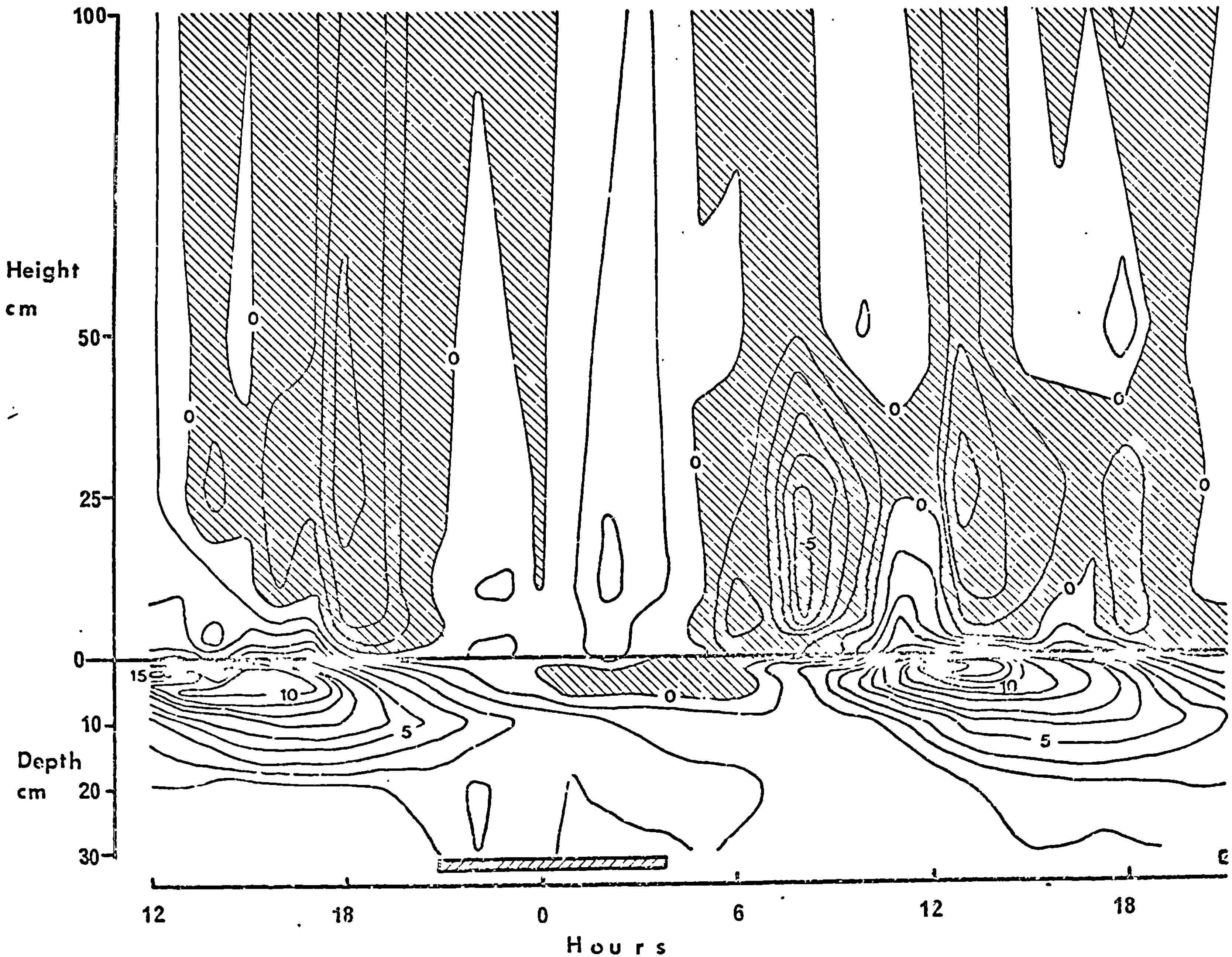


5 - 8

Fig.5-9

Experiment 2. The difference between stands III and II showing the effect on soil and air temperatures of vegetation removal alone. The presentation is the same as in Fig.5-4.

The hatched areas indicate times and heights when the site without vegetation was colder than the site with vegetation.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5 - 9

to 41% (Table 5-8). The vegetated stand II was generally about 4% lower than stands I and III during the day and about 14% higher at night. There was no cloud throughout the experimental period and no measurable precipitation.

The wind speed near the ground was between 2 and 5 $km.hr^{-1}$ at stands I and III during the daytime while it was never above 1.1 $km.hr^{-1}$ at stand II. There was no wind recorded near the ground at night. The data from Valley indicated a sea breeze effect occurred on both days.

<u>Morphology of *Festuca rubra* from stands I to IV. Experiment 1a.</u>

The morphology of 20 specimens of *Festuca rubra* taken from each stand in Experiment 1a was investigated; the results are given in Fig.5-10. (There was no *Festuca* right in the wet sites but the samples were gathered from the nearest possible points). The path examples all had shorter tillers and leaves, and reduced dry weight per plant and per tiller, Figs.5-10b, f, g and i. There were also increases in the proportion of dead material, Fig.5-10h; and in the percentage of dead tillers on the plants from the dry path stand, Fig.5-10c. There was an increase in the number of tillers and the number of live leaves per plant from the wet path stand, Figs.5-10a and d. Most of these changes could be anticipated

TABLE 5-8. EXPERIMENT 2

SELECTED MAXIMUM AND MINIMUM SOIL TEMPERATURES, RELATIVE HUMIDITIES AND MAXIMUM WIND SPEEDS

N.B. The extreme measurements given here did not necessarily occur on all stands at the same time.

	Stand I	Stand II	Stand III	Site Position 1.73 m high	Valley Meteorological Station
Soil temperature at 2 cm depth					
Max. 1200-1800	34.2	29.9	39.0	-	25.0*
Min. 1800-0600	15.9	15.0	14.4	-	15.6*
Max. 0600-1800	34.7	29.3	41.5	-	25.5*
Relative humidity %					
Min. 1200-1800	47	43	34	-	47
Max. 1800-0600	91	91	100	-	91
Min. 0600-1800	41	41	38	-	57
Wind speed km/hr					
Max. 1200-1800	5.4	1.1	4.1	8.7	16.6
Max. 1800-0600	0.2	0.0	0.0	3.2	11.1
Max. 0600-1800	4.7	1.0	4.5	8.7	18.5

* Air temperature

Fig.5-10

Festuca rubra. Morphology of samples taken from a 10 cm square quadrat near stands I and II and at stands III and IV, Experiment 1a.

a) tillers per plant

b) mean live tiller length

c) percentage of dead tillers

d) live leaves per plant

e) live leaves per tiller

f) mean length of live leaves cm

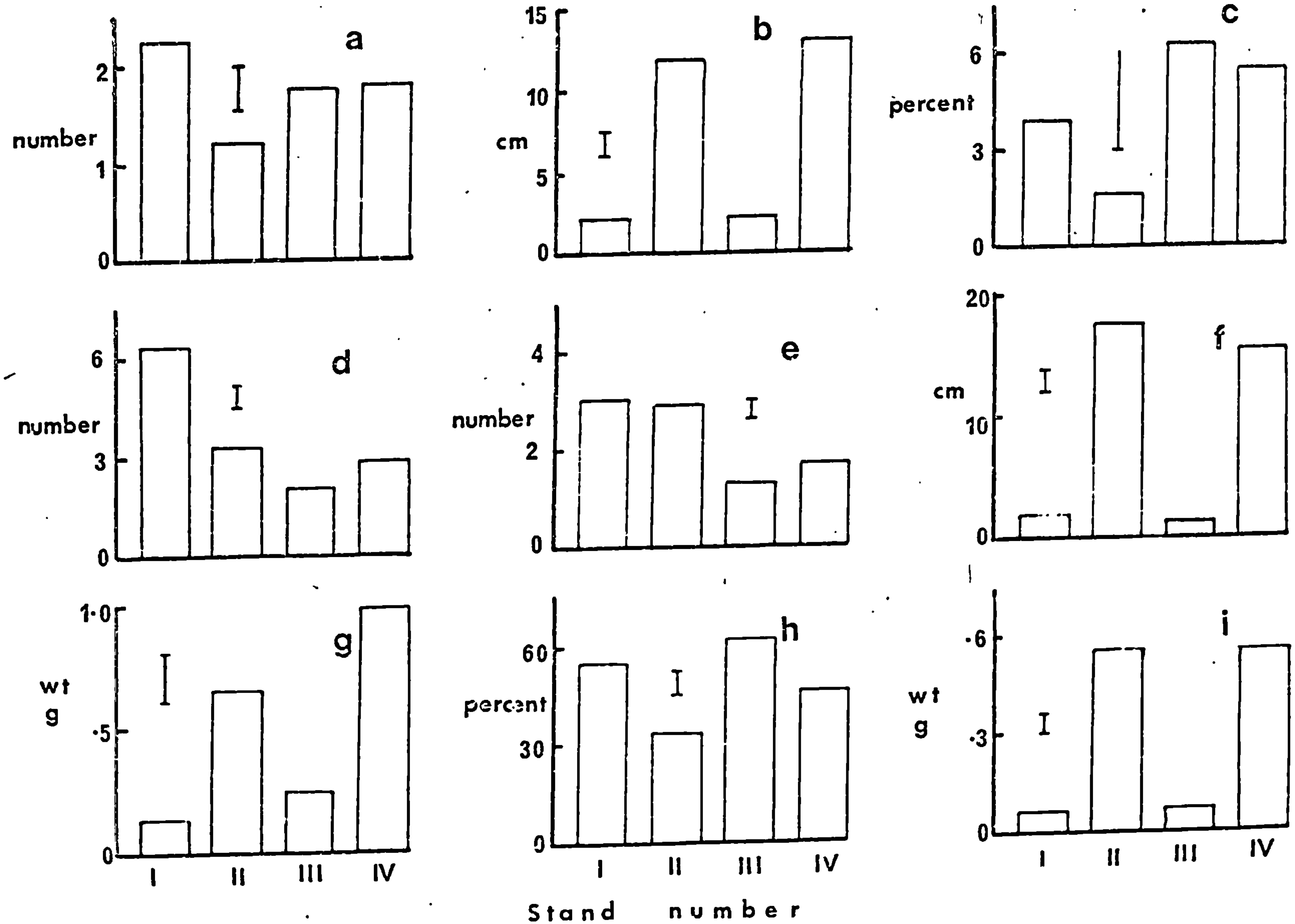
g) dry weight per plant g

h) percentage of dead material g

i) dry weight per tiller g

b), f), g) and i) all show obvious changes due to path effects. a),c), d) and e) tend to show soil water effects.

I 2 SE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g
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30
60
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·3
·6
I
II
III
IV
Stand number

5 – 10

but the marked increase in tiller and live leaf number on plants from near stand I were unexpected. Paper 1 also gave data on the increase in tiller number as a result of both shoot damage and soil compaction, so damage may have stimulated this response but it could have been inhibited at stand III because of limited water supply and possibly the more extreme thermal environment. The only parameter that responded to soil water alone was the higher number of live leaves per tiller.

GENERAL DISCUSSION

The effect of path creation was to extend the soil temperature range and to increase slightly the range in the air above the path, see Experiments 1a and 1b. The soil increase in range was only 3°C in winter but could be as much as 15°C in summer. The thermal characteristics of the soils were only slightly altered by compression in the dry areas in the summer, but in the wet area the diffusivity was markedly decreased. There was, however, an increase in diffusivity in the 'dry' area in the winter. This suggested that in dry sand dune pasture the major change was caused by the removal of the vegetation above ground.

The results of Experiment 2 also show that the process of vegetation removal has a greater influence than soil compression on the path microclimate under conditions of high incident radiation pertaining at the time of this experiment. There is evidence from this experiment that the soil compression operates in the opposite 'direction' to the effects of vegetation removal, i.e. it tends to reduce the soil temperature range.

The presence of high levels of soil moisture reduced the temperature ranges on paths and in the taller vegetation. As pointed out in Willis & Raney

(1971) compaction affects the heat content and transmission in soil by changing soil density, soil water relations and plant growth. The increase in density increases thermal conductivity unless water is replaced by a material of lower conductivity such as organic material. In the dry areas measured in the summer there was a small increase in conductivity but in the wet area the estimated path conductivity was lower than under the adjacent undisturbed vegetation and this suggested that there may have been a high organic content with low conductivity at the wet stands. Thermal diffusivity was only slightly affected by compaction in the dry areas but showed a marked decrease in the wet areas.

Sprague (1943) found that Festuca rubra would germinate at alternating temperatures of 31° - 40°C. whereas Poa pratensis did not germinate above 22° - 31°C. This difference may explain why Festuca occurs on sites with a mean of 11% water content whereas Poa sites had a mean of 15% and, therefore, have lower maximum temperatures. (See Paper 1).

The general effect of a path was to create a more continental climate than that of the tall vegetation but the areas of bare sand have even more extreme conditions than those found on the path. This indicates that primary colonisers may have a continental distribution, being specially adapted to withstand these conditions or they may avoid them as in the case of the winter annuals. The species found on the paths may be expected to have a wide continental distribution and the data on the most common species found at Aberffraw (Appendix 2) shows that this is correct.

This work suggests that the choice of species to sow for the regeneration of dune paths should be restricted to heat resistant species such as *Festuca rubra* and the more conventional *Poas* and *Lolium* be avoided. It would also be wise to sow early in the spring so that the seedlings can become well established before they are exposed to the high temperatures that can occur on the drier paths. It should also be noted that the application of nitrogenous fertilisers can lower the cold resistance of *Poa pratensis* (Carroll & Welton 1938) so they should also be used with care.

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```
HH1:=HH2;
HH2:=HH3;
HH3:=A[X+4];
"END"
"END";
"FOR" X:=2 "STEP" 1 "UNTIL" 30 "DO"
T[X,TIM]:=A[X];
"END";
"PRINT" ''L3'';
"PRINT" ALIGNED(1,4),''L'K IS  ',K,'    CM↑2 SEC↑-1';
"PRINT" ''L'';
"PRINT" ''L' TEMPERATURE PROFILES AT 2 5  10  20  AND 30';
ALIGNED(2,1);
"PRINT" ''L'';
"FOR" TIM:=1 "STEP" 1 "UNTILL" 16 "DO" "PRINT"
T[2,TIM];
"PRINT" ''L'';
"FOR" TIM:=1 "STEP" 1 "UNTILL" 16 "DO" "PRINT" T[5,TIM];
"PRINT" ''L'';
"FOR" TIM:=1 "STEP" 1 "UNTILL" 16 "DO" "PRINT" T[10,TIM];
"PRINT" ''L'';
"FOR" TIM:=1 "STEP" 1 "UNTILL" 16 "DO" "PRINT" T[20,TIM];
"PRINT" ''L'';
"FOR" TIM:=1 "STEP" 1 "UNTILL" 16 "DO" "PRINT" T[30,TIM];
"PRINT" ''L2'';
"FOR" TIM:=17 "STEP" 1 "UNTILL" 34 "DO" "PRINT" T[2,TIM];
"PRINT" ''L'';
"FOR" TIM:=17 "STEP" 1 "UNTILL" 34 "DO" "PRINT" T[5,TIM];
"PRINT" ''L'';
"FOR" TIM:=17 "STEP" 1 "UNTIL" 34 "DO" "PRINT" T[10,TIM];
"PRINT" ''L'';
"FOR" TIM:=17 "STEP" 1 "UNTILL" 34 "DO" "PRINT" T[20,TIM];
"PRINT" ''L'';
"FOR" TIM:=17 "STEP" 1 "UNTILL" 34 "DO" "PRINT" T[30,TIM];
"GOTO" L;
LEND: "END" PROGRAM;
```

'TEMP' PRINT OUT

```
K IS   0.0055    CM↑2 SEC↑-1

TEMPERATURE PROFILES AT 2 5  10  20  AND 30
17.5 18.0 18.0 17.6 17.4 16.9 16.4 15.4 15.0 14.5 14.1 14.1 13.8 13.6 13.5 13.1
16.1 17.0 17.3 17.2 17.1 16.9 16.5 16.0 15.5 15.1 14.7 14.6 14.4 14.1 14.0 13.7
15.5 15.9 16.3 16.5 16.5 16.5 16.4 16.3 16.0 15.7 15.5 15.2 15.1 14.9 14.7 14.5
15.0 15.1 15.3 15.4 15.6 15.8 16.0 16.1 16.1 16.1 16.1 15.9 15.7 15.6 15.4 15.2
15.5 15.0 15.1 15.4 15.5 15.9 16.2 16.2 16.3 16.2 15.9 15.7 15.5 15.4 15.4 15.3

13.0 13.1 13.0 13.5 14.5 15.6 16.8 18.0 19.5 19.5 19.2 18.7 18.4 18.0 17.2 16.5 15.9 15.5
13.5 13.5 13.4 13.6 14.1 14.9 15.8 16.7 17.8 18.4 18.4 18.3 18.1 17.9 17.4 16.9 16.4 16.0
14.3 14.1 14.0 14.0 14.1 14.4 14.9 15.4 16.1 16.8 17.2 17.4 17.4 17.4 17.3 17.1 16.8 16.5
15.1 15.0 14.9 14.6 14.7 14.7 14.8 14.9 15.1 15.4 15.8 16.1 16.3 16.4 16.6 16.7 16.7 16.7
15.3 15.3 15.3 15.3 15.3 15.2 15.3 15.3 15.7 15.8 15.9 15.9 16.0 16.2 16.4 16.5 16.5 16.6
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APPENDIX 2

DISTRIBUTION OF COMMON SPECIES FOUND AT ABERFFRAW

A list of the plant species common at Aberffraw according to their 'track preference index' derived in Paper 1. Their world distribution is listed in column three so that their relationship with the 'continental' track climate can be assessed.

Species	Track preference index	Distribution
Bellis perennis	10	Throughout British Is., Europe, W. Asia.
Poa pratensis	10	Throughout British Is., Europe, but only on mountains in S., temperate Asia, N. Africa, N. America, N. Zealand.
Juncus articulatus	9	Throughout British Is., S. Europe, Asia, N. Africa, eastern N. America; introduced S. Africa, Australia and N. Zealand.
Potentilla anserina	9	Throughout British Is., Europe (not Arctic) to N. Portugal, C. Spain, N. Italy, N. & C. Asia, N. Persia, W. Himalaya, Manchuria, Japan, N. America to New Jersey & N. California, S. America, Victoria, Tasmania, N. Zealand.
Brachythecium albicans	8	Throughout British Is., Europe, N. Africa, N. America and N. Zealand.
Taraxacum laevigatum	8	Lowland Britain & Ireland. Europe.
Agrostis tenuis	7	Throughout British Is., Europe, N. Asia, N. America; introduced Australia, N. Zealand, Tasmania.

Species	Track preference index	Distribution
Carex flacca	7	Throughout British Is., Europe, N. Africa, Siberia; introduced N. America, W. Indies & N. Zealand.
Festuca rubra	7	Throughout British Is., Europe, N. Africa, temperate Asia, N. America, on mountains in S.part of its range.
Galium verum	7	Throughout British Is., Europe except Russia, W. Asia.
Taraxacum officinale	7	Throughout British Is. & N. Hemisphere.
Trifolium repens	7	Throughout British Is., Europe, N. & W. Asia, N. Africa; introduced S. Africa, Atlantic Is., N. & S. America, E. Asia.
Agrostis stolonifera	6	Lowland British Is., Europe, C. Asia, Japan, N. America; introduced Australia, N.Zealand, S. Africa.
Leontodon autumnalis	6	Throughout British Is., Europe except Greece, N. & W. Asia, Africa, Greenland; introduced N. America.
Leontodon taraxacoides	6	British Is. to S. Scotland, Europe to Denmark, Gotland and C. Russia.
Thymus drucei	6	Throughout British Is., Greenland, Iceland, Faeroes, W.Norway, France, N.W. Spain.
Tortula ruraliformis	6	Throughout British Is., Europe, Asia Minor, N. Africa, N.America.

Species	Track preference index	Distribution
Anthoxanthum odoratum	5	Throughout British Is., Europe, Western N. Africa, Asia Minor, Caucasus, N. Asia only on mountains in S.; introduced N. America, Australia & Tasmania.
Camptothecium lutescens	5	Throughout British Is., Europe, Asia Minor, N. Africa, N.America.
Carex arenaria	5	Maritime British Is., coasts Europe, not Arctic. Black Sea, Siberia, N. America.
Lotus corniculatus	5	Throughout British Is., Europe to 71°N., Asia, N. & E. Africa. On mountains in tropics.
Ammophila arenaria	4	Maritime British Is. & W.Europe except Arctic.
Luzula campestris	4	Throughout British Is., S.Europe, N. Africa, N. America, Malaysia, N. Zealand, etc.
Potentilla reptans	4	Throughout British Is., S.Europe, Mediterranean region, W. Siberia, Turkistan, Persia, Himalaya; introduced N. & S. America.
Senecio jacobaea	4	Throughout British Is., Europe to 62°N, Caucasus, W. Asia, N. Africa; introduced N. America & N. Zealand.
Viola canina	4	Throughout British Is., Europe to C. Spain, Portugal, N. Italy, Macedonia, N.W. Asia Minor, C. Asia (rare).
Poa subcaerulea	3	N. British Is., N.W. Europe.

Species	Track preference index	Distribution
Prunella vulgaris	3	Throughout British Is., S. Europe, temperate Asia, N. Africa, N. America, Australia.
Viola tricolor	2	Throughout British Is., Europe from Iceland & Scandinavia to Corsica (mountains), N. Italy & Macedonia, Asia Minor, Caucasus, Siberia & Himalaya.
Linum catharticum	0	Throughout British Is., Europe, Iceland to N. Portugal, C. Spain, Corsica, C. Italy, Macedonia & Caucasus, Asia Minor, Persia.

FINAL DISCUSSION

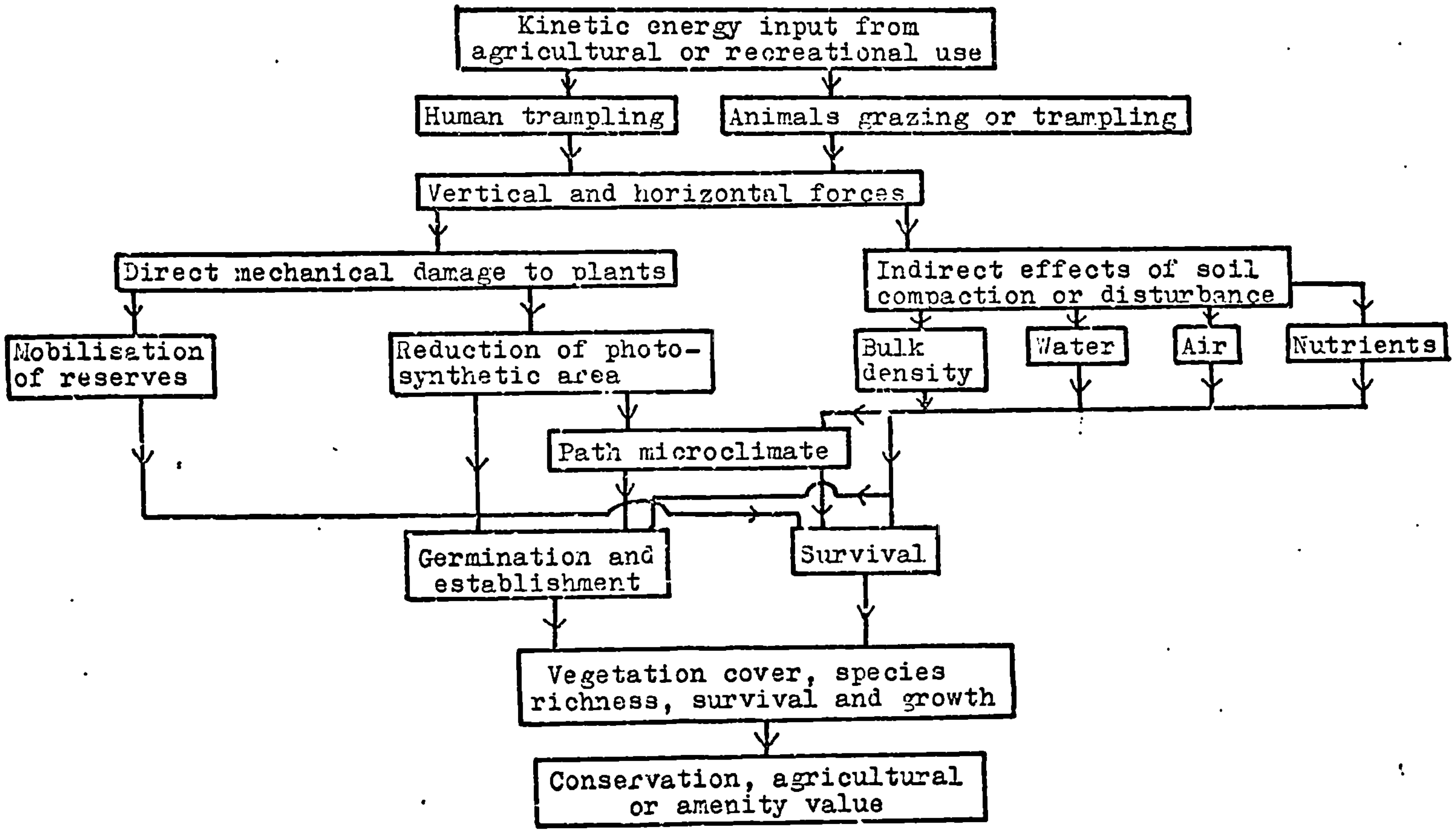
Ecological relationships

The various changes brought about by trampling are summarised in a logical model (Fig.6-1). This is derived from a more complicated original constructed in conjunction with Dr. J. Barkham. The postulated relationships are considered to be causal in nature but the parameters involved in each step are not necessarily all the same.

The vertical forces for static conditions range from 740 $g.cm^{-2}$ for sheep to 1,600 $g.cm^{-2}$ for cattle (Spedding 1971) and are from 160 $g.cm^{-2}$ to 206 $g.cm^{-2}$ for man (Paper 3), but the dynamic forces for men average 1,478 $g.cm^{-2}$ (Harper _et al_ 1961). Harper _et al_ (1961) also found that the horizontal forces may be up to 32% of the body weight. The vertical force exerted by a car was between 936 and 1,611 $g.cm^{-2}$ (Paper 3): the horizontal forces are extremely variable at the soil surface but are considerable.

The first visible effect of these forces is to reduce vegetation height (Gillham 1956). Even after a summer recovery season the height of the vegetation was still reduced by 15% after three times 16 passages (total 48) by a person walking the previous winter. A total of 384 passages applied and measured in the same

FIG.6-1. LOGICAL MODEL OF THE ECOLOGICAL EFFECTS OF TRAMPLING.



way reduced height by 55%. the biomass on an existing car track was only 13% of the adjacent natural vegetation but on a footpath it was 20% (Paper 2). Eight passages of a vehicle reduced live shoot biomass by 14% and in the field they increased soil bulk density by 12%; but an increase in bulk density of 32% produced a 15% rise in biomass when the vegetation was undamaged (Paper 1). The effect of 'trampling' is negative when only the direct effect on the plant was considered but it is indirectly positive through its effect on the soil.

The effect of trampling on the mobilisation of reserves is apparently unknown but severe defoliation of *Dactylis glomerata* resulted in mobilisation of labile reserves (Davidson & Milthorpe 1965), and defoliated tillers of *Poa pratensis* were shown to import assimilates from source tillers that they would not normally utilise (Nyahoza 1971). A reduction in the leaf size of *Trifolium repens* as a result of mechanical damage was noted by Bates (1934) and at one point on a wide sand dune track used by a van 40 times every other week for 20 weeks in summer a reduction of 57% in mean leaflet area was recorded. The consequence of these changes on establishment or survival has apparently not been measured but the common practice of restricting access to newly sown lawns is probably based on sound foundations.

The calculated regression lines of soil bulk density on the log of the number of passages had R^2 values of 0.86 and 0.91 for walkers and vehicles respectively. The penetrometer provided a more sensitive distinction between the two types of wear with R^2 values of 0.95 and 0.93 (see Paper 1). Data from established paths and tracks showed that there was an increase in soil water in dry areas and a reduction in very wet sites as a result of compaction (Fig.1-9). This difference is probably one of the reasons for the varying reports of this effect of trampling. In some instances the reduction in air filled pore space could lead to oxygen shortages but this was not measured directly (Fig.1-11b). The nitrogen content was up to 68% higher in compacted soils than in those artificially tilled, but phosphorus, potassium and sodium levels were higher in the dug soils (Paper 4). The effect on the mineral cycles is uncertain but tillage may accelerate the cycling of nitrogen.

The germination and establishment of <u>Festuca rubra</u> on compacted soil was only 57% of that on soil that had been tilled and of <u>Poa pratensis</u> only 24%. However, this failure was overcome by the use of fertilisers over a period of two growing seasons (Table 4-2).

Survival and growth of established plants was increased by compaction in greenhouse conditions. Light trampling has also been shown to stimulate growth of dicotyledonous species, such as Bellis perennis, Fig.2-6b, as has the low number of impacts of an experimental trampler on Phleum pratense (Bayfield 1971).

The extremes of the track thermal range were extended by 14°C as a result of vegetation removal (Fig.5-9), but soil compaction reduced this to 9°C (Fig.5-8). The soil changes again appear to have a beneficial effect on theplants' environment.

The effect of all these factors on the structure of the plant community depends on the dynamic balance of positive and negative components; if trampling ceases they are mainly positive and there is some evidence that a new edaphic climax may be created (Fig.s3-9a and b), especially in the sand dune situation. The changes in dynamic balance under different levels of trampling are illustrated by the change in the percentages of monocotyledonous and dicotyledonous species making up the total biomass (Figs.2-8a and b). There was an initial increase in the proportion of dicotyledonous species from below 40% to over 80% as a result of light trampling; this was accompanied by an increase in species number. The mechanism is probably the removal of tall monocotyledonous structures and a reduction in the competition for light. However, higher levels of trampling eliminated dicotyledonous species leaving only the monocotyledonous species present; the species number fell but there was a rise in the level of the realised diversity. The change in ratio was probably a result of the higher intrinsic resistance of monocotyledonous species to the effects of trampling; the reasons for this were not investigated but are probably not simple. The rise in realised diversity suggests that competition between species is reduced or absent.

The presence of species on trampled ground depends on the plant either being able to colonise the worn areas rapidly or to survive the direct effects of treading. The former strategy requires either a rapid growth rate in the case of vegetative invaders such as *Trifolium repens*, and possibly *Thymus drucei*, or a short life cycle. The relatively rapid rise and fall of the annual species on the field plots and turves (Figs.4-19 and 4-15) supports this suggestion, although the adverse factor in this case was the growth of other plants rather than trampling. Intrinsic resistance has been stated to depend primarily on the morphology of the plants (Bates 1935, 1938); a list of species able to survive on paths and one of resistant morphological characteristics appears in Speight (1973). This should also include the tussock form as mentioned in Paper 2. Tiller number may increase as a result ~~either~~ of shoot damage (Brougham et al 1960) and Fig.1-13a, or of a reduction in plant density (Lazenby & Rogers 1962), or of an increase in soil compaction (Fig.1-13a). All these stimuli may occur as a result of trampling and an increase in tiller number has been observed in the field (Fig.5-10a). This suggests that the apices may, in fact, have been destroyed and survival is the result of tillering potential; this is contrary to Bates' hypothesis (1935, 1938).

Trampling may act as an agent of genetic selection creating ecotypes in the field. Measurements showed that Festuca ovina collected from a Breckland track that had been closed for three growing seasons had a mean inflorescence length of 17 mm compared with 31 mm for inflorescences in nearby vegetation. Mean stem length was also reduced from 228 mm to 102 mm. The possibility of this being an edaphic effect cannot be ruled out, but experimental data suggest that it is unlikely.

Management implications

Carrying capacity

The factors affecting carrying capacity of sand dune pasture that were considered in this work are presented in the form of a model (Fig.6-2). Total relative cover, relative species number, relative diversity and relative cover of resistant species were used as parameters of the vegetation. The relationship between intensity of use and these parameters can be stated in the form of quadratic equations derived from regressions; these are given in Tables 6-1, 2, 3 and 4 and the graphs in Figs.6-3, 4, 5 and 6.

The choice of the appropriate equation depends on three dichotomous selections. The ideal situation requires that these choices should, in fact, be a continuous relationship between a wide range of levels of each variable, but in the experiment it was only possible to take two extremes, e.g. plus or minus recovery periods, walkers or vehicles and summer or winter seasons. (The effect of frequency is not considered further owing to limitations of the experimental method discussed in Paper 3). The first consideration is whether a period of recovery is to be allowed before mensuration. The experimental data allow predictions for one wear period of 20 weeks; to forecast the effect of sequential periods

FIG.6-2. MODEL FOR ESTIMATION OF CARRYING CAPACITY OF SAND DUNE PASTURE

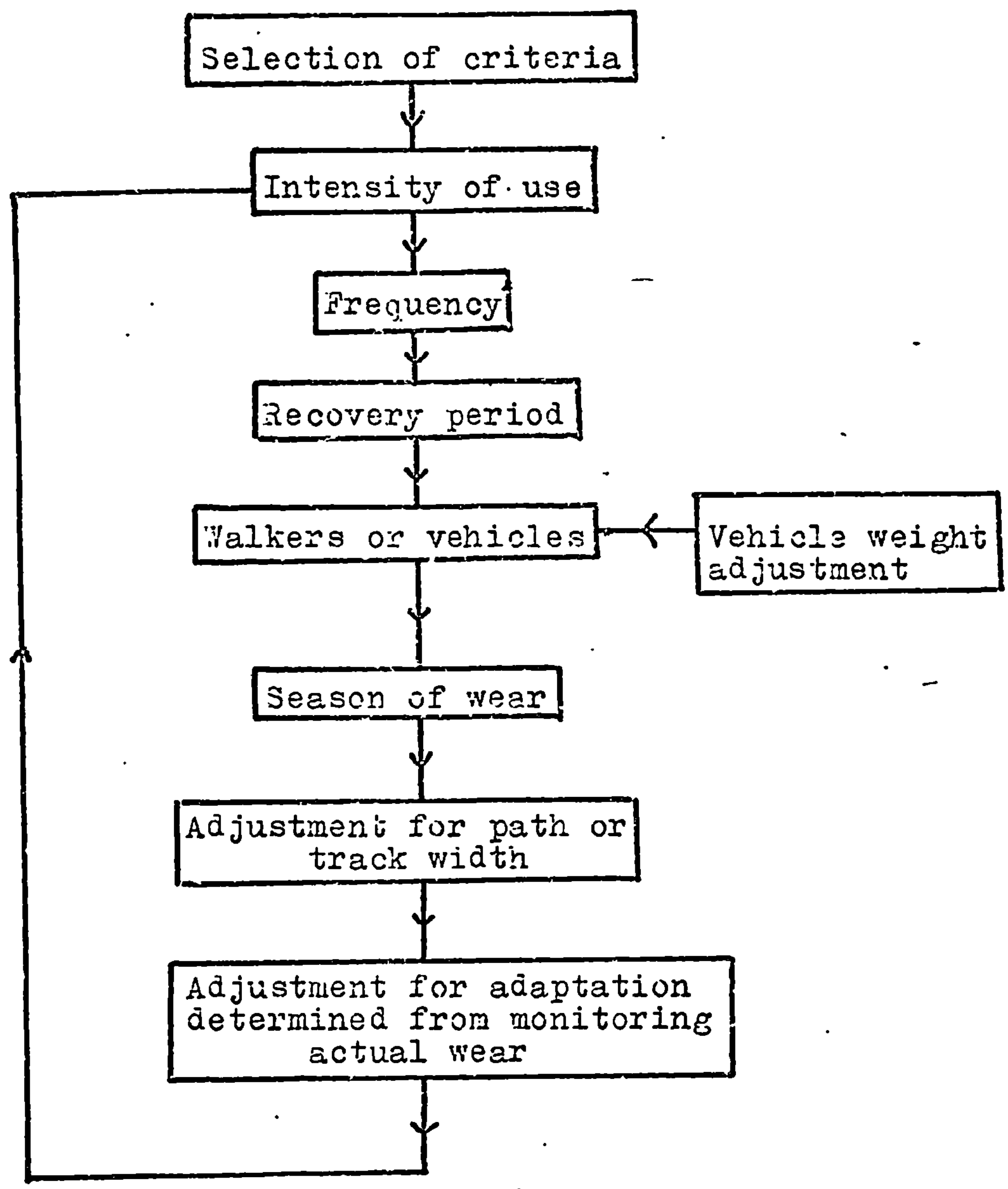


TABLE 6-1

TOTAL RELATIVE COVER

Regression data by which the amount of relative cover remaining after a given number of passages can be calculated.

Plus or minus recovery	Walkers or vehicles	Season of wear	a	b	c
- Recovery	Walkers	Summer	-7.51077	74.24034	-83.51968
		Winter	-5.83772	48.39095	-3.77198
	Vehicles	Summer	-4.87053	20.11019	80.67221
		Winter	-2.94225	3.30578	110.7533
+ Recovery	Walkers	Summer	-4.01773	42.54726	-1.40282
		Winter	-0.71194	10.80244	74.3022
	Vehicles	Summer	-4.28347	21.986	90.0171
		Winter	-5.66595	49.13928	13.30794

Based on quadratic regression equation

$$y = ax^2 + bx + c$$

y = percentage relative cover

x = number of passages

TABLE 6-2

RELATIVE SPECIES NUMBER

Regression data by which the relative species number remaining after a given number of passages can be calculated.

Plus or minus recovery	Walkers or vehicles	Season of wear	a	b	c
- Recovery	walkers	Summer	-2.20681	13.47227	81.12834
		Winter	-5.25787	49.51679	-20.35584
	vehicles	Summer	-2.57494	2.79114	111.7975
		Winter	-5.10044	27.46374	60.75092
+ Recovery	walkers	Summer	-1.07532	9.11433	84.49852
		Winter	3.28567	-38.58679	220.716
	vehicles	Summer	-4.85997	39.67365	24.33371
		Winter	1.20052	-10.13818	127.8927

Based on quadratic regression equation

$$y = ax^2 + bx + c$$

y = percentage relative cover

x = number of passages

TABLE 6-3

RELATIVE DIVERSITY

Regression data by which the relative diversity pertaining after a given number of passages can be calculated.

Plus or minus recovery	Walkers or vehicles	Season of wear	a	b	c
- Recovery	walkers	Summer	6.61304	-70.02952	275.9448
		Winter	5.76487	-60.21636	247.6899
	vehicles	Summer	6.20412	-61.87313	219.2987
		Winter	-9.265	86.77068	-97.00016
+ Recovery	walkers	Summer	1.5565	-26.31201	180.3504
		Winter	1.03042	-11.4318	136.9264
	vehicles	Summer	11.25942	-75.76316	212.5712
		Winter	2.38574	0.97705	58.75034

Based on quadratic regression equation

$$y = ax^2 + bx + c$$

y = percentage relative cover

x = number of passages

TABLE 6-4

RELATIVE COVER OF RESISTANT SPECIES

Regression data by which the relative cover of resistant species remaining after a given number of passages can be calculated.

Plus or minus recovery	Walkers or vehicles	Season of wear	a	b	c
- Recovery	walkers	Summer	-8.2399	84.50862	-106.6911
		Winter	-9.00083	84.48463	-95.39644
	vehicles	Summer	-7.29213	37.65307	63.91524
		Winter	-5.99482	27.93903	73.79995
+ Recovery	walkers	Summer	-5.71404	64.16438	-64.68238
		Winter	25.52389	-275.2738	832,5405
	vehicles	Summer	-5.57996	31.38729	77.00055
		Winter	5.44243	-49.49028	230.7517

Based on quadratic regression equation

$$y = ax^2 + bx + c$$

y = percentage relative cover

x = number of passages

Fig.6-3

The effect of different intensities of walking and driving on the total relative cover of sand dune pasture.

a) Walking

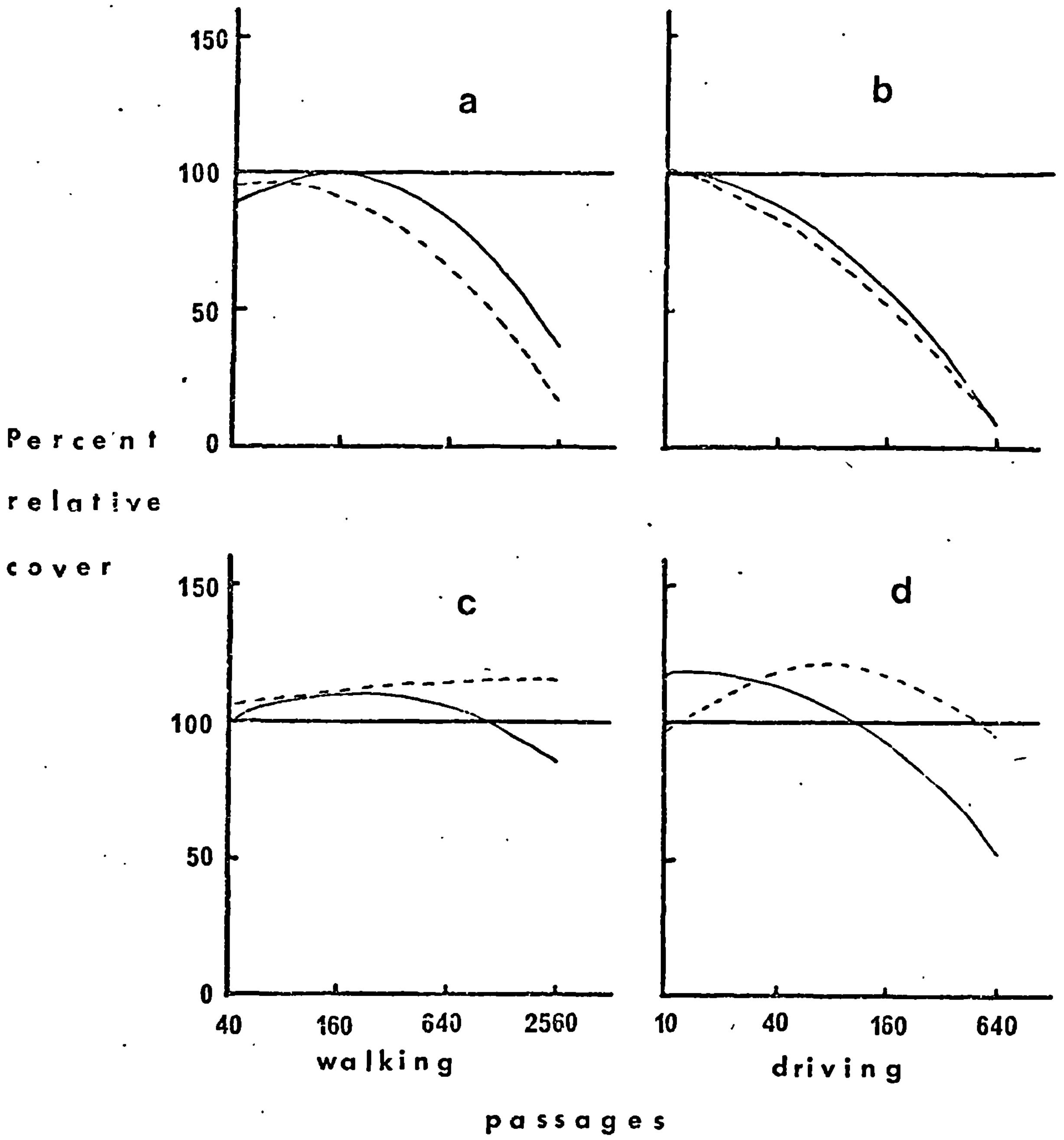
b) Driving

c) ~~20 weeks~~ Recovery after walking

d) ~~20 weeks~~ Recovery after driving

——— wear treatment carried out in the summer

- - - - wear treatment carried out in the winter



Percent relative cover
150
100
50
0
a
b
c
d
40
160
640
2560
walking
10
40
160
640
driving
passages

Fig.6-4

The effect of different intensities of walking and driving on the relative species number of sand dune pasture.

a) Walking

b) Driving

c) ~~20 weeks~~ Recovery after walking

d) ~~20 weeks~~ Recovery after driving

——————— wear treatment carried out in the summer

— — — wear treatment carried out in the winter

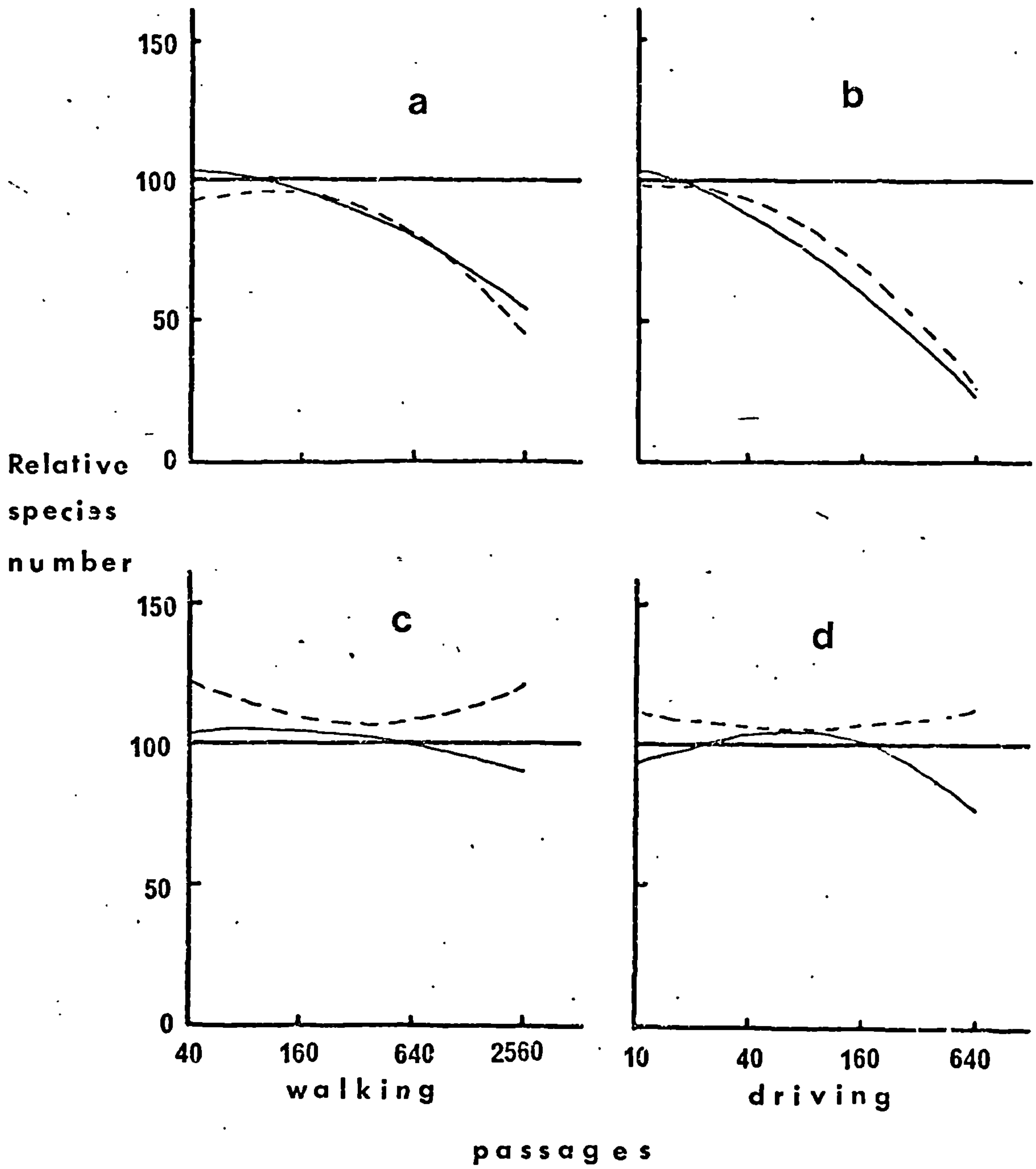

150
100
50
0
a
b
c
d
Relative
species
number
40
160
640
2560
walking
10
40
160
640
driving
passages

Fig.6-5

The effect of different intensities of walking and driving on the relative diversity of sand dune pasture.

a) Walking

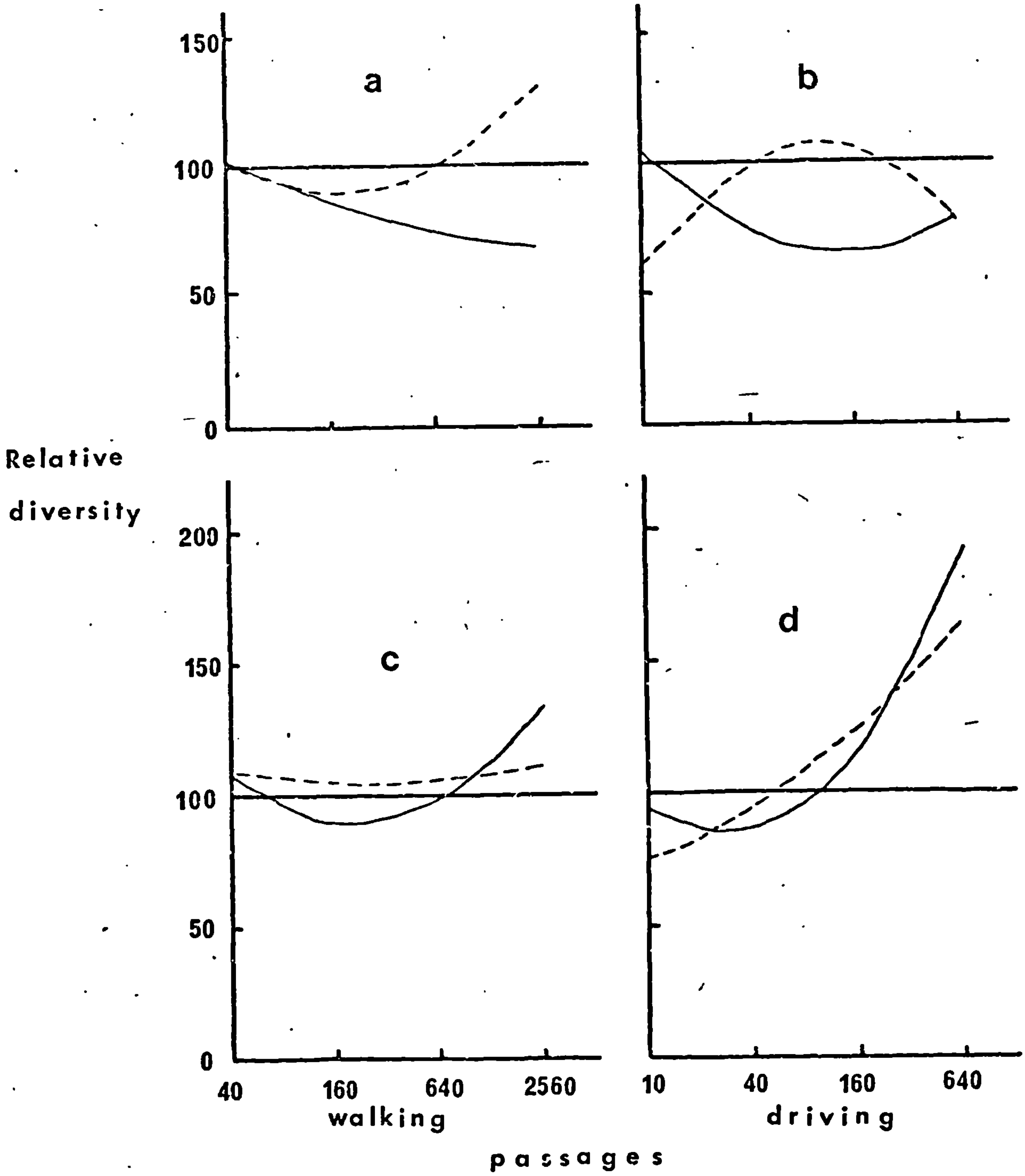
b) Driving

c) ~~20 weeks~~ Recovery after walking

d) ~~20 weeks~~ Recovery after driving

——— wear treatment carried out in the summer

– – – wear treatment carried out in the winter



a
b
c
d
150
100
50
0
200
150
100
50
0
Relative diversity
40
160
640
2560
walking
10
40
160
640
driving
passages

Fig.6-6

The effect of different intensities of walking and driving on the relative cover of resistant species of sand dune pasture.

a) Walking

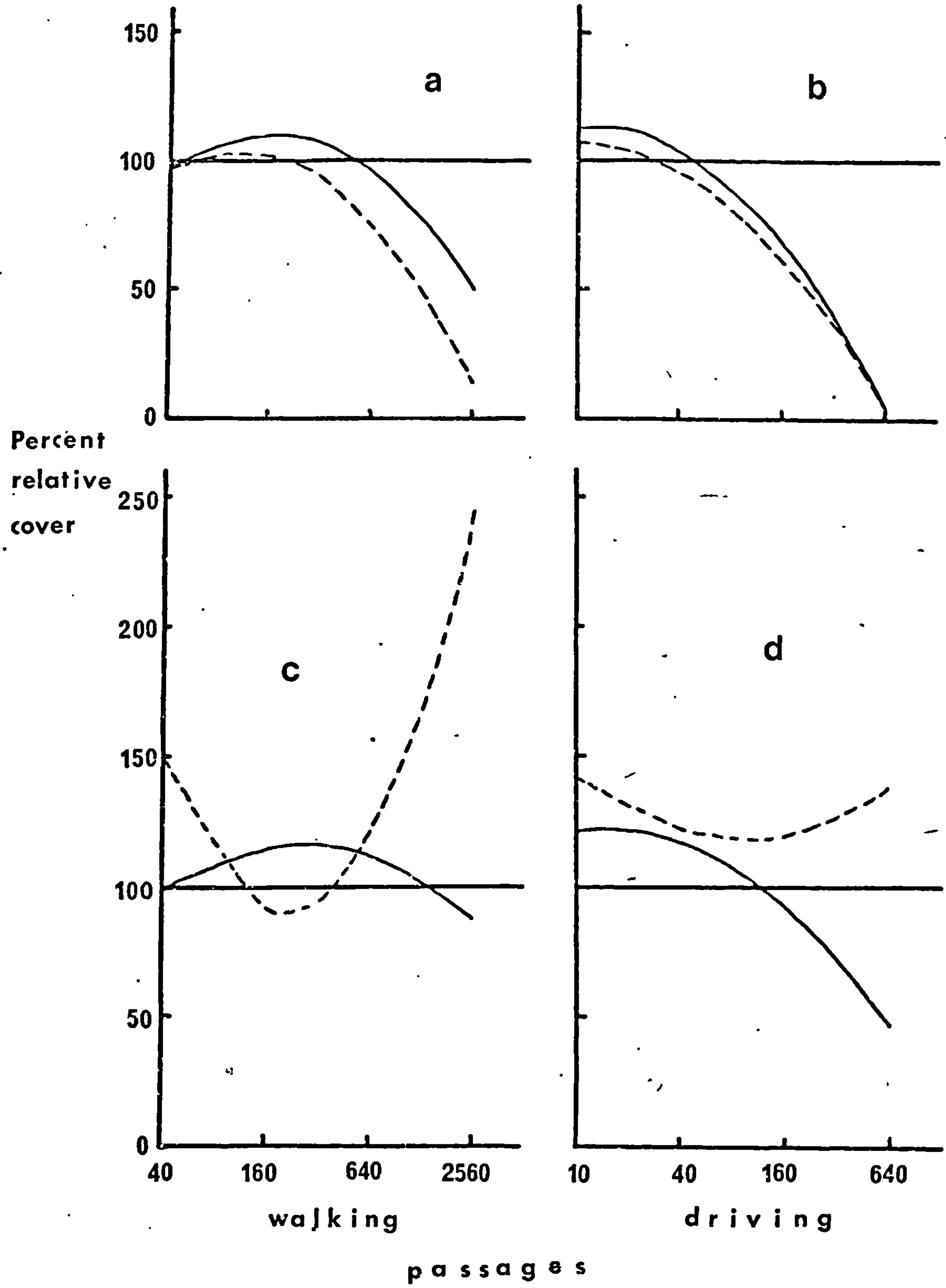
b) Driving

c) ~~20 weeks~~ Recovery after walking

d) ~~20 weeks~~ Recovery after driving

——— wear treatment carried out in the summer

— — — wear treatment carried out in the winter


a
b
c
d
Percent relative cover
150
100
50
0
250
200
150
100
50
0
40
160
640
2560
walking
10
40
160
640
driving
passages

of wear requires further data. The second choice is between wear by walkers or vehicles; if a mixture is allowed there may be an interaction but for practical purposes it is probably safe to use the effects in an additive way, e.g. 80 vehicles and 960 walkers both reduce the total relative cover by 25% in the summer, so if 50% cover is the acceptable minimum then this intensity of combined use is permissible. A correction factor for use with heavy vehicles is given in Paper 3, but this must be used with caution as it is based on data from a different habitat. The third choice is for wear in the summer or winter and if recovery is required then the other half of the year must be allowed for this, e.g. winter treatment and summer recovery.

The path width on which these calculations were based was approximately 25 cm. An estimate of the spread of people across the sand dune path based on the hardness at 12-18 cm depth (Fig.2-6a) and the data from the walking experiment (Fig.1-7d), gives a figure of 61% of passages on the central 25 cm quadrat. This means that on similar paths the permissible number of people derived from the equations can be multiplied by 1.5 to allow for spread of the wear across the path. The same calculation carried out for the track using data presented in Figs.2-5a and 1-7c gives a figure of

57% on the most used quadrat, producing a similar correction factor of approximately 1.5. But since the experimental rut width was about 12.5 cm (see photo 1-6) and the calculation is based on a 25 cm wide quadrat, a further factor of 2 must be allowed, so the final vehicle correction factor for track width is in the order of three times the experimental number of passages.

For example, suppose an estimate of the physical carrying capacity of sand dune pasture is required for a period of wear, the path is to be open to walkers only during the summer and a minimum cover of 75% must be maintained. The first equation in Table 6-1 or the graph in Fig.6-3a should be used. At 75% relative cover the number of passages is 843; this is multiplied by 1.5 to allow for path width giving a capacity of 1,686 passages by walkers on previously untrodden ground. The criteria presented in Figs.6-4, 5 and 6 can be used in the same manner.

The final 'box' in the model is to allow for adaptation of the flora to the effect of trampling over a period of time as found by La Page (1967); the calculated carrying capacity may, therefore, be gradually increased.

The technique of regressing the percentage of remaining vegetation cover on the log of the number of passages can also be utilised in an assessment of the vulnerability of different habitats. In the calculations presented in Paper 3 the number of passages that reduced cover to 50% were calculated from various data, a weight correction factor was introduced and a conversion factor to 'walker units' was used (Table3-12). These calculations allow the suggestion that tundra is between 5 and 187 times more vulnerable than sand dune pasture while a sown 'pasture' on a light silt loam may be twice as resistant as the sand dune pasture.

Maintenance of trampled sand dune pasture

The various cultural treatments described in Paper 4 suggest that if cover is the only important criterion of maintenance then an annual application of a slow release fertiliser (if possible one containing micronutrients) combined with seeding is likely to be the best treatment. Generally tillage should be avoided and in most circumstances only the top one or two cm of soil should be disturbed. The microclimatic measurements also indicate that tillage would create more extreme conditions which may adversely affect plant survival. If no cultivation is done a high diversity and species number may be achieved especially if the level of trampling is not excessive. A low level of trampling can itself be used to limit the growth of monocotyledonous species and allow an aesthetically pleasing turf dominated by dicotyledonous species to develop.

Bellis perennis was the most common track species recorded in the survey and Festuca rubra was the second most common. They occurred at mean volumetric soil water contents of 20% and 14% respectively; thus, the latter occurred in drier areas and it also made up a large proportion of the naturally occurring grassland. This species should, therefore, form the bulk of any seed mixture used in track maintenance. Poa pratensis and Bellis perennis could be used in the damper areas and in the wettest places Juncus articulatus and Carex flacca may be most successful. If only grass seed is available then Festuca rubra may be used in dry and Poa pratensis in the wet areas.

If a path is routed around the edge of a wet slack the more mesic resistant species such as Bellis perennis and Poa pratensis may be sown or allowed to colonise naturally. In the event of the breakdown of the soil crust, erosion will soon be halted by the presence of the water table near the surface. These species have very little dormancy and can, therefore, take advantage of any temporary withdrawal of trampling pressure. The problem of puddling is not likely to arise in sand dune soils.

The best recovery treatments for areas where trampling pressure has been lifted are probably those listed above; and it is of interest that Beardsley & Wagar (1971) and Herrington & Beardsley (1970) also found considerable merit in both seeding and fertilising. The use of a watering treatment was probably dictated by the climate at their experimental sites but in Britain the drier sand dune areas may well benefit from this technique if the cost is acceptable. The alternative of artificial path surfaces is, however, the solution commonly employed in the most vulnerable areas.

The morphological criteria upon which the selection of species resistant to trampling are selected for cultivation should be extended beyond the list in Speight (1973) to include the small tussock forms, especially grasses with a high tillering capacity.

There is a considerable urgency in the production of adequate management models for the various habitats subjected to high levels of public pressure, and this thesis attempts to provide some of the data required for such a model for sand dune pasture. There is, however, a need for further quantitative experimentation so that carrying capacities, maintenance treatments and management criteria can all be accurately defined. It should be possible to predict the effect of altering any aspect of management on the various vegetational parameters and when this can be done ecologists will have made an invaluable contribution to the preservation of one of our most precious resources.

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