Bryophyte recolonisation of burnt ground with particular reference to *Funaria hygrometrica*

A thesis submitted to the University of London
for the Degree of Doctor of Philosophy

-by-

Anne Lilian Denise Southorn

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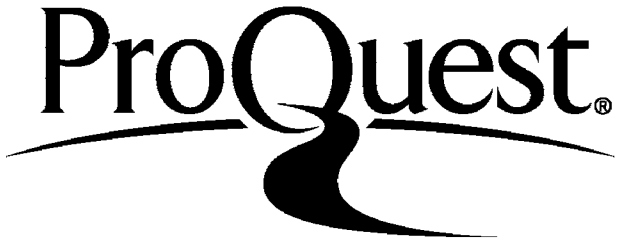


ABSTRACT

Field studies throughout England showed that the pattern of bryophyte recolonisation on a burnt site depends largely on the type of fire from which the site results. Two types of fire were distinguished, rapid fires and bonfires, these differing mainly in the amount of ash deposited and the duration of high temperatures, both being greater during a bonfire. On bonfire sites, after an initial period of growth inhibition, Funaria hygrometrica characteristically became abundant, whilst scattered shoots of Bryum argenteum, Ceratodon purpureus and tuberous species of Bryum were often found. Then, as the angiosperm cover increased these pioneer mosses were replaced by the pre-burn species. Rapid fire sites in contrast, were colonised largely by species characteristic of the pre-burn vegetation, these only becoming abundant when angiosperm recolonisation was slow.

Culture on inorganic nutrient agar showed that in the presence of adequate amounts of potassium and particularly phosphorus, growth of Funaria was stimulated by raising the level of nitrate nitrogen and soil analyses indicated some correlation between these requirements and conditions in bonfire soils. Addition of inorganic nutrients to unburnt soil however, did not stimulate growth. Thus under natural conditions soluble organic nutrients, present in high concentrations in bonfire soils, may be essential for growth, or alternatively a heat-labile inhibitor may prevent good growth of Funaria on unburnt soil, though this seems unlikely. The excessively high concentrations

of soluble substances found immediately after burning, together with the inhibition of nitrification, would explain the initial growth inhibition on bonfire sites, whilst the later disappearance of Funaria from bonfire sites could be linked with the gradual return of nutrient conditions to the pre-burn state and increasing angiosperm competition.

CONTENTS

INTRODUCTION

Fire is an ecological factor of considerable economic importance and thus it is not surprising that much attention has been paid to its effect on vegetation. Many of the investigations concern forest fires, see for example the review by Ahlgren & Ahlgren (1960), and later works by Cremer & Mount (1965), Remezov & Pogrebnyak (1969), but in Britain the commonest fires are those on heathland and moorland and work has concentrated on these. Notable investigations include those of Fritsch & Salisbury (1915); Summerhayes & Williams (1926); Fritsch (1927); Elliot (1953); Whittaker (1961) and Kayll & Gimmingham (1965). Both forest fires and heathland and moorland fires usually result in extensive areas of burnt ground and much less attention has been paid to the recolonisation of smaller burnt areas such as those resulting from bonfires. Descriptions of the recolonisation of such sites are however given by Benson & Blackwell (1926); Graff (1935) and Pettersson (1931). The majority of workers as would be expected have concentrated on the recolonisation by angiosperms, although bryophytes, often conspicuous in the early stages of the recolonisation, are commonly mentioned. A few authors describe the bryophyte recolonisation in greater detail, (Skutch, 1929; Graff, 1935; Doignon, 1949; Cremer & Mount, 1965; Hoffman, 1962).

It is apparent from the literature that certain species of bryophytes are found on burnt sites over a wide geographical range

the most notable of these being Funaria hygrometrica Hedw.. Table 1 gives a selection of references illustrating the wide geographical range of this species on burnt ground. References to the occurrence of Marchantia polymorpha L. and Ceratodon purpureus (Hedw.) Brid. on burnt ground are likewise frequent, whilst Bryum argenteum Hedw. has also been recorded for this habitat by several workers (Summerhayes & Williams, 1926; Doignon, 1949; Richards, 1963a), as also has Leptobryum pyriforme (Hedw.) Wils. (Richards, 1932; Watson, 1968; Remezov & Pogrebnyak, 1969). Crundwell & Nyholm (1964) have noted the association of several members of the Bryum erythrocarpum complex with Funaria hygrometrica and thus it is possible that these species too are able to grow on burnt ground, whilst Bryum bornholmense Wilkelm and Ruth, a member of the Bryum erythrocarpum complex has been reported by Miles (1967) to grow well on burnt heathland. Other bryophytes noted on recently burnt areas, include species of Campylopus (Richards, 1932 and 1963b; Cremer & Mount, 1965), Barbula convoluta Hedw. (Doignon, 1949), species of Pohlia (Summerhayes & Williams, 1926; Remezov & Pogrebnyak, 1969) and species of Polytrichum (Katz, 1926; Summerhayes & Williams, 1926; Skutch, 1929; Graff, 1936; Doignon, 1949; Lutz, 1956; Cremer & Mount, 1965; Remezov & Pogrebnyak, 1969). Funaria hygrometrica and Marchantia polymorpha appear to be the most abundant species in the pioneer stages of the recolonisation, species of Polytrichum often replacing these pioneers (Watson, 1964).

Table 1. The geographical range of Funaria hygrometrica.

Reference		Location
Bradshaw	1926	U.S.A. California
Clark	1904	U.S.A. Pennsylvania
Hoffman	1966a	U.S.A. E. Washington and N. Idaho
Svihla	1936	U.S.A. N.W. Washington
Wolfe	1924	U.S.A. Nebraska
Katz	1926	U.S.S.R. Western U.S.S.R.
Remezov & Pogrebnyak	1969	U.S.S.R. and Northern Europe
Duncan	1966	U.K. Scotland, Angus
Jones	1952	U.K. Berkshire and Oxfordshire
Paton	1969	U.K. Cornwall
Proctor	1956	U.K. Cambridgeshire
Smith	1964	U.K. Wales, Glamorgan
Pettersson	1930-31	South Finland
Bird	1962	Western Central Canada
Hill	1911	Canada, Br. Columbia
Cremer and Mount	1965	Tasmania
Richards	1963a	West Africa
Giesy & Richards	1959	Thailand
Doignon	1949	France

No attempt is made to list all records

Although most usually found in the early stages, the order in which the other species appear and their abundance appears to be variable.

Differences in the details of the recolonisation and the time taken for re-establishment of the preburn vegetation, will obviously vary according to a number of factors. These might include: the original soil and vegetation type, the prevailing climate, the season of burning and also the nature of the fire itself and subsequent biotic influences, but it is widely held (see for example Watson, 1964) that increases in the levels of soil nutrients due to burning are most important in determining the presence of the pioneer bryophyte species. This argument is reinforced for Funaria hygrometrica by the observation that the comparatively few non-burnt sites colonised by this species are also likely to be rich in minerals (e.g. Sheldon 1907; Parker 1931 and Flowers 1933). Little attempt however, has been made to determine experimentally the relative importance of the factors involved and the present work was therefore carried out in an attempt to verify and extend the existing information concerning the recolonisation of burnt ground by bryophytes and in particular by Funaria hygrometrica.

FIELD INVESTIGATIONS AND OBSERVATIONS

Field investigations were carried out in order to determine which species are involved in the recolonisation of burnt ground and to find which factors are most important in determining their establishment and subsequent replacement. The work described in this section falls into two parts: I. a detailed study of sites set up in the grounds of Royal Holloway College and II. a series of less detailed observations carried out on sites situated on a wide variety of soil and vegetation types throughout England.

All the burnt sites resulted from one of two sorts of fires referred to here as bonfires and rapid fires. Bonfires are characterised by the burning of large amounts of fuel in a localised area, whilst rapid fires are characterised by the rapid burning of large areas of vegetation. A list of all the sites studied together with a brief description of the pre-burn soil and vegetation type is given in appendix table 1 and their location shown in Fig. 1. Site numbers are given in appendix table 2.

As far as possible all the bryophytes occurring on the sites were identified, but where shoots were immature, material scanty or capsules lacking, this was not always possible. This was most commonly the case with species of Bryum. Unidentifiable species of this genus possessing rhizoid gemmae or tubers are referred to as tuberous species of Bryum (a list of the European species of Bryum

Fig. 1. Location of sites.

with tubers is given by Whitehouse, 1966). The succession of bryophytes on the sites was recorded and the importance of the following factors considered:

1. type and severity of fire;
2. season of burning and prevailing climate;
3. preburn soil and vegetation type;
4. edaphic conditions after burning;
5. angiosperm competition and animal disturbance.

I. THE COLLEGE SITES

1. Preliminary study of the recolonisation of bonfire sites

Bonfire sites B1, B2, B3, B4 and B5, were set up in December, 1965 and March 1966 and compared with control sites W1, W2, W3, W4 and W5 cleared of their vegetation by weeding. Sites B2, B4, W2 and W4 were situated in an area of fallow ground whilst B3, B5, W3 and W5 were on waste ground and B1 and W1 on rough pasture. The arable soil in all three areas overlay Bagshot sand and gravel. All the sites were covered with a grid made of plastic coated wire enclosed in a wooden frame, giving a sampling area of 1 sq.m. divided into 10 cm. squares. Sites B2, B3, W2 and W3 were used only for observation and sites B4, B5, W4 and W5 for soil sampling. B1 and W1, the sites set up in December, were used both for observation and

soil sampling.

In setting up the bonfire sites it was found that a pile of fuel 1.5 m.cu, provided that it contained a considerable proportion of heavy material, gave a depth of ash of 2-3 cm. over an area 1 m.sq. A site of this size was large enough to permit regular collection of small soil samples and provided a convenient size for recording the recolonisation. The fuel consisted of a mixture of tree and hedge trimmings resulting from the work of the college gardeners. The fires were allowed to burn themselves out, the ash being cool enough to handle within 24 hours, when it was spread out to form an even cover over the site. Thermocolour pyrometers as designed by Whittaker (1961) were used in a attempt to obtain an approximate measure of the temperatures of the fires, but many of the pyrometers in this experiment, were lost or shifted to the edge of the site during burning, as they were not anchored in position. The sites were visited at approximately fortnightly intervals and the recolonisation recorded by means of notes and estimations of percentage cover using the Domin scale (McVean and Ratcliffe, 1962), the bryophytes and angiosperms being considered as two separate layers. In addition recording the recolonisation by taking a series of close up vertical photographs of each site was tried, but this proved very time-consuming and it was difficult to build up a composite picture of each site from the prints obtained.

The recolonisation

Observations are summarised in table 2. The soil conditions of sites in this experiment and succeeding experiments are considered later.

A green film was seen on the sites within 3 months after burning, at approximately the same time as angiosperm growth was first noted. It is not possible to say however, whether the film was composed initially only of algae, since the surface soil was not regularly closely examined. On all the sites, both bonfires and controls, the percentage cover of bryophytes was small at all stages of the recolonisation but certain species were characteristic of the bonfire sites: Bryum argentum, Ceratodon purpureus, Funaria hygrometrica and tuberous species of Bryum. On the control sites Brachythecium rutabulum was the most abundant species.

Angiosperms recolonised the bonfire sites relatively slowly by invasion from the edges, whilst the control sites were colonised more rapidly by growth from seeds and surviving roots and stems scattered over the whole site. On both the winter bonfire site and the winter control site vigorous growth was delayed until the following spring.

As the angiosperm cover on the bonfire sites increased, the characteristic bonfire species of bryophytes became overgrown and disappeared. The importance of the shading effect of the angiosperms, in determining the disappearance of the bonfire species, was illustrated by one of the bonfire sites B2 which was covered very rapidly by Convolvulus arvensis, growing along the wires of the

Table 2. A summary of the recolonisation of sites in Experiment 1.

	B1	W1	B2	W2	B3	W3	
Green film 1st noted after	3	2	2	1	2	g)	
Angiosperms 1st noted after	3	2	2	1	2	1)	months
Time taken for angiosperm cover to reach 75%	9	6	6	3	6	6)	
Type of angiosperm recolonisation	I	S	I	S	I	S	
Occurrence of *Funaria hygrometrica*	+a	-	+a	-	+a	-	
" " *Bryum argenteum*	+	-	-	-	+	-	
" " *Tuberous spp. Bryum*	+	-	-	-	+l	-	
" " *Ceratodon purpureus*	+	-	+	-	+	+	
" " *Brachythecium rutabulum*	-	+a	+l	+a	+l	+a	
" " *Eurhynchium praelongum*	-	-	-	+	-	-	
" " *Barbula convoluta*	-	-	-	-	+l	+l	
" " *B. unguiculata*	-	-	-	-	+l	+l	
" " *Bryum sp.*	+	-	-	-	-	-	

a = most abundant species

l = found only towards end of observation period

g = gametophores present after 6 months

I = invasion

S = from scattered shoots and seedlings

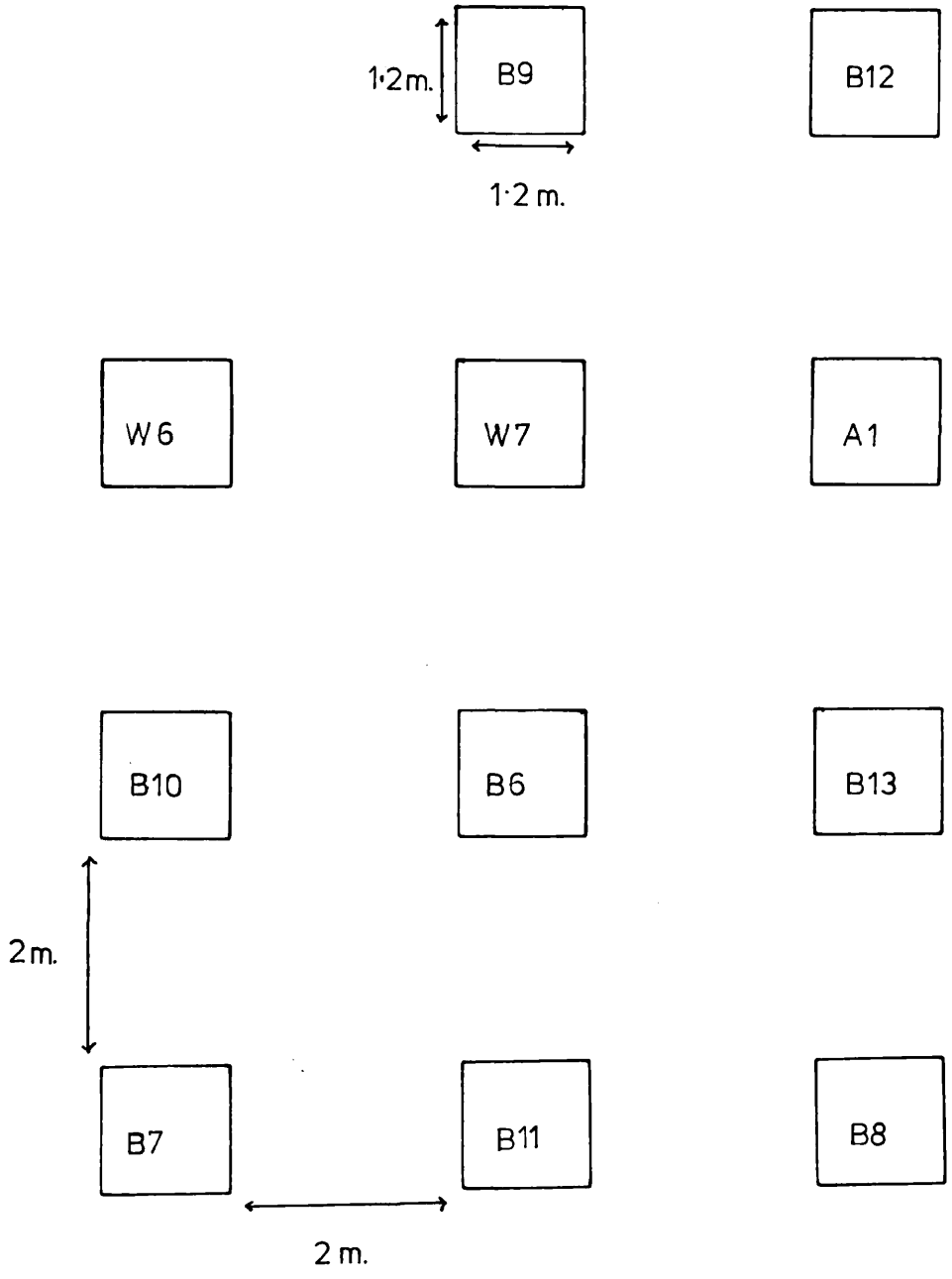
sampling frame. Within 6 months the few bryophytes which had managed to colonise this site had disappeared.

2. Detailed study of the recolonisation of bonfire sites

The preliminary experiment was ended after 12 months and with the aid of information obtained from this experiment, a more critical study was carried out on a series of plots, set up in April, 1967 in the grounds of the botany department. The sites were situated in an area of neglected lawn, the arable soil overlying Bagshot sand and gravel. The vegetation was dominated by grasses including Anthoxanthum odoratum, Dactylis glomerata and Holcus mollis. Other angiosperms abundant were Achillea millefolium, Glechoma hederacea, Ranunculus repens, Rumex acetosa and Trifolium dubium, Bryophytes, except for a few etiolated and unidentifiable shoots of a Bryum species, were absent from the dense vegetation.

Eleven plots were set up. Eight of these B6, B7, B8, B9 B10, B11, B12 and B13 were bonfire sites and three W6, W7 and A1 areas cleared of their vegetation by weeding, care being taken not to disturb the surface soil. The layout of the sites is shown in fig. 2. The type and amount of fuel used in setting up the bonfire sites and the duration of burning were as in the first experiment, but to ensure

Fig. 2. Lay out of sites in Experiment 2.



that the ash layer on each site was identical, the ash from all the sites was collected as soon as it was cool enough to handle, mixed and redistributed. Ash was not replaced on one of the bonfire sites B12 but instead was placed on weeded site A1. Approximate temperatures of the fires (table 3) were again measured using thermocolour pyrometers, these being secured to steel stakes to prevent them shifting and being lost.

Table 3. Maximum temperatures (^{o}C) at the soil surface during bonfires in Experiment 2.

Site							
B6	B7	B8	B9	B10	B11	B12	B13
805	805	805	640	900	805	900	900
900	805	715	715	900	715	715	715
805	900	715	715	900	900	-	715

The sites were visited at regular fortnightly intervals until the recolonisation was nearly complete, when less frequent visits were made. Observations were recorded by means of notes, estimations of percentage cover using the Domin scale and hand drawn maps. The angiosperm growth of one of the weeded sites, W7 and one of the bonfire sites, B13, was removed on each visit, care

being taken not to disturb the surface soil or any bryophytes which were present. Surface soil samples for chemical analysis were collected regularly from three of the bonfire sites, B9, B10 and B11, these sites not being used for recording. Soil samples were collected less regularly from weeded site W6 and only occasional samples for chemical analysis were removed from other sites. Fifty small surface soil samples each less than 1 gm. were removed from each of the bonfire sites, B6, B7 and B8, at fortnightly intervals for close examination for protonemata. The method of examination is given in the appendix p.268.Sampling grids identical to those used in Experiment 1 greatly facilitated recording and sampling and were placed over all sites in Experiments 2, 3 and 4.

The recolonisation of the bonfire sites B6, B7 and B8 and control site W6 is first described in detail and the vegetation changes then compared with those of the remaining sites, B12 and A1, B13 and W7. The results are illustrated by a selection of vegetation maps (for key to these see appendix p.287, whilst the time taken for completion of various stages in the recolonisation of sites is summarised in table 4. Changes in the bryophyte and angiosperm Domin ratings are given in tables 4 and 5 in the appendix.

Bonfire sites B6, B7 and B8

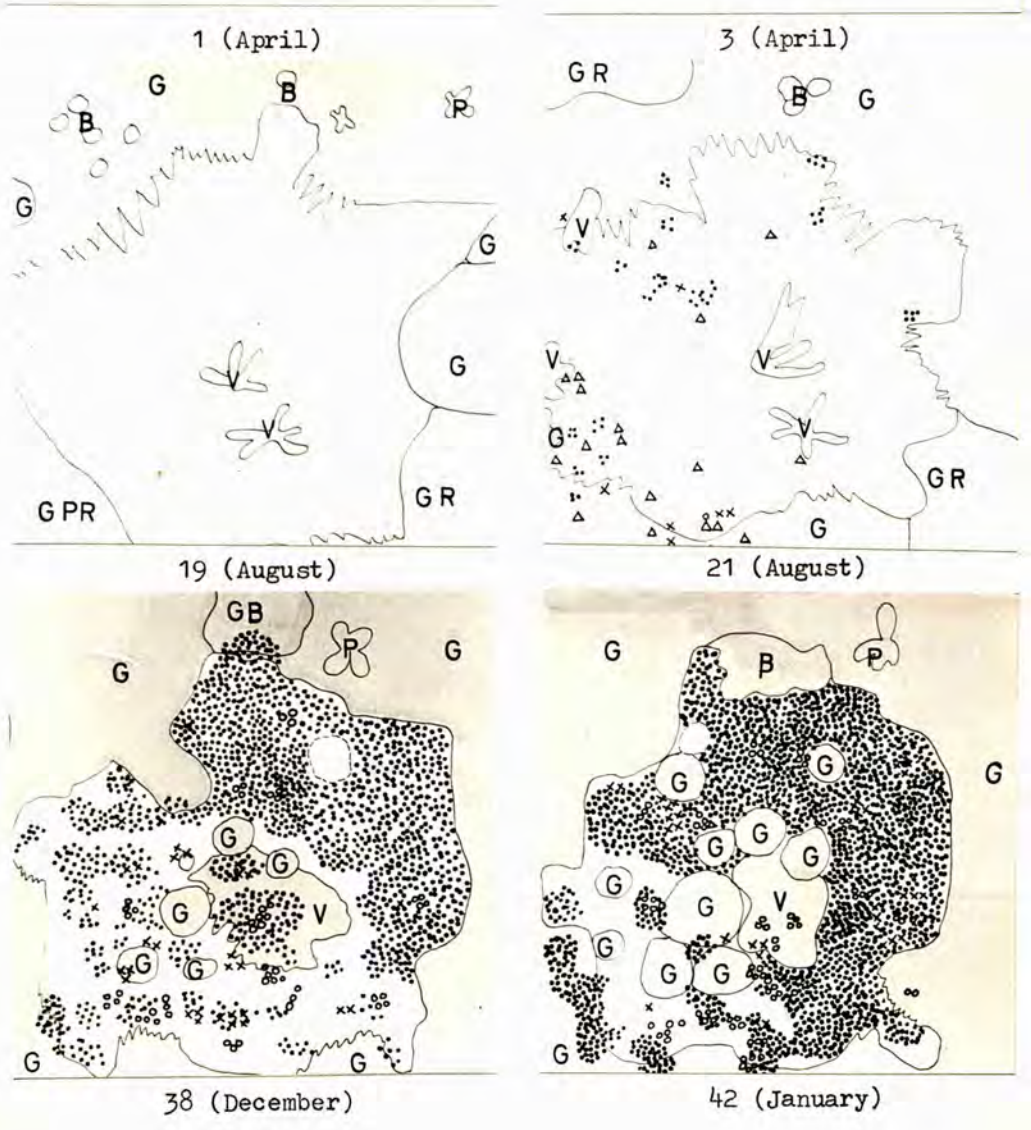
From fig. 3, 4 and 5 it can be seen that recolonisation of all three sites was very similar. The first angiosperm growth

Table 4. A summary of the recolonisation of sites in Experiment 2.

FACTOR	AGE OF SITE IN MONTHS							
	B6	B7	B8	B12	A1	B13	W7	W6
Algae first recorded	3	3	3	-	-	-	-	3
Protonemata first recorded	9	9	9	-	-	-	-	7
Angiosperms first recorded	5	5	5	9	1	-	-	1
Gametophores first recorded	18	18	18	18	13	13	9	11
Angiosperm cover reached 25-33%	18	18	18	18	5	-	-	3-5
Angiosperm cover reached 33-50%	19	19	13-18	21	7-9	-	-	5
Angiosperm cover reached 50-75%	23	23	18	23	9	-	-	7
Angiosperm cover reached 75-95%	67	67	67	25	13	-	-	9
Bryophyte cover reached 25-33%	29	25	38	x	x	25-27	27	x
Bryophyte cover reached 33-50%	42	29	x	x	x	27	x	x
Bryophyte cover reached 50-75%	x	42	x	x	x	38	x	x
Bryophyte cover reached 75-95%	x	x	x	x	x	x	x	x

x = not achieved

Fig. 3. The recolonisation of site B6.



No's = age of site in weeks.

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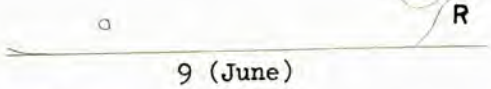

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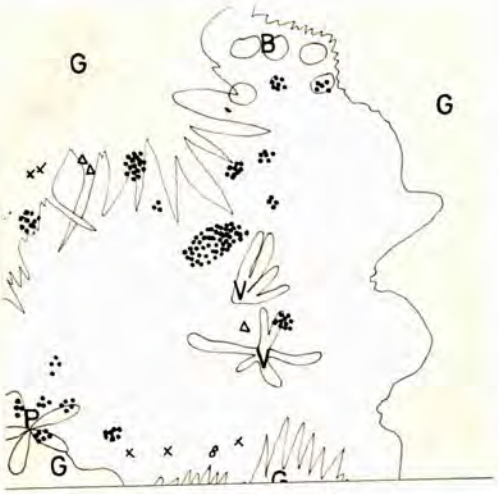

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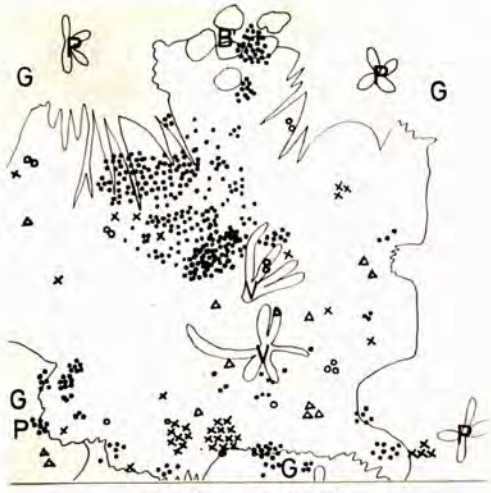

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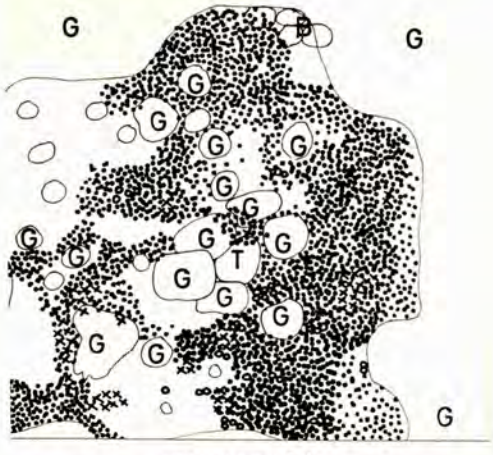
46 (February)



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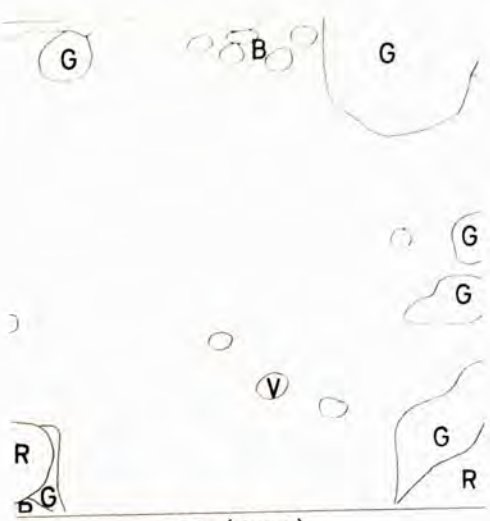

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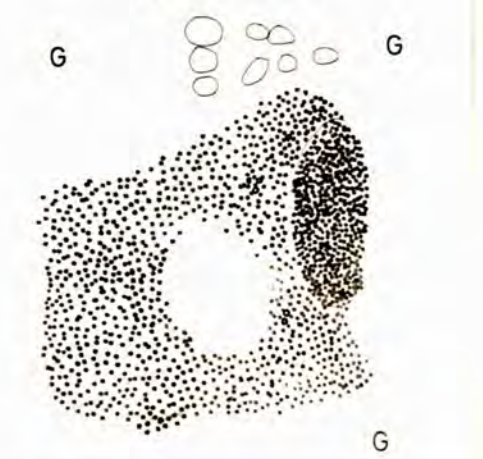
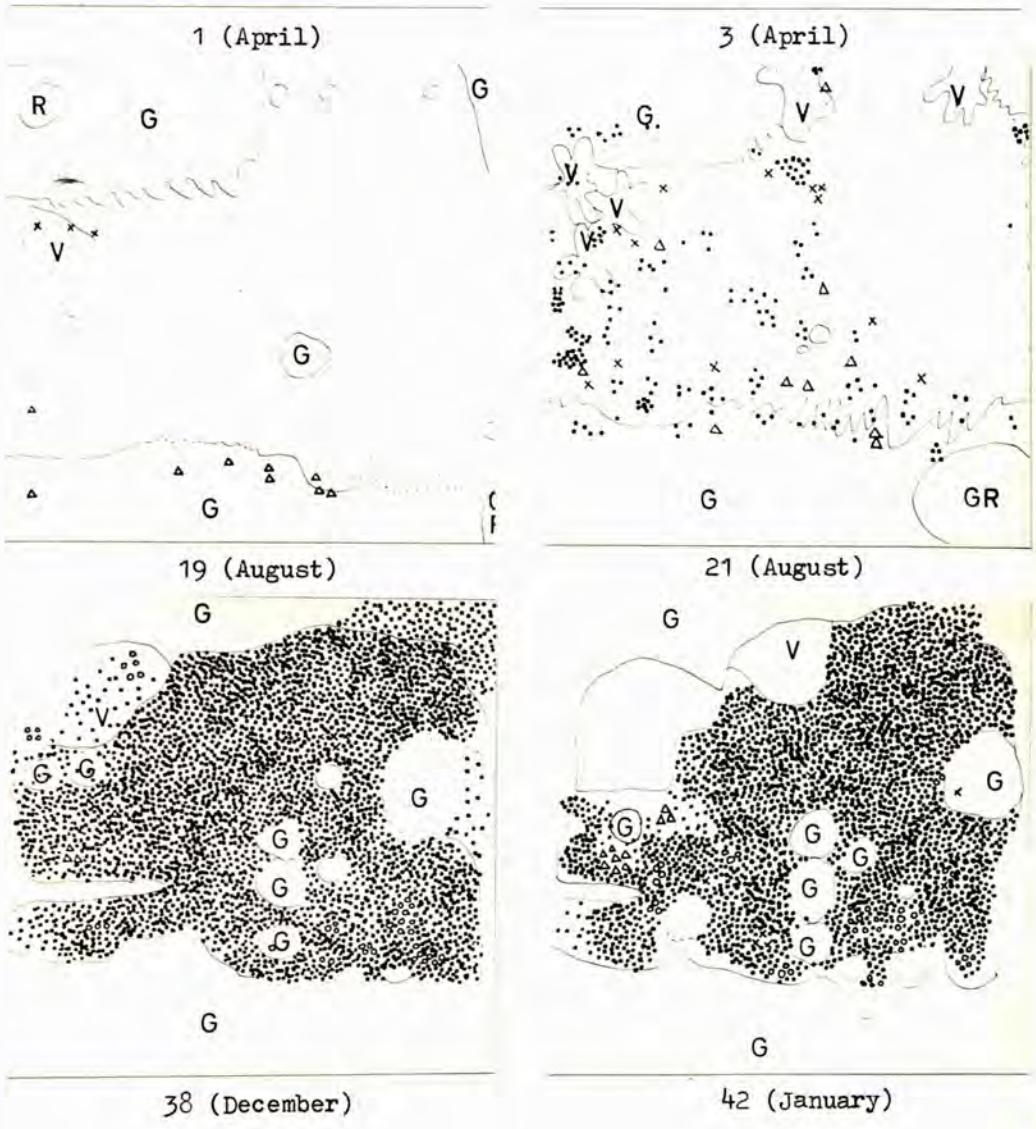


67 (July)

Fig. 4. The recolonisation of site B7.



No.'s = age of site in weeks.

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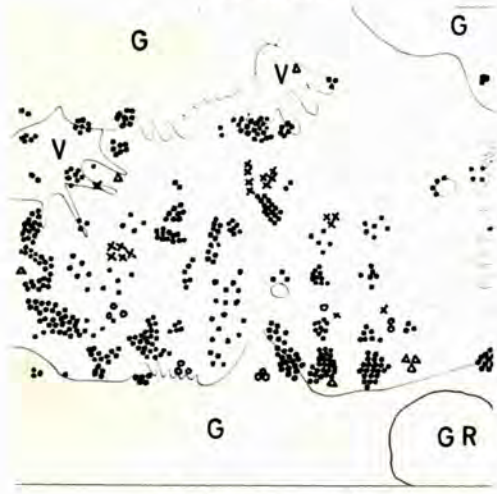

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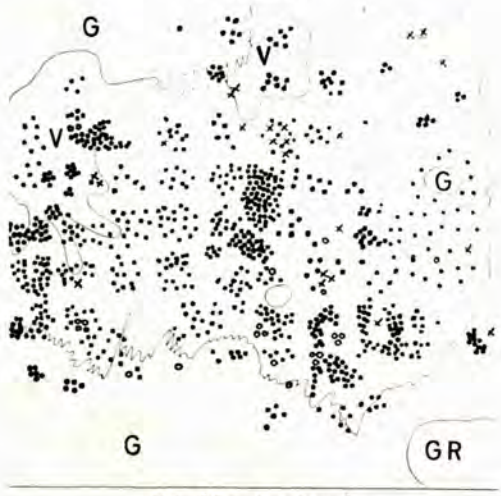

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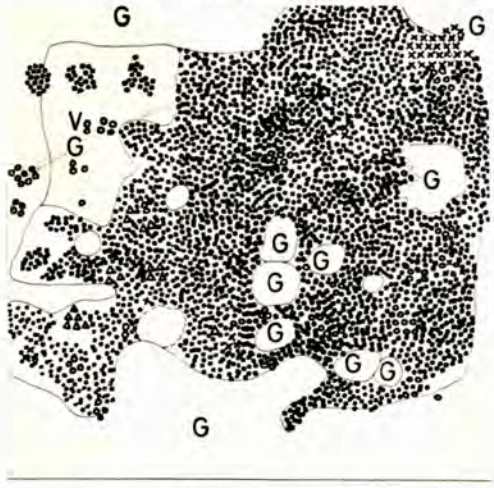

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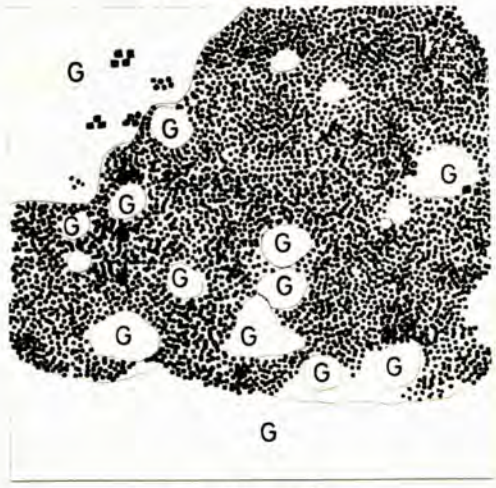

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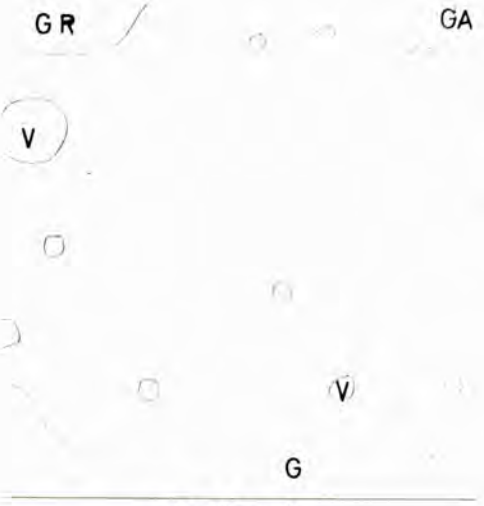

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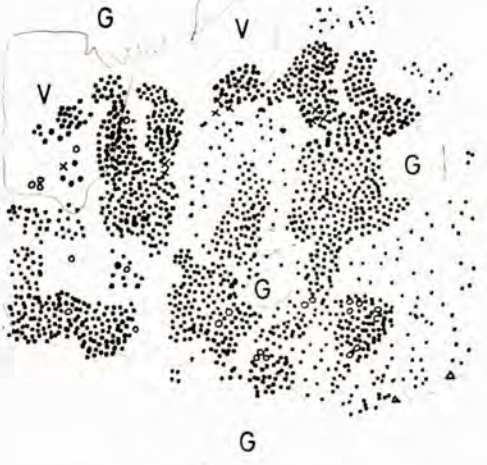

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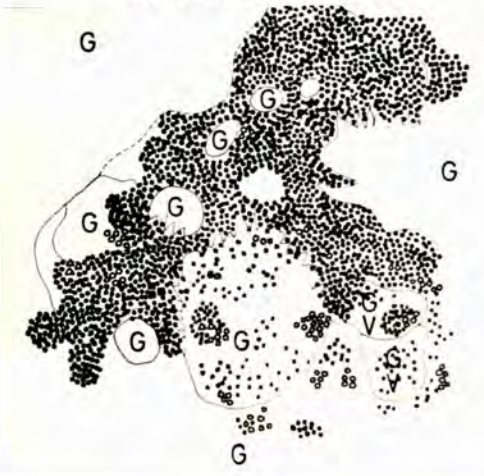

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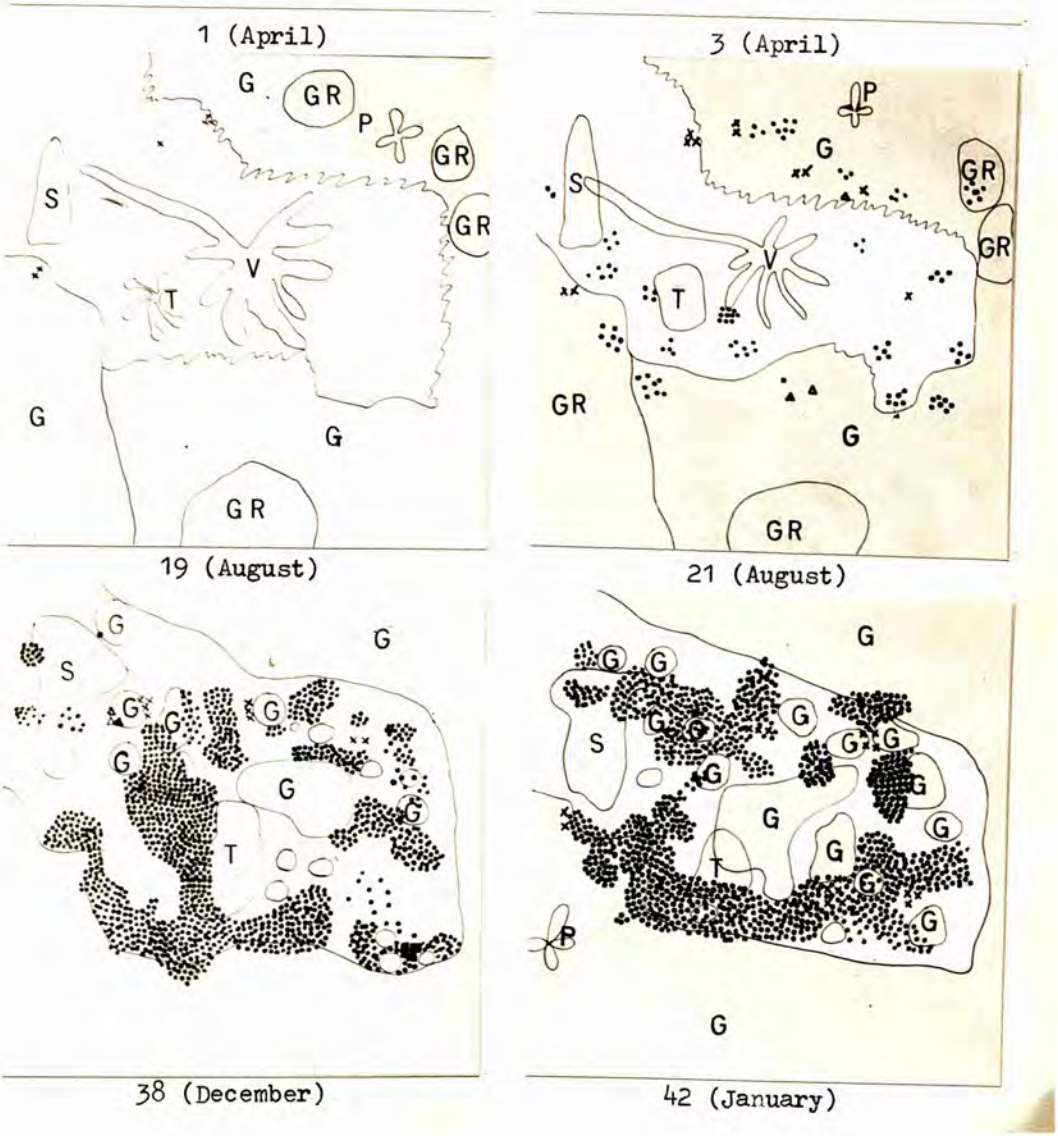
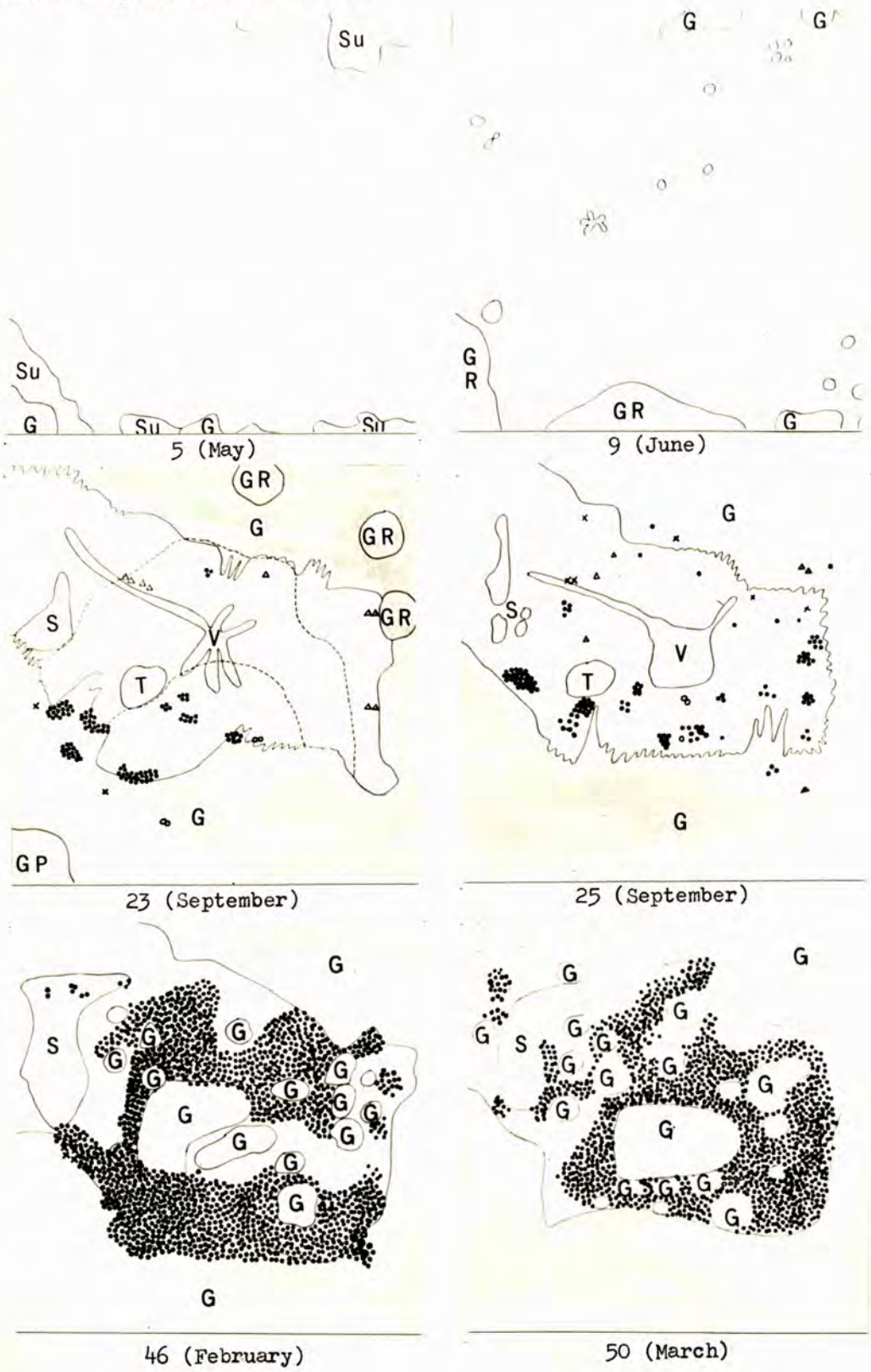
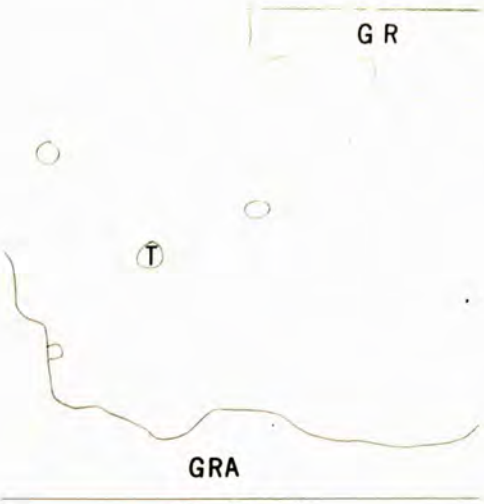
Fig. 5. The recolonisation of site B8.



No.'s = age of site in weeks.





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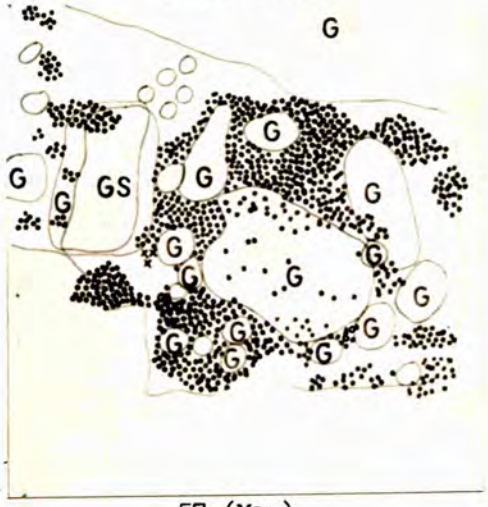
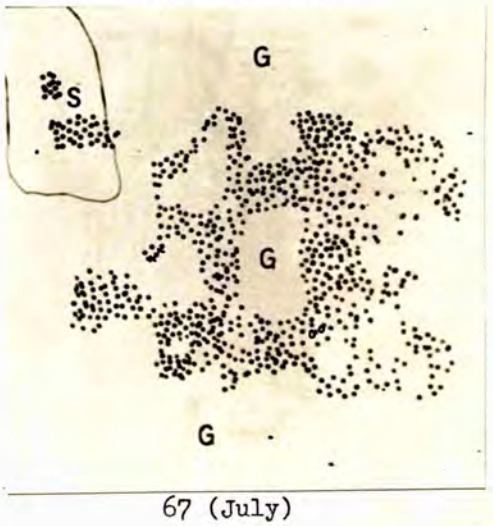
29 (October)

33 (November)



57 (May)



67 (July)

appeared five weeks after burning, a few scattered shoots and seedlings being found at the edges of the sites particularly on areas which had only been scorched by the fire. At this time a green film was also apparent on the soil surface. Initially this was not contributed to by protonemata, since close laboratory examination of the surface soil showed that although algae were present within three weeks, protonemata did not appear until nine weeks after burning (fig. 6).

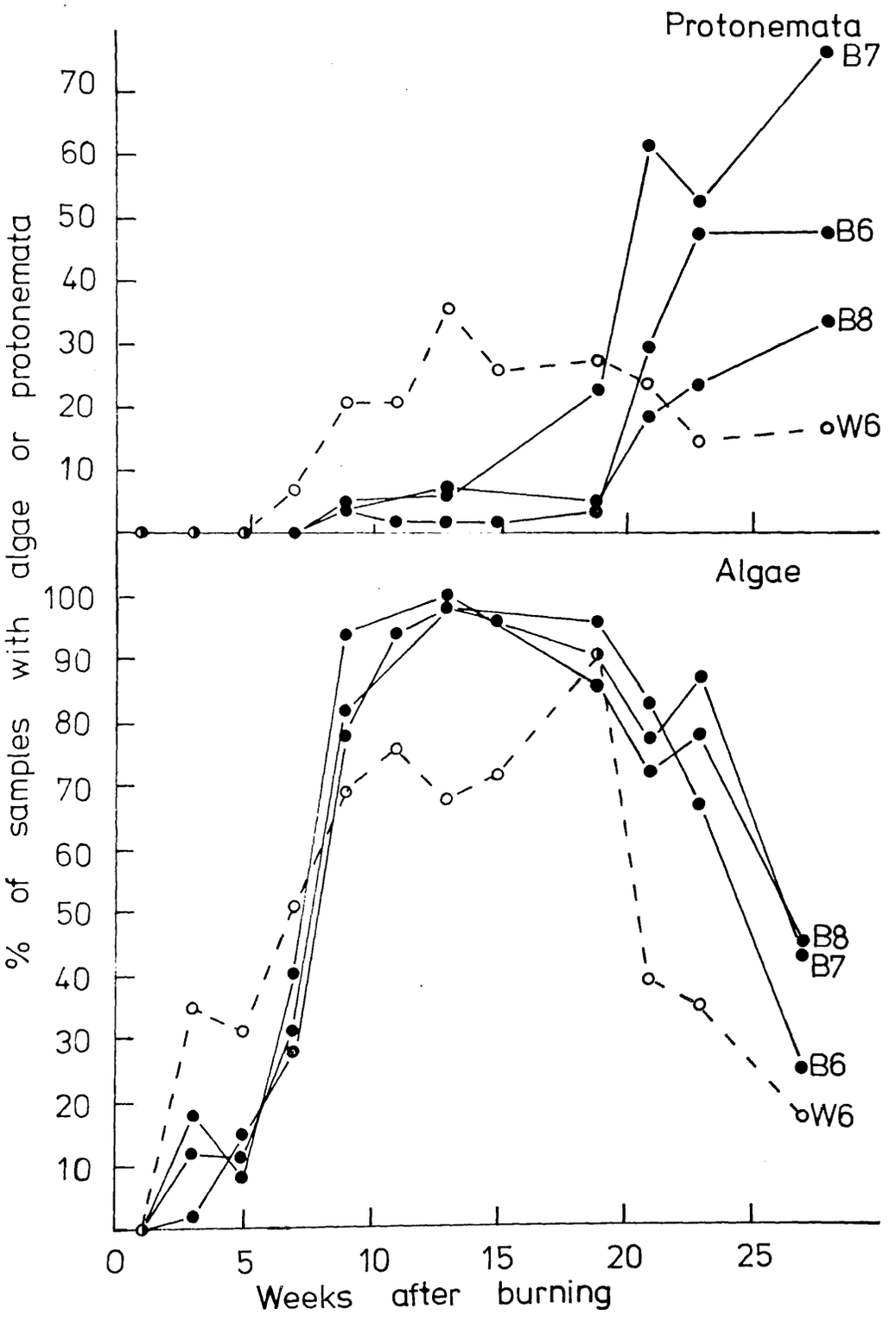
By the time protonemata first appeared, several species of angiosperms were recognisable in the invading vegetation including grasses characteristic of the unburnt vegetation, plus Achillea millefolium, Plantago lanceolata, Rumex acetosa, Trifolium repens, Vicia sativa and species of Compositae.

Gametophores were first visible in the field 18 weeks after burning, scattered leafy shoots being present on all three sites. Although most of these were immature and could not yet be identified, a few shoots of Bryum argenteum were noted on sites B7 and B8, this species being easy to recognise because of its distinctive shoot form and colour.

Angiosperms by this time covered 33-50 percent of sites B6 and B7 and 50-75 percent of site B8. Grasses and Rumex acetosa were the most important colonisers, whilst in addition to the species already mentioned the following were now present: Ranunculus repens, Trifolium dubium and Veronica chamaedrys.

Between the 19th and the 21st weeks a notable increase in the abundance of bryophyte gametophores and protonemata was found in

Fig. 6. The recolonisation of sites B6, B7, B8 and W6 by protonemata and algae.



the surface soil, whilst the percentage frequency of algae decreased (fig. 6). As shown by the vegetation maps an increase in the number of gametophores was also seen in the field. Moss shoots were more mature and in addition to Bryum argenteum, it was now possible to recognise Funaria hygrometrica as the most abundant species and to distinguish a third species, later found to be Ceratodon purpureus.

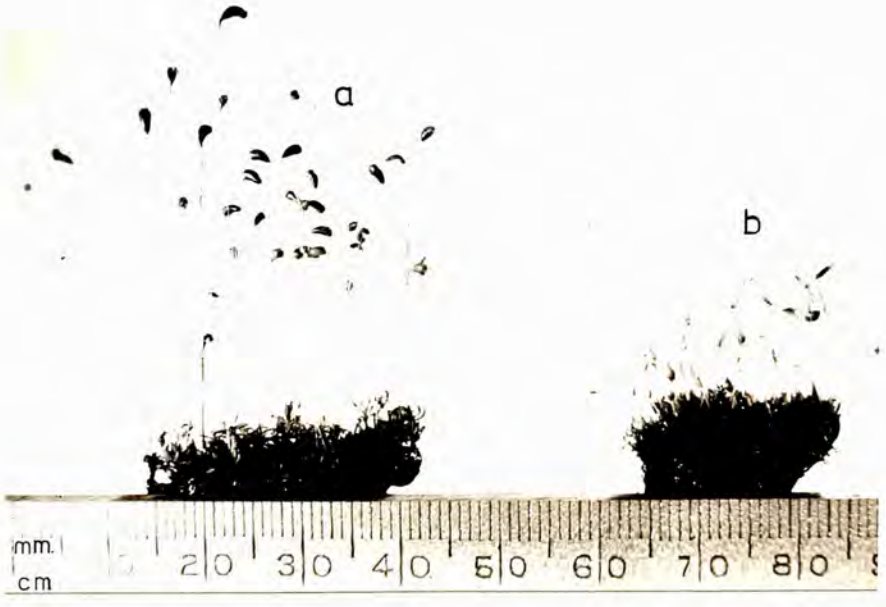
The angiosperm cover continued to increase up to the beginning of September, 23 weeks after burning, by which time it covered at least 50 percent of all three sites. Further encroachment of the sites however, was slow, until the early summer of the following year when active angiosperm growth was again resumed. In fact there was some decrease in the shading effect of the angiosperms during the winter months due to the dying back of flowering heads and vegetative shoots, which in some species had reached a third of a metre or more in height during the summer. Although close laboratory examination of the surface soil was discontinued after 29 weeks, it was apparent from field observations that in contrast to the angiosperms, the bryophytes continued to increase in abundance. By the 29th week, in mid-October, Funaria hygrometrica was very conspicuous, forming large pure colonies, whilst Bryum argenteum and Ceratodon purpureus occurred as scattered shoots or small colonies amongst the Funaria hygrometrica. A few shoots of a tuberous species of Bryum were also found, on B8, whilst Barbula convoluta was noted on B7, 31 weeks after burning and had formed two colonies, some 2 cm. across, by the 42nd week. Sporogonia were also first noted on Funaria hygrometrica

after 31 weeks.

Snow and ground frost appeared to have some effect on both Funaria hygrometrica and Bryum argenteum, many shoots during the winter months, November to February, appearing brownish and possessing leaves with blackened edges. In addition most of the Funaria hygrometrica capsules produced at this time were abnormal in appearance, although cultures maintained at a temperature just above freezing in a nearby greenhouse, formed large numbers of normal capsules (fig. 7). Mature capsules containing viable spores were not abundant in the field until May 1968. In spite of the adverse effects of cold weather the bryophytes reached their maximum percentage cover during the winter and early spring. By mid-December Funaria hygrometrica covered most of the exposed surfaces of sites B6 and B7 although Bryum argenteum, Ceratodon purpureus and tuberous species of Bryum still occurred as scattered shoots and colonies amongst the Funaria hygrometrica. On site B8, Funaria hygrometrica was also abundant but possibly due to the disturbance of this site by moles 23 weeks after burning (fig. 5) and its more rapid recolonisation by angiosperms, the bryophyte cover never reached a Domin rating higher than 6, whereas sites B6 and B7 reached Domin ratings of 7 and 8 respectively.

In May 1968, 57 weeks after burning, the new season's growth of angiosperms began to be apparent and much of the bryophyte growth which had become established during the winter months became hidden.

Fig. 7.



a) Funaria hygrometrica grown in the greenhouse.

b) Material of comparable age, collected from the field in January, showing the effect of cold weather on capsule development.

By early June all three sites were almost completely covered by angiosperms and shoots of all the bryophyte species were etiolated and much overgrown by roots (fig. 8). Funaria hygrometrica however, remained abundant and Bryum argenteum and Ceratodon purpureus could still be found, although Bryum argenteum was absent from site B6 by July. Funaria hygrometrica and Ceratodon purpureus were still present in October but much of their growth appeared dead and from the angiosperm point of view it was difficult to distinguish the bonfire sites from the surrounding unburnt vegetation.

Control site W6

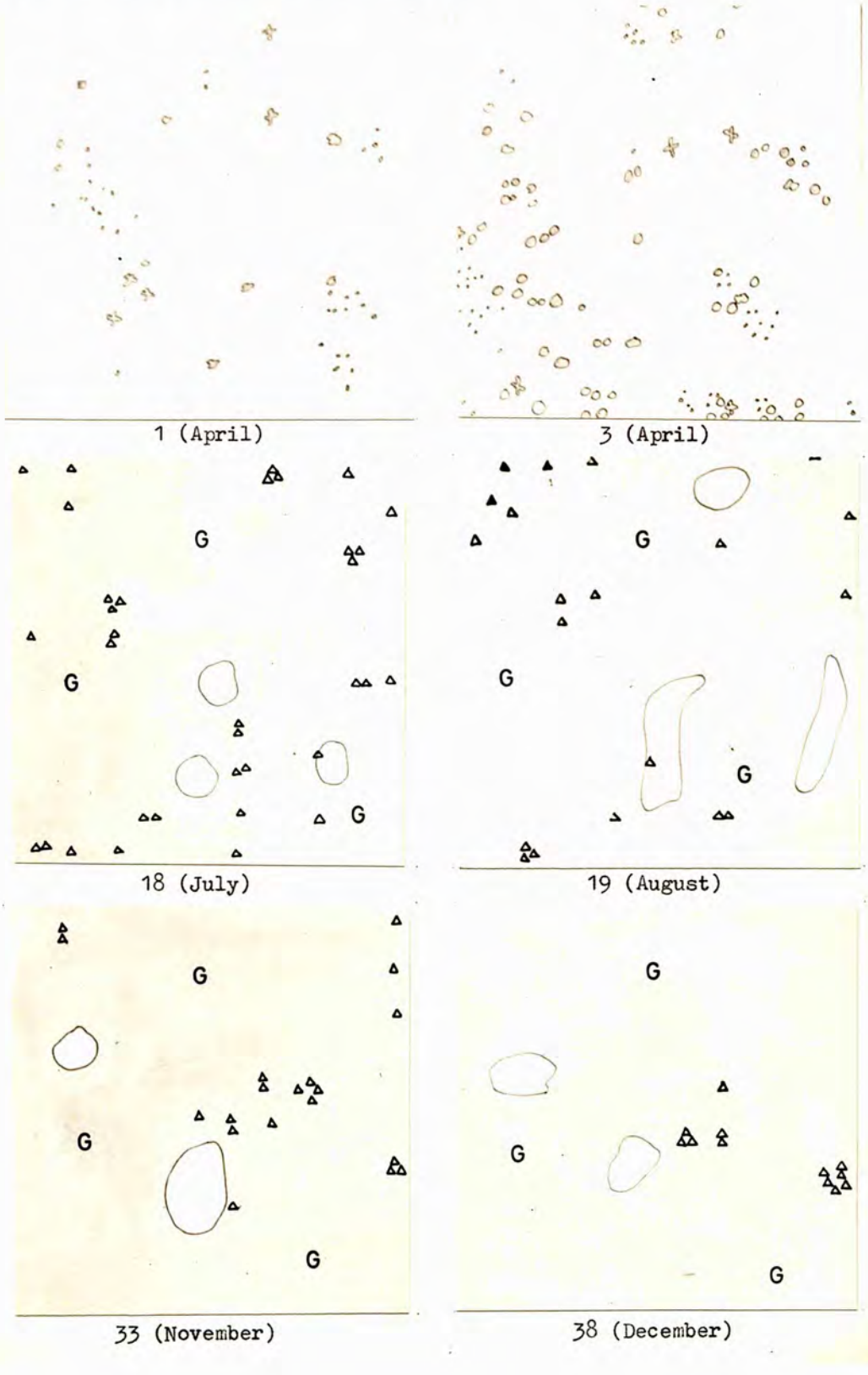
Changes in the angiosperm and bryophyte cover of this site are shown in fig. 9.

Recolonisation of the site was very rapid. Seedlings and new angiosperm shoots were found within the first week after weeding scattered over the whole site and not confined to the edges as they were on the bonfire sites. Within 11 weeks angiosperms covered 75 percent of the site and after 18 weeks 90 percent, all the species being characteristic of the surrounding unburnt vegetation. Close examination of the surface soil showed that as on the bonfire sites, algae were present within 3 weeks but protonemata were present a little earlier, after 7 weeks (fig. 6). Gametophores were also visible in the field sooner than on the bonfire sites, i.e. after 11 weeks, but increased in number gradually and did not show a sudden increase in abundance from the 19th to the 21st week. Throughout

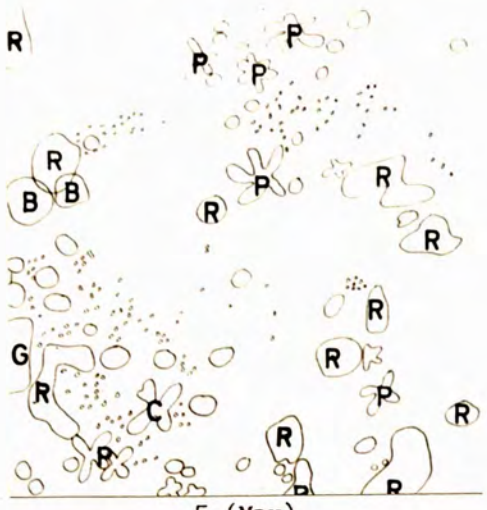
Fig. 8.

Etiolated shoots of Funaria hygrometrica collected from B8, when the site had become almost completely covered by angiosperms.

Fig. 9. The recolonisation of site W6.



No.'s = age of site in weeks.



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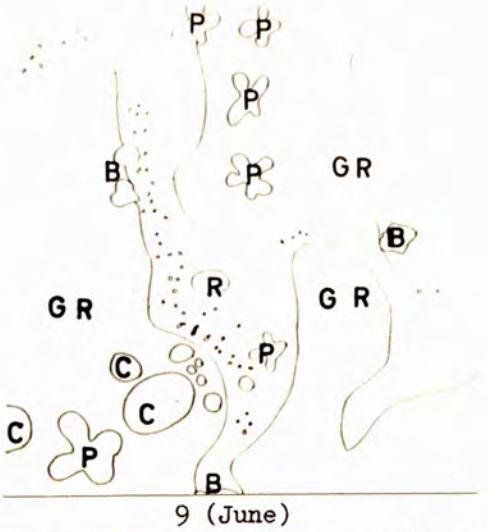

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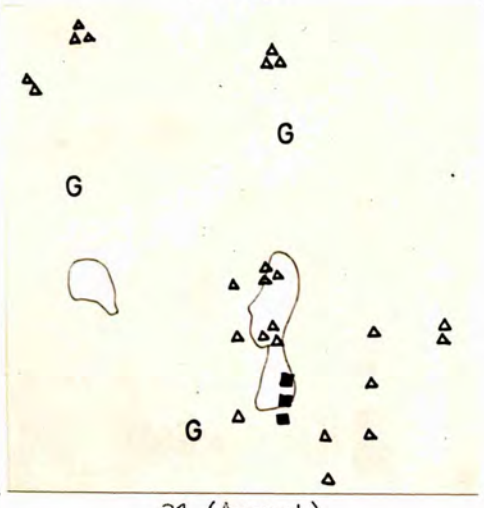

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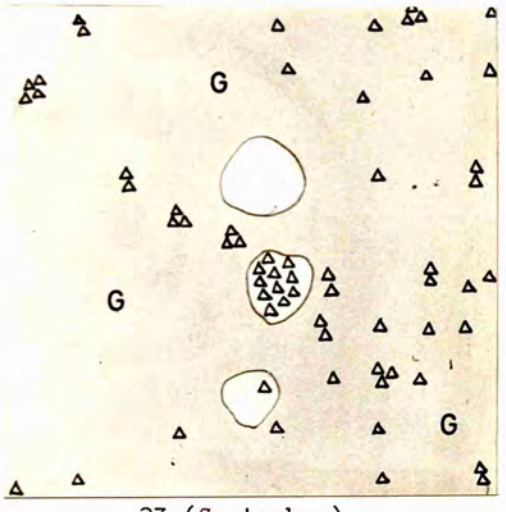

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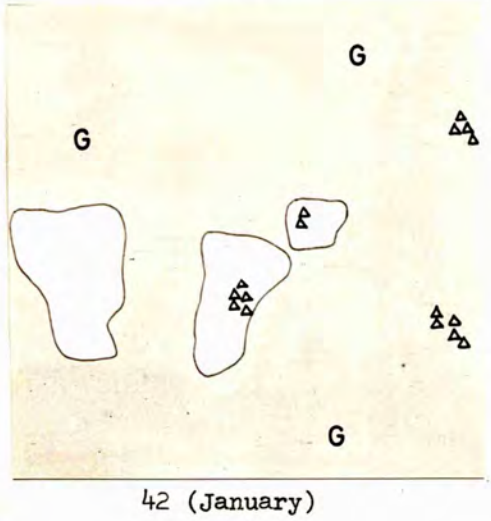

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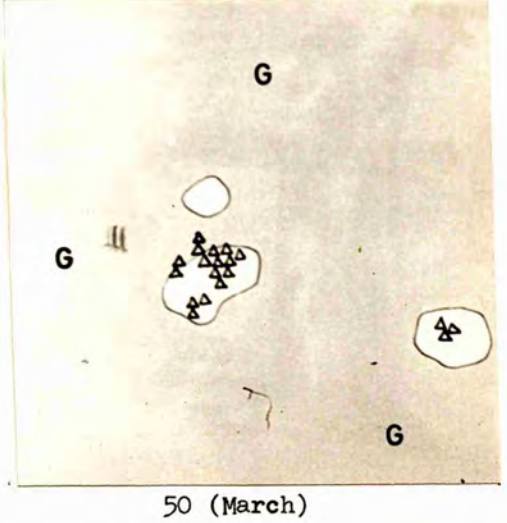

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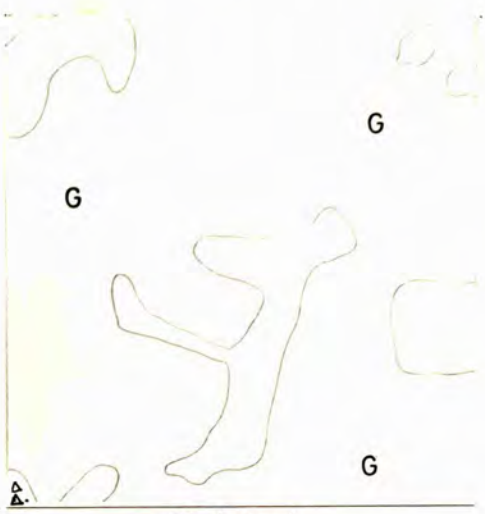

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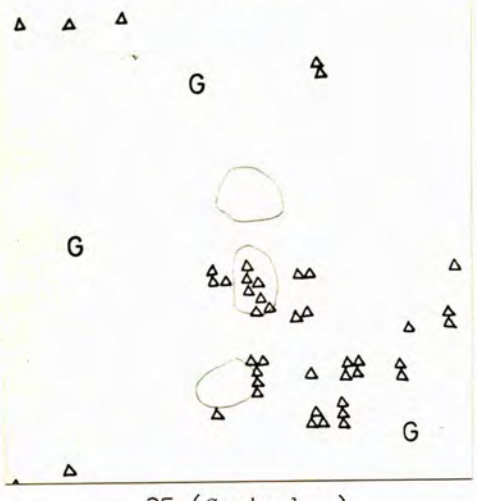
13 (June)



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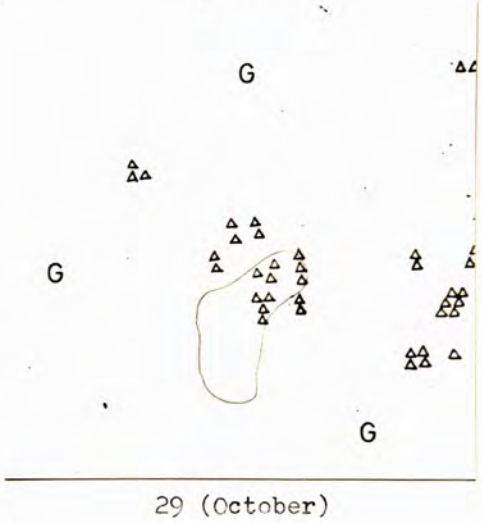

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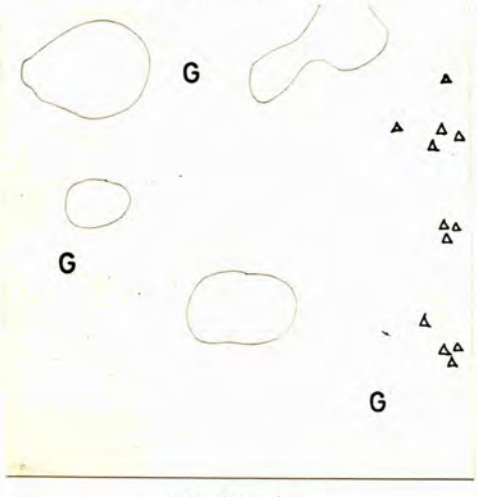


57 (May)

the period of observation bryophyte shoots remained scattered and had an etiolated appearance due to the shading effect of the angiosperms. Most of the shoots were of a species of Bryum which proved impossible to identify but shoots of Brachythecium rutabulum and a tuberous species of Bryum were also found. The maximum Domin rating of 4 was achieved in September 23 weeks after weeding, numbers of gametophores then decreasing. In October 1968 when the last visit to the site was made, no bryophytes could be found and angiosperms covered the whole site.

The study of sites B6, B7, B8 and W6, thus both confirmed and extended the information obtained in experiment 1 the major features of bonfire site recolonisation having been as follows:

1. Recolonisation by angiosperms and initially by bryophytes was slower than on the weeded control sites, but on both controls and bonfire sites, algae appeared after 3 weeks, reached their highest percentage frequency after about 3 months and then decreased in abundance.

2. Angiosperm recolonisation took place largely by invasion from the edges of the sites, whereas on the control sites, growth took place over the whole site from seeds and from roots and stems which had survived burning.

3. Protonemata were found 9 weeks after burning and although initially there were more bryophytes on the control sites, after 5 months bryophytes became more abundant on the bonfire site and

eventually had a much greater percentage cover. Bryophytes never became abundant on the control sites.

4. In spite of some evidence of damage to both shoots and capsules during cold weather, the maximum cover of mosses on the bonfire sites was reached during the late summer and winter of the first year after burning. This coincided with the dying back of angiosperm growth.

5. Funaria hygrometrica was the most conspicuous bryophyte, Bryum argenteum, Ceratodon purpureus and tuberous species of Bryum occurring as scattered shoots or small colonies amongst the Funaria hygrometrica. On the control sites however, the most abundant moss was an unidentifiable species of Bryum and other species present were Brachythecium rutabulum and tuberous species of Bryum.

6. The bryophytes were crowded out by the dense angiosperm growth in the second summer after burning. On the control sites where angiosperm recolonisation was more rapid, bryophytes began to decrease in abundance after the first summer.

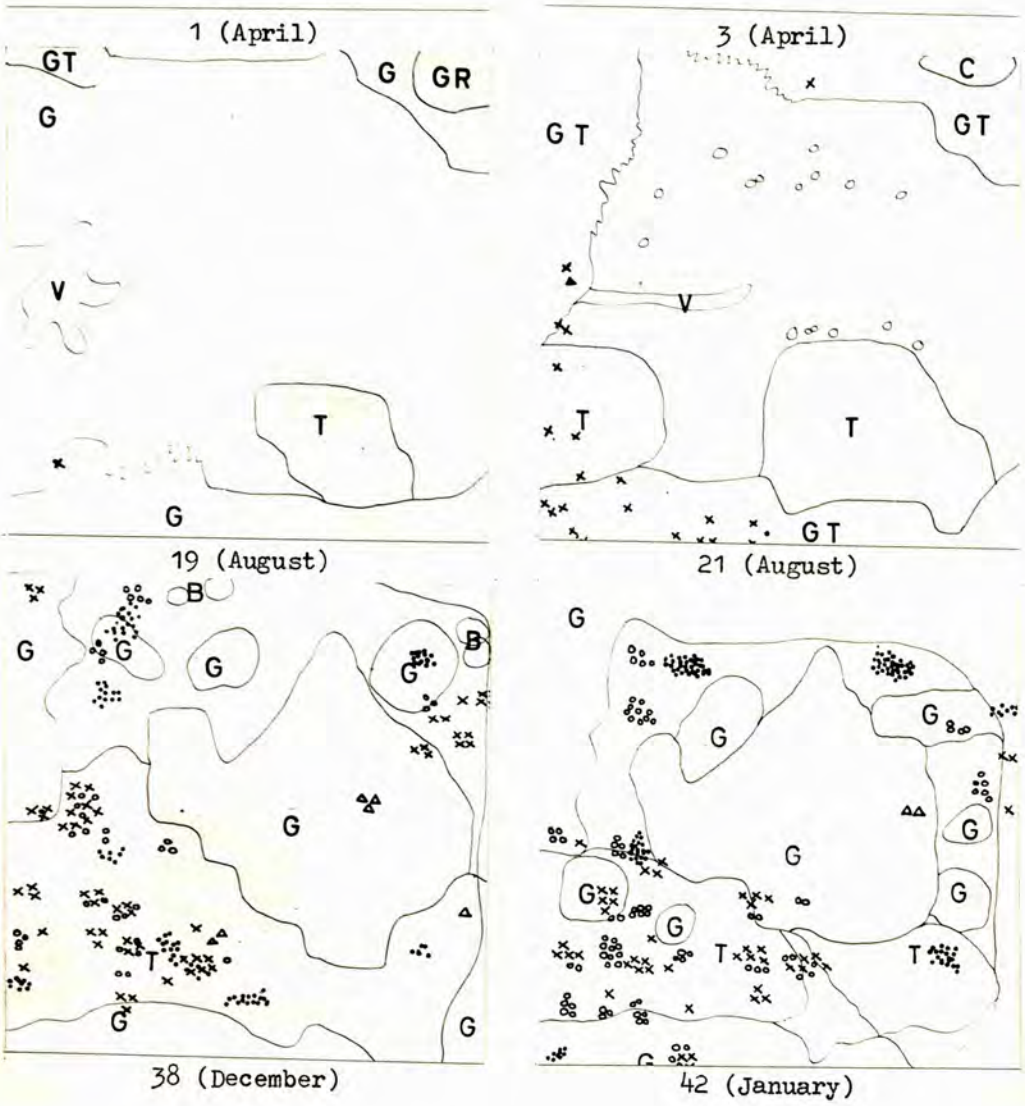
7. Disturbance of the soil surface as on site B8, appeared to reduce the abundance of mosses.

Further information about the factors influencing the course of the recolonisation emerged from the study of the other sites.

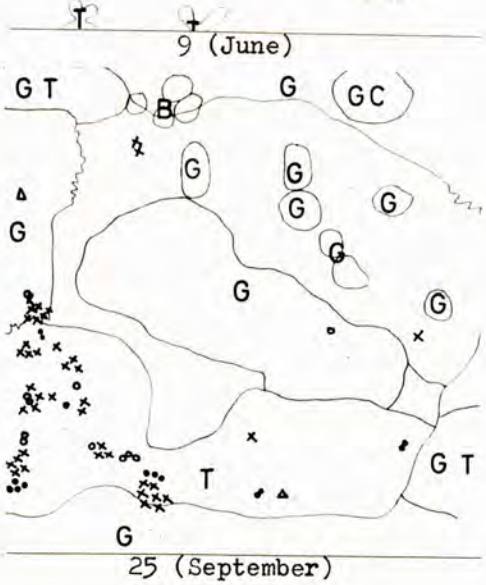
Site B12, the bonfire site from which the ash was removed and site A1 to which ash was added

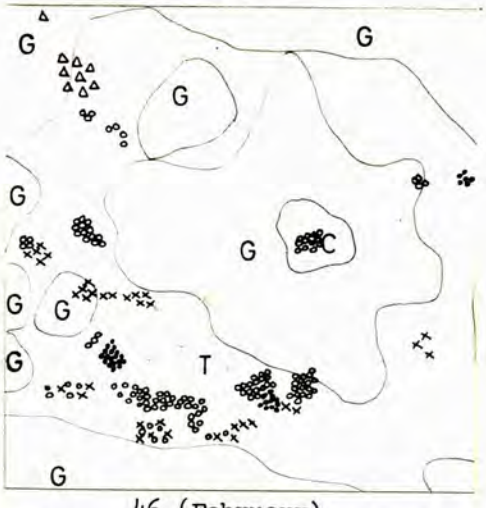
Fig. 10 and 11 illustrate changes in the bryophyte and angiosperm covers of these sites.

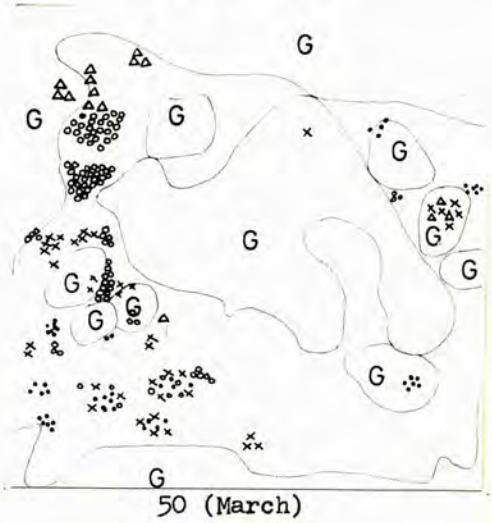
Fig. 10. The recolonisation of site B12.

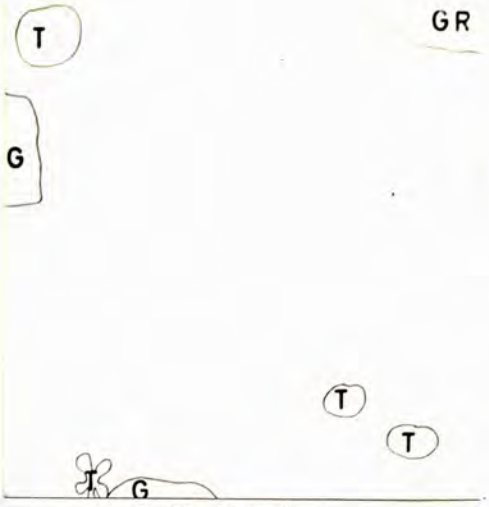


No.'s = age of site in weeks.









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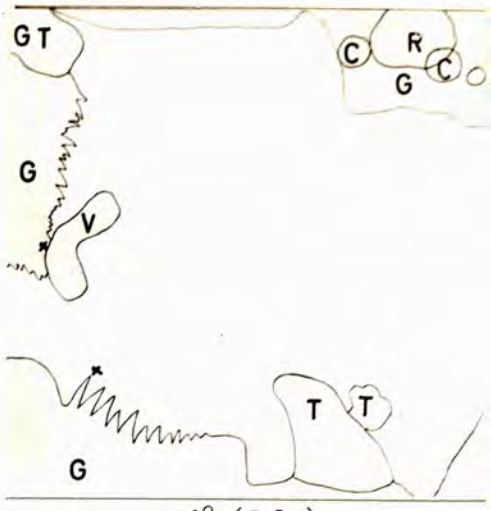

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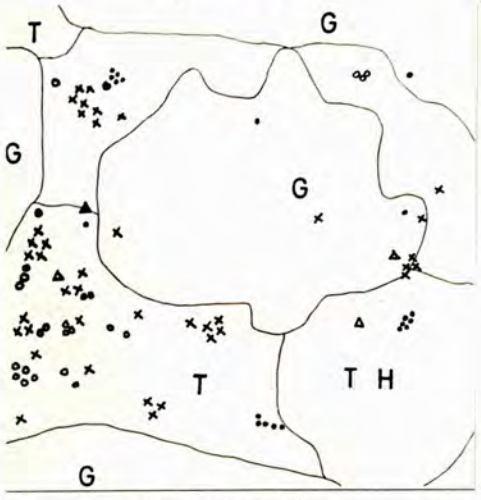

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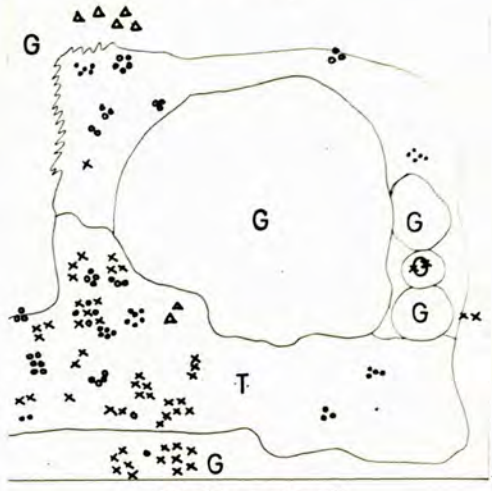

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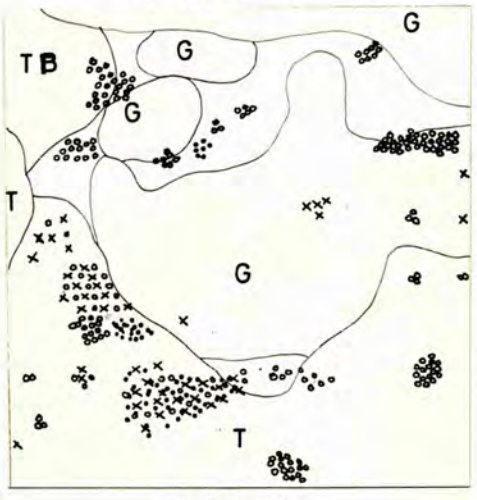
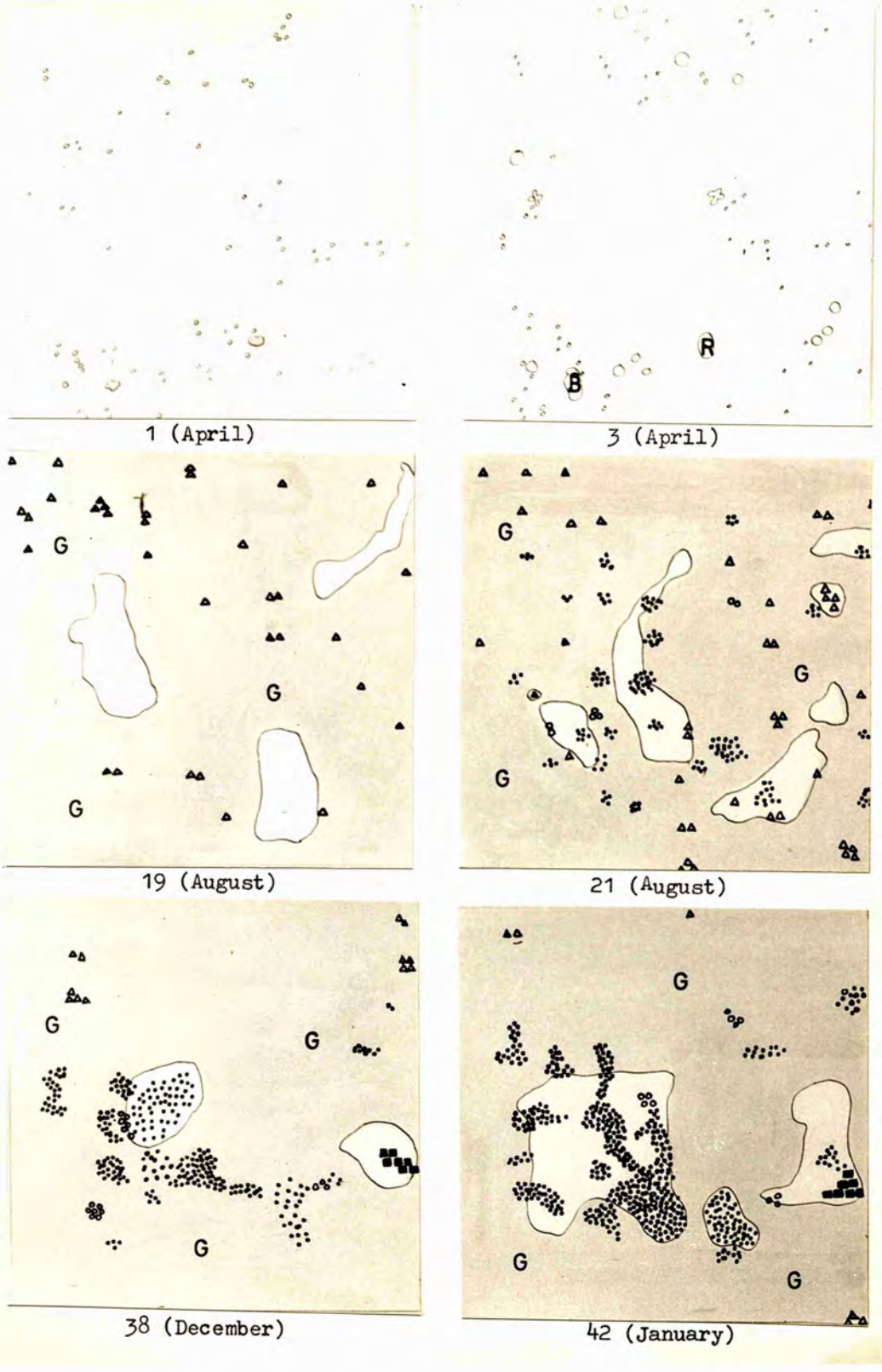


57 (May)

Fig. 11. The recolonisation of site A1.

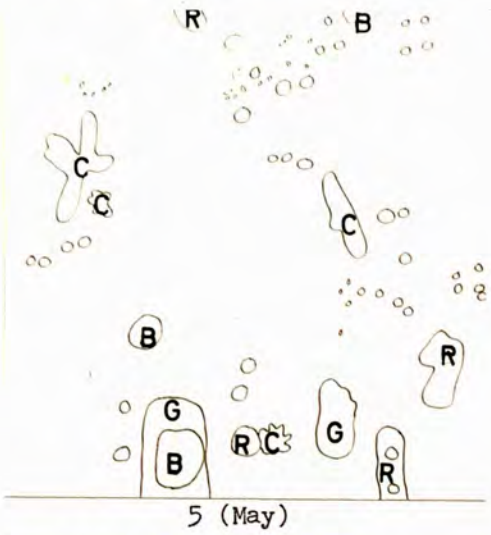


1 (April) 3 (April)

19 (August) 21 (August)

38 (December) 42 (January)

No's = age of site in weeks.



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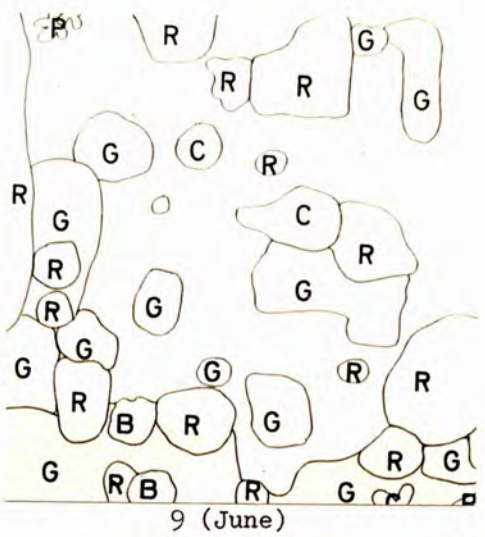

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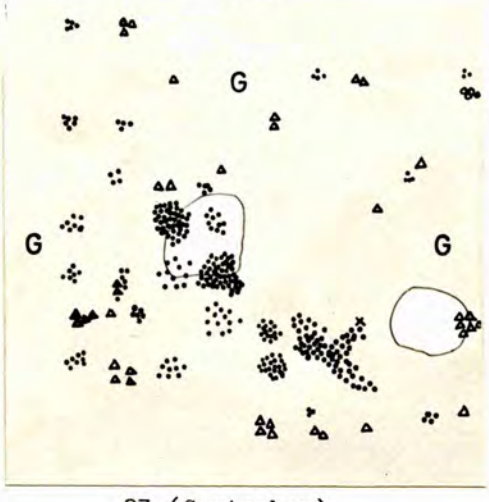

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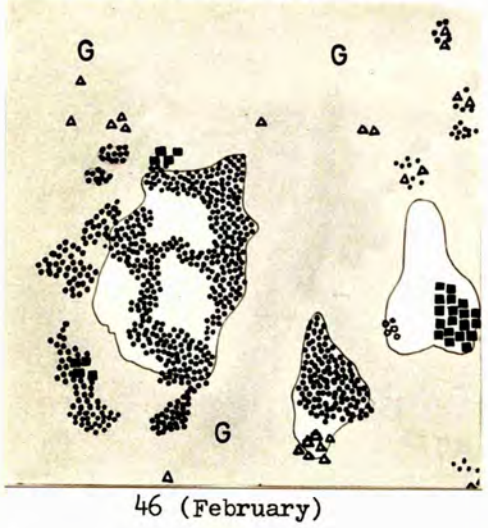

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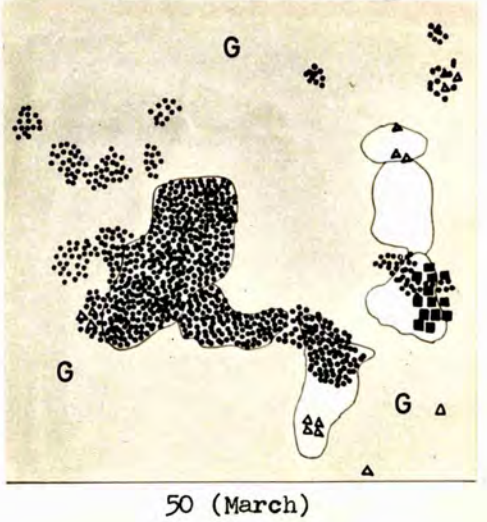

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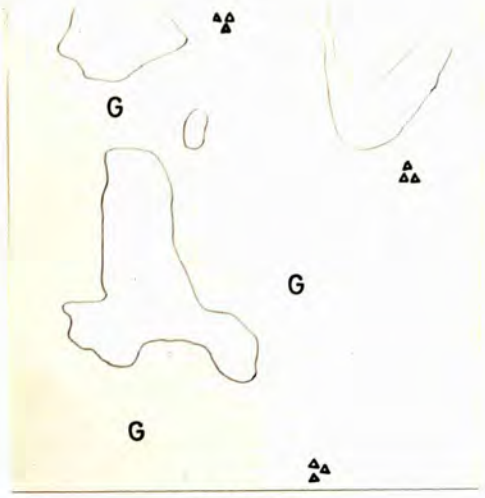

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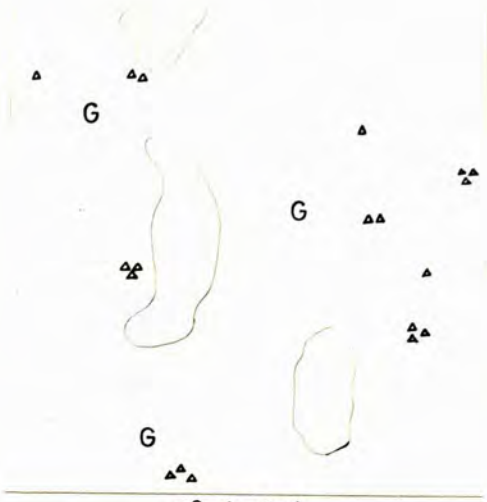

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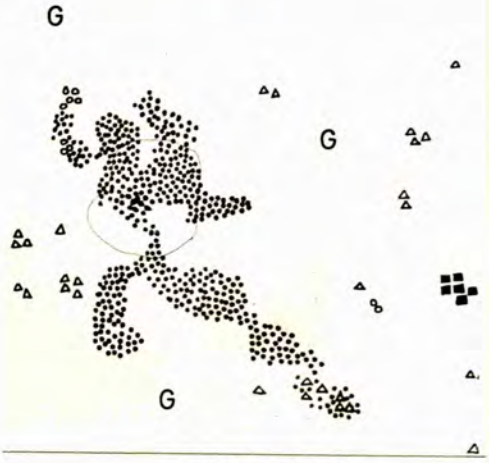

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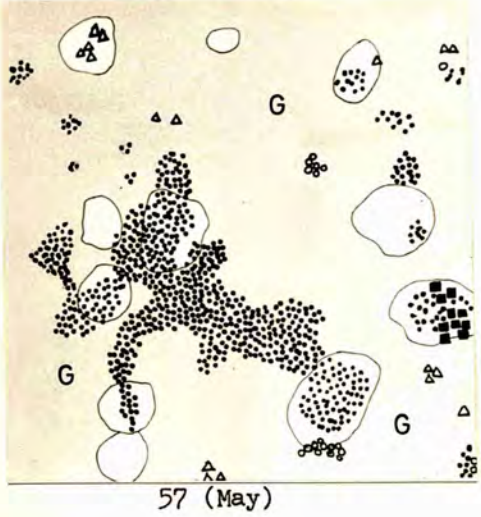

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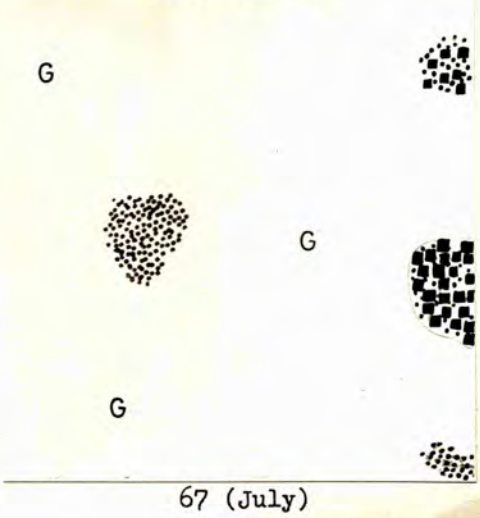


67 (July)

Angiosperms were found on site A1 in the first week after the setting up of the site and within 13 weeks covered nearly the whole site, all the species being characteristic of the pre-burn vegetation. Thus recolonisation took place as rapidly as on the control site W6 though growth was more luxuriant and not so dense. On site B12 however, angiosperms first occurred mainly at the edges of the site, 9 weeks after burning. As on the bonfire sites recolonisation was largely by invasion, with grasses and Trifolium repens being the most conspicuous species. Angiosperms did not attain a percentage cover of 75 percent until 25 weeks after burning, recolonisation thus being slower than on the control sites but more rapid than on the bonfire sites.

The recolonisation of site A1 was thus similar to that of a control site and of site B12 more similar to that of a bonfire site, the angiosperm recolonisation of neither being much affected by the deposition or removal of ash. In contrast the growth of bryophytes was significantly affected by the presence or absence of ash. On site A1 gametophores were visible in the field a little earlier than on the bonfire sites, after 13 weeks, but as on the bonfire sites, there was a notable increase in their abundance from the 19th to the 21st week. By this time it was possible to recognise Funaria hygrometrica as the most abundant species, Ceratodon purpureus also being present. Later it became possible to identify the other shoots present as Bryum argenteum and tuberous species of Bryum. Though the characteristic bonfire species of bryophytes were present, shoots

particularly of Bryum argenteum did not reach such a high percentage cover as on bonfire sites B6, B7 and B8. A cover of 20 percent reached by August of the first year increased only slightly and then decreased when the new growth of angiosperms began in the following year. In June 1968, 61 weeks after burning, Funaria hygrometrica was still present together with shoots of Ceratodon purpureus. Funaria hygrometrica however, then became less abundant, shoots of a tuberous species of Bryum, Bryum rubens, increasing in number and becoming the most conspicuous moss by October 1968. On site B12 as on the bonfire sites, bryophytes were first visible in the field 18 weeks after burning. Bryum argenteum was the first species recognisable, with Funaria hygrometrica and Ceratodon purpureus becoming identifiable a little later. In contrast to the bonfire sites however, Bryum argenteum became the most abundant species on the site and remained the most conspicuous moss until February 1968 when Ceratodon purpureus became more abundant. By June 1968 the bryophytes had become overgrown by angiosperms and whilst a few shoots of Funaria hygrometrica and Ceratodon purpureus were still present, Bryum argenteum had disappeared.

The deposition of ash therefore appears to promote the growth of the bonfire species of bryophytes on weeded ground, but the removal of ash from a bonfire site was not sufficient to prevent them colonising this site. On neither site however, did Funaria hygrometrica form an extensive turf or bryophytes reach a Domin rating of more than 5.

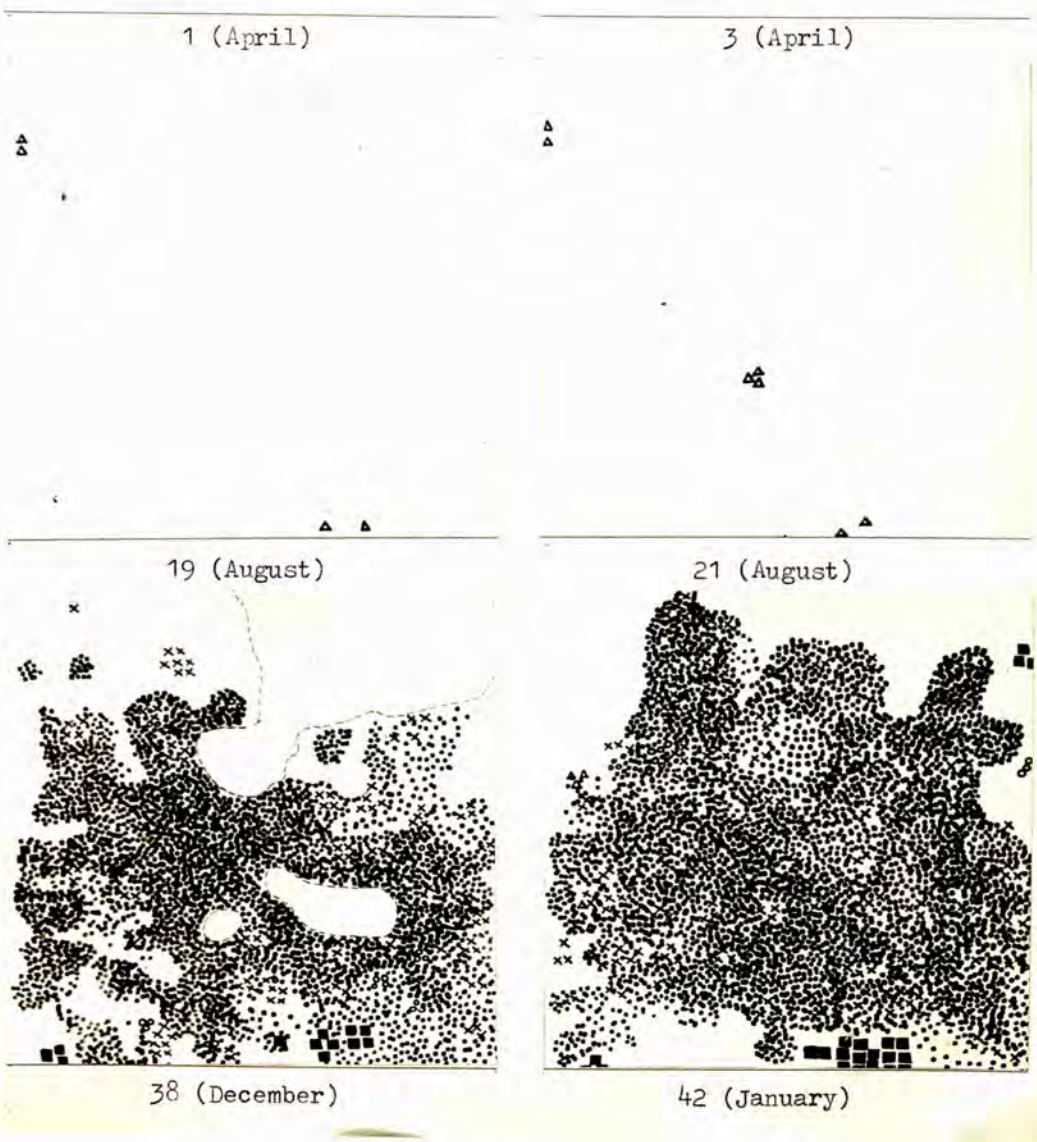
Bonfire site B13 and weeded site W7, the sites kept free of angiosperms by continued weeding.

Changes in the bryophyte cover of these two sites are shown in fig. 12 and 13.

Bryophytes appeared a little sooner than on the comparable bonfire and weeded sites. On bonfire site B13 leafy shoots of Brachythecium rutabulum and Bryum argenteum were first seen 13 weeks after burning at the edges of the site. A notable increase in the abundance of bryophytes occurred from the 23rd to the 25th weeks when Funaria hygrometrica, Ceratodon purpureus and tuberous species of Bryum appeared alongside the increased numbers of Bryum argenteum shoots. Funaria hygrometrica continued to increase in abundance becoming more anundant than on any of the other sites and reaching its maximum percentage cover by mid-February, 46 weeks after burning. At this stage other species characteristically only occurred as scattered shoots, although Bryum argenteum was fairly abundant. In spite of the lack of angiosperm competition bryophytes never covered the whole site. The edges of the site did not seem to be colonised, possibly because these had not been subjected to the full effect of the fire, whilst disturbance by small mammals and birds resulted in the baring of small patches. Bryophytes mainly Funaria hygrometrica still had an extensive cover when observations of the site were terminated in October 1968.

On site W7, gametophores of an unidentifiable species of Bryum were found 9 weeks after the initial weeding. As on the

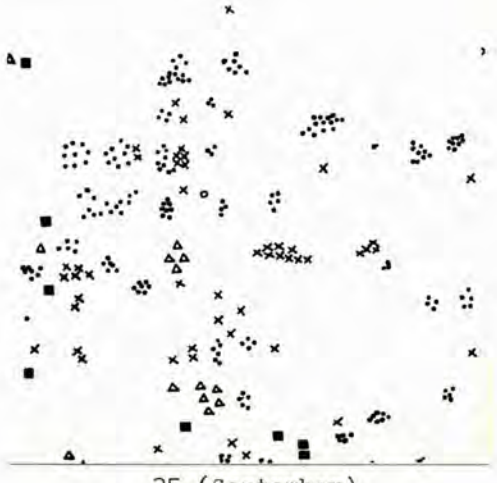
Fig. 12. The recolonisation of site B13.



No.'s = age of site in weeks.

5 (May)

9 (June)



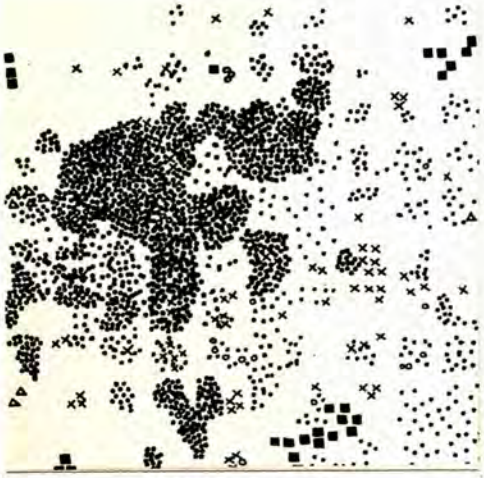
23 (September)

25 (September)

46 (February)

50 (March)

13 (June)



18 (July)

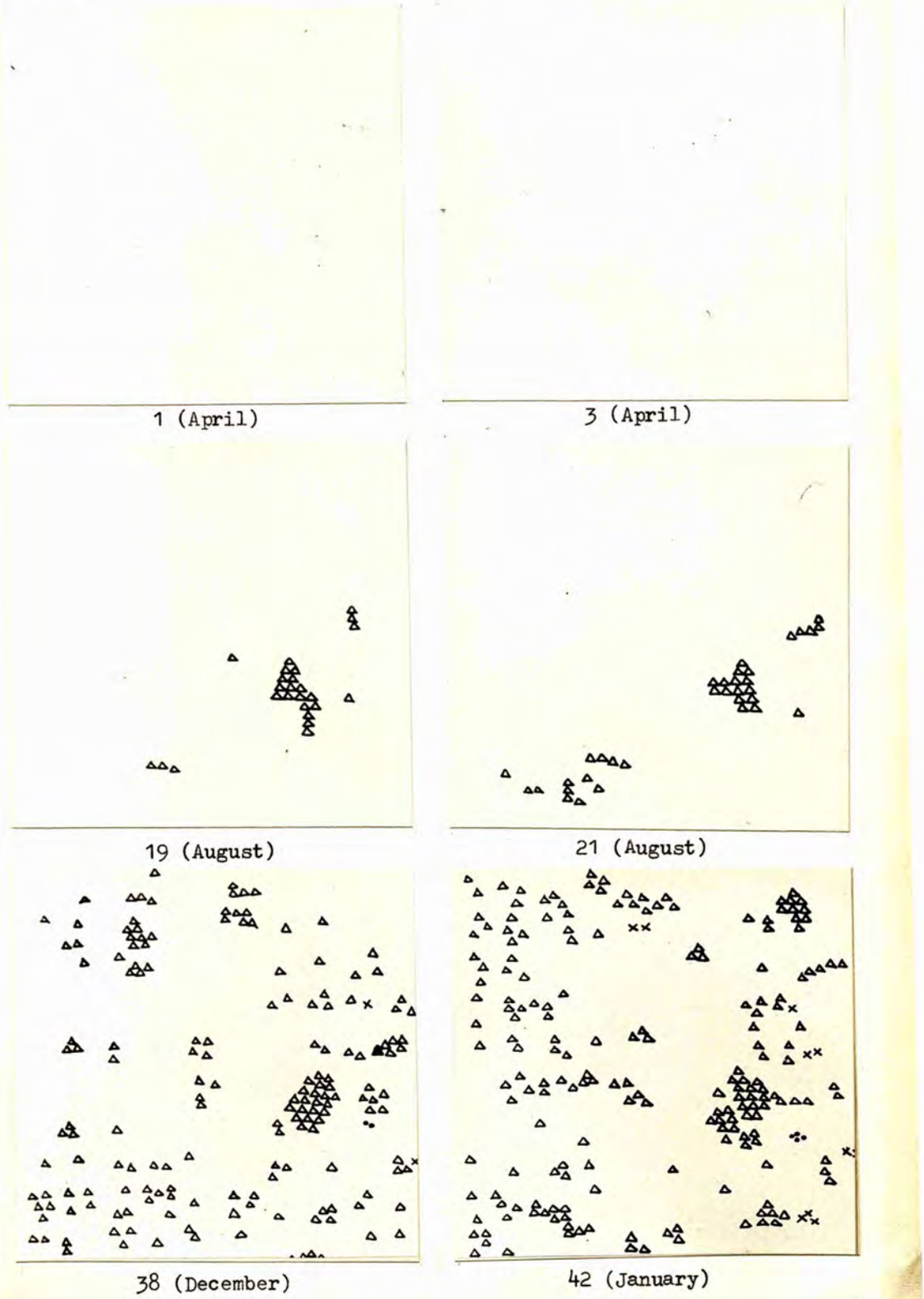
29 (October)

33 (November)

57 (May)

67 (July)

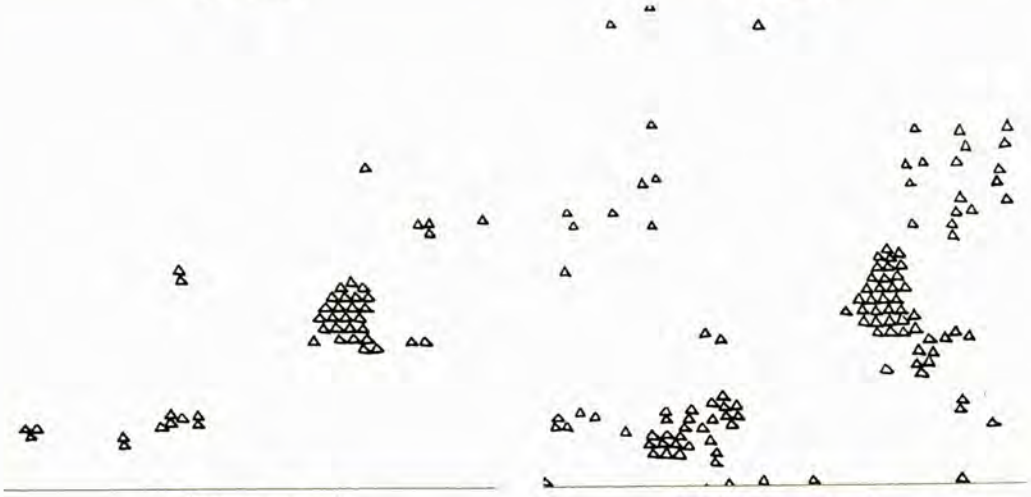
Fig. 13. The recolonisation of site W7.



No.'s = age of site in weeks.

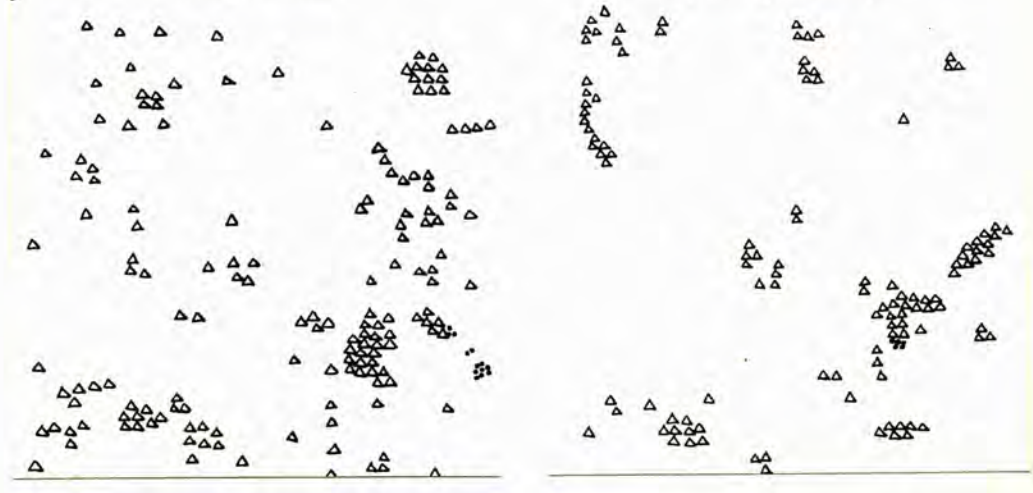
5 (May)

9 (June)



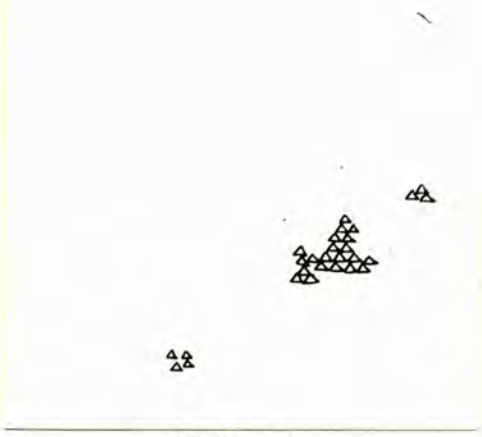
23 (September)

25 (September)

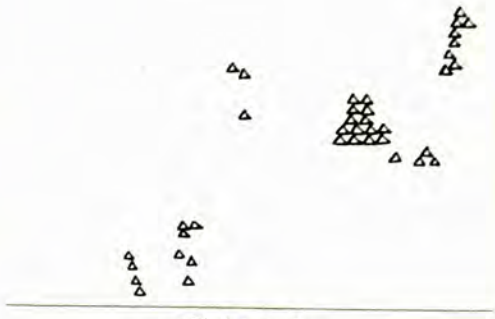


46 (February)

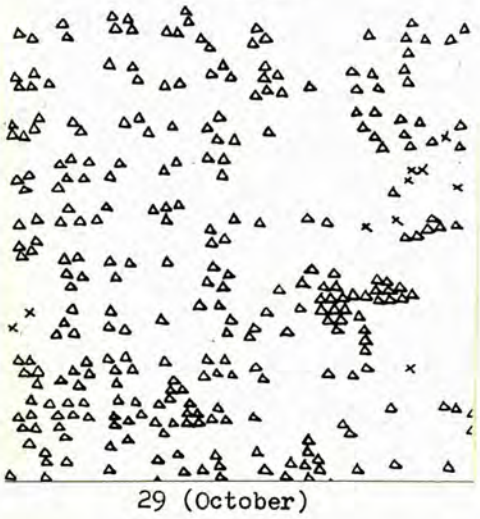
50 (March)



13 (June)

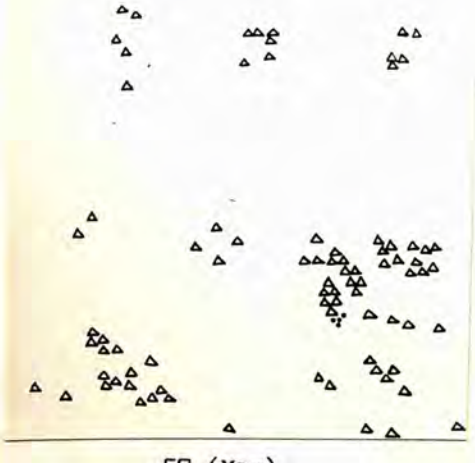


18 (July)

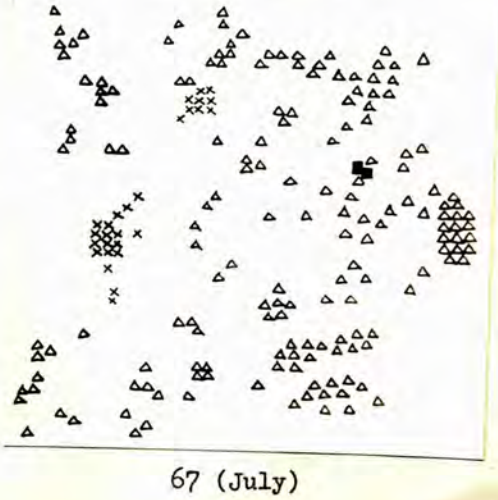


29 (October)

33 (November)



57 (May)



67 (July)

bonfire site the bryophytes increased noticeably from the 23rd to the 25th week, most of these shoots still being of an unidentifiable species of Bryum. After 18 weeks a second species, Leptobryum pyriforme was found.

Although the bryophyte cover attained a Domin rating of 6 (25-33 percent) within 27 weeks, shoots remained scattered. The cover of bryophytes appeared to decrease slightly during the winter, but increased to reach the same cover again by October 1968. By then Leptobryum pyriforme and tuberous species of Bryum were abundant, ~~and~~ whilst a small fruiting colony of Pottia truncata had been present since the 33rd week, together with a single rosette of Riccia glauca. A few shoots of Funaria hygrometrica were first noted in December 1967, 38 weeks after burning and Bryum argenteum occurred sporadically; neither of these two species however, became abundant.

The recolonisation of site B13 indicated that angiosperm competition is largely responsible for the decline in abundance of the bonfire bryophytes on the bonfire sites. Bryophytes remained abundant at the end of the second season of growth although on other bonfire sites they were scarce by this time. Removal of the angiosperms however, as was shown by site W7, was not in itself sufficient to promote the formation of the bonfire association of bryophytes, although scattered shoots of the bonfire species were

found on this site.

In experiment 2 seedlings were less frequent on the bonfire sites than on the weeded sites and were confined mainly to the edges of the sites. After 14 months when the numbers of seedlings on sites B13 and W7 were counted before weeding, a difference in both the number and variety of seedlings present was found, both being less on the bonfire site (table 5). Bonfire soil thus appears to have an inhibitive effect on seedling growth, which continues for a considerable time after burning.

Table 5. Seedlings present on sites B13 and W7 after 14 months (numbers of individuals).

Genus or family of seedling	Site	
	B13	W7
Compositae	4	8
Epilobium	8	3
Euphorbia	2	32
Ranunculus	0	5
Rumex	3	5
Trifolium	11	48
Veronica	14	9
Total no. of species	6	8
Total no. of seedlings	42	110

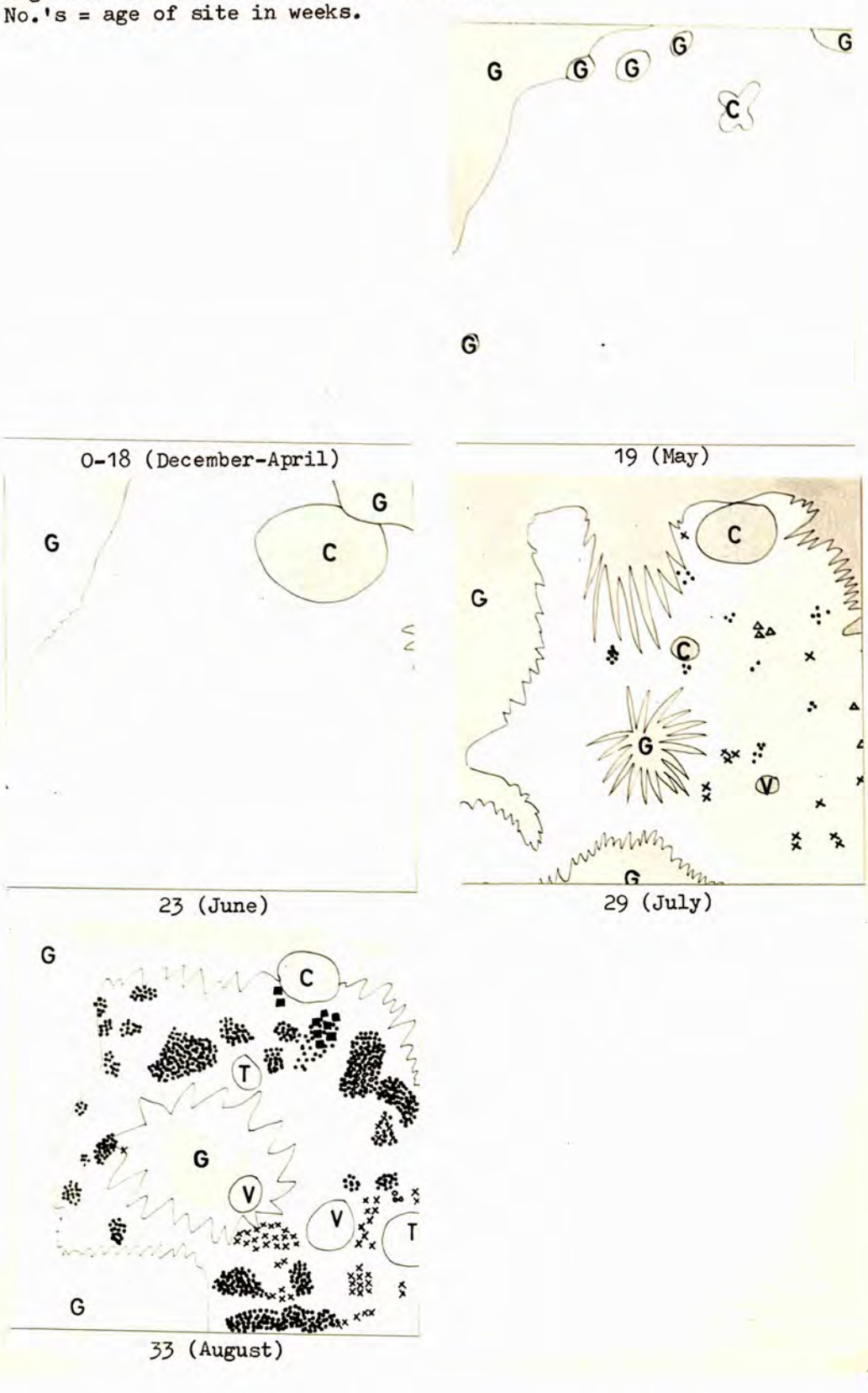
3. The effect of season on bonfire recolonisation

All the sites in Experiment 2 were set up in the spring; an additional bonfire site, B15 was therefore set up adjacent to the sites in Experiment 2 in December 1967, to find whether season of burning had any effect on recolonisation.

Recolonisation of this site by angiosperms followed a very similar course to that of the bonfire sites in Experiment 2, although as found for site B1 in Experiment 1, it was a little slower, vigorous growth not taking place until the early summer of the following year (fig. 14).

Recolonisation by bryophytes and algae as illustrated by fig. 15 was also delayed. Close examination of the surface soil showed that although algae were present as on the other bonfire sites, 3 weeks after burning, they did not become abundant until May of the following year, 19 weeks after burning. Protonemata were not found at all until 25 weeks after burning, first appearing in June as they did on the spring burnt sites. The bryophytes which were later identifiable as Funaria hygrometrica, Bryum argenteum, Ceratodon purpureus and tuberous species of Bryum formed a typical bonfire community.

Fig. 14. The recolonisation of site B15.
No.'s = age of site in weeks.



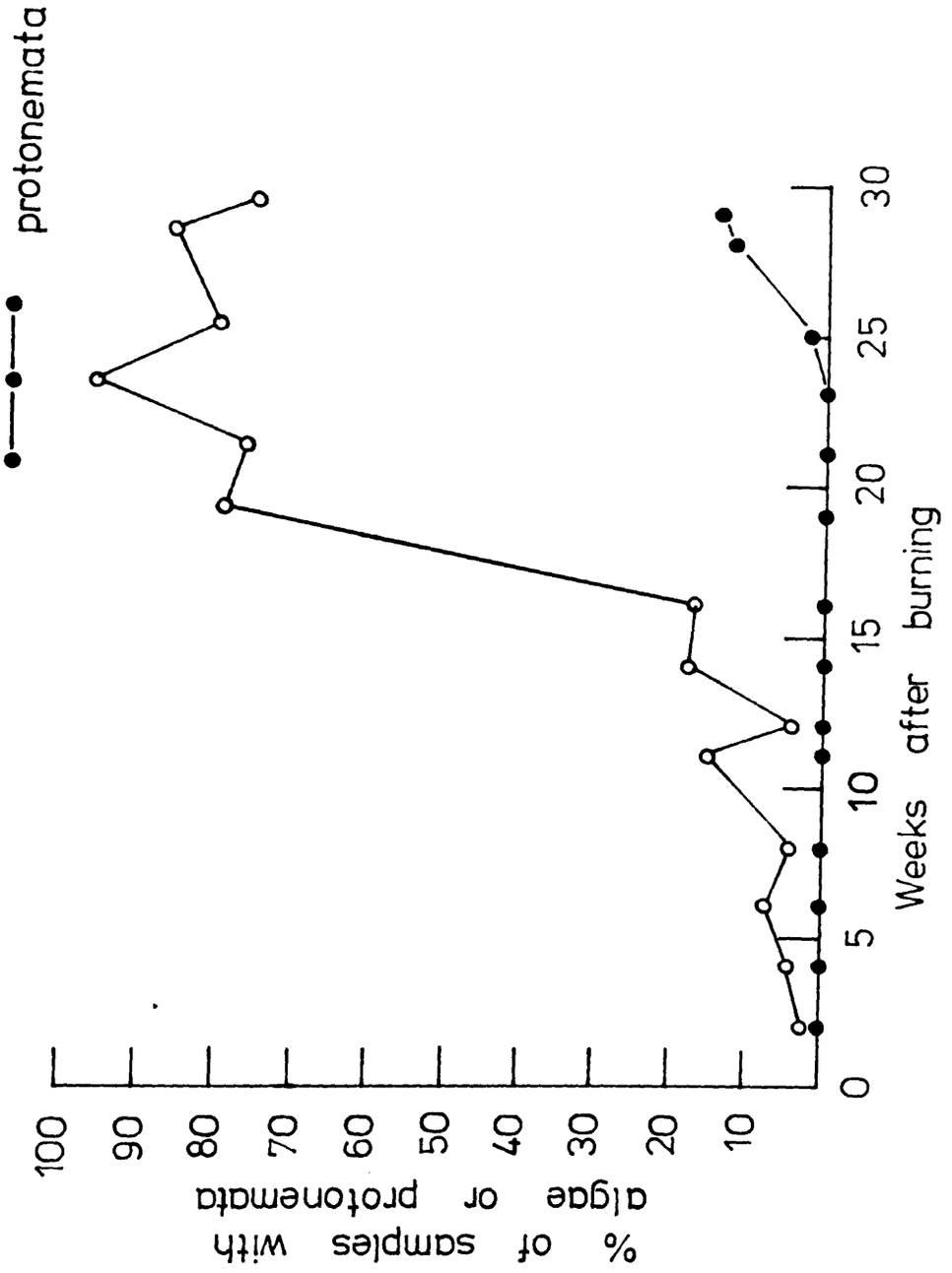


Fig. 15. The recolonisation of site B15 by protonemata and algae.

4. Recolonisation of simulated rapid fire sites

Three rapid fire sites R1, R2 and R3 were set up in April 1968, close to the sites in Experiment 2. Angiosperms were removed from R3 before burning, in order to produce the effect of a rapid fire without the deposition of ash. Rapid fire sites were simulated by running a Mc'Allen hooded flame gun over the surface of the ground for 30 minutes so that the surface soil was scorched and the vegetation of sites R1 and R2 also removed. Very little ash was present on any of these sites and particularly R3. Recolonisation was recorded in the same way as in Experiment 2, although time did not allow for such regular visiting of the sites, or for close examination of the surface soil for protonemata.

Within the first month after treatment, all three sites were abundantly colonised by seedlings and new shoots, which extended over the whole site, but no bryophytes were found. After 7 weeks, like the weeded site W6 in Experiment 2, all three sites were at least half covered by angiosperms. Gametophores were found a few weeks later but right up to the end of the sampling period in October 1968, 26 weeks after burning, these were confined to a few scattered shoots of an unidentfiable species of Bryum. Removal of the vegetation from site R3 before burning appeared to have no effect on the subsequent recolonisation.

The effect of the relatively light burning was thus not sufficient to retard the recolonisation by angiosperms, or to

promote the formation of the characteristic bonfire community of bryophytes.

5. The effect of adding nitrogen and phosphorus to unburnt soil

Cremer & Mount (1965) found that the stimulating effect of burning on growth of Funaria hygrometrica, could be reproduced on unburnt soil, by the addition of nitrogen and phosphorus in the form of blood and bone fertiliser. To test this observation fertilised plots were set up in July, 1968 close to the plots in Experiment 2. Four plots, each 0.6 m.sq., were weeded and the soil forked over. Blood and bone fertiliser was then mixed with the surface soil of two of the plots F1 and F2 in the amounts shown in table 6, the remaining two plots W8 and W9 being left as controls. A large bonfire B16, resulting from the burning of an old fence, lay close to the plots and since the fire occurred at approximately the same time as the sites were set up, this site was used for comparison. The sites were visited about once a month and notes made of any species present. Angiosperms were periodically removed by careful weeding, since Experiment 2 had indicated that angiosperm competition limited the growth of Funaria hygrometrica.

Table 6. Amount of blood and bone fertiliser added to Sites F1 and F2.

	gm. added	gm. N and P contained in fertiliser	
		N	P
Dry Blood	120	16.2	0
Bone Meal	360	14.4	34.6

Percentages of nitrogen and phosphorus in blood and bone fertiliser based on Figures supplied by C.D. Sutton (personal communication).

Protonemata and scattered gametophores were found on all the plots after 5 weeks but by the beginning of October, 13 weeks after the beginning of the experiment shoots were most abundant on the controls. A tuberous species of Bryum was the most conspicuous moss on all the sites, whilst scattered shoots of Brachythecium rutabulum were present on the control plots and a small clump of Bryum argenteum on one of the fertilised plots F1. Later a few shoots of Ceratodon purpureus and Pseudoscleropodium purum were found on the control sites. Bryophytes became abundant on all the plots, but remained as scattered shoots or colonies until observations were ended in January 1969, 26 weeks after the sites were first set up. Funaria hygrometrica was never seen on the fertilised sites although it was very conspicuous on the adjacent bonfire site, B15. Bryum argenteum and Ceratodon purpureus were also present on this site, but unusually Marchantia polymorpha was the most abundant bryophyte.

Thus the addition of nitrogen and phosphorus in the form of dried blood and bone meal did not promote the growth of Funaria hygrometrica. The presence of Marchantia polymorpha on the bonfire site is interesting because this was the only burnt site in this area on which it was found to occur.

II. SITES ON OTHER PARTS OF ENGLAND

In some cases sites were set up especially for this investigation, whilst the remainder resulted from accidental fires or the work of other persons in which case as much information as possible was obtained regarding the type and severity of the fire, the major components of the fuel and the date of burning. The majority of sites were in places where public access was either limited or controlled so that disturbance was reduced to a minimum.

Observations were carried out on both rapid fire sites and bonfire sites. The recolonisation of rapid fire sites was studied in an area of heather moorland on Cronkley Fell in Yorkshire and on Calluna Heath at South Haven Peninsula in Dorset. Bonfire sites were studied in both these areas and in addition on chalk grassland at Coombe Hill, Bucminghamshire and in a deciduous wood, Waterperry Wood, Oxfordshire.

The sites were visited as often as possible and in most cases every 3-4 months. Soil samples were collected and changes in the vegetation recorded by estimating percentage cover using the Domin scale, photographs, and in some cases hand drawn maps.

In addition to the sites mentioned above, other burnt sites were examined and records made of the species present. Again as much information as possible was obtained about the previous history of the sites, the date of burning and the type of fire from which they resulted. These sites were visited only once, or at the most infrequently so that the process of recolonisation was not followed, but a knowledge of the species present, together with the age of the site, provided valuable supplementary data for the study of recolonisation on the other sites.

Burrel (1917) working in Leeds and Gilbert (1968) working in Newcastle, found that the species of bryophytes found on bonfire sites in the present investigation were the only widespread ones in areas of high industrial pollution. Gilbert noted that Funaria hygrometrica appeared on walls, a habitat from which it was absent outside the polluted area. Investigations were carried out to confirm these observations.

The sites studied in detail at Coombe Hill, Waterperry Wood, South Haven Peninsula and Cronkley Fell are described first and then the effect of industrial pollution considered. All the other sites examined are described in table 9 (p.79).

Coombe Hill

Coombe Hill, an area of chalk grassland with a characteristic rendzina soil was, at the time of the investigation being encroached by shrubs, mainly Crataegus monogyna, Quercus robur and Sambucus nigra. Of the herbaceous plants Festuca ovina was the most conspicuous species, whilst Poa pratensis and Poterium sanguisorba were the only other species present in any abundance. Bryophytes were very scarce and only Eurhynchium praelongum and Pseudoscleropodium purum were found. It is probable that heavy grazing in the area was responsible for the poverty of both angiosperm and bryophyte species.

Activities of the Conservation Corps, aimed at clearing the encroaching shrubs, resulted in a number of burnt and disturbed sites. The recolonisation of one such site, A2 was followed, although little information could be obtained regarding its previous history. The site was about 0.7 m.sq. and appeared to consist of a pile of ash removed from other sites.

In March 1966 felled shrubs were used as fuel to set up a bonfire site B17. The size of the fire and its maximum temperature, 900°C, were similar to those of sites in Experiment 2 (table 3) but in Experiment 2 (table 3) but in contrast it was only allowed to burn for 3 hours and was also in a more exposed position, thus the soil rapidly lost the typical appearance of a bonfire soil, light ash particles being removed by wind and rain.

The area was visited at the followimg times after the setting up of the bonfire site B17; 2 weeks, 5, 8, 11, 14, 15, 17, 20 and 32 months.

Ash pile site A2

Observation of this site was started in August 1966, at which time a few shoots of an unidentifiable moss were present. 3 months later several other species of bryophytes were distinguishable including Funaria hygrometrica and Bryum argenteum. By February 1967, Phascum cuspidatum and the bonfire species Funaria hygrometrica, Bryum argenteum, Ceratodon purpureus and tuberous species of Bryum, Bryum ruderale and Bryum klinggraeffii, could all be recognised. Funaria hygrometrica however, was only present in small amounts and by May Phascum cuspidatum had become the most abundant species. During 1967 bryophytes formed a close turf and throughout the observation period angiosperms never became abundant. By November 1967 a mixed community of bryophytes was present composed of Funaria hygrometrica, Barbula convoluta, Brachythecium rutabulum, Bryum caespiticium, Bryum capillare, Ceratodon purpureus, Phascum cuspidatum and tuberous species of Bryum including Bryum klinggraeffii. 12 months later in November 1968 Barbula convoluta and a Bryum species without tubers were the most conspicuous mosses, but Funaria hygrometrica, Ceratodon purpureus and tuberous species of Bryum were still present.

Bonfire site B17

Cirsium arvense, abundant in the surrounding disturbed area, rapidly invaded the site, achieving a percentage cover of over 50 percent by August, 5 months after burning. Although this growth

died back in the autumn much of the soil surface (which had already lost the typical appearance of a bonfire soil) was still covered by dead leaves and stems. Colonisation by bryophytes was considerably delayed in comparison with that on spring bonfire sites, described in Experiment 2. Even though a green film, probably contributed to by both algae and protonemata, was noted after 5 months, gametophores were not found until February 1967, 11 months after burning. By this time most of the dead Cirsium growth had disappeared and only a few scattered angiosperms wars present. The bryophytes were scarce although Funaria hygrometrica was characteristically the most abundant species. Ceratodon purpureus and an unidentifiable species of Bryum were also present. It was obvious that from this time both the site and the surrounding area were much disturbed by sheep and cattle and so it was not surprising that little further colonisation of the site took place during the rest of the year (fig. 16). Various grasses and a new growth of Cirsium arvense were the most common angiosperms, but growth of the Cirsium was not so successful as in the previous year. Bryum argenteum was recorded in May and all the bryophyte species now present were characteristic of bonfire sites, but remained very scarce. No bryophytes at all could be found in August, and in November, Funaria and Bryum argenteum were the only species present. When the site was last visited in November 1968, 32 months after burning, it was still distinct from the chalk grassland vegetation. Dead remains of the previous years growth of angiosperms were abundant together

Fig. 16.

Site B17, Coombe Hill, 17 months after burning.

with living plants of Urtica dioica and grasses. Funaria hygrometrica and Bryum argenteum had disappeared and the only bryophytes present were a few scattered shoots of a tuberous species of Bryum.

Site B17 was of particular interest since it was never successfully colonised by bryophytes although as can be seen from table 9, Funaria hygrometrica was abundant on other nearby bonfire sites. It seems most likely that the early removal of ash by wind and rain, rapid colonisation by Cirsium arvense, and disturbance of the soil surface were responsible for the scarcity of bryophytes. In contrast to B17 the ash pile site A2 was more protected, being surrounded by felled shrubs, which made it less accessible to grazing animals and less exposed to wind and rain. This site was successfully colonised by bryophytes. It is possible, however that the surface of this site was covered by a mixture of ash and soil and not just ash and thus species other than the characteristic bonfire species were present and Funaria hygrometrica never became the most abundant moss.

Waterperry Wood

Waterperry Wood is a mixed deciduous wood on a clay-loam soil, the tree and shrub layers being composed mainly of the following species; Betula pendula, Betula pubescens, Corylus avellana, Crataegus monogyna, Fraxinus excelsior, Ligustrum vulgare, Populus sp., Prunus spinosa, Quercus robur, Rosa sp., Rubus caesius,

Rubus fruticosus, Thelycrania sanguinea, Salix cinerea ssp. atrocinerea, Salix caprea and Viburnum opulus. As part of the management programme of the wood, ten glades each 30 x 50 m.sq. were formed by chopping down trees and shrubs. In some of the glades the resulting cut down material was piled up and burnt and thus a number of bonfire sites of different ages were present. The mixed composition of the wood resulted in considerable variation in the ground flora of the glades, but the two bonfire sites, B18 and B19, studied in detail, were situated in adjacent glades the flora of which was alike and since both fires were recent, the whole process of recolonisation could be followed. The depth of ash and the size of the sites were very similar to those of the bonfire sites in Experiment 2, but about 15 percent of site B18 was occupied by a charred tree stump. Burning took place in January, 1966 and observations were made at the following intervals after burning; 4½, 8, 10, 13, 16, 19, 22 and 34 months.

When the area was first visited in May 1966, recolonisation was beginning, a green film being present on the surface of both sites, but signs of animal disturbance were also evident. A protective cage was therefore erected over site B18 so that the importance of animal disturbance as a factor in determination of the bryophyte succession could be investigated. The cage (fig. 17), assembled in the wood, was constructed of four frames, each 1 m.sq. and one, the lid, 1.2 m.sq. These were made of steel dexion with a plastic coated wire mesh.

Fig. 17.

Site B18, Waterperry Wood, showing protective cage.

Subsequent bryophyte recolonisation of the caged site was rapid, mosses covering almost three-quarters of the site by the 10th month, November. Funaria hygrometrica which was first noted in August with a percentage cover of 5 percent, was by November, easily the most conspicuous species, although Bryum argenteum occurring as scattered shoots amongst the Funaria was also abundant. Both species were found on the charred tree stump, but their growth here was not so robust. A few young thalli of Marchantia polymorpha were found on the tree stump just outside the cage. Angiosperm recolonisation was taking place largely by invasion from the edges of the site, Agrostis canina and Poa pratensis being the most abundant species and showing good growth inside the cage. Outside the cage however the effects of grazing and trampling were evident. The non-caged site B19 was also much disturbed and although by November some invasion by angiosperms had taken place at the periphery of the site and a few shoots of Funaria hygrometrica were found at the inner edge of this growth, the rest of the site consisted of bare mud.

Between November, 1966 and February, 1967 angiosperms on the caged site increased in number, Agrostis canina, Anthoxanthum odoratum and Poa pratensis all being abundant. With this increase, the bryophyte cover diminished and by February occupied only half of the site. There was no sign of ~~the~~ Marchantia polymorpha and Bryum argenteum was now as abundant as Funaria hygrometrica.

Funaria hygrometrica was fruiting but as on the bonfire sites in Experiment 2, at this time of the year the capsules did not develop normally. By May 16 months after burning the angiosperms cover on this site had reached 60 percent (fig. 18a) and the bryophyte cover had decreased still further to 25 percent, of which only 15 percent was not shaded by angiosperms. Funaria hygrometrica and Bryum argenteum were still the only species present. In contrast the non-caged site, B19 showed little colonisation by angiosperms and was obviously much disturbed (fig. 18b). A few scattered shoots of Funaria hygrometrica were the only mosses present.

In August no exposed bryophytes were found on the caged site, B18 and only a few living shoots of Funaria hygrometrica were found under the grasses. Most shoots were dead and much overgrown by roots. Bryum argenteum was now restricted entirely to the tree stump whilst etiolated shoots of Eurhynchium praelongum had appeared both on the tree stump and amongst the angiosperms. The vegetation in both glades was now a metre high. The non-caged site had been completely recolonised by angiosperms and on this visit and all subsequent visits to the area, could not be distinguished from the rest of the glade.

By November Bryum argenteum had disappeared from the caged site B18 and living shoots of Funaria hygrometrica were restricted to the tree stump, together with shoots of Ceratodon purpureus, recorded for the first time. A single shoot of a

Fig. 18.

a) Site B18, Waterperry Wood, 16 months after burning. Note the luxuriant angiosperm growth resulting from protection by the cage.

b) Site B19, Waterperry Wood, 16 months after burning, showing obvious signs of animal disturbance.

Brachythecium species was found amongst the angiosperms in November 1968, 12 months later, whilst Funaria hygrometrica and Ceratodon purpureus were still found on the tree stump, together with Bryum argenteum, which had reappeared. Although recolonisation of the rest of the site by angiosperms was complete, the soil was still more friable than that of the rest of the clearing.

Bryophyte recolonisation of the caged site B18 was thus similar to that of the bonfire sites in Experiment 2. Bonfire species of bryophytes reached their maximum abundance by the first winter after burning, then with increase in the angiosperm cover, were crowded out, growth of Bryum argenteum being restricted to the tree stump before that of Funaria hygrometrica. Bryum argenteum however, was nearly as abundant as Funaria hygrometrica at certain stages of the recolonisation, Ceratodon purpureus occurred only at later stages in the recolonisation and tuberous species of Bryum were never found. This was one of the few sites for which Marchantia polymorpha was recorded, although only a few plants were found. Both Funaria hygrometrica and Bryum argenteum grew on the charred tree stump, although Funaria in particular appeared to prefer the soil as a habitat.

South Haven Peninsula

South Haven Peninsula forms the southern arm of the entrance to Poole Harbour. The eastern larger part on which all

the sites were situated, has been built up in the last 350 years by the wind deposition of sand from the Bagshot beds composing the floor of Studland Bay. A series of ridges has formed, the oldest of which, Ridge 3 is covered with typical lowland heath vegetation, whilst the younger ridges show various stages in the succession from bare sand to Calluna heath. The vegetation of this area has been fully described by Good. (1935), Alvin. (1960) and Wilson. (1960). Accidental fires of the rapid fire type are common in this area and sites resulting from two such fires were studied.

Rapid fire site 4

This site was situated on Ridge 1 in an area where the succession has reached the dune-heath stage. Here the sand is covered by a thin layer of humus and has a pH of 3.9 - 4.5. The burnt area was relatively small, approximately 11 x 27 m. and the ground was sloping and uneven. The site was burnt in August 1964 and was visited at the following times after burning; 22, 24, 26, 29, 30, 33, 36 and 43 months.

When first visited in June 1966, nearly 2 years after burning, the site was still largely bare of vegetation and clearly distinguishable from the surrounding unburnt area. Only species characteristic of dune heath were present on the burnt site, Calluna vulgaris the dominant, having regenerated from plants which had

survived the burning, rather than grown from seed. Other angiosperms present on the site at this time included Ammophila arenaria, Carex arenaria, Carex flacca, Erica cinerea and Jasione montana. With regard to bryophytes Campylopus brevipilus was abundant, but provided relatively little cover whilst small amounts of Polytrichum juniperinum and Dicranum scoparium were also recorded.

Little change was noticed in the vegetation cover on any of the succeeding visits, recolonisation of this site being very slow. In March, 1968 3½ years after the fire (fig. 19) it was still clearly distinguishable from the surrounding vegetation mainly by the large percentage of bare ground. Campylopus brevipilus remained the most abundant bryophyte whilst Campylopus flexuosus, C. fragilis, C. introflexus, Dicranum scoparium, Pohlia nutans and Polytrichum juniperinum made up the rest of the bryophyte component of the vegetation.

Rapid fire site 5

This site was situated on Curlew Heath, in an area of damp Callunetum where Erica tetralix was relatively abundant. The site was burnt in May 1966 and covered approximately 1 acre. One corner was occupied by scorched birch, willow and gorse scrub, together with Pteridium aquilinum, whilst one assumes that the remainder was covered, before burning, with species typical of damp lowland heath. Indications were that the surface soil of the heath area had

Fig. 19.

Site R4, South Haven Peninsula, $3\frac{1}{2}$ years after burning.

Fig. 20.

Site R6, Cronkley Fell, 3 years after burning. The large tussocks of Polytrichum commune are conspicuous.

only been lightly scorched and little ash was to be seen. In the area of scrub however, patches of red ash were found suggesting that in places, possibly where a log had burnt, temperatures had been high (see p.233).

The site was visited eight times over a period of 22 months following the fire. As was the case with the other burnt site in this area, recolonisation was very slow and all the species which occurred on the site were characteristic of the unburnt vegetation. Of the bryophytes Campylopus brevipilus and C. fragilis were the most abundant species, C. flexuosus also being present. Leucobryum glaucum and Sphagnum species were producing new shoots from scorched. tussocks. Erica tetralix, Calluna vulgaris and Molinia caerulea were the dominant angiosperms. Even though the fire appeared to have been hotter in the scrub area, with greater deposition of ash, a bonfire community of bryophytes was still not found, Bryum bornholmense, Pohlia nutans and Polytrichum juniperinum being the only species recorded. Growth of both bryophytes and angiosperms, however, was more luxuriant in this area.

Recolonisation of both rapid fire sites was thus very slow and only species of angiosperms and bryophytes characteristic of the pre-burn vegetation were recorded.

Cronkley Fell

The sites were situated at an altitude of 381-564 m., the unburnt vegetation of this region consisting of typical upland

heather moor with a blanket peat soil. The land is used for sheep grazing and rearing grouse and as part of the management programme, areas are subjected to controlled burning of the rapid fire type. Burning takes place twice yearly (in spring and autumn) in different plots and thus a number of rapid fire sites of varying age were available for study. Four sites R6, R7, R8 and R9 burnt in 1963, 1964, 1965 and 1966 respectively were selected. These were in areas topographically and floristically similar except for the 1963 burn R6, which received drainage water from higher ground and supported a richer bryophyte flora. In addition a bonfire site B20 and an ash pile site A3 were set up.Protective cages like the one used in Waterperry Wood were set up over a small part of each of the rapid fire sites, in order to assess the effects of disturbance by sheep and grouse and were also used to protect the bonfire site and ash pile site,

The rapid fire sites were visited somewhat infrequently at intervals of 4, 12, 16, 28 and 37 months after the first visit in April, 1966, observations being made in the late spring and early summer in order to avoid the grouse rearing and shooting seasons and periods of snow cover. Complete bryophyte species lists for each of the sites are given in appendix table 6.

Rapid fire site R6 (burnt in 1963)

When first visited 3 years after the fire angiosperms covered less than 50 percent of the site. Bryophytes, however

formed a rich growth covering at least half the soil surface, species of Campylopus and Polytrichum being particularly abundant (fig. 20).

The site showed little further change over the next 3 years. At the end of the observation period in May 1969, angiosperms had not yet formed a closed community and Calluna vulgaris plants were only 10 cm. high. Bryophytes especially species of Polytrichum were still very abundant.

Rapid fire site R7 (burnt 1964)

2 years after burning, dead Calluna stems and bare ground still accounted for at least three-quarters of the site. Species of Campylopus were the most abundant bryophytes. In August, 1967 it was noted that Pohlia nutans had exceeded the Campylopus species in abundance, having a cover of about 25 percent. Campylopus species however were still conspicuous and Polytrichum gracile fairly abundant.

5 years after burning in May, 1969 plants of Calluna were about 3 cm. high and covered about half the ground. Ceratodon purpureus and Pohlia nutans were abundant and lichens were also frequent.

Rapid fire site R8 (burnt 1965)

Species of Campylopus were the most abundant bryophytes when the site was first visited 1 year after burning, but the

vegetation cover was small. 12 months later Pohlia nutans had become very conspicuous, although Campylopus species were still fairly common. These plants remained abundant up to the end of the observation period, when the site was 4 years old. Leafy liverworts were also frequent by this time although angiosperms still covered less than 20 percent of the site.

Rapid fire site R9 (burnt 1966)

No growth had occurred by the time the site was first visited and dead stems of Calluna vulgaris covered most of the ground surface. The litter layer had not been removed by the fire and was 3-4 cm. deep.

Orthodontium lineare was the only bryophyte species to be recorded in August 1966, although several angiosperm species all characteristic of the preburn vegetation were present. These, however were scattered and covered only 5 percent of the ground. By April, 1967, 1 year after the fire several bryophyte species had colonised the site, including Eurhynchium praelongum, Plagiothecium undulatum, Pohlia nutans and Calypogeia trichomanis. Campylopus brevipilus, Hypnum cupressiforme, Mnium hornum, Polytrichum species and Gymnocolea inflata were recorded in addition to the above species, in the following August. By this time Pohlia nutans was the most abundant species, whilst Hypnum cupressiforme and Gymnocolea inflata were also fairly abundant, but cover of both angiosperms and bryophytes was still small, bare ground accounting for over three-quarters of the site (fig. 21a).

Fig. 21.

× 1/10

a) A small portion of site R9, Cronkley Fell, 16 months after burning.

b) Part of the same site which had been protected from animal disturbance.

Little change was noted on subsequent visits and by May 1969 vegetation still covered less than a third of the site. Pohlia nutans and Campylopus brevipilus were the most conspicuous bryophytes.

Although plant growth inside the cages was more luxuriant than that outside, the presence of the cages on the rapid fire sites had no effect on species colonising the sites (fig. 21b).

Bonfire site B20

The bonfire site was set up in April 1967 close to the rapid fire sites. Calluna vulgaris freshly cut from the surrounding moorland was the major fuel. The fire was allowed to burn for 2 hours and thermocolour paints showed it to have been fairly hot, maximum temperatures ranging from 715°C-805°C. An area approximately 30 cm.sq. was burnt and ash 3 cm. deep, formed an even layer over it.

The site was first visited in August 1967, 4 months after burning. Nothing was growing on it and much of the ash had disappeared due to wind action. Calluna vulgaris seedlings and Scirpus caespitosus were present in the scorched area surrounding the site and close examination of the surface soil showed the presence of algae, but not protonemata.

By August 1968, 16 months after burning bryophytes were abundant on the site. Ceratodon purpureus was the most common species and Pohlia nutans was fairly abundant. Funaria hygrometrica formed four distinct colonies and scattered shoots of Bryum argenteum

were also present. Ceratodon purpureus, Plagiothecium undulatum and Pohlia nutans and scattered shoots of Funaria hygrometrica were growing in the scorched area, amongst seedlings of Calluna vulgaris.

After 2 years in May, 1969 angiosperms were still not present on the site itself and bryophytes were conspicuous, (fig. 22). Ceratodon purpureus the most abundant species covered over half the site, whilst Pohlia nutans had a cover of 25 percent. Funaria was fairly abundant and scattered shoots of Bryum argenteum were found. All species were fruiting.

Ash pile site A3

An ash pile site similar to that set up in Experiment 2 (site A1) was set up on Cronkley Fell in March, 1968, to find what effect the more severe climatic conditions and the different pre-burn soil and vegetation type would have on the colonisation of such a site. Ash was collected from a 14 day old bonfire site in the grounds of Royal Holloway College, the same fuel being used for this fire as for those in Experiment 2. The ash was spread out to form a layer 2-3 cm. deep in a shallow depression, dug in the area of the 1963 burn, site R6. The depression was made to prevent the ash from blowing away, whilst a snow cover at the time of setting up the site made the 1963 burn the only recognisable and accessible area.

In August, 1968, 5 months after the site was first set up, Funaria hygrometrica and Bryum argenteum were already present. Campylopus fragilis, Pohlia nutans and Polytrichum species were also recorded, but were found only at the edge of the site.

Fig. 22.

× 1/10

Site B20, Cronkley Fell, 2 years after burning showing the abundance of mosses. The capsules of Funaria hygrometrica are conspicuous.

Fig. 23.

Site A3, Cronkley Fell, in May 1969.

By May, 1969 bryophytes, as shown in fig. 23, were abundant. Funaria hygrometrica covered three-quarters of the site surface, whilst Bryum argenteum and Ceratodon purpureus occurred as scattered shoots. Pohlia nutans and Polytrichum species were still only found at the edge of the site. As shown in fig. 23, one edge of the site was not colonised at all, possibly because ash and leachates had accumulated at the other side of the site due to strong wind and rain action. The only angiosperms present were one plant of Rumex acetosa and one of Cardamine flexuosa.

Recolonisation of the rapid fire sites on Cronkley Fell was thus very similar to those on South Haven Peninsula. Recolonisation was very slow and at the end of the observation period angiosperms had not formed a closed community on any of the sites, even on R6 the 1963 burn, which was 6 years old at the end of the observation period. Other sites on Cronkley Fell indicated that a closed community was not formed until at least 8 years after burning. As on South Haven Peninsula the only species of bryophytes and angiosperms to colonise the rapid fire sites were those found in the pre-burn vegetation. Acrocarpous species of bryophytes were abundant in the open community stage of the recolonisation and although the recolonisation of none of the sites was followed to completion, pleurocarpous species appeared to become more abundant at later stages.

In contrast, the bryophytes recolonising the bonfire site B20 were no longer those characteristic of Callunetum, Funaria hygrometrica and Bryum argenteum being present in addition to the other species. The early removal of ash and thus potential mineral nutrients, may have accounted for the fact that Funaria hygrometrica was not as abundant on the bonfire site as it usually is in such a habitat. On the scorched area around the site, where there was never much ash, only a few scattered shoots of Funaria hygrometrica were found.

The presence of ash alone was sufficient to promote the growth of the bonfire species of bryophytes on Cronkley Fell. In fact Funaria was considerably more abundant on site A3 than on the bonfire site, probably because the ash had been placed in a depression and so had been prevented from blowing away. Colonisation of this site by bryophytes was also more successful than on the ash pile site A1 in Experiment 2, in spite of the more severe climatic conditions. Lack of angiosperm competition due to the slow recolonisation of the moorland vegetation was probably important in determining this.

The occurrence of the bonfire bryophytes in areas of industrial pollution

The bryophyte flora of brick and stone walls and brick rubble was examined in the industrially polluted centre of Newcastle and compared with that of similar sites in two less polluted areas, Thursley Village and Farnham both in Surrey. The results are given in tables 7 and 8.

Table 7. Bryophytes found on stone and brick walls and brick rubble in the centre of Newcastle.

SITE	SPECIES RECORDED
Stone wall	Bryum argenteum B. radiculosum Ceratodon purpureus Funaria hygrometrica Tortula muralis
Stone wall	Ceratodon purpureus Funaria hygrometrica Leptobryum pyriforme
Brick wall	Ceratodon purpureus Funaria hygrometrica (a few dead shoots) Tortula muralis
Brick wall	Bryum argenteum Ceratodon purpureus Funaria hygrometrica
Brick wall	Marchantia polymorpha (on detritus at bottom of wall)
Brick wall	Brachythecium sp. (1 shoot) Bryum radiculosum Ceratodon purpureus
Brick wall	Bryum radiculosum Ceratodon purpureus Marchantia polymorpha (on detritus at bottom of wall)
Brick wall	Bryum argenteum Ceratodon purpureus Funaria hygrometrica Leptobryum pyriforme

(cont.)

Table 7. (cont.)

SITE	SPECIES RECORDED
Brick and stone wall	Bryum radiculosum Ceratodon purpureus Funaria hygrometrica Leptobryum pyriforme
Sandstone wall with large detritus filled gaps	Bryum argenteum B. capillare Ceratodon purpureus Funaria hygrometrica Tortula muralis
Brick rubble on a demolition site. No obvious signs of burning but very probable that waste materials burnt on the site.	Bryum argenteum Ceratodon purpureus Funaria hygrometrica (very abundant) (and fruiting)

If walls had been recently repointed no mosses were found on the mortar; otherwise mosses were found on mortar, stone and brick work and in detritus filled cracks.

Table 8. Bryophytes found on stone and brick walls in Thursley Village and at Farnham in Surrey.

11 walls were examined:

Barbula convoluta
Barbula fallax
Barbula recurvirostra
Brachythecium rutabulum
Bryum capillare
Bryum argenteum
Camptothecium sericeum
Ceratodon purpureus
Grimmia pulvinata
Orthotrichum diaphanum
Tortula muralis

It can be seen that in Newcastle, Funaria hygrometrica, Bryum argenteum and Ceratodon purpureus were the most widespread species in the habitats examined. The performance of all the species however, was poor except on the last site, where it was possible that burning had taken place and growth of Funaria hygrometrica was as good as on bonfire sites in less polluted areas. On all the sites examined in Surrey the growth of bryophytes was much more luxuriant and the species found were those generally considered to be characteristic of brick and stonework. Thus although Bryum argenteum and Ceratodon purpureus were recorded, Funaria was not seen.

III. DISCUSSION

A clear difference was found between the recolonisation of bryophytes on sites resulting from rapid fires and those resulting from bonfires.

Recolonisation of rapid fire sites

Thirteen rapid fire sites were examined on lowland heath and upland heather moor, six over a period of time, and on both types of Callunetum, the recolonisation was similar, The major species of lowland heath and upland heather moor are slow growing shrubs and since during the process of recolonisation of sites in the present investigation, no other species attained a high percentage cover, the

Table 9. Other sites examined.

(The pre-burn soil and vegetation of the areas are described in table 1 in the appendix pp.)

Location		Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
BUCKS. Coombe Hill. Chalk grassland. Whole area much disturbed by activities of Conservation Corps and grazing.	a.	B	?	Funaria hygrometrica	F. hygrometrica covered the whole site.
	b.	B	?	Brachythecium rutabulum Ceratodon purpureus Funaria hygrometrica Tuberous species Bryum	C. purpureus F. hygrometrica only on charred log.
	c.	B	?	Ceratodon purpureus Funaria hygrometrica	F. hygrometrica abundant.
	d.	B?	?	Funaria hygrometrica	Disturbed site no. obvious signs of burning. Pure community of F. hygrometrica.
DORSET. Morden Bog. Lowland Calluna heath 71 simulated rapid fire sites set up by S.B. Chapman (Nature Conservancy). Each plot 10 m.sq. subjected to controlled burning and various	a.	R	1 - 6	Heathland bryophytes conspicuous, species of Campylopus being particularly abundant	Where Campylopus sheltered by Calluna, shoots survived burning.

(cont.)

Table 9 (cont.)

Location		Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
additional treatments applied to some sites e.g. clipping vegetation before burning. (Plots very close together and counted as one site).					
	b.	B	?	Campylopus spp. Ceratodon purpureus Dicranum scoparium Polytrichum juniperinum	Possibly an old burn
South Haven Peninsula Lowland Calluna heath.	a.	B	3	Ceratodon purpureus Tuberous species Bryum	Fuel unknown but ash produced apparently toxic to both angiosperms and bryophytes. Site observed over period of 3 years during which very little recolonisation took place. Only a few scattered moss shoots ever present and these at edge of site.

(cont.)

Table 9 (cont.)

Location		Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
Calcareous road verges. Verges periodically trimmed and resulting cut material burnt on the verges.	b.	B	< 1	Barbula convoluta Funaria hygrometrica	F. hygrometrica abundant.
	c.	B	< 1	Barbula convoluta Ceratodon purpureus Funaria hygrometrica	F. hygrometrica abundant.
	d.	B	< ½	Bryum argenteum Tuberous species Bryum	Only a few shoots of each.
	e.	B	-?	Brachythecium velutinum Funaria hygrometrica Tuberous species Bryum	Tuberous species Bryum covered 3/4 of site. Other species represented only by scattered shoots.
ESSEX. Stour Wood Deciduous woodland regularly coppiced. Trimmings burnt in the coppiced clearings ∴ a no. of bonfire sites of different ages present. Size of sites and amount of ash indicated that fires large.	a.	B	4	Ceratodon purpureus Dicranella heteromalla Eurhynchium praelongum Funaria hygrometrica Lophocolea sp.	Angiosperms 75% cover. Bonfire species of bryophytes being replaced by woodland species.
	b.	B	3	Dicranella heteromalla	Angiosperms 75% cover.
	c.	B	2	Ceratodon purpureus Eurhynchium praelongum Funaria hygrometrica	M. polymorpha most abundant species. Others present

(cont.)

Table 9 (cont.)

Location	Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs)	Bryophyte species recorded	Notes
			Polytrichum commune Tuberous species Bryum Marchantia polymorpha	as scattered shoots and except for F. hygrometrica only at the edge of the site.
d.	B	2	Funaria hygrometrica Marchantia polymorpha	M. polymorpha 75% cover F. hygrometrica 25%.
e.	B	2	Funaria hygrometrica	F. hygrometrica covered $\frac{1}{2}$ site, but much of growth infected by fungus and dead.
f.	B	2	Funaria hygrometrica Leptobryum pyriforme Marchantia polymorpha	F. hygrometrica covered nearly whole site, other species scattered
g.	B	2	Funaria hygrometrica Marchantia polymorpha	F. hygrometrica 33% cover. Only a few thalli of Marchantia polymorpha present.

(cont.)

Table 9 (cont.)

Location	Fire Type B=Bonfire R=rapid Fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
h.	B	2	Ceratodon purpureus Funaria hygrometrica Marchantia polymorpha	F. hygrometrica abundant. Other species scattered and scarce.
i.	B	1	Funaria hygrometrica	Angiosperms 50% cover and only a few small colonies of moss present.
j.	B	1	Ceratodon purpureus Tuberous species Bryum Marchantia polymorpha	All species scarce.
k.	B	1	Ceratodon purpureus Tuberous species Bryum Marchantia polymorpha	All species scarce.
l.	B	(1-2 mths.)	Funaria hygrometrica	A few scattered shoots at edge of site.
m.	B	(1-2 mths.)	Funaria hygrometrica	A few scattered shoots at edge of site.

(cont.)

Table 9 (cont.)

Location		Fire Type	Site age at time of observation	Bryophyte species recorded	Notes
OXFORDSHIRE. Waterperry Wood					
Deciduous woodland. Bonfire sites resulted from the clearing of areas within the wood, cut down material being burnt in theclearings.	a.	B	2 - 3	-	Angiosperms 100% cover.
	b.	B	2 - 3	Funaria hygrometrica	Angiosperms abundant and only a few over-grown moss shoots present.
	c.	B	1	Funaria hygrometrica	Fairly abundant.
	d.	B	?	Funaria hygrometrica	F. hygrometrica 95% cover.
SURREY. Box Hill					
Chalk grassland. Sites resulted from the burning of cut down, invading scrub.	a.	B	?	Barbula spp. Ceratodon purpureus Funaria hygrometrica	Much overgrown by angiosperms.
	b.	B	?	Barbula spp. Ceratodon purpureus Funaria hygrometrica	Much overgrown by angiosperms.
	c.	B	?	Barbula spp. Ceratodon purpureus Funaria hygrometrica	Much overgrown by angiosperms.

Table 9 (cont.)

Location		Fire Type B=bonfire R=rapid fire	Site age at time of observation(yrs.)	Bryophyte species recorded	Notes
Chobham Common Lowland Calluna heath, repeatedly burnt by accidental rapid fires.	a.	R	<1	Bryum sp. Campylopus pyriformis Pohlia nutans Polytrichum juniperinum Gymnocolea inflata Lophozia ventricosa	
	b.	R	<1	Bryum sp. Campylopus pyriformis Pohlia nutans Polytrichum juniperinum Gymnocolea inflata Lophozia ventricosa	
	c.	R	<1	Bryum sp. Campylopus pyriformis Pohlia nutans Polytrichum juniperinum Gymnocolea inflata Lophozia ventricosa	
	d.	R	<1	Bryum spp. Campylopus pyriformis Pohlia nutans Polytrichum juniperinum	

(cont.)

Table 9 (cont.)

Location		Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
	e.	R	< 1	Bryum spp. Ceratodon purpureus Polytrichum commune P. juniperinum	
Royal Holloway College					
Neglected apple orchard. Bonfire site resulted from burning of builders waste.	a.	B	1	Ceratodon purpureus Funaria hygrometrica Tuberous species Bryum	Tuberous species Bryum very abundant.
Building site, formerly kitchen garden. Several large bonfires were made in this area but continued disturbance made individual sites difficult to distinguish.	b.	B	1	Bryum argenteum Ceratodon purpureus Funaria hygrometrica Tuberous species Bryum	All 4 species abundant.
Lorry tracks on neglected lawn close to building site.	c.	-	1	Ceratodon purpureus Ditrichum cylindricum Funaria hygrometrica Pottia truncata Tuberous species Bryum Weissia sp.	No obvious signs of burning.

(cont.)

Table 9 (cont.)

Location		Fire Type (B = bonfire, R = rapid fire)	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
Rough pasture.	d.	B	?	Funaria hygrometrica	3/4 of site covered by moss.
Fallow ground.	e.	B	?	Barbula convoluta Funaria hygrometrica	F. hygrometrica very abundant.
	f.	B	?	Funaria hygrometrica	Much overgrown by angiosperms and moss scarce. Probably an old burn.
Thursley Common Lowland Calluna heath. Bonfire sites resulted from the burning of Calluna, Pteridium aquilinum and invading scrub mainly pine trees. Rapid fire sites from accidental fires.	a.	B	?	Barbula unguiculata Bryum argenteum Ceratodon purpureus Funaria hygrometrica Polytrichum juniperinum	F. hygrometrica abundant. Other species present as scattered shoots, P. juniperinum only at the edge of the site.
	b.	B	?	-	Probably a recent burn.

(cont.)

Table 9 (cont.)

Location		Fire Type B=bonfire R=rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
	c.	B	$1\frac{1}{2}$?	-	Possibly a more recent burn than would appear from the information obtained.
	d.	B	$1\frac{1}{2}$	Funaria hygrometrica Polytrichum juniperinum	F. hygrometrica abundant. P. juniperinum found only at edge of site.
	e.	B	$\frac{1}{2}$	-	
	f.	B	$\frac{1}{2}$	-	
	g.	B R	?	Polytrichum juniperinum	Bonfire site (probably recent) on rapid fire site.
Wet heath.	h.	R	?	Heathland species of bryophytes abundant particularly species of Polytrichum	Polytrichum species regenerating from underground stems, Campylopus species from protonemata.
	i.	B	$1\frac{1}{2}$	Brachythecium rutabulum Bryum argenteum Bryum spp. Ceratodon purpureus Funaria hygrometrica	F. hygrometrica abundant and only scattered shoots of other species present. Brachythecium rutabulum on a charred log. (cont.)

Table 9. (cont.)

Location		Fire Type B= bonfire R= rapid fire	Site age at time of observation (yrs.)	Bryophyte species recorded	Notes
	j.	B	$1\frac{1}{2}$	Brachythecium rutabulum Bryum argenteum Ceratodon purpureus Funaria hygrometrica Polytrichum juniperinum	F. hygrometrica 33% cover, C. purpureus 5%. Other species scattered shoots, B. rutabulum on a charred log.
	k.	B	$1\frac{1}{2}$	Bryum sp.	Only a few moss shoots present.
	l.	B	$\frac{1}{2}$	Aulacomnium androgynum Bryum argenteum Ceratodon purpureus Funaria hygrometrica	F. hygrometrica covered $\frac{1}{2}$ site and other species present only as scattered shoots. A. androgynum on a charred log.
	m.	B	?	-	Probably a recent burn. Algal film present.
	n.	B	?	-	Probably a recent burn.
Pine wood.	o.	B	$\frac{1}{2}$	-	Protonemata present.

(cont.)

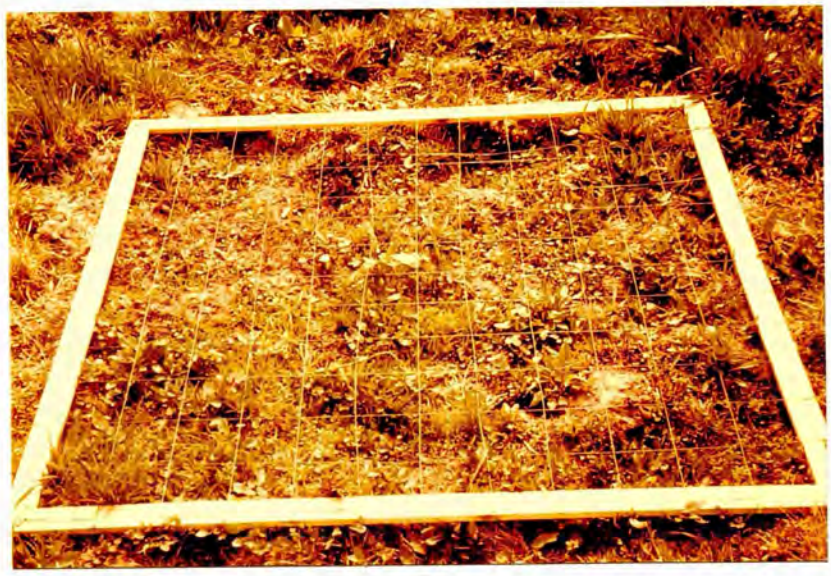
Table 9 (cont.)

Location		Fire Type B = bonfire R = rapid fire	Site age at time of observation (yrs)	Bryophyte species recorded	Notes
YORKS/DURHAM. Barnard Castle					
Rough grassland. History of site not known.	a.	B	?	Funaria hygrometrica. Other species also present but not recorded	F. hygrometrica most abundant species.
Lowland pasture. History of site not known.	b.	B	?	Bryum argenteum Ceratodon purpureus Funaria hygrometrica Tortella tortuosa	F. hygrometrica most abundant species.

formation of a community with an angiosperm density similar to that of the unburnt vegetation was slow. As with angiosperms, it was only bryophytes species characteristic of the unburnt vegetation which colonised the burnt ground. Detailed examination of the soil was not carried out, so that the first occurrence of bryophytes was not accurately determined, but on sites 6 months old, bryophytes were abundant on areas free of angiosperms. Acrocarpous species particularly Ceratodon purpureus, Pohlia nutans and species of Campylopus and Polytrichum were the most important early colonisers. Dicranum scoparium, and pleurocarpous mosses as found by Fritsch & Salisbury 1915, did not become abundant until later in the succession when the angiosperm cover was more complete and provided some shelter.

The recolonisation of three simulated rapid fire sites on rough grassland at Royal Holloway College, was similar to the recolonisation of rapid fire sites on Callunetum, in that only species characteristic of the preburn vegetation colonised the sites. Recolonisation by angiosperms, however, was much more rapid (fig. 24), complete recolonisation being accomplished within a few months of burning and the only bryophytes recorded were a few scattered shoots of a species of Bryum.

Fig. 24.



Site R2, Experiment 4, 6 weeks after burning.

Recolonisation of bonfire sites

Sixty four sites, situated on a wide range of soil and vegetation types throughout England were studied and a characteristic bryophyte community was found to be recognisable in early stages of the recolonisation.

Recolonisation by angiosperms, taking place mainly by invasion from the edges of the site as shown in fig. 25, was slower than on control weeded sites and even after 14 months, the number and variety of seedlings present was found to be less. Bryophyte growth was also at first delayed. On spring burnt sites in Experiment 2, the soil of which was closely examined, protonemata were not found until after 9 weeks and gametophores after 4-5 months. After the initial delay period, however, the number of shoots increased rapidly, the bryophytes usually reaching their maximum abundance at the end of the first year after burning (fig. 26). The following species most commonly composed this first association of bryophytes on the bonfire sites; Funaria hygrometrica, Ceratodon purpureus, Bryum argenteum and tuberous species of Bryum. Other authors investigating the recolonisation of sites resulting from various sorts of fires, e.g. Summerhayes & Williams (1926) and Doignon (1949); have found these species occurring in varying orders. On the bonfire sites studied here however, none of the bonfire mosses characteristically occurred before the others. Funaria hygrometrica, rapidly became the most abundant bryophyte whilst the other species occurred as scattered shoots amongst the Funaria.

Fig. 25.

Site B6, Experiment 2, 1 month after burning, showing the invasion of angiosperms beginning at the edge of the burnt area.

Fig. 26.

Site B7, Experiment 2, 12 months after burning, showing its maximum growth of bryophytes.

Fig. 27.

Site B7, Experiment 2, 15 months after burning, showing bryophytes becoming overgrown by angiosperms.

Bryophytes other than those mentioned above were also found at this stage of the recolonisation, but as shown in table 10, each was found on only a few sites and shoots were scarce and usually confined to the edges, where the full effect of the fire had not been felt.

In the second growing season the bonfire species of bryophytes were crowded out by angiosperms (fig. 27) and eventually bryophytes characteristic of the pre-burn vegetation appeared.

The bonfire association of bryophytes

Funaria hygrometrica was found on forty eight of the sixty four bonfire sites examined. Nine of the sixteen sites from which it was absent were still young at the time of examination and it is probable that Funaria would have occurred later. On three sites the succession was advanced and was probably past the Funaria stage, whilst the ash of a further site, bonfire site a. at South Haven Peninsula, appeared to be toxic to both bryophyte and angiosperm growth (table 9). Its absence from the three remaining sites (Stour Wood j. k. and Thursley Common c.), cannot readily be explained. All bryophytes were scarce on these sites.

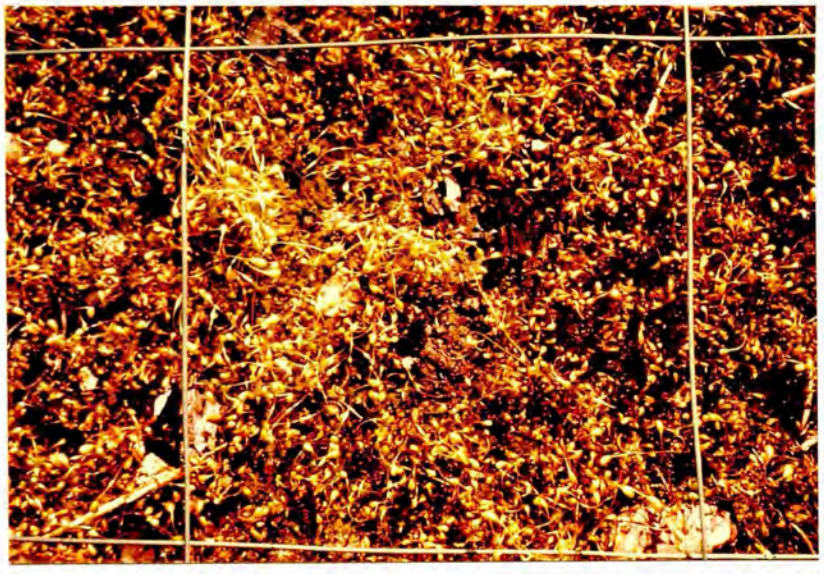
Funaria hygrometrica was usually the most conspicuous bryophyte as shown in fig. 28. On 28 of the 48 sites on which it occurred, it was abundant and on only 7 of the other sites were other species more abundant, three of these sites being dominated by Marchantia polymorpha (fig. 29). On one site several species were

Table 10. The occurrence on bonfire and ash pile sites of bryophytes other than the bonfire species.

SPECIES	A	E	L	TOTAL NO. OF OCCURRENCES
Aulacomnium androgynum	-	-	-	1
Barbula convoluta	-	-	2	6
B. unguiculata	-	-	-	2
Brachythecium rutabulum	-	2	2	8
B. velutinum	-	-	-	1
Bryum caespiticium	-	-	1	1
B. capillare	-	-	1	1
Campylopus fragilis	-	1	-	1
Dicranella heteromalla	-	-	2	2
Dicranum scoparium	-	-	-	1
Eurhynchium praelongum	-	1	2	3
Leptobryum pyriforme	-	-	-	1
Phascum cuspidatum	1	-	-	1
Plagiothecium undulatum	-	1	-	1
Pohlia nutans	1	1	-	2
Polytrichum commune	-	1	-	1
P. juniperinum	♀	3	-	6
Tortella tortuosa	♀	-	-	1

A = abundant
E = at edge of site only
L = occurring only at late stages of the succession

Fig. 28.



× 7/10

Funaria hygrometrica on site B7, Experiment 2.

Fig. 29.

× 1/5

Marchantia polymorpha on site B16, Experiment 5.

equally abundant to Funaria hygrometrica and on the remaining 12 sites all bryophytes were scarce. The other bonfire species were less widely distributed, but on 33 sites Funaria hygrometrica was associated with one or more of the other species. After Funaria hygrometrica, Ceratodon purpureus was the most widespread species. The finding of Burrell (1917) and Gilbert (1968) that Funaria hygrometrica, Bryum argenteum and Ceratodon purpureus were the most widespread species in areas of industrial pollution was confirmed.

The environmental factors influencing the bryophyte recolonisation

Both bonfire and rapid fires caused an alteration to almost every environmental factor, but the greatest difference between these two sorts of fires was in the amount of ash deposited and the intensity of heat (the temperature and its duration) produced during burning and presumably therefore, in their effect on edaphic factors. It is likely therefore that edaphic factors are of primary importance in determining the presence or absence of the bonfire species of bryophytes. No temperature measurements were made during rapid fires, but the works of Lloyd (1968) on grassland fires and Whittaker (1961) and Kenworthy (1963) on moorland fires, showed that during such rapid fires, temperatures near the surface of the soil may be very high reaching 800-900°C, but the duration of such temperatures was short. Both Lloyd and Whittaker also showed

that heat penetration into the soil was negligible. On most of the rapid fire sites examined in the present investigation, combustion was incomplete and the surface soil was covered with charred plant remains (fig. 21a. p. 70) rather than ash. In addition several plants including some bryophytes survived burning. In contrast during a bonfire most of the fuel was reduced completely to ash, and because of the large quantity of fuel per unit area a much greater depth of ash was formed. Usually no plants survived burning. Temperatures at the surface of the soil during burning were usually found to be in the range 640-900°C (table 3 p.19), but in contrast to the high temperatures of rapid fires must have been prolonged, since the bonfires continued to burn over one place for several hours. In spite of the excellent insulating properties of soil, with such prolonged high temperatures, temperatures in the surface soil must also have been high and with reference to the work of Humphreys & Lambert (1965) (fig. 30) were probably in the range 150-500°C.

Both the addition of ash and the heating effect of the fires appeared to be important. The addition of ash by itself, as was shown by the three ash pile sites, was sufficient to promote the growth of the bonfire species. The removal of ash from a site, however, did not prevent its colonisation by the bonfire bryophytes, although their growth was not as good as on the ash pile sites. It would seem therefore that the addition of ash may be more important than the heating effect. The effect produced by either, however, in

Fig. 30. Penetration of heat into soil during bonfires (heaps of burning slash and logs). Taken from Humphreys & Lambert 1965.

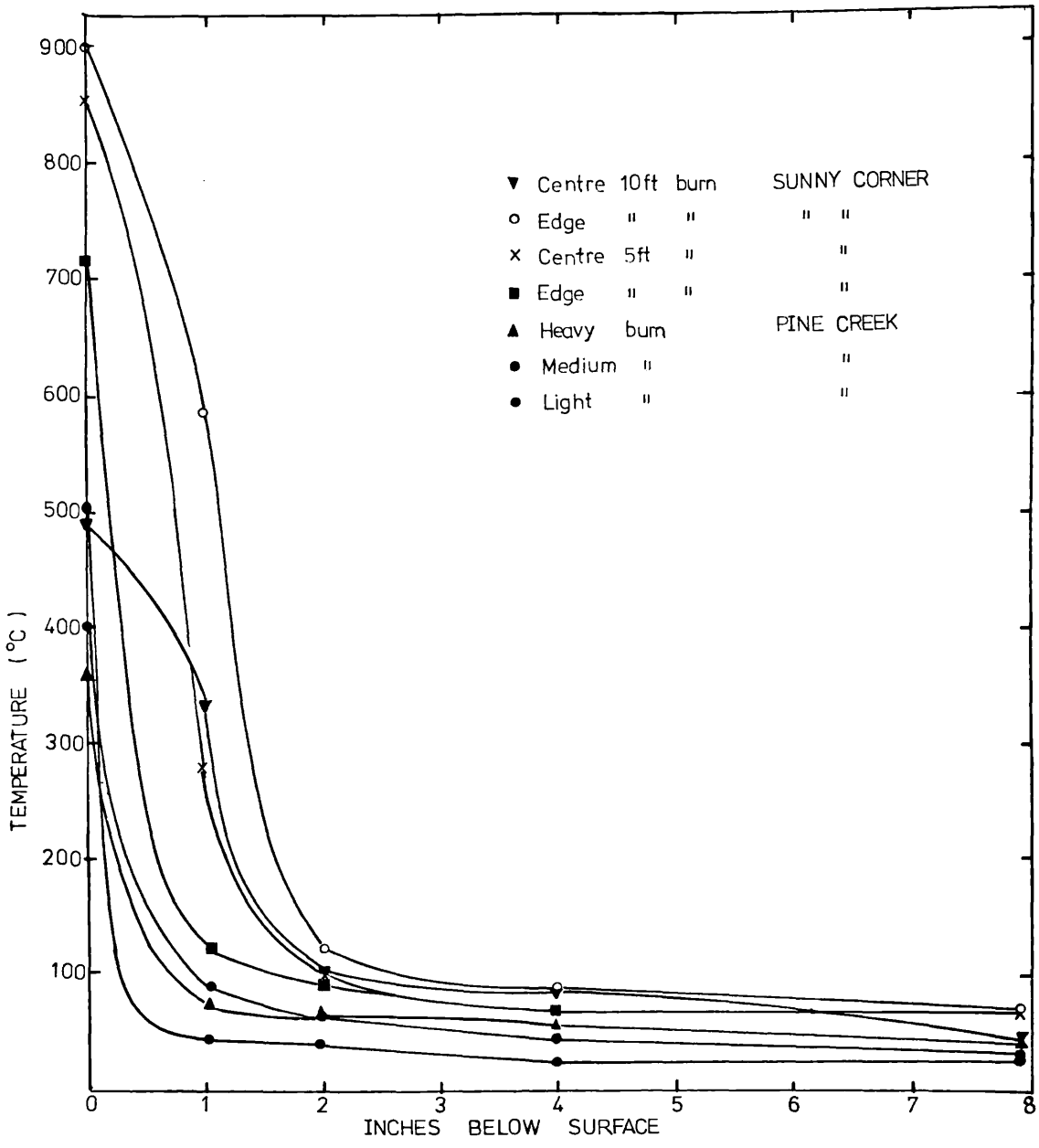


FIG. 1. - Maximum temperatures (°C) reached at various depths below the soil surface under burns of different intensity.

contrast to the findings of Cremer & Mount (1965), could not be simulated by the addition of blood and bone fertiliser.

Several other factors played some part in determining the succession, although these were of secondary importance. These included angiosperm competition, animal disturbance, prevailing weather conditions and season of burning; altitide and the original nature of the soil and vegetation, being important in their effect on these factors. Angiosperm competition, itself closely related to edaphic conditions, was shown to be the next most important factor. Although some shading by angiosperms was beneficial presumably due to increased humidity, excessive shading and competition was obviously detrimental. Under such conditions shoots became etiolated and sporophytes when present were less mature than sporophytes of comparable age on non-shaded sites. Thus reduction of angiosperm competition was beneficial to growth of bryophytes on both rapid fire sites and bonfire sites. Removal, however, of angiosperms from a non-burnt site was not sufficient to promote colonisation by the bonfire species. Even where angiosperm recolonisation was prevented by continued weeding, the characteristic bonfire community was not found. Neither did a bonfire association develop on rapid fire sites where the angiosperm recolonisation was slow.

Angiosperm competition was usually largely responsible for ousting the bonfire species from a site. When a bonfire site was kept free of angiosperms by continued weeding, bonfire species were still abundant on the bonfire sites at the end of the second

growing season, although on non-weeded bonfire sites they had disappeared by this time. Bryum argenteum appeared to be particularly sensitive to angiosperm competition being one of the first species to disappear. Where recolonisation of a bonfire site by angiosperms was very rapid (e.g. B2 Experiment 1) the bonfire species were not able to colonise the site successfully.

The soft open ground and growth of young shoots usually found on burnt sites frequently attracted animals to the burnt ground and the resulting disturbance of the surface soil prevented successful colonisation by the bonfire bryophytes. Similarly the removal of ash by wind and rain also affected the colonisation and thus prevailing climate is of some importance.

The season of burning affected the time taken for the succession to reach completion, both bryophyte and angiosperm colonisation being delayed on a winter bonfire site until the following spring. Fig. 31 shows the winter bonfire site B15, 24 weeks after burning, in the following spring. Recolonisation is at the same stage as that of the 4 week old spring burnt site shown in fig. 25. As far as Funaria hygrometrica is concerned the initial delay in colonisation of winter bonfire sites may be contributed to by the effect of cold weather on the fertility of the moss and the consequent reduction in the availability of spores. The harmful effects of cold weather on sporophyte formation have also been noted by Benson-Evans & Brough (1966) who noted that low temperatures retard the development of sex organs, and plants may take a whole season to recover from this damage.

Fig. 31.

Site B15, Experiment 3, 24 weeks after burning.

MINERAL NUTRIENT STUDIES

I. INTRODUCTION AND THE LITERATURE

Field experiments supported the widely held view that changes in the levels of soil nutrients are of primary importance in determining the colonisation of burnt sites by the bonfire species of bryophytes. The following investigations were carried out with Funaria hygrometrica, the most prominent coloniser, in order to examine more closely its growth on different soil types and to determine its nutrient requirements. In the time available it was not possible to extend the study to all the bonfire bryophytes although a few experiments were carried out with other species.

Much experimental work has been carried out with [illegible] bryophytes and Funaria hygrometrica (referred to as Funaria in the remainder of this work) readily available and easy to grow in culture has very often been chosen as the experimental subject. The majority of investigations however, have been concerned with developmental morphology, and of the comparatively small number of papers concerned with mineral nutrition, most were published some years ago. Of the more recent works the most important are those of Kofler (1959) and Hoffman (1962, 1966a and 1966b). Both these authors include comprehensive reviews of the early literature.

It is apparent that Funaria can tolerate a wide range of nutrient solutions although its morphological response to different solutions may vary. The chemical composition of seven

commonly used solutions including those used in the present work are shown in table 11. The type of substrate, with the exception of liquid ones, appears to have little effect on performance. It is difficult to draw any further general conclusions from the works of these early authors because of the large variety of culture conditions and techniques employed. Points relevant to the present study in the work of individual authors are, however, commented on later.

Kofler's own work was restricted to the study of protonemal growth and early gametophore development, and emphasised the influence which genetical stock can have on the plant's responses. Altering the total concentration of the nutrient solution (in most experiments solidified with agar) had a greater effect on growth than altering the concentration of individual nutrients, whilst the addition of ammonia nitrogen was found to result in abnormal growth. Omission of micronutrients severely inhibited development. Hoffman's study is especially interesting since observations were not restricted to early stages of growth and experiments were carried out primarily to link the nutrient requirements of Funaria with its ecological distribution. Growth was studied both on modified soils (1962 and 1966a) and nutrient sand and agar (1962, 1966a and b). Funaria was again found to grow well on a wide range of nutrient solutions, although Hoffman concluded that relatively high concentrations of nigrogen and phosphorus and the balance between these two nutrients was particularly important.

Table 11. The chemical composition of seven nutrient solutions commonly used for growing bryophytes (mgm./l.).

Ion \ Medium	Kofler Medium A	Benecke	Knop's I	Knop's II	Marchal	Voth's solution 5 (used in present investigation)	Hoagland's 100% solution (used by Hoffman)
NO_3	518.6	154.9	525.1	26.26	774.6	211.4	930.1
SO_4	235.2	39.0	97.4	48.7	763.9	101.4	192.1
PO_4	170.3	69.8	174.5	87.2	412.8	38.0	95.0
NH_4	112.7	45.1	-	-	303.7	-	-
K	169.7	28.7	202.9	84.2	224.4	46.9	234.6
Ca	42.4	36.1	169.7	84.9	116.4	28.0	200.4
Mg	24.7	9.9	24.7	12.3	49.3	34.1	48.6

The concentrations of nutrients in Benecke's, Knop's I, Knop's II and Marchal's solutions were all calculated from recipes given by Kofler (1959).

Preliminary investigations directly relevant to the present work were carried out by . Lodge at Royal Holloway College in 1963. This work has not been published and so with Lodge's permission it is briefly described here. The culture techniques and growing conditions were the same as those used for the nutrient agar experiments of the present investigation, described later (p.144). As in Hoffman's investigation, experiments extended over several months and observations were not restricted to early stages of development.

The first series of experiments was designed to determine the effect of varying the concentration of the nutrient solution. Growth was tested on ten different concentrations of a nutrient solution, solutions 1-10, prepared according to Voth (1943) and solidified with agar, Oxoid No. 3. Concentrations of nutrients in each solution are shown in table 12. Solution 2, the second most concentrated solution, is stated by Voth to be approximately the same concentration as solutions used to grow greenhouse plants e.g. tomatoes. As shown in tables 13, 14 and 15. Funaria was able to grow on all the media, but showed considerable variation in performance even in the early stages of growth. Best growth was found in cultures with nutrients in the middle of the range of concentrations. With dilution of the solution below the concentration of solution 6, there was a progressive decrease in the number of shoots present and in their leaf size. Shoots became spindly and distinctly yellowish in colour, whilst rhizoidal filaments and rhizoids became

Table 12. Concentrations of nutrients in Voth's solutions (mgm./l.).

Solution no.	Relative concentration	Osmotic concentration (atm.)	K	Mg	Ca	NO_3	PO_4	SO_4
1	$\frac{160}{160}$	1.83	468.5	340.5	280.1	2113.8	380.1	1014.3
2	$\frac{80}{160}$	0.94	234.3	170.3	140.1	1056.9	190.1	507.2
3	$\frac{48}{160}$	0.59	140.6	102.2	84.0	634.1	114.0	304.3
4	$\frac{32}{160}$	0.37	93.7	68.1	56.0	422.8	76.0	202.9
5	$\frac{16}{160}$	0.21	46.9	34.1	28.0	211.4	38.0	101.4
6	$\frac{12}{160}$	0.18	35.1	25.5	21.0	158.5	28.5	76.1
7	$\frac{8}{160}$	0.13	23.4	17.0	14.0	105.7	19.0	50.7
8	$\frac{4}{160}$	0.08	11.7	8.5	7.0	52.9	9.5	25.4
9	$\frac{2}{160}$	0.05	5.9	4.3	3.5	26.5	4.8	12.7
10	$\frac{1}{160}$	0.01	2.9	2.1	1.8	13.2	2.4	6.4

(cont.)

Table 12. (cont.)

Solution 1 as prepared by Lodge contained the following concentrations of micronutrients:

2 mgm./l.	$MnSO_4$
2 mgm./l.	$ZnSO_4$
2 mgm./l.	$Na_2B_4O_7$
2 mgm./l.	$FeCl_3$

Table 13. Experiment a. (Lodge); Growth of Funaria on media prepared from Voth's solutions.

Solution from which medium prepared	No. of shoots present after		
	11 wks.	22 wks.	24½ wks.
1	-	137	406
2	128	595	1109
3	655	2134	2201
4	1070	1792	-
5	1014	1460	1469
6	1404	1491	1519
7	1031	1544	-
8	740	882	879
9	690	829	799
10	523	546	644

Three cultures were set up on each medium, cultures being discarded after the shoots were counted.

Table 14. Experiment b. (Lodge); Growth of Funaria after 3 weeks, on media prepared from Voth's solutions.

Solution from which medium prepared	No. of buds			Notes
	Culture 1	Culture 2	Culture 3	
1	0	0	0	Chloronemal filaments abundant.
2	10	39	13	Buds very immature, chloronemal filaments abundant.
3	10	20	34	Some buds with leaves, chloronemal filaments abundant.
4	30	46	48	All buds very immature, chloronemal filaments abundant.
5	94	112	78	Leafy shoots abundant, rhizoidal filaments present and chloronemal filaments fairly abundant.
6	56	73	45	Buds immature, rhizoidal filaments present and chloronemal filaments fairly abundant.
7	50	48	36	Buds very immature, rhizoidal filaments abundant.
8	28	32	26	Buds very immature, rhizoidal filaments abundant.
9	12	20	8	Buds very immature, rhizoidal filaments abundant.
10	0	0	0	Rhizoidal filaments abundant.

Table 15. Experiment c. (Lodge); Growth of Funaria after 11 weeks on media prepared from Voth's solutions. (Each result is the mean result of two cultures).

Solution from which medium prepared	No. of shoots	Oven dry wt. (105°C) per shoot (mgm.)*
1	138	0.060
2	391	0.079
3	450	0.079
4	586	0.077
5	993	0.057
6	1239	0.048
7	851	0.058
8	721	0.051
9	638	0.038
10	466	0.033

* Calculated from the total wt. of moss shoots clipped off at the surface of the agar.

very abundant, giving cultures an overall red-brown appearance. In cultures with high concentrations of nutrients, inhibition of growth was also found. Shoots were light green and the number of shoots and their height decreased with increase in the concentration of the solution, until on media prepared from solution 1, shoots were very stunted. Chloronemal growth became progressively more extensive, but the number of rhizoidal filaments and rhizoids decreased, none at all being found on media prepared from solutions 1 and 2.

A second series of experiments was carried out to determine the effect of adding potassium and nitrogen to a nutrient-deficient medium. Potassium chloride, potassium nitrate and ammonium nitrate were added to Voth's solution 10 in varying amounts giving concentrations of potassium within the range of solutions 1-10, as shown in tables 16, 17 and 18. Again all the solutions were solidified with Oxoid agar No. 3. At the end of the growing period potassium analysis was carried out on unwashed shoots using emission spectrophotometry. High levels of potassium did not compensate for the low concentrations of other nutrients, nor in the presence of inadequate amounts of other nutrients were high concentrations of potassium toxic. Except on media with very low potassium concentrations, the potassium content of the moss shoots was very similar (table 16). The addition of both potassium and nitrate nitrogen however, did result in some improvement in growth as is shown in table 17, although even at the highest concentrations mineral deficiency symptoms were still evident. The addition of

Table 16. Experiment d. (Lodge); Growth of Funaria after 11 weeks, on media prepared from Voth's solution 10 plus varying amounts of potassium chloride. (Each result is the mean result of three cultures).

Mgm./l.K in the modified Voth's solution 10	No. of shoots	Oven dry wt. (105°C) per shoot (mgm.)*	Mgm.K./gm. moss
486.5	494	0.015	37.2
234.3	492	0.015	42.1
140.6	477	0.015	39.9
93.7	489	0.015	39.9
46.9	515	0.015	40.7
35.1	528	0.016	40.0
23.4	476	0.016	39.0
11.7	453	0.016	40.4
5.9	485	0.014	7.3
2.9	457	0.018	8.2

*Calculated from the total wt. of moss shoots clipped off at the surface of the agar.

Table 17. Experiment e. (Lodge); Growth of Funaria after 14 weeks, on media prepared from Voth's solution 10 plus varying amounts of potassium nitrate. (Each result is the mean result of three cultures).

Mgm./l.K in the modified Voth's solution 10	Mgm./l.NO_3 in the modified Voth's solution 10	No. of shoots	Oven dry wt. (105°C) per shoot (mgm.)*
313.4	505.7	528	0.062
157.4	258.2	488	0.079
94.9	158.7	532	0.074
63.4	109.2	538	0.060
32.4	59.7	466	0.064
24.4	47.2	433	0.069
16.4	35.2	349	0.075
8.9	22.2	394	0.055
4.9	16.2	383	0.058
2.9	13.2	357	0.041

*Calculated from the total wt. of moss shoots clipped off at the surface of the agar.

Table 18. Experiment f. (Lodge); Growth of Funaria after 11 wks, on media prepared from Voth's solution 10 plus varying amounts of ammonium nitrate. (Each result is the mean result of three cultures).

Mgm./l. NH_4 in the modified Voth's solution 10	Mgm./l. NO_3 in the modified Voth's solution 10	pH of medium after 11 wks.*	No. of shoots	Oven dry wt. (105°C) per shoot (mgm.)**
306.5	1068.2	3.39	213	0.025
154.0	542.2	3.39	232	0.028
92.5	330.2	3.70	262	0.048
61.5	224.7	3.79	293	0.039
31.0	118.7	4.50	372	0.054
23.0	92.7	4.90	437	0.056
15.5	65.7	5.30	485	0.051
7.5	39.7	5.30	519	0.049
4.5	29.2	5.30	455	0.045
0.0	13.2	5.95	286	0.036

* determined electrometrically

** Calculated from the total wt. of moss shoots clipped off at the surface of the agar

ammonia nitrogen in low concentrations also resulted in some enhancement of growth, but at high concentrations, growth was progressively inhibited with increase in concentration of the salt (table 18) indicating its toxicity. After 11 weeks an obvious increase in the acidity of the medium correlated with the concentration of ammonium nitrate was found (table 18).

II. INVESTIGATIONS INTO THE NUTRIENT REQUIREMENTS OF FUNARIA

Experiments were of three main types: germination and early growth were first examined on soil from various sites and on unheated and heated soil. Growth over a longer period was then tested on unheated and heated soil with added nutrients and lastly, under more controlled environmental conditions on nutrient agar.

In the making up of all media, freshly distilled water and wherever possible analar chemicals were used. In order to obtain a readily available source of fresh spores for experiments and to reduce the possibility of variation due to genetical factors, a stock of Funaria was cultured in the greenhouse. Garden soil covered with a layer of bonfire ash and charcoal and, contained in earthenware flower pots, was steam-sterilised for 3 hours. A spore suspension, prepared from capsules freshly collected from a single colony of Funaria, was sprinkled over the surface of the cooled soil and ash. The pots were then stood in a tray of distilled water in a

north-facing greenhouse and covered with polythene bags. After 3 months, when gametophores were abundant and the cultures more resistant to drying out, these bags were removed. Ripe capsules were present after 5 months and further cultures were set up at 3 monthly intervals so that fresh mature capsules were always available. Subsequent cultures however, were not sprinkled with a spore suspension, but were placed among the sporing cultures for 1-2 days before being enclosed in the polythene bags.

It is generally agreed (Allsopp & Mitra, 1958) that two main types of filament can be distinguished in the primary moss protonema, i.e. the protonema developed directly from the spore. Although these differ both morphologically and physiologically they appear to be modifications of the same basic type of filament and many transitional forms between the two types occur. The first type of filament, characterised by the abundance of chlorophyll, hyaline cell walls and perpendicular cross walls, is referred to in the present work as a chloronemal filament. The second type, with little or no chlorophyll, pigmented cell walls and oblique cross walls, is termed a rhizoidal filament.

Germination and early growth on soil

Spores in suspension (see appendix p.269) were inoculated onto a membrane filter paper, (Millepore, cellulose ester) separated by a layer of Whatman's filter paper No. 1, from the soil-water mixture contained in a petri dish, diameter 5 cm.. The cultures were incubated at 18°C, under day-light fluorescent tubes which gave a

light intensity of 285 fc. for daily 12 hour periods. Some of the tests were set up under sterile conditions, but where no special precautions were taken, infection was never a problem as the growing period was so short.

Bonfire sites were not colonised by Funaria until at least 2 months after burning, whilst growth on some older bonfire sites, rapid fire sites and unburnt sites was poor or non-existent. In the first two experiments therefore growth was tested on soil from some of these sites to find whether this inhibition of growth could be directly linked with the soil.

Germination and early growth on bonfire ash of different ages (i.e. collected at different times after burning)

In this first series of tests the soil:water ratio, the soil sterilising procedure and the time allowed for growth were varied (see table 19) in order to determine the best methods for further experiments. Results were recorded by determining the percentage of spores germinated, 100-300 spores being counted unless otherwise indicated in the table. Alternatively the length of the protonemal filament of 20 spores was measured and the average length calculated.

Because of differences in method it was not surprising that the results shown, in table 20, are rather variable. A tendency can be seen however, both in the number of spores germinated and in the length of the protonemal filament, for growth to be inhibited on young bonfire ash, both on sterilised and non-sterilised

Table 19. Summary of methods used to examine germination and early growth of Funaria on bonfire ash of different ages.

Test no.	Site from which soil collected*	Gm. soil	Ml. water	Germination time (hrs.)	Soil sterilisation procedure	Growth parameter used
1	B4	1	5	72	Soil + water autoclaved	Percent. germ., all swollen green spores ± filament counted as germinated.
2	B5	2	1	72	Soil + water autoclaved	As for test 1
3	B5	2	2	72	Soil autoclaved before addition of water	Percent. germ., all spores with a filament at least ½ diam. of spore in length counted as germinated
4	B4	2	2	72	Soil autoclaved before addition of water	As for test 3
5	B11	2	2	84	Not sterilised	As for test 3
6	B10	2	2	84	" "	As for test 3
7	B11	2	2	72	" "	Average length of protonemal filament of 20 spores

(cont.)

Table 19. (cont.)

Test no.	Site from which soil collected*	Gm. soil	Ml. water	Germination time (hrs.)	Soil sterilisation procedure	Growth parameter used
8	B9	2	2	72	Not sterilised	As for test 7
9	B10	2	2	72	Soil heated to 150°C for 3 hrs. before addition of water	As for test 7
10	W6	2	2	84	Not sterilised	As for test 3
11	W6	2	2	72	" "	As for test 7

Cultures in tests 3-11 were lightly stained with methylene blue before observation.

* B = bonfire site
  W = weeded site

Table 20. Germination and early growth of Funaria on bonfire ash of different ages.

Test no.	Site from which soil collected	½	1	3	4	5	7	9	14	18
1	B4	80			82			80	86	87
2	B5	0			0			95	100	98
3	B5	0			0			97	99	
4	B4				37				92	
5	B11		0 0 [0]	20 18 24						
6	B10		[18] 14 [12]	[12] 17 12		13 40 20	[14] * *			

percentage spores germinated

(cont.)

Table 20 (cont.)

Test no.	Site from which soil collected	½	1	3	4	5	7	9	14	18	
7	B11		0	467		345	1272				average length of protonemal filament (μ)
			0	459		375	919				
			0	*		349	*				
8	B9		127	(477)		473	294				
			93	335		530					
			116	201		246					
9	B10		0	260		371	306				
			0	261		331	387				
			0	263		415	281				
10	W6		⌈9⌋	⌈28⌋							percentage spores germinated
			24	18							
			18	20							
11	W6		214	515		177	526				average length of protonemal filament (μ)
			344	339		176	309				
			269	297			335				

⌈ ⌋ = less than 100 spores counted
( ) = less than 15 spores measured
* = germination too advanced to count or measure spores

soils. Spores were able to germinate on all the unburnt soils.

Two phases can be recognised in spore germination: 1. swelling of the spore and 2. protrusion of the protonemal filament (Valanna, 1966). Although the first phase is usually distinct in Funaria and was used both in the first two tests here and in experiments of other authors e.g. Kofler, it has been found that this phase is little effected by external conditions and may be completed without further development taking place (Krupa, 1964). In aggreement with Valanne, it was therefore decided that the second phase was a better criterion to use and in further tests with reference to the defination of Hoffman (1962), germination was considered to have taken place when a filament at least half the diameter of the spore in length was present. These protonemal filaments were clearly visible if the cultures were lightly stained with methylene blue. Measurement of the length of the filament was very time-consuming and was therefore discontinued.

A ratio of 2 ml. of water to 2 gm. of soil gave a mixture which was dry enough to support the filter paper, but which did not dry out too much during the growing period and was employed in subsequent tests. Dry-heating which proved the most convenient way of sterilising the soil, and a growing period of 72 hours found to be sufficient to allow growth on favourable soils, were also used in further tests.

Comparison of germination on ash and soil from various sites

All the soils tested here were sterilised by dry-heating to 150°C for 3 hours.

Table 21 shows that usually where Funaria was present on the site spores showed positive germination on soil from the site. Spores were thus able to germinate on most bonfire soils but not on soil from rapid fire sites. A few exceptions were found however. On unburnt soil at Coombe Hill positive germination was shown although Funaria was not present in the field, whilst on soil from the ash pile site in this area A2, no germination was found even though in the field Funaria was present. Since with the exception of one sample collected from Cronkley Fell in Yorkshire, all samples were collected several months after burning, the age of the sample probably had little effect on germination. Germination, however as expected, was inhibited on the young ash sample from Cronkley Fell.

Both experiments therefore indicate that the colonisation of burnt sites by Funaria can be linked with the nature of the soil.

Germination on heated soil

It was becoming apparent from soil analyses (p.231) that heating soil, particularly to the temperatures used in sterilising soil, 100°C-150°C had a marked effect on its chemistry. Germination was therefore tested on aliquots of soil heated to different temperatures.

Table 21. Germination of Funaria on ash and soil from various sites. (Results are the means of at least 2 and in some cases 3 tests).

Area	Site from which soil collected	Age of site when sampled (mths.)	Percentage spores germinated	Funaria present (P) or absent (A) in Field at time sample collected
Coombe Hill	B17	8	2	A
	B17	11	98	P
	A2	8	0	P
	Bonfire site adjacent to B17	?	43	P
	Bonfire site adjacent to B17	6 mths. after first sample collected	98	P
	Unburnt soil	-	87	A
Waterperry Wood	B18	7	85	P
	B18	10	88	P
South Haven Peninsula	R4	24	0	A
	R4	26	0	A
	R4	22	0	A
	R4	30	0	A
	R4	33	0	A
	R5	½	0	A
	R5	3	0	A

(cont.)

Table 21 (cont.)

Area	Site from which soil collected	Age of site when sampled (mths.)	Percentage spores germinated	*Funaria* present (P) or absent (A) in field at time sample collected
	R5	4½	0	A
	R5	11	0	A
	Bonfire site a.	25	0	A
	Bonfire site b.	12?	100	P
Cronkley Fell	B20	(1 day)	0	A
	B20	4	100	A
	R9	18	0	A
Stour Wood	Bonfire site c.	18	99	P
	Bonfire site d.	18	100	P
	Bonfire site l.	2	90	P
	Bonfire site a.	36	100	P

Garden soil, collected from the grounds of the Botany Department was sieved (brass sieve B.S. 410 mesh no. 5), air-dried and all recognisable plant and animal material removed. Separate aliquots were then heated in an oven to one of the following temperatures: 50°C, 100°C, 150°C, 200°C, 250°C, 300°C, 350°C, 400°C 450°C, 500°C, 550°C, 600°C, 650°C and 700°C. Spore germination was tested on each aliquot, six series of tests being carried out and a fresh spore suspension used for each of the series.

The percentage of spores germinated in each test is shown in table 22. Complete inhibition of growth was found on soil samples heated to temperatures between 100°C and 300°C. Good growth however, was usually found on soils heated above and below these temperatures, although there was a tendency for growth of the protonemata to be less advanced on soils heated to 100°C and on soils heated to the highest temperatures as is shown in fig. 32.

In series 6, the results were unusual in that no germination took place on the unheated soil and growth was advanced on the soil heated to 700°C. Cultures were checked to ensure that the soils had not become mixed, but since the soil heated to 700°C had a distinctive colour, it was easily recognisable and it was clear that this had not happened.

Growth of Funaria is thus markedly affected when soil is heated and, this must obviously be taken into account in interpreting the results of the first two germination and early growth experiments, where some soils were heat sterilised.

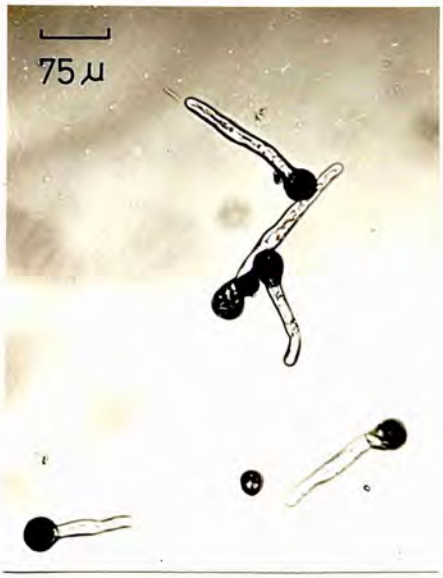
Table 22. Germination of Funaria spores on heated soils (percentage spores germinated).

Temp. to which soil preheated	Series					
	1	2	3	4	5	6
unheated	98	100	94	94	97	0
50	-	100	100	87	95	5
100	98	97	97	74	95	85
150	0	0	-	0	0	0
200	0	0	0	0	0	0
250	-	0	0	0	0	0
300	40	89	95	98	97	96
350	-	-	-	78	95	95
400	-	-	-	60	95	96
450	-	-	-	76	96	93
500	-	50	73	73	95	-
550	-	-	-	71	94	94
600	-	-	-	64	97	94
650	83	94	94	74	96	96
700	-	-	-	68	96	96

Fig. 32. Growth of Funaria on soils preheated to different temperatures;

a) unheated soil,

b) soil preheated to 100°C,

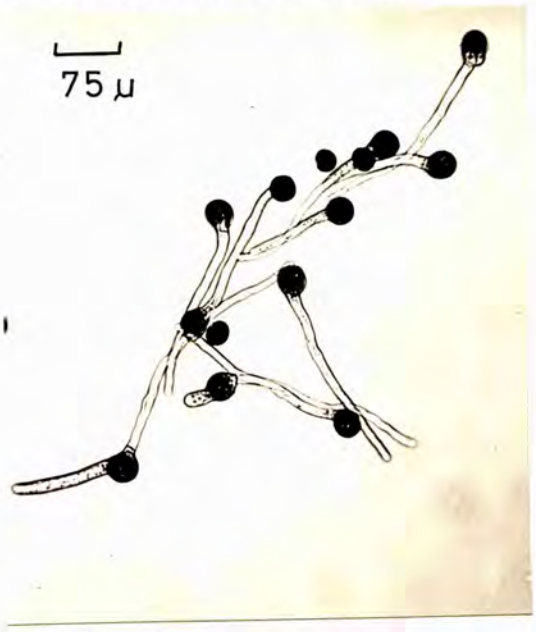


c) soil preheated to 200°C,

Fig. 32 (cont.).

d) soil preheated to 400°C,

e) soil preheated to 700°C.



Growth on unheated and heated soils with added nutrients

Garden soil from the grounds of Royal Holloway College was used as the basic soil and before treatment was air-dried, sieved (mesh 0.5 cm.) and all recognisable plant and animal material removed. The amounts of nutrients added to the soils were somewhat arbitrary since soil analysis results were not yet available. The treated soils were placed in earthenware flower pots. These were stood in china dishes of distilled water in the north-facing greenhouse amongst the sporing stock cultures, soils not being directly inoculated with a spore suspension.

Growth on unheated soil plus potassium, calcium, nitrogen and phosphorus

Potassium, calcium, nitrogen and phosphorus were added to the basic soil in the amounts shown in table 23. With the exception of potassium sulphate, which because of its low solubility was first mixed with a minimal amount of water, the dry salts were mixed with the soil with the aid of a glass rod. All the treatments were set up in triplicate. The cultures were examined at weekly intervals and any angiosperm growth which appeared during the course of the experiment carefully removed.

The first occurrences of protonemata and shoots are noted in table 24 together with the percentage covers of the main species present after 26 weeks. Initially cultures on all the soils showed some infection by algae and fungi, but the bryophytes soon overcame this. Most of the soils were colonised by mosses fairly rapidly,

Table 23. Nutrients (ppm.) added to unheated soil in tests on growth of Funaria.

Treatment no.	K	Ca	NO_3	PO_4	Other nutrients
1	2674	-	4088	233	-
2	8022	-	12264	699	-
3	2578	-	4088	-	-
4	96	-	-	233	-
5	960	-	-	2330	-
6	3496	-	-	-	Cl 3171
7	2991	-	-	-	SO_4 3675
8	-	1222	3779	-	-
9	-	969	-	1531	-
10 (Control)	-	-	-	-	-

Salts used: KNO_3, KH_2PO_4, KCl, K_2SO_4, $Ca(NO_3)_2$, $Ca_3(PO_4)_2$.

Table 24. Bryophyte growth on unheated soil plus varying amounts of potassium, calcium, nitrogen and phosphorus.

Treatment no.	1st occurrence (wks. after beginning of experiment)		Percentage cover of shoots after 26 weeks (Domin ratings)			
	Protonemata	Shoots	*Brachythecium rutabulum*	Tuberous species of *Bryum*	*Funaria*	
1	8	11	5	-	4	
	4	6	5	-	2	
	7	11	4	-	4	
2	7	14	2	2	3	
	8	14	-	-	-	
	11	12	-	1	-	
3	3	3	5	-	4	
	3	4	1	1	6	
	4	4	5	2	6	
4	4	8	1	-	1	*
	4	5	2	-	2	
	6	11	2	1	-	
5	3	3	6	-	2	
	3	3	3	-	3	+
	3	3	8	5	5	
6	3	3	1	1	4	
	3	3	6	1	6	
	3	3	6	1	3	

(cont.)

Table 24 (cont.)

Treatment no.	1st occurrence (wks. after beginning of experiment)		Percentage cover of shoots after 26 weeks (Domin ratings)		
	Protonemata	Shoots	*Brachythecium rutabulum*	Tuberous species of *Bryum*	*Funaria*
7	5	11	3	-	3
	3	11	3	-	3
	11	14	1	2	-
8	3	3	7	1	2
	3	3	7	1	1 *
	3	3	7	4	3 *
9	6	11	2	-	4
	5	11	2	1	5
	3	4	2	-	2
10 (control)	3	3	2	-	6
	3	3	5	1	2
	3	6	6	2	3

* a few shoots of *Leptobryum pyriforme* present.

\+ 1 plant of *Marchantia polymorpha* present.

protonemata and shoots being present on several soils by the third week. Little difference was found in the growth on the various soils throughout the experiment, differences being as great between soils of the same treatment as between soils of different treatments. As shown in table 24, Funaria occurred on nearly all the soils, but its growth was not very good and was no better than on the control untreated soil. Tuberous species of Bryum were present in many of the pots and Brachythecium rutabulum, present on most of the soils, often exceeded Funaria in abundance.

Growth on heated soil plus potassium, calcium, nitrogen and phosphorus

The above experiment was repeated, using soil which was first steamed for 3 hours. Treatments in this experiment were duplicated.

Cultures were again examined at weekly intervals. After 24 weeks the oven-dry weights of samples of leafy shoots and sporogonia were determined by collecting sample cores from predetermined positions in each culture, using a number 12 cork borer. Shoots and sporogonia were clipped off at soil level, separated and bulked samples for each culture dried at 105°C for 24 hours.

All the soils as in the previous experiment were initially covered by a growth of fungi and algae, which except in the one pot of treatment 2 was soon overgrown by bryophytes. The main differences between the results of this experiment and the previous one lay in the better growth of Funaria in all treatments. Except on the soil

of treatment 2, heavily infected with green algae, sporogonia were present (table 25) and other species were scarce and scattered. Other differences lay in the rate of colonisation by mosses which was slower and less varied in this experiment than on the unheated soils of the previous experiment (table 26). Protonemata were found on all the treated soils after 9 weeks, whilst shoots did not appear until after 13 weeks at the earliest. Colonisation of one pot of the control soil 10 (heated but no nutrients added) was a little more rapid, protonemata being found after 5 weeks. After 20 weeks many shoots had blackened leaves. As shown in table 25 this symptom was most marked on soils to which high concentrations of potassium had been added, but since it was also seen in shoots on soil to which no potassium was added, it cannot have been directly due to excess quantities of this nutrient. After 24 weeks little difference could be seen between the treatments as shown in table 25, although as in the previous experiment poorest growth was shown on soils of treatment 2 which had the highest concentrations of nutrients.

Heating the soil thus provided a greater stimulating effect on growth of Funaria than the addition of potassium, calcium, nitrogen or phosphorus in varying combinations, and no further stimulation of growth was found on addition of these nutrients to the heated soil.

A direct comparison of growth on heated soil, unheated soil and unheated soil plus nutrients.

Soils were steam sterilised for 3 or 7 hours and then air-dried again so that their initial moisture contents were equivalent to

Table 25. Growth of Funaria after 20 and 24 weeks, on heated soil plus varying amounts of potassium, calcium, nitrogen and phosphorus.

Treatment no.	Presence of black leaves after 20 wks.	Performance of leafy shoots after 24 wks.	Presence or absence of sporogonia after 24 wks.	Oven dry wt. (105°C)/sample after 24 wks. (mgm.)	
				Shoots	Sporogonia
1	(B)	Growth very good	Present	0.12	0.02
	(B)	Growth good	A few present	0.08	0.01
2	(B)	Growth good	A few present	0.07	0.01
	*(B)	" "	Absent	0.14	0.00
3	(B)	Growth very good	Present	0.16	0.04
	(B)	" " "	"	0.12	0.03
4		Growth very good	Present	0.12	0.04
	B	" " "	"	0.12	0.05
5		Growth very good	Present	0.15	0.02
	B	" " "	"	0.09	0.07
6	(B)	Growth very good	Present	0.08	0.07
	(B)	" " "	"	0.06	0.02
7	(B)	Growth very good	Present	0.10	0.04
	(B)	" " "	"	sample lost	sample lost
8		Growth very good	Present	0.12	0.02
	B	" " "	"	0.13	0.03

(cont.)

Table 25 (cont.)

Treatment no.	Presence of black leaves after 20 wks.	Performance of leafy shoots after 24 wks.	Presence or absence of sporogonia after 24 wks.	Oven dry wt. (105°C)/sample after 24 wks. (mgm.)	
				Shoots	Sporogonia
9	B	Growth very good	Present	0.08	0.03
		" " "	"	0.11	0.01
10 (control)	B	Growth good	Present	0.14	0.01
		Growth very good	"	0.16	0.04

(B) = many shoots with black leaves B = only a few shoots with black leaves

* = heavily infected by algae throughout experiment

Table 26. Rate of colonisation by Funaria of heated soil plus varying amounts of potassium, calcium, nitrogen and phosphorus.

Treatment no.	1st occurrence (wks. after beginning of experiment)		Cover reached 50% (wks. after beginning of experiment)	
	protonemata	shoots	protonemata	shoots
1	9	15	11	16
	9	14	11	16
2	9	15	11	18
	9	17	*	*
3	9	14	11	16
	9	14	*	15
4	9	13	11	15
	9	13	11	14
5	9	13	11	15
	9	14	11	15
6	9	14	11	15
	9	13	11	16
7	9	14	11	15
	9	14	11	16
8	9	13	11	14
	9	14	*	15
9	9	13	11	14
	9	13	11	14
10	9	13	*	15
	5	13	11	13

* 50% cover never reached

those of the unheated soils. 100 ml. of distilled water, containing in some treatments, tri-ammonium orthophosphate and ammonium nitrate (NH_4NO_3), was added to each aliquot, the levels of nutrients added being much lower than in the two previous experiments. Puddling was avoided by first placing the soil in a polythene jar and gradually mixing in the water by rolling the jar. Each treatment was set up in triplicate, details of the different treatments being given in table27.

Cultures were examined weekly and after 13 weeks the number of shoots of each species touching a thin wire stretched across the surface of each culture were counted. 5 transects, each 14 cm. long and dissecting the centre of the pot, were laid out in each pot, a 2 cm. border being left at the edge in case of edge effects.

As in the previous experiments, initial colonisation by bryophytes of the non-heated soils was more rapid, but again the addition of nitrogen and phosphorus to soils resulted in no difference in growth of Funaria. As seen in table 27 Funaria was the species showing best growth on the heated soils, although no differences could be seen in its growth on soils steamed for 3 hours and those steamed for 7 hours. Some cultures showed poor growth of all species. This however was not obviously due to fungal or algal infection and is difficult to explain. Tuberous species of Bryum were only abundant on the non-heated soils.

Growth on nutrient agar

Work was continued along the same lines as the

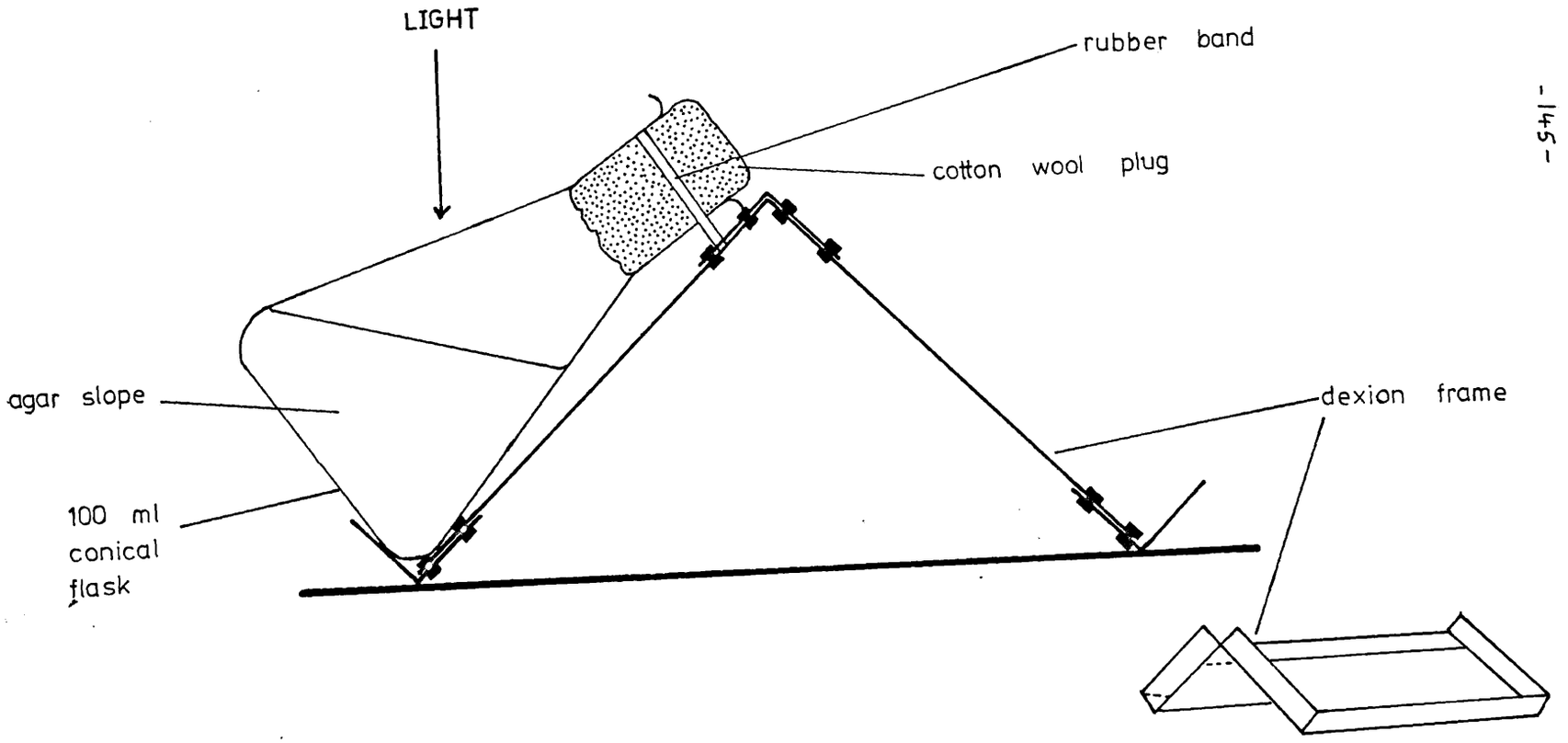
Table 27. Bryophyte growth after 13 weeks on heated soil, unheated soil, and unheated soil plus nitrogen and phosphorus.

Treatment no.	Culture no.	No. of hrs. soil steamed	Ppm. nutrients added			No. of shoots occurring along 5 transects across each culture			Notes
			NH_4	NO_3	PO_4	Funaria	Tuberous species of Bryum	Other species	
1	1	3	0	0	0	7	0	0	Funaria the only abundant species, growth very good on 3.
	2					4	0	0	
	3					109	0	0	
2	1	7	0	0	0	92	0	5	Funaria the only abundant species on 1 and 3, a few shoots present on 2.
	2					0	0	0	
	3					137	3	2	
3	1	0	0	0	0	1	1	0	Tuberous species of Bryum most abundant species, but growth of Funaria good on 2.
	2					59	41	0	
	3					7	44	0	
4	1	0	33	124	29	85	66	4	Tuberous species of Bryum and Funaria both abundant on 1.
	2					33	97	0	
	3					27	12	0	

investigation by Lodge. Experiments were carried out to investigate the toxicity of ammonia nitrogen and to find whether nutrients added singly or in varying combinations would stimulate growth of Funaria on a mineral-deficient medium. The possible toxicity of high concentrations of nutrients was also investigated and experiments carried out to determine the relative importance of micronutrients and osmotic concentration.

Mineral solutions were solidified with 1 percent agar, Oxoid no. 3 and sterilised by autoclaving for 15 minutes at 15 lbs/sq.in.. 100 ml. Pyrex Erlenmeyer flasks were used to contain the media, since the agar dried up less readily in these than in petri dishes. The medium was sloped in the flasks to increase the surface area for growth, whilst the positioning of the flasks in specially designed racks (fig. 33) resulted in a second gentler slope, thus avoiding possible harmful effects due to the accumulation of excess water (Ward, 1960). The position of the flasks also ensured that the cultures received the maximum amount of light from the light source which was unavoidably situated in the top of the incubator. All the cultures were set up under sterile conditions; details of the preparation of the spore suspension and the inoculation technique being described in the appendix p.269. As in the germination and early growth tests cultures were incubated at 18°C under day-light fluorescent tubes giving a light intensity of 285 fc. for daily 12 hour periods. In most experiments growth was allowed to continue for 10 weeks by which time on favourable media, large numbers of

Fig. 33. The position of cultures during incubation.



robust gametophores were present. All the treatments were set up in triplicate.

Parameters used for measuring growth included number of shoots, area or largest diameter of colony and oven-dry weight per shoot. To determine the dry weights, shoots were clipped off at the surface of the agar and dried at 105°C for 12 hours. Where possible 300 shoots were used for the determination. The performance of Funaria in the various cultures was compared with growth on a nutrient-deficient medium prepared from Voth's solution 10 (V10), a satisfactory medium prepared from Voth's solution 5 (V5) and in some cases with growth on a medium prepared from Voth's solution 1 (V1), where nutrient concentrations were too high. The appearance of cultures on these media was very similar to that found by Lodge, growth on Voth's solutions 5 and 10 media being shown in fig. 34.

On the Voth's solution 1 medium, growth of the chloronemal filaments was very extensive covering the whole surface of the agar, but rhizoidal filaments were absent and shoots stunted, pale green and very few in number.

Growth on media prepared from Voth's solution 10 plus varying amounts of nitrogen and phosphorus added in the form of ammonium salts.

Nitrogen and phosphorus were added in the form of ammonium nitrate NH_4NO_3 and tri-ammonium orthophosphate, in the amounts shown in table 28. The amount of ammonia nitrogen added in the two series was the same.

Fig. 34.

10 weeks growth of Funaria on media prepared from;
a) Voth's solution 5 b) Voth's solution 10.

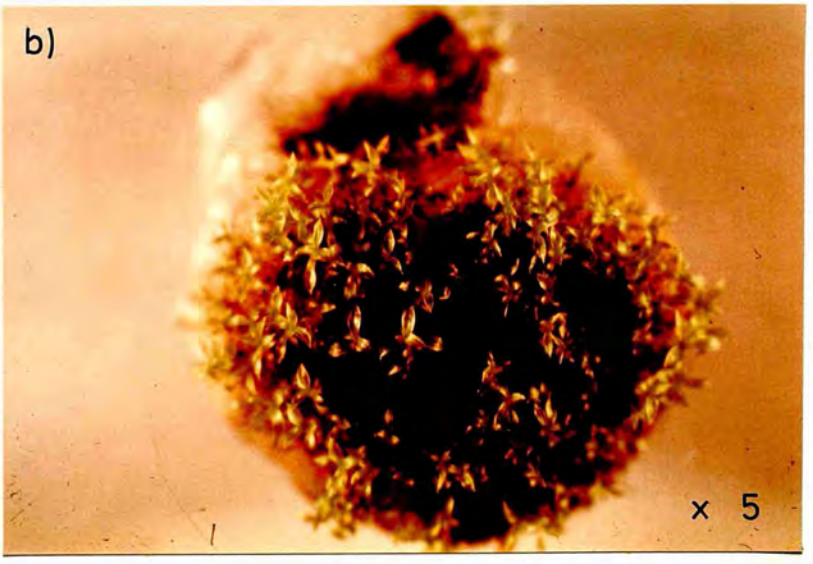


Table 28. Protonemal growth of Funaria after 2 weeks, on media prepared from Voth's solution 10 plus varying amounts of nitrogen and phosphorus, added in the form of ammonium salts.

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)			pH*	Protonemal growth - = no growth, + = growth poor, ++ = growth good		
	NO_3	PO_4	NH_4		1	2	3
N_1	3100.5	-	902.0	5.25	+	+	+
N_2	1860.3	-	541.2	5.45	+	+	+
N_3	620.1	-	180.4	5.70	++	++	++
N_4	310.0	-	90.2	5.55	++	++	++
N_5	62.0	-	18.0	5.65	++	++	++
N_6	6.2	-	1.8	5.65	++	++	++
P_1	-	1582.9	902.0	8.60	-	-	-
P_2	-	949.8	541.2	8.60	-	-	-
P_3	-	316.6	180.4	8.55	-	-	-
P_4	-	158.3	90.2	8.60	+	+	+
P_5	-	31.7	18.0	7.30	++	++	++
P_6	-	3.2	1.8	6.35	++	++	++
Voth's solution 5	-	-	-	5.55	++	++	++

(cont.)

Table 28 (cont.)

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)			pH*	Protonemal growth - = no growth, + = growth poor, ++ = growth good		
	NO_3	PO_4	NH_4		1	2	3
Voth's solution 10	-	-	-	5.60	++	++	++

* determined electrometrically before autoclaving.

Even after 2 weeks, better growth was found on media to which only small amounts of ammonia nitrogen had been added particularly in the phosphorus series (table 28).

Between 6 and 10 weeks the appearance of the cultures did not alter much. As shown in fig. 35a very little growth was found on P1, P2 and P3 which had the highest concentrations of ammonia nitrogen in this series. On the media with lower concentrations, P4, P5 and P6 growth improved as the concentration of ammonia nitrogen decreased. On P4 and P5 protonemal growth was extensive, but the colonies were yellow-brown in colour and the few gametophores present, although large-leaved, were stunted and dark green. Shoots on medium P6 closely resembled those on the Voth's solution 10 medium.

Growth in the nitrate series was also poor, growth however again improving with decrease in the concentration of ammonia nitrogen as shown in fig. 35b. More growth occurred on media with the highest concentrations of ammonia nitrogen N1, N2 and N3 than on P1, P2 and P3, but after 10 weeks much of the growth appeared dead. The cytoplasm in the brown filaments was contracted and the chloroplasts were very pale green. As shown in fig. 36 some filaments also showed abnormal cell division. After 10 weeks a few gametophores were present on N2 and N3 but these were stunted and dark green. The leaves were malformed bearing peculiar projections, whilst nerves and borders were often absent (fig. 37). Shoots were not present on N4, but were more abundant on N5 than on N2 and N3 and were less

Fig. 35. Growth of Funaria after 10 weeks, on media prepared from Voth's solution 10 plus varying amounts of a) phosphorus and b) nitrogen added in the form of ammonium salts. (For details of treatments see table 28).

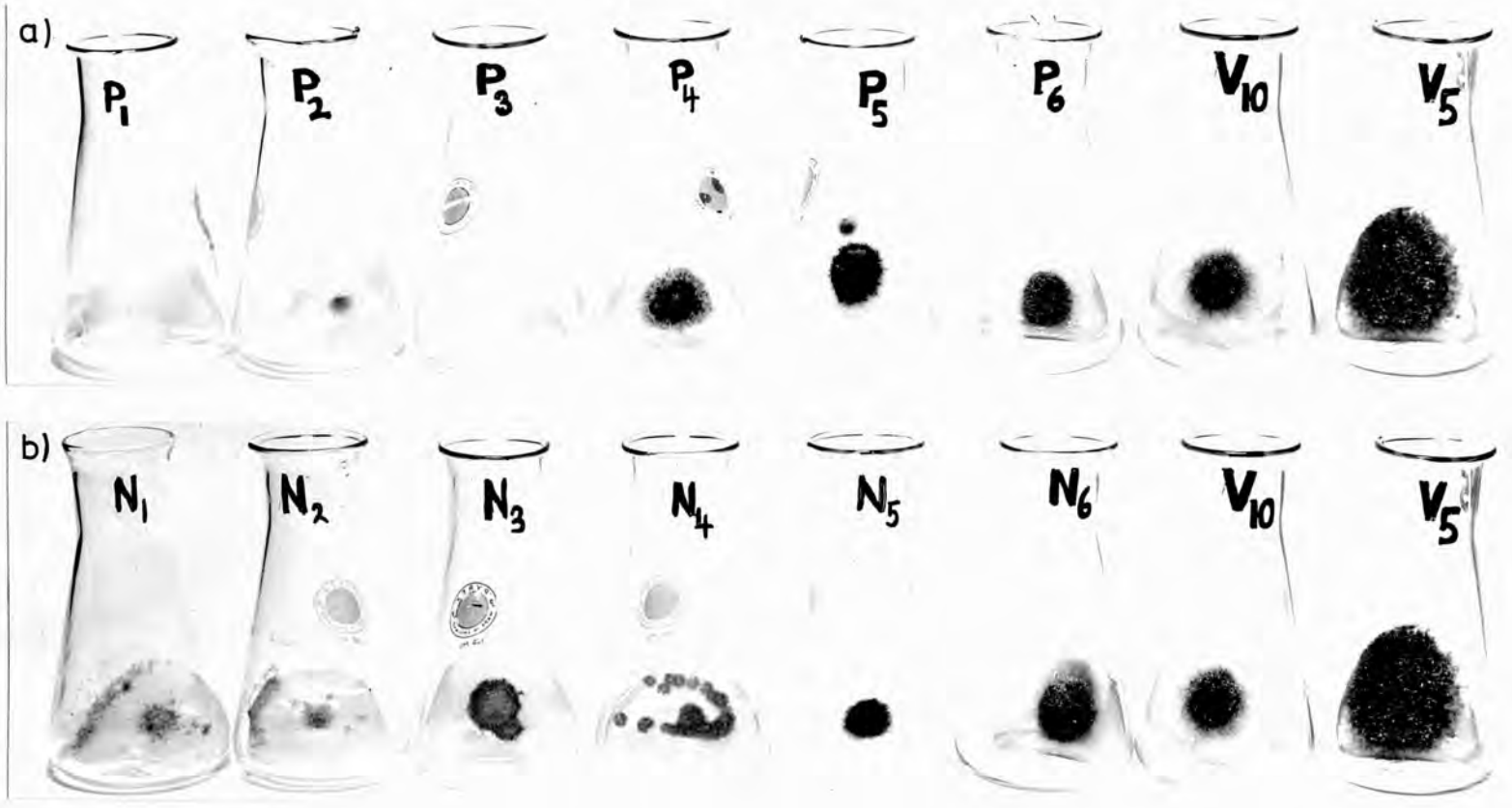


Fig. 36. Chloronemal filaments from a 10 week old culture of Funaria grown on a medium containing ammonium nitrate

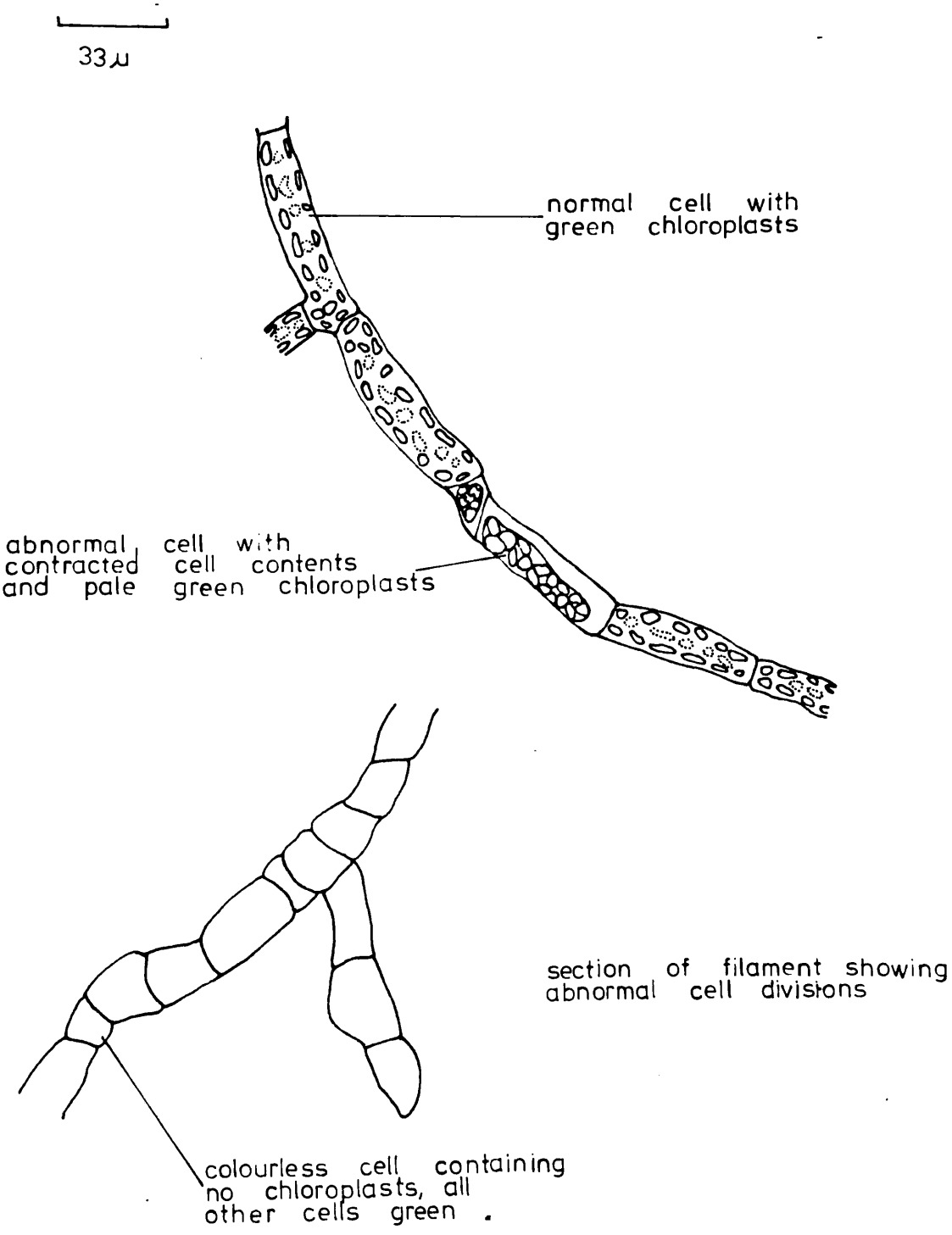
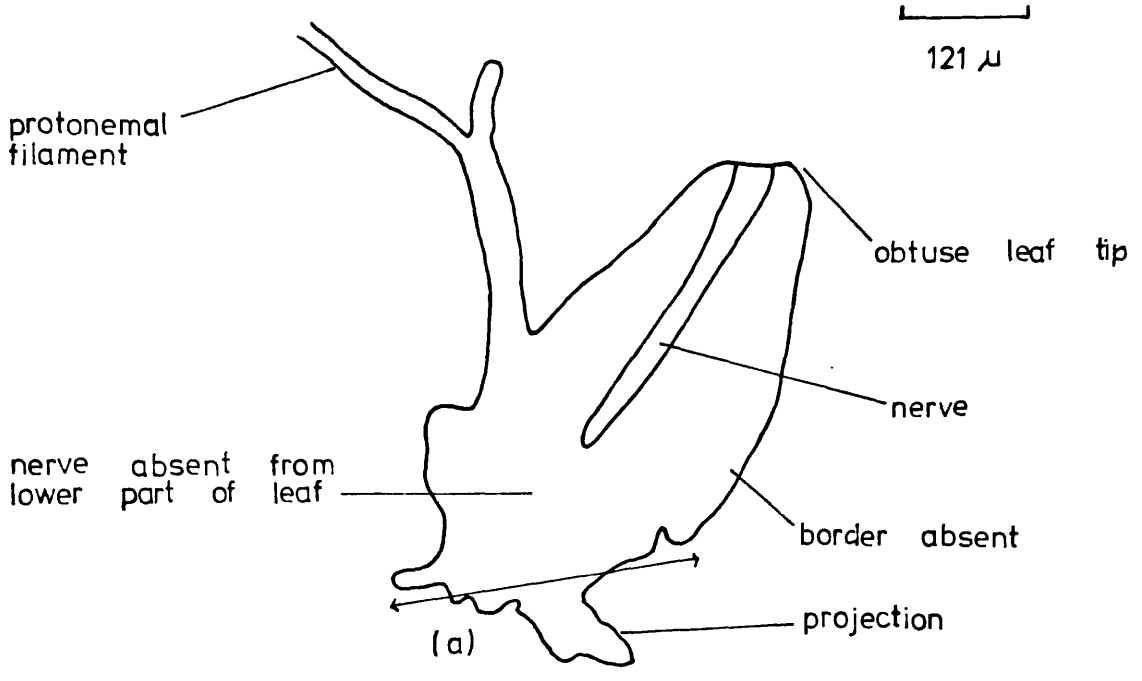
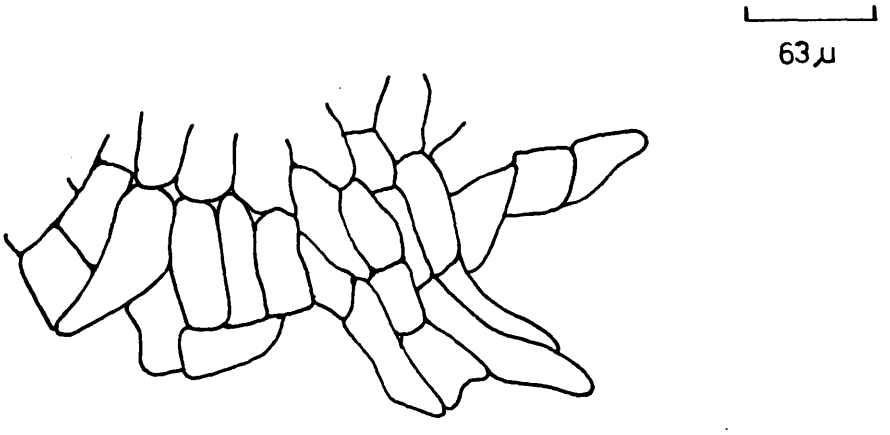


Fig. 37. A malformed leaf from a 10 week old culture of Funaria grown on a medium containing ammonium nitrate



(a) abnormal structure of lower part of leaf



stunted and malformed. Shoots on medium N6, like P6, closely resembled those of the Voth's solution 10 cultures.

Growth on media prepared from Voth's solution 10 plus varying amounts of phosphorus added in the form of ammonium salts.

Phosphorus was added to Voth's solution 10 in the form of three ammonium salts, ammonium di-hydrogen orthophosphate, $NH_4H_2PO_4$, di-ammonium hydrogen orthophosphate, $(NH_4)_2H\ PO_4$ and tri-ammonium orthophosphate. (The assumption was made that phosphorus was not taken up differentially from different salts). The concentrations of phosphorus were varied at two different levels of ammonia concentration as shown in table 29.

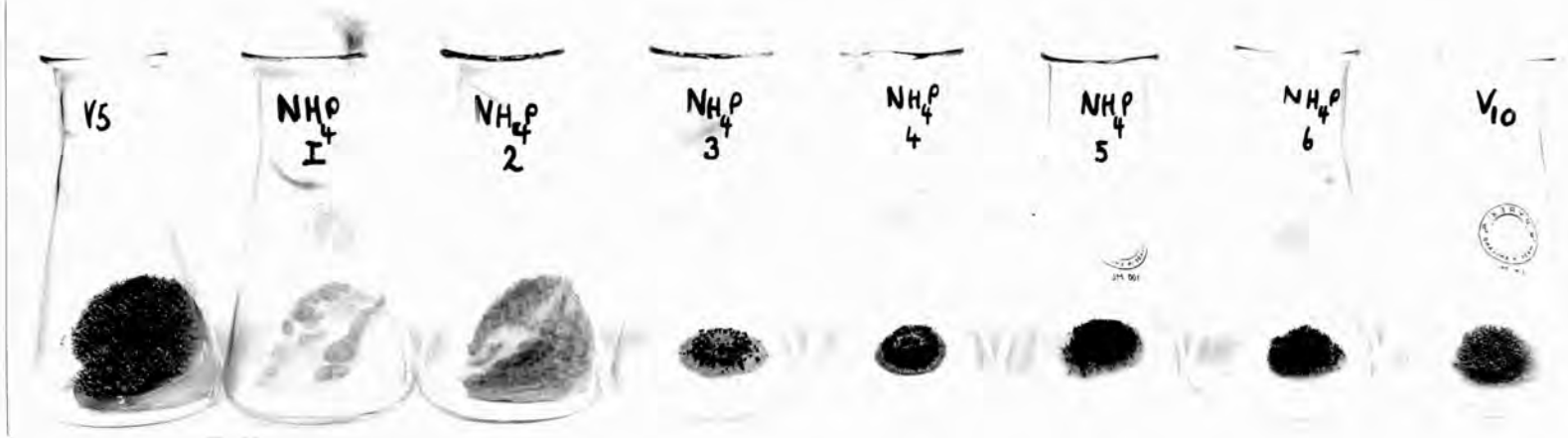
The appearance of the cultures after 10 weeks is summarised in table 29 and illustrated in fig. 38. On media with the higher concentrations of ammonia nitrogen, protonemal growth was yellow-brown and shoots, where present, were dark green and stunted, showing abnormal leaf forms as in the nitrate series of the previous experiment. On the media with the lower concentrations of ammonia nitrogen shoots were similar to those of Voth's solution 10, but were darker green and still possessed a few abnormal leaves. In addition, at both concentrations of ammonia nitrogen a slight improvement in growth could be linked with decreasing concentration of phosphorus. On medium NH_4P_6, which had the lowest concentrations of both ammonia nitrogen and phosphorus, growth was nearly as good as on the Voth's solution 10 medium.

Table 29. Appearance of Funaria cultures after 10 weeks, on media prepared from Voth's solution 10 plus varying amounts of phosphorus added in the form of ammonium salts.

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)		pH*	Appearance of cultures
	PO_4	NH_4		
NH_4 P 1	189.95	36.08	5.05	Yellow-brown protonemal growth, no gametophores.
NH_4 P 2	94.98	36.08	7.35	Yellow-brown protonemal growth with a few dark green, stunted gametophores.
NH_4 P 3	63.32	36.08	7.75	Yellow-brown protonemal growth with scattered dark green, stunted gametophores.
NH_4 P 4	94.98	18.04	5.25	Pale green protonemal growth with scattered dark green gametophores.
NH_4 P 5	47.49	18.04	7.05	Pale green protonemal growth with scattered dark green gametophores.
NH_4 P 6	31.66	18.04	7.30	Growth very similar to that of Voth's solution 10 cultures, but gametophores darker green.

* determined electrometrically before autoclaving

Fig. 38.



Growth of Funaria after 10 weeks, on media prepared from Voth's solution 10 plus varying amounts of phosphorus added in the form of ammonium salts. (For details of treatments see table 29).

The toxicity of ammonium phosphate was thus related mainly to the ammonium ion, greatest differences in growth being found between cultures on media with different concentrations of ammonia nitrogen. Some inhibition of growth could however, be related to the phosphate ion, the concentration of which was fairly high in the media of both this experiment and the previous one, in comparison with Voth's solution 5 (table 12).

Growth on media prepared from Voth's solution 10 plus nitrogen and phosphorus added either in the form of the ammonium or calcium salts.

Media were prepared containing three different concentrations of nitrate nitrogen and phosphorus as shown in table 30. The ions were added either in the form of their ammonium salts, NH_4NO_3 and tri-ammonium orthophosphate, or their calcium salts, $Ca(NO_3)_2 \cdot 4H_2O$ and $CaH_4(PO_4)_2 \cdot H_2O$.

The appearance of the cultures after 10 weeks is summarised in table 30. On media containing nitrate nitrogen and phosphorus in the form of the ammonium salt, growth showed the characteristic symptoms of ammonia toxicity. These symptoms as expected were more marked in the media with the higher concentrations of ammonium salts. On media with nitrate nitrogen and phosphorus added in the form of the calcium salts, growth was better than that of the Voth's solution 10 cultures. Shoots however, were still small and spindly and rhizoidal filaments and rhizoids abundant. As indicated by the dry weight figures shown in table 30, shoots were not nearly so

Table 30. Growth of Funaria on media prepared from Voth's solution 10 plus nitrogen and phosphorus, added either in the form of ammonium or calcium salts.

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)				pH*	Oven dry wt. (105°C) per shoot (mgm.)**	Appearance of Cultures
	Ca	NH_4	NO_3	PO_4			
NH_4NP_1	-	108.24	248.03	63.32	7.60	×	Protonemal growth yellow-brown and only a few stunted, dark-green shoots present.
NH_4NP_2	-	54.12	124.02	31.66	7.15	×	Protonemal growth yellow-brown and only a few stunted, dark-green shoots present.
NH_4NP_3	-	27.06	62.01	15.83	6.90	×	Protonemal growth yellow-brown; some shoots stunted other spindly as on Voth's solution 10 medium.
CNP_1	93.52	-	248.03	63.32	4.30	0.035	Rhizoidal filaments, rhizoids and small-leaved shoots abundant.
CNP_2	46.76	-	124.02	31.66	5.08	0.016	Rhizoidal filaments, rhizoids and small-leaved shoots abundant.

(cont.)

Table 30 (cont.)

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)				pH*	Oven dry wt. (105°C) per shoot (mgm.)**	Appearance of Cultures
	Ca	NH_4	NO_3	PO_4			
CNP_3	23.38	-	62.01	15.83	5.25	0.039	Rhizoidal filaments, rhizoids and small-leaved shoots abundant.
Voth's solution 5	-	-	-	-	5.05	0.108	Growth normal
Voth's solution 10	-	-	-	-	5.80	0.011	Growth normal

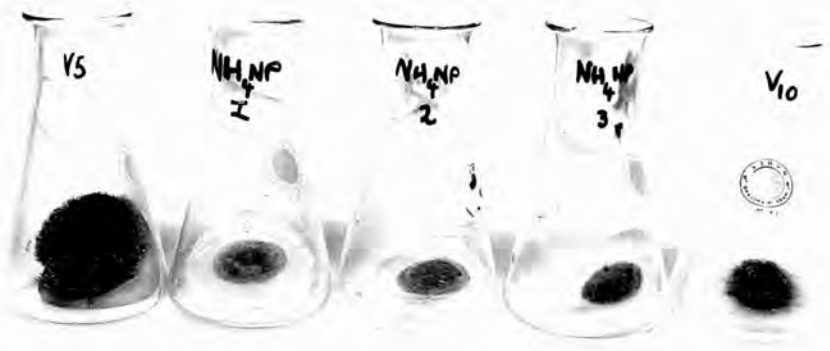
* determined electrometrically before autoclaving

** only calculated for 1 culture of each treatment

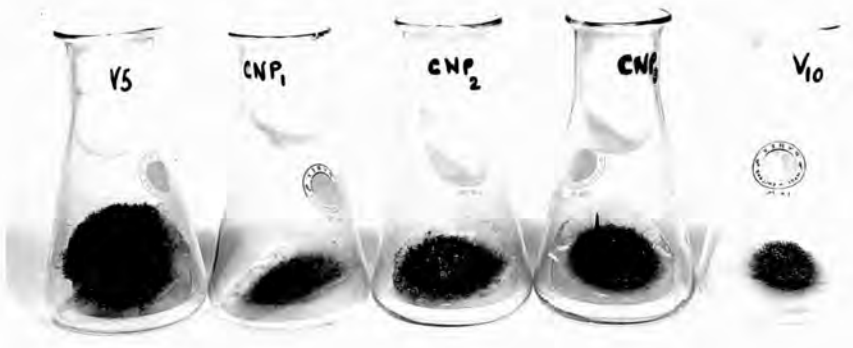
× insufficient shoots for determination

Fig. 39. Growth of Funaria after 10 weeks, on media prepared from Voth's solution 10 plus nitrogen and phosphorus added in the form of a) ammonium salts and b) calcium salts. (For details of treatments see table 30).

a)



b)



robust as those grown on the Voth's solution 5 medium. There was no difference in the appearance of cultures in the three treatments, although the oven-dry weight per shoot for medium CNP2 was low.

The addition of nitrate nitrogen and phosphorus in the form of the ammonium salt as expected rendered the medium toxic, but when the same concentrations of nitrate nitrogen and phosphorus were added in the form of the calcium salts, there was a slight improvement in growth over that of Voth's solution 10 cultures. Raising the concentration of added salts however, did not result in a corresponding increase in growth and on all three media mineral deficiency symptoms were still evident.

Growth on media prepared from Voth's solution 10 plus varying combinations of potassium, calcium, nitrate nitrogen and phosphate phosphorus.

Calcium, potassium, nitrate nitrogen and phosphorus, were added to Voth's solution/10 in various combinations, final concentrations however being kept as close as possible to those of Voth's solution 5. Two other media were prepared in which a) levels of the four nutrients were similar to those in Voth's solution 1, KCNP2 and b) levels of potassium and phosphorus were similar to those of Voth's solution 5, but levels of calcium and nitrate nitrogen were very high KCNP3. The concentrations of nutrients in all the solutions are shown in table 31.

The number of shoots per colony, dry weight per shoot and colony areas are given in table 32. The dry weights were very

Table 31. Amounts of potassium, calcium, nitrate and phosphate added to Voth's solution 10 in tests on growth of Funaria.

Treatment	Nutrients added to Voth's solution 10 (mgm./l.)				pH*
	Ca	K	NO_3	PO_4	
CN	46.89	-	124.02	-	5.2
KN	-	91.10	124.02	-	5.2
CP	46.89	-	-	32.29	5.0
KP	-	91.10	-	31.34	5.2
KNP	-	91.10	124.02	31.34	5.0
CNP	46.89	-	124.02	32.29	5.2
KCP	46.89	91.10	-	32.29	5.2
$KCNP_1$	46.50	91.50	124.02	31.35	5.2
$KCNP_2$	458.41	585.56	2101.01	377.62	5.2
$KCNP_3$	239.68	57.67	809.86	35.60	5.2

*determined with indicator papers before autoclaving.

Salts used: KNO_3, $Ca(NO_3)_2$, $4H_2O$, $CaH_4(PO_4)_2.H_2O$, KH_2PO_4, KCl, $CaCl_2.2H_2O$

Table 32. Growth of Funaria on media prepared from Voth's solution 10 plus varying combinations of potassium, calcium, nitrogen and phosphorus.

Treatment	No. of shoots per culture	Average no. of shoots	Oven dry wt. (105°C) per shoot (mgm.)	Average wt. per shoot (mgm.)	Area of colony (sq.cm.)	Average area of colony (sq.cm.)
CN	199		0.074		3.55	
	232	205	0.082	0.067	5.04	4.86
	183		0.046		6.00	
KN	163		0.186		5.32	
	215	151	0.067	0.099	5.74	4.91
	76		0.043		3.66	
CP	171		0.068		2.23	
	-	-	-	-	-	-
	-		-		-	
KP	299		0.038		4.40	
	17	162	0.012	0.043	3.64	3.69
	169		0.079		3.04	
KNP	233		0.056		11.94	
	333	306	0.194	0.107	10.06	10.13
	353		0.070		8.53	
CNP	136		0.052		8.49	
	82	127	0.010	0.034	9.32	8.92
	162		0.040		8.94	
KCP	164		0.085		3.53	
	-	-	-	-	-	-
	-		-		-	

(cont.)

Table 32. (cont.)

Treatment	No. of shoots per culture	Average no. of shoots	Oven dry wt. (105°C) per shoot (mgm.)	Average wt. per shoot (mgm.)	Area of colony (sq.cm.)	Average area of colony (sq.cm.)
KCNP I	124		0.028		14.79	
	246	193	0.013	0.019	11.38	12.20
	208		0.016		10.43	
KCNP 2	434		0.074		14.26	
	431	425	0.121	0.100	16.00	16.17
	409		0.106		18.26	
KCNP 3	233		0.077		12.25	
	229	222	0.071	0.073	14.93	13.22
	213		0.070		12.47	
Voth's solution 5	115		0.038		16.66	
	43	137	0.042	0.076	12.15	14.07
	253		0.149		13.40	
Voth's solution 1	0		0.000		14.19	
	10	7	0.050	0.020	21.13	18.06
	10		0.010		18.85	
Voth's solution 10	187		0.056		2.36	
	133	143	0.048	0.056	3.32	2.85
	109		0.066		2.87	

variable and the differences indicated could not be related to the visual appearance of the shoots. In many of the cultures, particularly those showing mineral deficiency symptoms, rhizoids were very abundant and extended up the shoot stems and were therefore included in the dry weights. The numbers of shoots per culture were also very variable.

The visual appearance of cultures after 10 weeks

CN, CP, KN, KP: two cultures on medium CP were contaminated and therefore discarded. All other cultures had small spindly shoots with abundant rhizoidal filaments and rhizoids. The shoots on medium KN were a little larger than those of the other media, whilst the colony areas of cultures on CN, KN and KP media although small, were generally larger than those of the Voth's solution 10 cultures.

KCP: two cultures were discarded because of infection. The colony of the remaining culture was small and composed of spindly shoots with abundant rhizoidal filaments and rhizoids.

KNP, CNP: the cultures formed were large and on two of the CNP media and all three of the KNP media shoots were large-leaved and robust. Shoots, however were more abundant on the KNP media.

KCNP 1: the colonies were large and all the shoots large-leaved and robust. In two cultures shoots were abundant.

KCNP2, KCNP 3: colonies were large particularly on the KCNP 2 media, shoots however, were scattered and although they were large-leaved and robust were short-stemmed and dark green in comparison with those of the Voth's solution 5 medium. Rhizoidal filaments and rhizoids were scarce.

Voth's solutions 1, 5 and 10: growth was as expected, except that shoots were abundant in only one of the Voth's solution 5 cultures.

Thus only on the media to which all four nutrients were added in concentrations similar to those of Voth's solution 5 was growth as good as on Voth's solution 5 medium. Where high concentrations of all these nutrients (KCNP2), or just calcium and nitrate nitrogen (KCNP3) were present, symptoms of nutrient excess were exhibited, although these were not as marked as those of Voth's solution 1 cultures. Growth on all the other media, showed signs of mineral deficiency, although some improvement in growth over that on Voth's solution 10 medium was found, particularly on addition of potassium, nitrate nitrogen and phosphorus when growth approached that of Voth's solution 5 cultures. Of the other media next best growth was found on media with added calcium, nitrate nitrogen and phosphorus, and potassium and nitrate nitrogen.

The importance of micronutrients

Two solutions were prepared, one containing macronutrients in the concentration of Voth's solution 1 and the other micronutrients in the concentration of the same solution. Media were prepared from dilutions of these solutions containing concentrations of nutrients as shown in table 33. Additional potassium, calcium, nitrogen and phosphorus were added to medium 7 so that concentrations of these nutrients were equivalent to those of Voth's solution 5. All the media were prepared with double glass-distilled water and special

Table 33. Nutrient concentrations of solutions used to test importance of micronutrients to growth of Funaria.

Solution no.	Conc. of macronutrients equivalent to	Conc. of micronutrients equivalent to	pH*
1	Voth's solution 5	Voth's solution 5	5.2
2	" " 5	" -	5.2
3	" " 10	" " 10	5.2
4	" " 10	" " 5	5.2
5	" " 5	" " 3	5.2
6	" " 5	" " 7	5.2
7	" " 10	" " 5	5.2
	+ 57.67 mgm./l. K 42.01 " " Ca 198.20 " " NO_3 35.60 " " PO_4		

* determined with indicator papers before autoclaving.

care was taken in the cleaning of glassware. Analar chemicals were used from previously unopened bottles, but no further attempt was made to purify them.

The number of shoots per colony, the oven-dry weight per shoot and the colony areas are all shown in table 34 and the appearance of cultures in fig. 40. Although figures for dry weight per shoot and number of shoots show considerable variability, both these parameters like colony area, indicated that best growth was found on media containing macronutrients or just calcium, potassium, nitrogen and phosphorus in concentrations equivalent to those of Voth's solution 5, regardless of the concentration of micronutrients. Even when the micronutrient solution was completely omitted from the medium or a concentration equivalent to that of Voth's solution 3 was added, growth did not seem to be affected.

The importance of osmotic concentration

Solutions were prepared containing nutrients in the concentrations of Voth's solution 5, but with the osmotic concentrations adjusted until they were equivalent to those of other Voth's solutions, as shown in table 35. An additional solution was prepared with nutrients in the concentration of Voth's solution 7 and an osmotic concentration the same as that of Voth's solution 5. The osmotic concentrations of the Voth's solutions were taken from Voth (1943). Concentrations were adjusted using mannitol (nutritionally

Table 34. Growth of Funaria after 10 weeks, on media containing various concentrations of micro- and macronutrients.

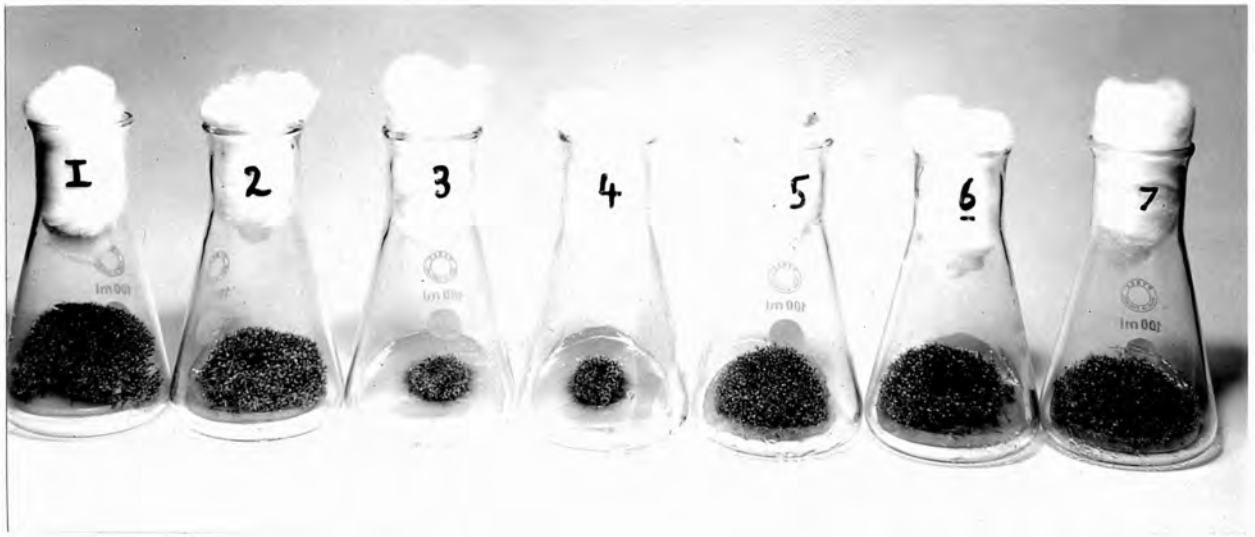
Medium prepared from solution no.	No. of shoots per culture	Average no. of shoots	Oven dry wt. (105°C) per shoot (mgm.)	Average oven dry wt. (105°C) per shoot	Area of colony (sq. cm.)	Average area of colony (sq. cm.)
1	392		0.148		11.08	
	298	452	0.159	0.155	9.57	10.85
	667		0.158		11.91	
2	244		0.130		10.94	
	665	438	0.107	0.144	13.62	11.45
	406		0.195		9.79	
3	151		0.049		3.17	
	175	182	0.071	0.057	2.62	2.97
	220		0.051		3.11	
4	136		0.033		2.40	
	105	145	0.090	0.055	1.09	1.70
	193		0.041		1.62	
5	270		0.206		12.00	
	354	305	0.170	0.177	9.38	10.58
	292		0.155		10.36	

(cont.)

Table 34. (cont.)

Medium prepared from solution no.	No. of shoots per culture	Average no. of shoots	Oven dry wt. (105°C) per shoot (mgm.)	Average oven dry wt. (105°C) per shoot	Area of colony (sq. cm.)	Average area of colony (sq. cm.)
6	294		0.137		11.04	
	576	364	0.133	0.126	13.70	12.33
	223		0.107		12.26	
7	337		0.179		12.06	
	337	416	0.164	0.156	12.49	11.66
	573		0.125		10.42	

Fig. 40.



Growth of Funaria after 10 weeks, on media containing various concentrations of micro- and macronutrients. (For details of treatments see table 33).

Table 35. Nutrient and osmotic concentrations of solutions used to test the importance of osmotic concentration to growth of Funaria.

Treatment no.	Conc.. of nutrients equivalent to Voth's solution	Ml. 1M mannitol / l.	Osmotic conc. (atm.)	Osmotic conc. equivalent to Voth's solution	pH*
V5	5	-	0.21	5	5.10
V5-4	"	6.60	0.37	4	5.15
V5-3	"	15.80	0.59	3	5.10
V5-2	"	30.40	0.94	2	5.10
V5-1	"	67.40	1.83	1	5.15
V7-5	7	3.30	0.21	5	5.10
V7	"	-	0.13	7	5.30

* determined electrometrically before autoclaving.

inert to many plants) and the new values calculated from the formula given by Hale (1958).

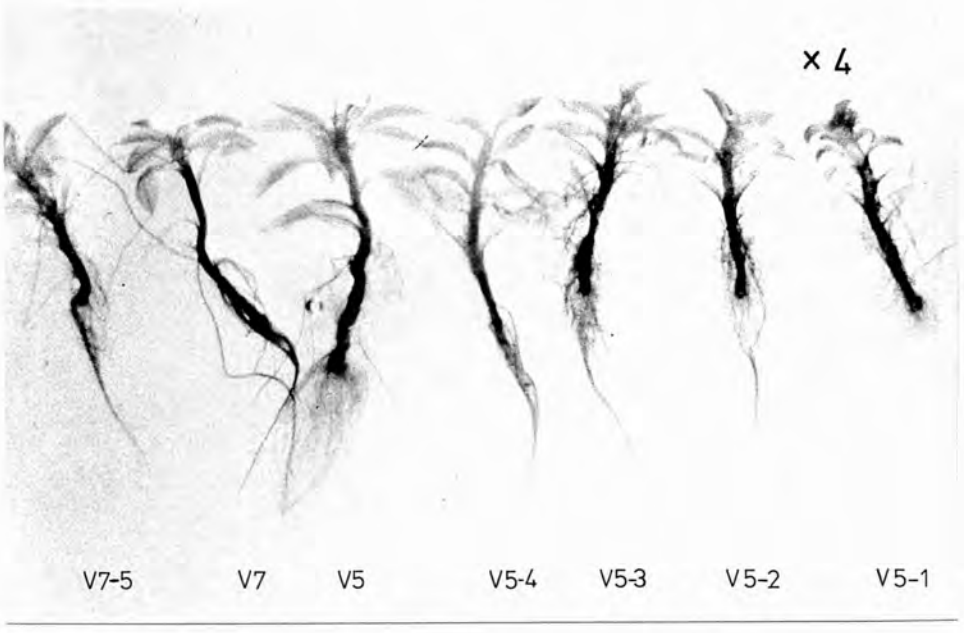
After 4 weeks all the cultures on media with added mannitol showed better growth of protonemata than on the control media, Voth's solution 5 and Voth's solution 7. Growth improved progressively with increase in the concentration of mannitol except at the highest concentration V5-1. Buds were present on all the media except the controls. After 7 weeks however, best growth was found on Voth's solution 5 and V5-4. Growth of the Voth's solution 7 cultures, as expected, showed some signs of nutrient deficiency. Cultures on medium V7-5 could not be distinguished from those on Voth's solution 7 media. As shown in fig. 41, on Voth's solution 5 with high concentrations of added mannitol, V5-3 to V5-1, shoots were shorter, leaves smaller and rhizoidal filaments and rhizoids more abundant. These symptoms increased progressively with increase in the concentration of mannitol.

III. INVESTIGATIONS INTO THE NUTRIENT REQUIREMENTS OF OTHER SPECIES

Greenhouse culture of Bryum argenteum, Ceratodon purpureus and Marchantia polymorpha.

Bryum argenteum from spore and shoot fragments and Ceratodon purpureus from spores were both successfully grown in the same way as stock cultures of Funaria (pp.118-9). Growth and

Fig. 41.



Shoots of Funaria from 7 week old cultures grown on media containing varying amounts of mannitol. (For details of treatments see table 35).

development of gametophores and sporogonia however was much slower in both species and cultures were rapidly invaded by Funaria unless kept in a separate part of the greenhouse. Marchantia polymorpha also grew well on heat-sterilised soil plus bonfire ash and charcoal, either from gemmae or the growing tips of thalli. Cultures were less susceptible to invasion by Funaria, growth being rapid and gemmae produced abundantly.

Germination of Bryum argenteum and Eurhynchium praelongum on heated soil

The germination of Bryum argenteum was tested on soils heated to temperatures ranging from 50°C-700°C for 3 hours, using the same soil and techniques as for Funaria spores (p.129). Germination of Eurhynchium praelongum was tested on the soil aliquot heated to 150°C. Three trials were carried out with each species, using a fresh spore suspension each time.

Unlike Funaria spores, split spore coats could not be seen attached to the swollen germinated spores of Bryum argenteum or identified as separate bodies. Since there were apparently large numbers of ungerminated spores in all the cultures, even where protonemal development was good, it is possible that spore coats had a similar appearance to, and were confused with, the ungerminated spores. Percentage germination was therefore not determined.

As with Funaria, germination of Bryum argenteum was completely inhibited on soil heated to temperatures between 100°C and

300°C (fig. 42a) and spores of Eurhynchium praelongum showed no germination on the soil heated to 150°C. Bryum argenteum spores germinated on all soils heated above and below these temperatures as shown in fig. 42b and c, although growth was less advanced on soils heated to the higher temperatures.

Growth of Bryum argenteum on nutrient agar

Unless otherwise stated culture techniques and growing conditions were the same as those for Funaria (p.144). Spore suspensions were prepared from capsules collected from a single colony of the moss.

Growth on media prepared from Voth's solutions

A comparison was made of growth on Voth's solutions 1, 3, 5, 7 and 9 over a period of 14 weeks.

The number of shoots formed on each medium and the areas of the colonies, as shown in table 36, indicated that best growth occurred on the Voth's solution 5 medium. This was also apparent visually (fig. 43). In cultures on this medium (fig. 44a) chloronemal and rhizoidal filaments were equally abundant and the majority of shoots were large and robust. Growth however, was dense and thin etiolated shoots were also present amongst the more robust shoots. On media containing higher concentrations of nutrients protonemal growth was extensive and composed mainly of chloronemal filaments, whilst shoots were small and stunted, particularly on Voth's solution 1 media (fig.44b). Where concentrations of nutrients were lower than in

Fig. 42. Early growth of Bryum argenteum on soils pre-heated to different temperatures.

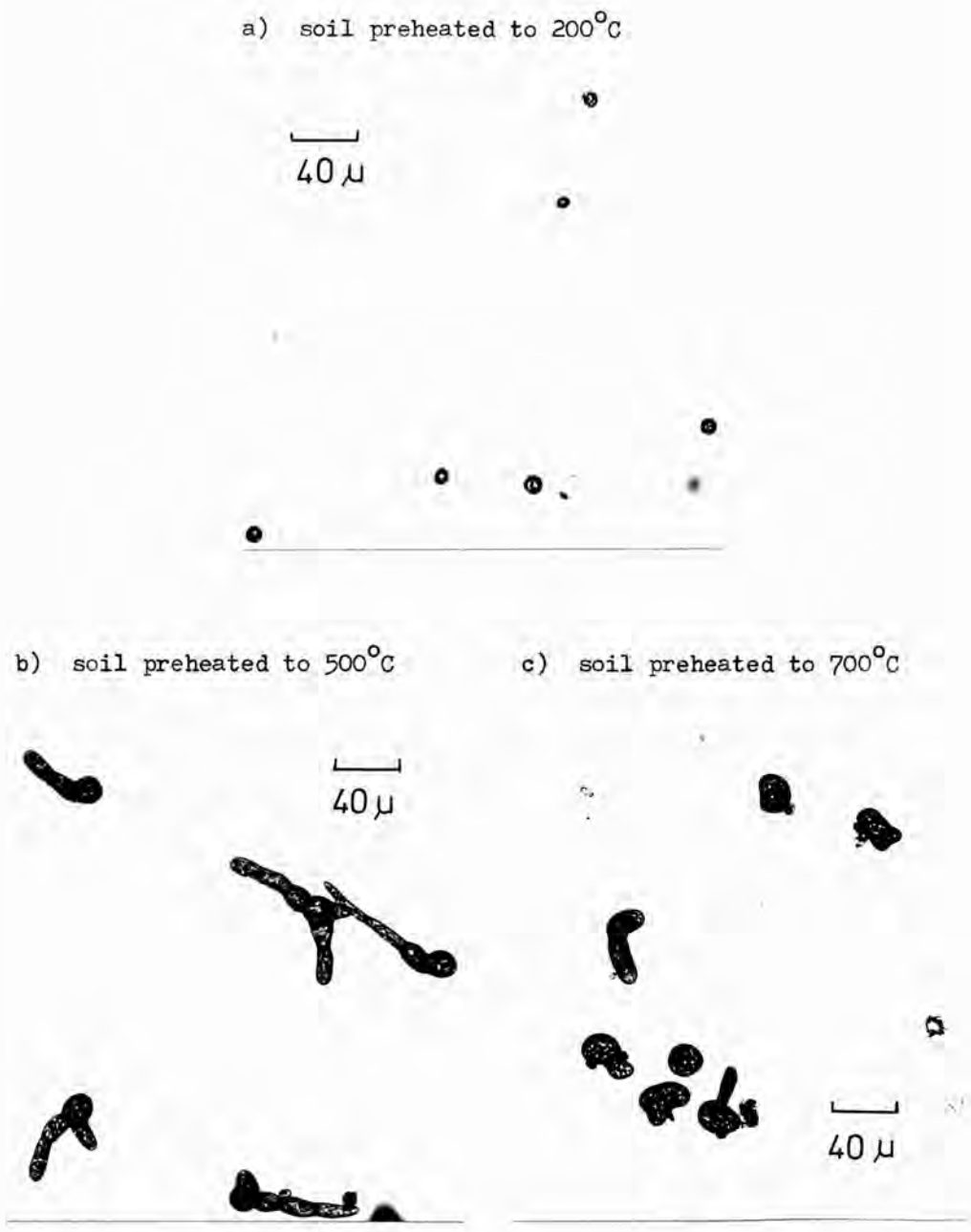


Table 36. Growth of Bryum argenteum on media prepared from Voth's solutions.

Solution from which medium prepared	No. of shoots per culture	Average no. of shoots	Area of colony (sq. cm.)	Average area of colony (sq. cm.)
1	122		8.77	
	139	121	11.15	10.52
	103		11.64	
3	594		15.19	
	257	405	16.76	15.65
	363		15.00	
5	987		19.19	
	786	819	14.47	16.36
	684		15.43	
7	447		11.74	
	515	451	10.09	10.63
	391		10.06	
9	386		5.06	
	121	245	4.45	5.20
	229		6.08	
10	145		2.98	
	172	149	5.47	4.53
	130		5.13	

Fig. 43. Growth of Bryum argenteum after 14 weeks, on media prepared from Voth's solutions 1(V1), 3(V3), 5(V5), 7(V7), 9V9) and 10(V10).

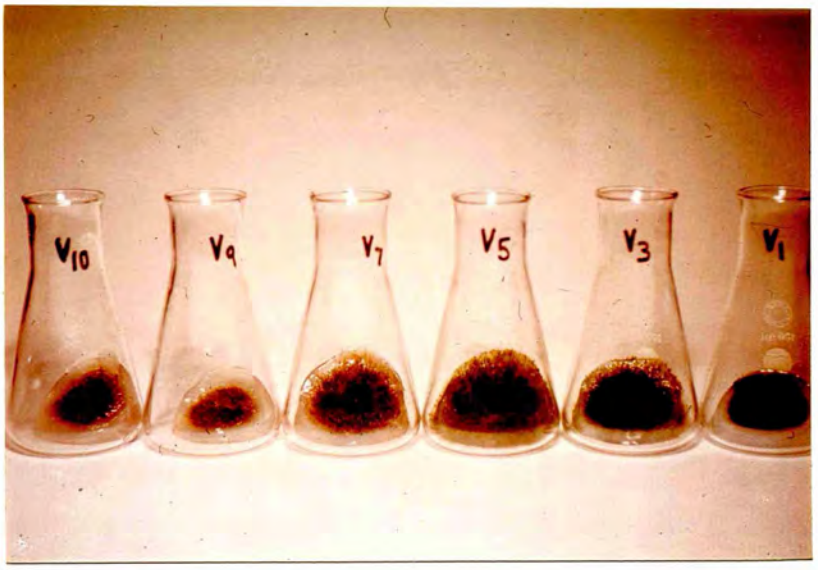
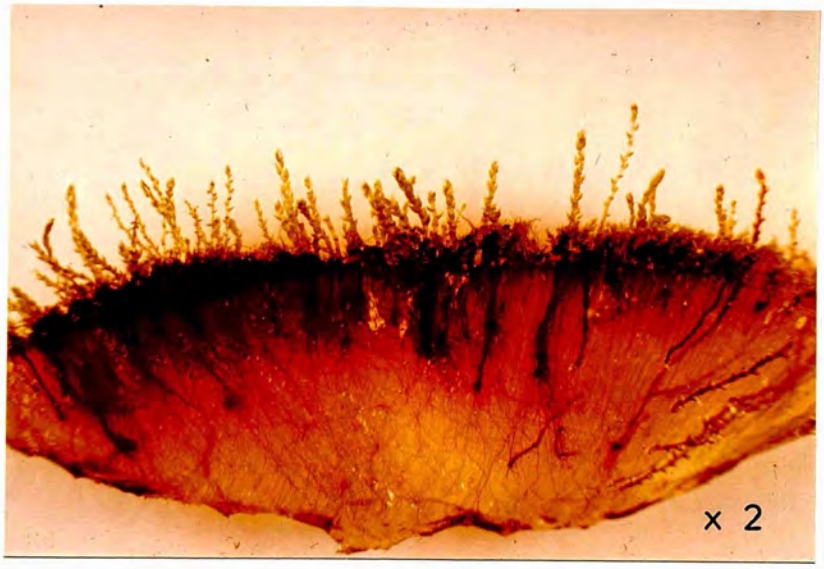


Fig. 44. Growth of Bryum argenteum after 14 weeks on media prepared from;

a) Voth's solution 5,



b) Voth's solution 1,

Fig. 44 (cont.).

c) Voth's solution 10.

Voth's solution 5, rhizoidal filaments became progressively more abundant and shoots smaller and more spindly (fig.44c).

The appearance of cultures of Bryum argenteum on Voth's solutions were thus very similar to those of Funaria, best growth again being found on media with nutrient concentrations in the middle of the range.

The effect of adding ammonium nitrate to Voth's solution 5 on growth of Bryum argenteum.

To test the supposed nitrophilous tendencies of Bryum argenteum (Watson, 1968) varying amounts of ammonium nitrate, as shown in table 37, were added to Voth's solution 5 to find whether additional nitrogen would improve growth. Duplicates of each medium were prepared and growth allowed to continue for 6 weeks.

Table 37. Amounts of nitrogen added to Voth's solution 5 in order to test nitrophilous tendencies of Bryum argenteum.

Solution no.	NH_4 mgm./L.	NO_3 mgm./L.
1	36	124
2	18	62
3	9	31
4	-	-

After 4 weeks all cultures showed good protonemal growth and had scattered shoots. Differences between the cultures were not noticeable, although shoots seemed to be darker green on media with added nitrogen. After 6 weeks however, no difference at all could be seen between the cultures. Growth in all was good, large robust shoots being present.

The presence of additional nitrogen in Voth's solution 5 therefore, did not result in any noticeable improvement of growth. It was of interest that in contrast to its effect on Funaria, ammonia nitrogen appeared to have no adverse effect on Bryum argenteum.

IV. DISCUSSION

Growth on soil

The preheating of soil was found to have a significant effect on growth. Germination of Funaria was completely inhibited on a garden soil preheated to temperatures between 100°C and 300°C for 3 hours, although spores were able to germinate on soils heated to lower or higher temperatures. Spores of Bryum argenteum behaved in the same way whilst spores of a non-bonfire species, Eurhynchium praelongum, were also unable to germinate on the aliquot heated to 150°C. In more long-term experiments however, growth of Funaria on a garden soil, steam-heated for 3-7 hours was much better than on unheated soil, this observation agreeing with Hoffman's finding that

growth of Funaria was stimulated on soils heated to 200°C-300°C. This author also reports that soils heated to temperatures above and below this supported much less growth. In spite of this overall stimulation of growth, as might have been expected from the results of the germination tests, colonisation of heated soils was initially delayed. This delay must have been due to the initial toxicity of the soil and not destruction of spores and vegetative propagules in the soil as a result of heating, since spores were abundant in the greenhouse atmosphere.

Since heating the soil alone is sufficient to stimulate good growth, the good growth of Funaria and probably also that of Ceratodon purpureus and Marchantia polymorpha on heated soil, plus ash and charcoal, cannot have been entirely due to addition of the latter. Hoffman however, did show that the presence of ash and charcoal resulted in additional stimulation of growth of Funaria. The addition of potassium, calcium, nitrogen and phosphorus in varying combinations to heated soil had little effect on growth of Funaria, nor was the poor growth on unheated soil improved by the addition of these nutrients, even though the amounts added were high. Hoffman also reports that attempts to simulate the growth on burnt soil by the addition of calcium, magnesium and potassium were unsuccessful, whilst under semi-natural conditions, addition of macronutrients including nitrogen but not phosphorus also proved unsuccessful. The addition of nitrogen particularly in combination with phosphorus to a

soil preheated to 600°C and low in these nutrients did however, stimulate growth, but addition of calcium and phosphorus singly or in combination to this soil provided little stimulus.

Reasons for the initial inhibition of growth and later stimulation of growth cannot be explained until the characteristics of heated soil have been described. Similarly the results of germination tests on bonfire ash of different ages and soils collected from a variety of burnt and non-burnt sites, cannot be properly interpreted until the effect of heat on soil is known, as some of the soils in these tests were heat-sterilised. Results of these tests appear to support the evidence of field experiments that there is a strong link between the colonisation of sites by Funaria and the nature of the soil, but detailed consideration of this is postponed until later (pp. 260-261).

Growth on nutrient agar

Measurement of growth: the visual appearance of shoots and protonemata was usually consistent in cultures on the same medium, but in order to express growth quantitatively other criteria were used. Of these the size of the colony, as also noted by Kofler, was a good indicator of growth. It was easy to measure and gave results which could be related to the visual appearance. Shoot numbers per culture were sometimes variable, but often gave useful information. Growth ratings based on shoot weight however, in many

experiments did not correspond with those based on visual appearance and showed considerable variability in cultures on the same medium. This unreliability of shoot weight as a growth indicator, which was also reported by Hoffman, may have been at least partly due to the variation in numbers of rhizoids on the stems of shoots. Although not used in the present investigation, shoot length and leaf dimensions, as used by Hoffman, would probably have provided further useful data.

Hydrogen ion concentration and renewal of the medium: except for some solutions in which ammonium ions were present and one other solution, the initial pH values of the nutrient solutions fell within a narrow range 4.9-6.1. Media however were not renewed during the course of experiments and some change in pH undoubtedly took place, particularly as phosphate concentrations were usually low. Although Funaria appears to be able to grow on substrates with a wide range of pH (Schweizer, 1930; Meyer & Ford, 1943 and Hoffman), the possibility that the availability of some ions and growth may have been affected at extremes of pH cannot be discounted. In addition to changes in pH, depletion of ions, changes in nutrient balance, accumulation of plant secretions and lack of aeration may all have affected ion uptake and growth. Techniques described by Bopp (1963) provide a practical way of renewing a solid medium whilst maintaining the purity of the cultures and would be useful in further more critical studies.

Altering the total concentration of the nutrient solution: both Funaria

and Bryum argenteum were able to show some growth on media with a wide range of nutrient concentrations, this ability in Funaria also being evident from the investigations of Hoffman and Kofler and the reports of earlier workers e.g. Schoene (1906) and Gurlitt (1918). Optimum growth for both species, however, was found in the middle of the range of concentrations, where the nutrient solutions had osmotic concentrations ranging from 0.18-0.21 atm.. Such solutions are rather dilute when compared with those commonly employed for culturing higher plants which usually have osmotic concentrations in the range 0.4-1.0 atm. (Hewitt, 1966). This preference of bryophytes for fairly dilute solutions has been noted by other authors (Garjeanne, 1932; Griggs & Ready, 1934 and Voth, 1943).

Marked morphological differences were found in the growth of both species on media with different nutrient concentrations. It is therefore rather surprising that Hoffman found little difference between the growth of Funaria on Voth's solution 5 and on three concentrations 25, 50 and 100 percent, of Hoagland's solution. The morphological responses of Funaria and Bryum argenteum found in the present investigation were much alike and were also very similar to those of Marchantia polymorpha grown on the same range of solutions (Voth, 1943). In addition the production by various bryophyte species growing on mineral-poor media of large numbers of rhizoidal filaments and rhizoids, a mineral deficiency symptom noted in the present study, has often been reported (see Kofler and Allsopp & Mitra, 1958). It seems therefore that the symptoms of nutrient deficiency and nutrient

excess described on pp.108&114, may be characteristic of bryophytes in general.

The extensive growth of chloronemal filaments and poor growth of gametophores on media with high nutrient concentrations, supports Hoffman's observation for Funaria, that protonemata are more tolerant to solutions of high osmotic concentration and differences between the requirements of protonemata and gametophores probably exist. As Hoffman points out however, combinations and concentrations of nutrients must promote both protonemal and gametophore growth for the plant to be successful.

The effect produced by altering the concentration of the nutrient solution from its optimum, may be directly due to deficiency or excess of certain nutrients, an unsuitable osmotic concentration, or a combination of these factors. Growth of Funaria on media containing nutrients in the concentrations of Voth's solutions 5 or 7, but with the osmotic concentrations adjusted by means of mannitol, showed varying responses according to the amount of mannitol added. If mannitol is nutritionally inert it can be assumed that the osmotic concentration itself is directly responsible for the growth response. Some doubt however, arises as to whether mannitol is nutritionally inert with respect to Funaria. Growth responses were very similar to those demonstrated by Mitra & Allsopp (1959) for Pohlia nutans on media with added sucrose and glucose. Since these authors found that the effects of mannitol at the lowest concentration added (which was high

compared with concentration added in the present work) were different from those of glucose at the same concentrations, they concluded that the effect of glucose at these concentrations was not entirely osmotic. Since the effect of mannitol in similar concentrations on the growth of Funaria were like those found by Mitra & Allsopp for glucose, it would seem that in this case, as with glucose, its effect was not entirely osmotic. In addition growth on media containing Voth's solution 7 with mannitol added to give an osmotic concentration equivalent to that of Voth's solution 5, initially showed better growth than Voth's solution 5 cultures, although growth would have been expected to remain similar to that on Voth's solution 5 or 7 media if mannitol is nutritionally inert. The extent of the effect of osmotic concentration on growth of Funaria is thus still uncertain, although it is most likely that the inhibition of growth which occurrs on concentrated media is at least partly due to osmotic effects.

Altering the concentration of individual nutrients: taking into consideration the results both of Lodge's investigation and those of the present work, the robust growth found on Voth's solution 5 media could not be simulated on Voth's solution 10 media by the addition of potassium, or the addition of any combination of 2 or 3 of the following: potassium, calcium, nitrogen and phosphorus. Some improvement in growth however was found on addition of nitrate nitrogen in the form of the potassium salt, particularly when phosphorus was

also added, growth in this case being nearly as good as on Voth's solution 5. Growth was also improved on addition of both nitrate nitrogen and phosphorus in the form of the calcium salt, but was not as good as when potassium, nitrate nitrogen and phosphorus were added. Only slight improvement in growth was found on addition of the following combinations; potassium and phosphorus, calcium and phosphorus, calcium and nitrate nitrogen, and calcium, potassium and phosphorus, suggesting the importance of the addition of nitrate nitrogen in the presence of either potassium or phosphorus. Best growth was found when potassium, calcium, nitrate nitrogen and phosphorus were all added. A balance between these four nutrients seems to be important, since when their relative concentrations were similar to those of Voth's solution 5, growth was indistinguishable from that of Voth's solution 5 cultures, in spite of the apparently low concentrations of magnesium, sulphur and micronutrients.

In the following paragraphs the terms 'low' and 'high' are used in comparison with the concentrations of nutrients in Voth's solution 5. High concentrations of potassium chloride or potassium nitrate in the presence of low concentrations of other nutrients, resulted in no signs of nutrient excess and in fact Funaria showed symptoms of mineral deficiency on these media. Analysis of plants grown on media with varying concentrations of potassium chloride showed that except on media with the very low concentrations, there was little difference in the amounts of potassium taken up. This suggests that the potassium requirements under these conditions may

have been low and that some active control of potassium uptake exists. Analysis of both the plant and the medium at the end of the growing period is obviously important in further investigations on the role of individual nutrients in growth. Symptoms of nutrient excess were seen in the presence of high concentrations of calcium and nitrate nitrogen, together with moderate levels of potassium and phosphorus and low concentrations of other nutrients, and also on media with concentrations of calcium, potassium, nitrate nitrogen and phosphorus similar to those of Voth's solution 1. Symptoms on these two media however were not as marked as those of Voth's solution 1 cultures, where concentrations of magnesium, sulphur and micronutrients were also high.

For good growth, Funaria thus appears to require relatively high concentrations of calcium, potassium, nitrogen and phosphorus in proportions similar to those of Voth's solution 5, nitrate nitrogen in the presence of phosphorus and potassium being especially important. The requirement for magnesium and sulphur seems to be lower. The toxicity of concentrated media however, appears to result from the combined effects of all nutrients. From the results of nutrient agar and nutrient sand experiments Hoffman came to similar conclusions, growth in the absence of any one of the macronutrients being poor and nutrient deficiency symptoms exhibited. It should be noted that the blackening of the tissue due to calcium deficiency described by Hoffman was never observed in nutrient agar cultures here, although

the symptoms of nitrogen, phosphorus and potassium deficiency as described by this author were marked in some cultures. It is possible that the calcium requirement of plants growing on Voth's solution 10 was relatively low and hence the addition of nitrogen and phosphorus in the form of the calcium salt was less stimulating than the addition of potassium, nitrate nitrogen and phosphorus. With regard to the relative importance of individual nutrients, Hoffman's work, in agreement with results of the present investigation, suggested that the absence of calcium and potassium from the medium had a greater effect than the absence of magnesium and the absence of nitrogen and phosphorus had a greater effect than the absence of sulphur, although it was suggested that the plant may have derived some sulphur from the atmosphere.

The conclusions arrived at by Kofler concerning the role of individual nutrients on early development, also show some agreement. Altering the concentration of magnesium sulphate or even complete omission of magnesium from the medium had little effect on growth. Kofler suggests that some magnesium may have been supplied by the agar but notes that although magnesium has been found to be important for the growth of other species (Bequerel, 1906 and Servettaz, 1913), Von Ubisch (1913) reports the apparent unimportance of magnesium to growth of Funaria. Altering the concentration of potassium sulphate, phosphates and calcium nitrate, also had little effect on early growth, although Kofler suggests that like magnesium some calcium may have been supplied by the agar. The work of Patschovsky (1926) cited by

Kofler indicates the importance of nitrate nitrogen. Altering the concentration of nitrate nitrogen was found to have the same effect as altering the total concentration of the medium, whilst the role of nitrate nitrogen in determining morphology was greater than that of phosphorus.

Except for the addition of nitrogen to Voth's solution 5, the effect on Bryum argenteum of varying the concentration of individual nutrients was not investigated. In spite of the supposed nitrophilous tendencies of this species, addition of nitrogen did not result in any improvement of growth. Thus it appears that the nitrogen requirements of Bryum argenteum are fully satisfied by Voth's solution 5.

The toxicity of ammonia nitrogen: the addition of even small amounts of ammonium nitrate was found to limit growth of Funaria. The toxicity of ammonium phosphate appeared to be still greater, but this can probably be attributed to the relatively high concentrations of phosphorus present. Although addition of small amounts of ammonium nitrate was found by Lodge to stimulate growth of Funaria, the presence of high concentrations of this salt resulted in inhibition of growth. It has been reported by Garjeanne (1932) that bryophytes are able to utilise either nitrate or ammonia nitrogen, although some species show a preference for one or the other. Reports of bryophytes cultured on media containing ammonia nitrogen are not uncommon, e.g. Physcomitrium turbinatum (Meyer 1940), Sphaerocarpus texanus (Schuler et al., 1955) and Atrichum undulatum (Burkholder 1959), whilst in the

present investigation it has been shown that Bryum argenteum is able to grow well on a medium containing ammonia nitrogen. The toxicity of ammonia to Funaria however, as found in the present investigation, is also clearly evident in the work of Kofler, who found abnormal cell divisions and death of protonemata, inhibition of bud formation and the production of abnormal leaves, symptoms very similar to those found here. In addition it is possible that the degeneration of chloronemal cells in Funaria, which was observed by Sironval (1947) was due to the presence of ammonia nitrogen in the medium. Ammonia nitrogen also appears to be toxic to Leptobryum pyriforme, since the presence of ammonium nitrate was found by Pringsheim (1921) to result in poor protonemal growth and retardation of bud formation in this species.

The utilisation of different forms of nitrogen by higher plants has been much studied and it is found that the response of different species to the various forms are influenced by numerous interrelated factors, the most important of which include; pH and ionic composition of the culture solution, the carbohydrate status of the plant and its stage of development (Street and Sheat, 1958). It is most likely that similar factors will effect bryophytes and because of the large number of variables involved it is not too surprising that some investigators have found it possible to obtain good growth of Funaria on media containing ammonia nitrogen e.g. Brown (1919), Patschovsky (1926) and Porter (1935). It is worth noting however, that the cultures of these three authors were not set up under sterile

conditions and also that the addition of nitrogen and phosphorus in the form of ammonium salts to unheated and non-sterilised soil in the present work, did not result in the production of the symptoms of ammonium toxicity. Micro-organisms may therefore reduce the toxicity of media to which ammonia nitrogen has been added, probably by oxidation of the ammonia.

It is impossible in the present state of our knowledge to suggest specific reasons for the toxicity of ammonium salts of Funaria, although Kofler and Pringsheim (1921) have both discounted the acid drift of media containing ammonia nitrogen (also noted by Lodge see p.118) as being the main cause.

The importance of micronutrients: results showed that high concentrations of micronutrients were not toxic, but also indicated that the presence of micronutrients was not essential to growth. This is most unlikely and the investigations of both Kofler and Hoffman suggest the contrary. Sufficient nutrients to satisfy requirements must therefore have been supplied as contaminants in the macronutrient salts and the agar.

Of the individual micronutrients Kofler found that manganese was of particular importance and concluded that the stimulating effect found on addition of iron salts to nutrient deficient media was probably due to the contamination of the salts with manganese. Iron did not appear to be essential to growth. Results of Hoffman's work, on the other hand, suggested that iron is the most important micronutrient. Hoffman notes however the difficulty of explaining the

stimulus offered by iron from an ecological point of view, since soil conditions after burning would be expected to render iron less available for plants. Before any more definite conclusions can be reached, it is obvious that there is a need for more critical studies employing methods for the elimination of contaminating ions, such as those suggested by Hewitt (1966) for work with higher plants.

CHARACTERISTICS OF BURNT SOIL

I. INTRODUCTION AND THE LITERATURE

In this last part of the work an attempt was made to link the performance of Funaria on burnt and heated soil and its nutrient requirements, with particular chemical conditions in the soil. Investigations were therefore carried out to find what effects bonfires and rapid fires had on the surface soil (the top 2 cm.), and to determine what changes took place with time after burning. Experimentally heated soils were analysed to find what changes took place as a direct effect of heat and in addition changes occurring with time in sterile and non-sterile soils were compared, in order to assess the role of micro-organisms in determining the changes.

The majority of works dealing with the effect of fire on soil are related to the growth of crop plants and so do not specifically refer to the top 2 cm. of soil. Much of the information given however, is likely to be relevant, the effects described probably being intensified in the surface soil. The literature concerning the overall effects of fire on the soil has been reviewed by Ahlgren & Ahlgren (1960) and Hare (1961). The main importance of the effect of fire on the physical nature of the soil appears to lie in its related effect on the moisture relations between the soil and the plant. Removal of the ground flora and the litter layer causes the mineral soil plus ash to be completely exposed to climatic influences. The direct force of rain may lead to a breaking up of

soil aggregations and the blocking of soil pores with fine particles washed down from above. In addition burning may result in a reduction in the number of channels made by decaying roots and burrowing animals. The water holding capacity may be raised, but most workers agree that it is not affected. The heat of the fire may cause direct changes in the soil texture, although most natural fires are not hot enough for this. All these effects can cause decreased infiltration leading to increased runoff, erosion and flooding. Some reports of increased porosity and filtration after burning are, however, found. Blackening of the soil surface as a result of burning, has been reported to increase the absorption of heat. This together with the increased exposure of the soil to climatic influences, results in wider daily and seasonal fluctuations in temperature and humidity.

With regard to the chemical nature of the soil, it is agreed that a general increase in the amounts of available macronutrients is shown after burning. Most reports indicate a loss in total organic matter particularly after severe forest fires, but variation in intensity (temperature and duration) of fires and the amount of organic matter broken down, together with the activity of micro-organisms after burning, may all be responsible for the reports of both increased and decreased nitrogen after burning. It is reasonable to assume that the rise in pH which is usually found after burning, is due to the increase in concentration of basic salts, although Eden (1924) points out that the destruction of organic acids and buffers may also contribute to changes in pH. The greater solubility of the plant

nutrients leads to their rapid removal after burning by leaching, but increased run off and micro-organism activity may also in part account for their removal. Recolonising plants will absorb some of the nutrients, but often the removal occurs by leaching, run off and micro-organism activity, before a significant amount of the nutrients can be incorporated into the biological cycle. Moreover the destruction of living vegetation, litter and organic matter, removes the major source of further nutrients. Thus burning and particularly repeated burning, may eventually lead to decreased soil fertility. The effect of fire on the soil trace elements is less well known. Present evidence suggests that these micronutrients may reach toxic levels immediately after burning, but subsequent leaching can reduce their concentration below the preburn level.

Although deposition of ash will probably be the most important source of the increased nutrients found after burning, the heat of the fire may also have a direct effect on the chemical nature of the soil. The effect of heat has been the subject of much investigation because of the accepted horticultural practice of heat-sterilising soil. Early literature on this subject has been summarised by Seaver & Clark (1912). It was found that heating increased the amount of soluble matter present, amounts being directly proportional to the organic content of the soil before heating. Seaver & Clark themselves reported that both soluble organic and inorganic matter, including nitrogen, increased as heating became more intense. Mukerjee (1954) considering later work,

found the following points generally agreed on: total soluble matter both organic and inorganic, organic nitrogen, ammonia nitrogen, potassium and phosphoric acid, all increased when the soil was heated. Other ions for example calcium, magnesium, iron and aluminium showed varying changes. The effect of heating the soil increased in direct proportion with increase in temperature, until at high temperatures breakdown of both soluble organic and inorganic material occurred. The characteristics of heated soil gradually disappeared when the soil was stored. Mukerjee himself found that there was an increase in soluble organic matter including nitrogen, together with an increase in ammonia nitrogen, phosphates and other inorganic salts. Nitrate nitrogen levels were, however, initially depressed. On heating soils for periods longer than 1 hour at 200°C the amount of organic matter coming into solution decreased as complete breakdown of organic matter took place, the amount of soluble inorganic matter continuing to increase. Later work e.g. that of Hoffman (1966a) confirmed the earlier findings.

Burning will also affect the activity of the soil micro-organisms which in turn may also affect the concentration of available nutrients particularly nitrogen. Initially if the fire is hot enough, a decrease in bacterial numbers particularly at the surface of the soil would be expected. Subsequently however,

bacterial numbers and activity will depend very much on other environmental factors, such as soil pH. Reports of both increased and decreased bacterial activity after burning are found in the literature (Ahlgren & Ahlgren, 1960). The most important effect of heating soil on micro-organisms activity is the initial partial blocking of the nitrogen cycle at ammonia. This effect, which is also seen in soils partially sterilised by irradiation and chemical means, leads to an accumulation of ammonia nitrogen, until the number and the activity of the nitrifiers subsequently increases, when the ammonia nitrogen is rapidly oxidised, leading eventually to an increase in the level of nitrate nitrogen (Russel, 1961; Mukerjee, 1954; Florence & Crocker, 1962; Dawson, Johnson, Adams & Last, 1965 and Wolcott, Fang & Kirkwood, 1967).

Air-drying soil has also been shown to affect the level of available nutrients. On remoistening the soil available nutrients are released and a temporary increase in microbial activity occurs. A flush of ammonification followed by increased nitrification as found in heated soils, also occurs (Stevenson, 1956; Russel, 1961; Funke & Harris, 1968). Such effects are obviously important to soils of burnt areas, which are much more liable to periodic drying out and rewetting, than soils with a vegetation cover.

II. COLLECTION AND ANALYSIS OF SOIL SAMPLES

Samples were collected from sites in Experiments 1 and 2 at Royal Holloway College at regular intervals after burning. All these sites were covered by a permanent quadrat frame (p.) and at each sampling period, random co-ordinates were used to select a square in the quadrat, the top 2 cm. of soil from this square being removed. Samples were collected less frequently from other sites and therefore it was felt unnecessary to use a random sampling technique. Approximately 100 gm. of the top 2 cm. soil was collected on each visit, small amounts being removed from a large number of places on the site. All samples were contained in self-seal polythene bags and initially stored in a deep freeze refrigerator maintained at 0°C. Subsequently samples were thawed at room temperature and left to air-dry for a minimum of 1 week. The air-dry soils were sieved using a brass sieve (B.S. 410 mesh no. 5) and stones, together with all recognisable plant and animal material, removed. Samples were then ground to remove any remaining coarse particles such as charcoal and soil aggregates. The only exception to this procedure was, that at first phosphorus, total nitrogen and pH were all determined on field-moist soil. An aliquot of the thawed, undried sample was therefore sieved and replaced in the deep freeze, the sieved samples being rethawed just before analysis. Later it was felt that greater speed, accuracy and compatibility of results within the investigation, would be obtained by eliminating the weighing out of

wet soil and the subsequent determination of soil moisture content. The bulk of determinations were therefore carried out on air-dry soil. Figures derived from determinations on field-moist soil are indicated in the tables and graphs.

Time was concentrated on methods which as far as possible would determine the soil nutrients available to higher plants, the assumption being made that such soil nutrients would also be available to bryophytes. Methods also had to be found which could be applied to small amounts of soil, since only the surface soil was used and many of the sites were small, whilst in addition the analytical procedures chosen had to be applicable to different types of soil as the various soils to be analysed had a very wide range of physical and chemical characteristics.

Full details of the analytical procedures are given in the appendix (pp.270-280). pH was determined electrometrically and organic matter by loss on ignition. Total nitrogen was determined by a modified Kjeldahl procedure. Initially ammonia nitrogen was determined by a modified Nessler method and nitrate nitrogen by an ultra-violet absorption method (Cawse, 1967). Later analyses however, were carried out using the double distillation technique described by Piper (1950). Exchangeable metallic cations were determined on an ammonium acetate extract, using E.D.T.A. titration methods and flame photometry, whilst total exchangeable bases were determined according to Brown's method (Brown, 1943). Available phosphorus was estimated colorimetrically on a dilute acid-fluoride extract, using the ammonium molybdate stannous chloride method described

by the American Public Health Association (1955).

Regression analysis was used to determine the best fit of a line to available data for some graphs. Four lines were considered a parabola, a straight line and two types of exponential curve and the best of these selected by the least squares method. For a few graphs where the points were widely scattered little difference was found in the fit of the four types of line. In such cases, the expected trend for the nutrient and the trend shown by the nutrient on other graphs was taken into consideration in choosing the line.

III. THE EFFECTS OF BONFIRES AND RAPID FIRES ON THE CHEMICAL NATURE OF THE SOIL

In general soil extracts of many of the bonfire soils were yellow-brown in colour in comparison with the unburnt and rapid fire soils particularly in soils collected in the first few months after burning. In addition loss on ignition values and levels of exchangeable metallic cations and available phosphorus, fluctuated

considerably from one sampling date to the next in soils from the bonfire sites in Experiments 1 and 2, when compared with those of the weeded sites (fig. 47-52).

pH

Fig. 45 and 46 show that the pH of soils from bonfire sites in both Experiments 1 and 2 rose sharply after burning, values ranging from 9.05-10.95 in contrast with the soils of the weeded plots the pH of which ranged from 5.25 - 6.61 throughout the investigation period. The pH of the bonfire soils then decreased, but did not reach the levels found in the unburnt soils during the sampling period even in Experiment 2 after 18 months.

Soils from bonfire site B17 at Waterperry Wood also had a very high pH 7.95 - 8.40 in comparison with the pH of 4.78 of the unburnt soil, but the pH of bonfire site a., at South Haven Peninsula, 4.50 - 5.75, which was not successfully colonised by the bonfire bryophytes was low in comparison with other bonfire soils of comparable age (16-18 months), although it was probably higher than the adjacent unburnt soil. The pH

Fig. 45. Changes in the pH of soils from sites in Experiment 1 (determined on field – moist soil).

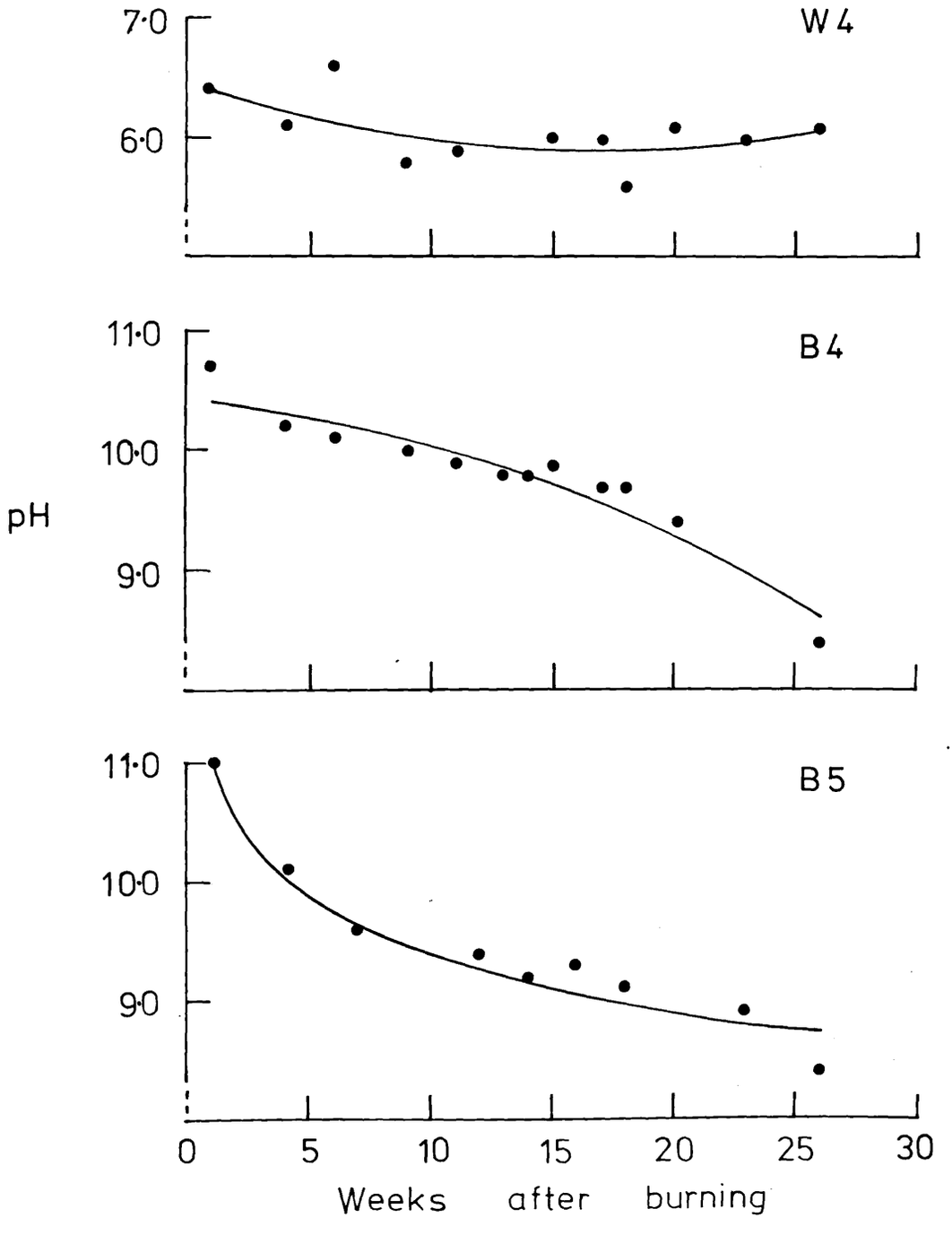
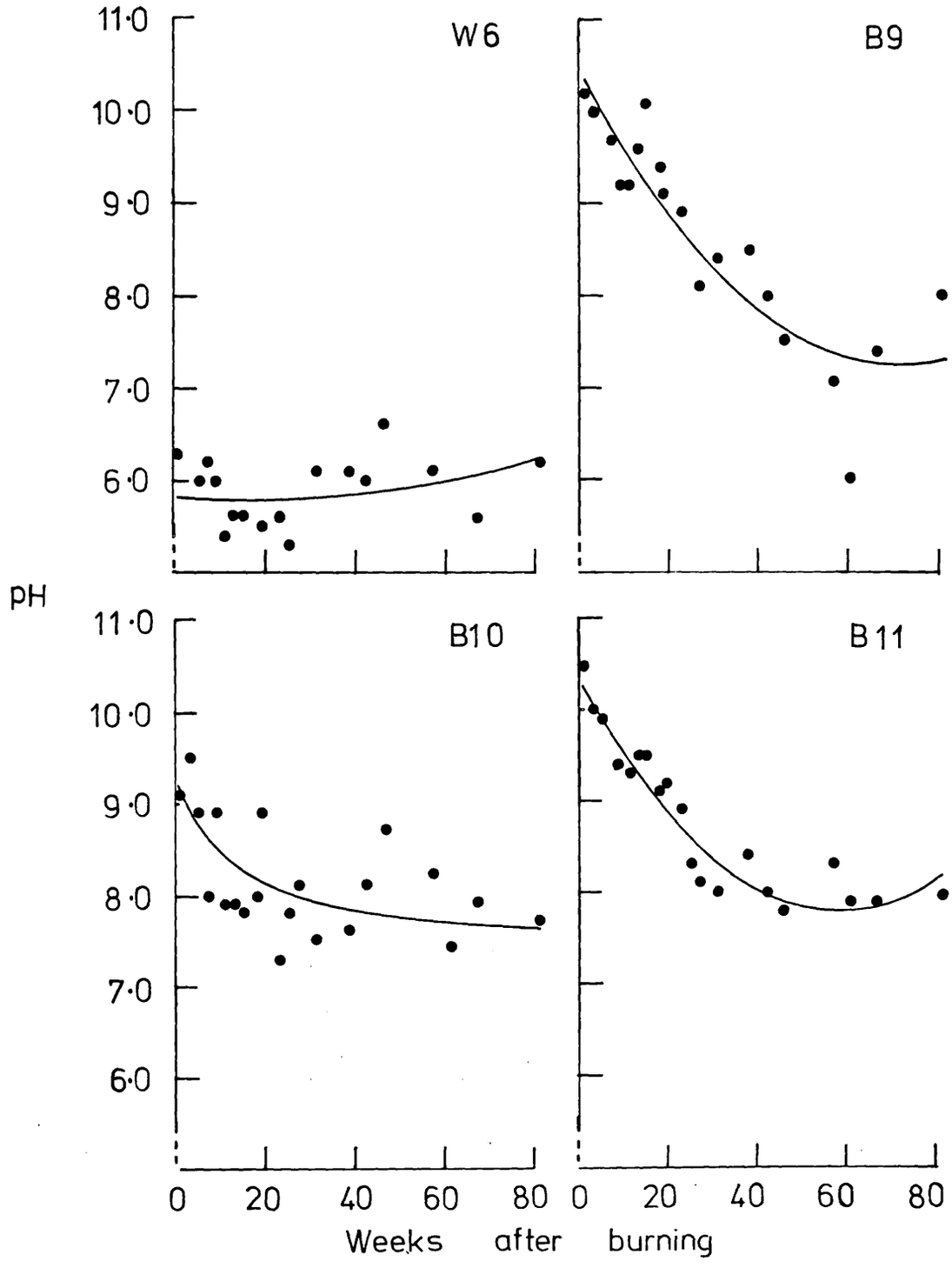


Fig. 46. Changes in the pH of soils from sites in Experiment 2.



of rapid fire sites R6-R9 at Cronkley Fell in Yorkshire; and R4 and R5 at South Haven Peninsula ranged from 3.85-4.60 and was probably similar to the unburnt soil of these areas (table 38). A second series of determinations made on soils collected from burnt areas of different ages on Cronkley Fell, (table 39), confirmed this and in addition showed that there was no correlation between age of the site and the soil pH.

Total organic matter

The bonfire sites in Experiments 1 and 2, initially showed a slightly higher loss on ignition value than the unburnt soil (table 40 and fig. 47), and in soils from both bonfire sites and the weeded site in Experiment 2, gradually decreased over the sampling period (fig. 47).

The main differences in the loss on ignition figures for other sites, were between different pre-burn soil types and it was not possible to link any differences with the type of fire or different ages of the site (table 38).

Exchangeable metallic cations

Immediately after burning levels of calcium, magnesium, potassium and sodium, were much higher in soils from the bonfire sites in Experiments 1 and 2, than in soils from the unburnt weeded sites (tables 40 and 41) and even during the relatively short 18 week

Table 38. pH and nutrient levels of soils from sites not studied in detail.

Site		Age of site when sampled (mths.)	pH (* = determined on field-moist soil)	Loss on ignition (% of oven-dry soil)	Mgm./gm. air-dry soil (*= determined on field-moist soil mgm./gm. oven-dry soil)				
					P	Ca	Mg	Na	K
Coombe Hill, Buckinghamshire	B17	5	-	-	0.40	-	-	-	-
		8	-	21.18	-	-	-	-	-
		11	-	-	0.62	-	-	-	-
		14	-	-	0.32	-	-	-	-
		17	-	-	0.25	-	-	-	-
	A2	8	-	9.20	-	-	-	-	-
Cronkley Fell, Yorkshire	R9	5	4.55*	95.58	0.16*	1.10	0.62	0.16	0.41
		7	4.20*	90.30	0.12*	0.54	0.20	0.18	0.28
	R8	17	4.30*	95.77	0.12*	0.61	0.17	0.15	0.20
		19	-	94.82	0.12*	0.65	0.17	0.28	0.36
	R7	29	4.40*	95.37	0.20*	0.40	0.20	0.17	0.85
		31	4.15*	95.74	0.25*	0.82	0.29	0.13	0.80
	R6	41	4.30*	90.64	0.09*	0.13	0.09	0.09	0.24
		43	4.30*	91.15	0.12*	0.34	0.04	0.11	0.26
	B20	< 1	-	-	3.78	-	-	-	-
		1	-	-	1.10	-	-	-	-
		4	-	-	1.01	2.29	1.81	0.03	0.78
		25	-	-	1.76	-	-	-	-
	A3	5	-	-	5.28	7.92	1.16	0.02	2.10

(cont.)

Table 38 (cont.)

Site	Age of site when sampled (mths.)	pH (*= determined on field-moist soil)	Loss on ignition (% of oven-dry soil)	Mgm./gm. air-dry soil (*=determined on field-moist soil mgm./gm. oven-dry soil)				
				P	Ca	Mg	Na	K
Royal Holloway R1	1	-	6.72	0.15	1.10	0.00	0.05	0.32
College, Surrey	1.5	-	-	0.17	1.24	0.02	0.05	0.41
R2	1	-	4.13	0.14	1.76	0.37	0.09	0.31
South Haven R5	< 1	3.95*	46.13	0.03*	0.45	0.16	0.21	0.31
Peninsula, Dorset	3	3.95*	34.83	0.04*	0.30	0.14	0.13	0.16
	5	3.85*	67.18	0.06*	0.44	0.16	0.13	0.17
R4	22	3.95*	9.73	0.01*	0.15	0.04	0.04	0.04
	24	4.60*	3.66	0.002*	0.06	0.01	0.03	0.10
	26	4.35*	4.71	0.004*	0.09	0.02	0.03	0.03
bonfire site a.	16	5.75*	10.39	0.04	1.20	0.91	0.09	0.06
	18	4.50*	17.57	0.03	0.69	0.00	0.06	0.05

(cont.)

Table 38 (cont.)

Site		Age of site when sampled (mths.)	pH (* = determined on field-moist soil)	Loss on ignition (% of oven-dry soil)	Mgm./gm. air-dry soil (*=determined on field-moist soil mgm./gm. oven-dry soil)				
					P	Ca	Mg	Na	K
Stour Wood, Essex	l	1-2	-	-	0.62	-	-	-	-
	i	12	-	-	1.53	-	-	-	-
	j	12	-	-	1.14	-	-	-	-
	c	24	-	-	0.82	-	-	-	-
	d	24	-	-	1.17	-	-	-	-
	f	24	-	-	1.40	-	-	-	-
	g	24	-	-	1.01	-	-	-	-
	a	48	-	-	0.46	-	-	-	-
Waterperry Wood B18 Oxfordshire		8	8.40	20.25	1.08	4.27	1.06	0.10	1.00
		10	7.95	18.37	1.11	4.12	1.52	0.10	1.00
		13	-	-	1.01	-	-	-	-
		16	-	-	1.03	-	-	-	-
		19	-	-	1.15	-	-	-	-

Table 39. pH of soils from rapid fire sites, of different age, on Cronkley Fell.

Unburnt site	Age of sites when sampled				
	6 mths.	2 yrs.	3 yrs.	4 yrs.	5 yrs.
3.6	3.2	3.3	3.2	3.3	3.2
3.4	3.1	3.4	3.2	3.4	3.4
3.3	3.2	3.6	3.5	3.3	3.3
3.5	3.2	3.4	3.4	3.4	3.2
3.3	3.3	3.5	3.4	3.5	3.3
3.4	3.3	3.8	3.3	3.5	3.3
3.4	3.3	3.3	3.5	3.4	3.5
3.3	3.2	3.5	3.2	3.4	3.4
3.4	3.3	3.4	3.2	3.5	3.2
3.5	3.1	3.6	3.5	-	3.2

10 samples were collected from each site and pH determined on the field moist soil.

Table 40. Nutrient levels of soils from sites in Experiment 1.

	Loss on ignition (% of oven-dry soil)		P* (mgm./gm. oven-dry soil)		Ca (mgm./gm. air-dry soil)		Mg (mgm./gm. air-dry soil)		K (mgm./gm. air-dry soil)		Na (mgm./gm. air-dry soil)	
Wks. after burning / Site	B4	B5	B4	B5	B4	B5	B4	B5	B4	B5	B4	B5
1	21.63	20.88	1.49	1.70	6.12	3.76	1.46	2.05	36.00	38.00	0.90	0.80
4	8.94	8.66	0.99	1.99	4.92	4.04	0.91	1.63	8.80	18.40	1.10	0.50
9	33.21	11.85	1.94	2.13	5.31	4.39	1.25	1.36	4.00	3.00	0.10	0.50
13	23.16	13.06	2.45	2.04	5.18	3.70	1.13	1.20	3.20	2.00	0.10	0.00
18	14.67	9.03	1.33	1.73	2.92	2.45	0.70	0.65	1.80	1.60	0.10	0.00
Site	W4	W5	W4	W5	W4	W5	W4	W5	W4	W5	W4	W5
	13.25	5.81	0.27	0.25	2.37	0.43	0.60	1.42	0.10	0.20	0.00	0.00

* determined on field-moist soil.

Fig. 47. Changes in the loss on ignition values of soils from sites in Experiment 2.

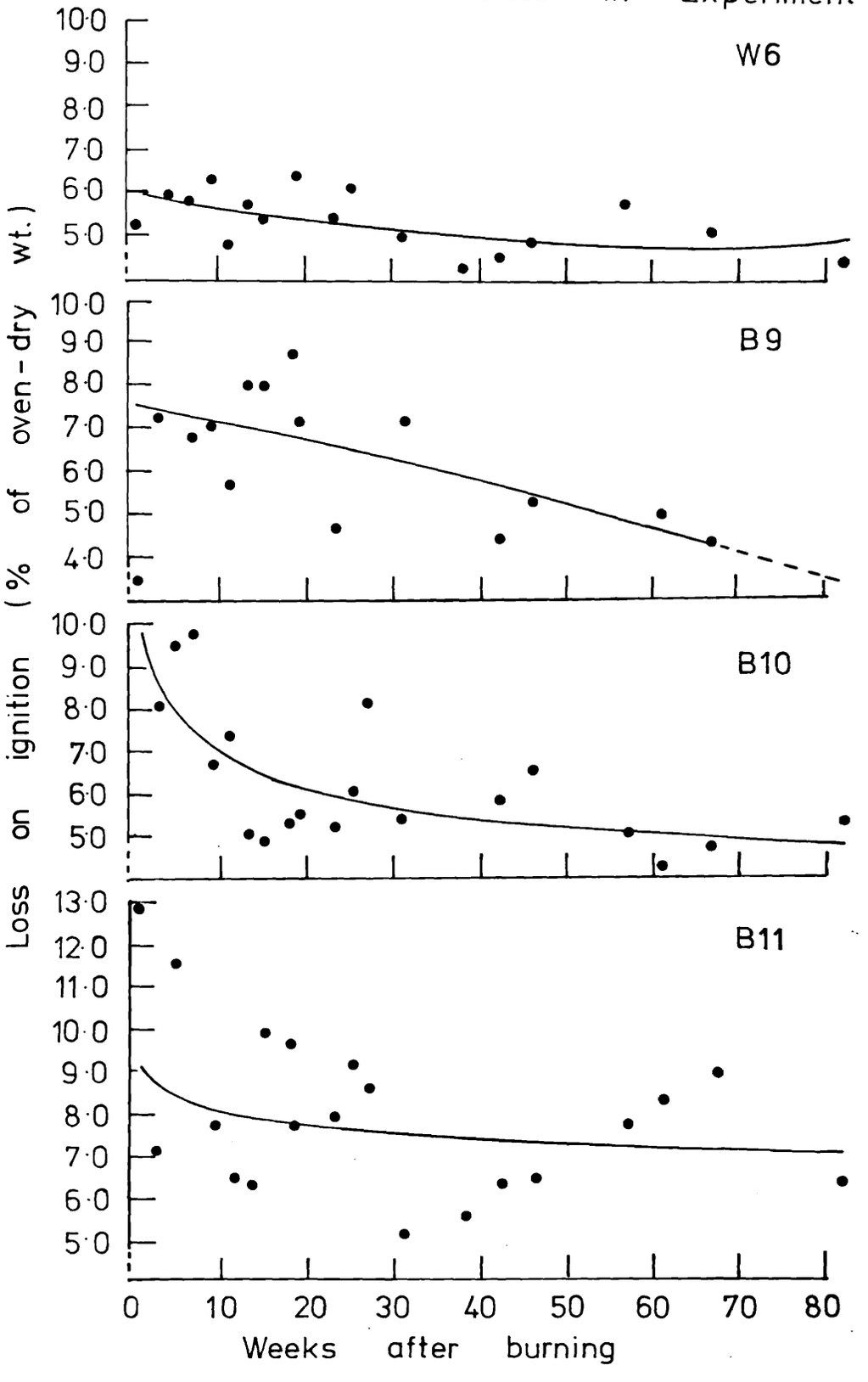


Table 41. Initial increases in nutrient levels after burning, of soils from sites in Experiment 2.

Nutrient	(Av. nutrient conc. of burnt soils in 1st mth. after burning) ÷ (Av. nutrient conc. of unburnt soil from site W6)
Ca	4
Mg	3
K	126
Na	14
P	14

sampling period of Experiment 1, as shown in table 40 the soils showed a definite decrease in the levels of magnesium, potassium and sodium, levels of potassium dropping very sharply in the first 4 weeks. There was however, no clear decrease in the calcium levels. In Experiment 2, as shown in fig. 48, decreases in the levels of calcium during the 18 month sampling period were also very slight. Magnesium in contrast (fig. 49), decreased rapidly at first and then more gradually, reaching the unburnt soil levels in site B9 soil and approaching levels in soil from site B10 within 18 months. Levels in site B11 soil were still high at the end of the sampling period. Sodium levels in addition to the potassium levels, dropped very sharply in the first few months after burning and then more gradually, reaching the unburnt soil levels within 12 months (fig. 50). Potassium approached the unburnt soil level in soils from site B9 after 18 months, although levels remained a little high in soil from sites B10 and B11 (fig. 51).

Table 38 shows that in rapid fire soils, levels of calcium were lower than in any of the bonfire soils except those of bonfire site at South Haven Peninsula. Magnesium, sodium and potassium however, were in some cases as high as those of the College bonfire sites and other bonfire sites, although the very high levels present immediately after burning were not found.

Fig. 48. Changes in the calcium levels of soils from sites in Experiment 2.

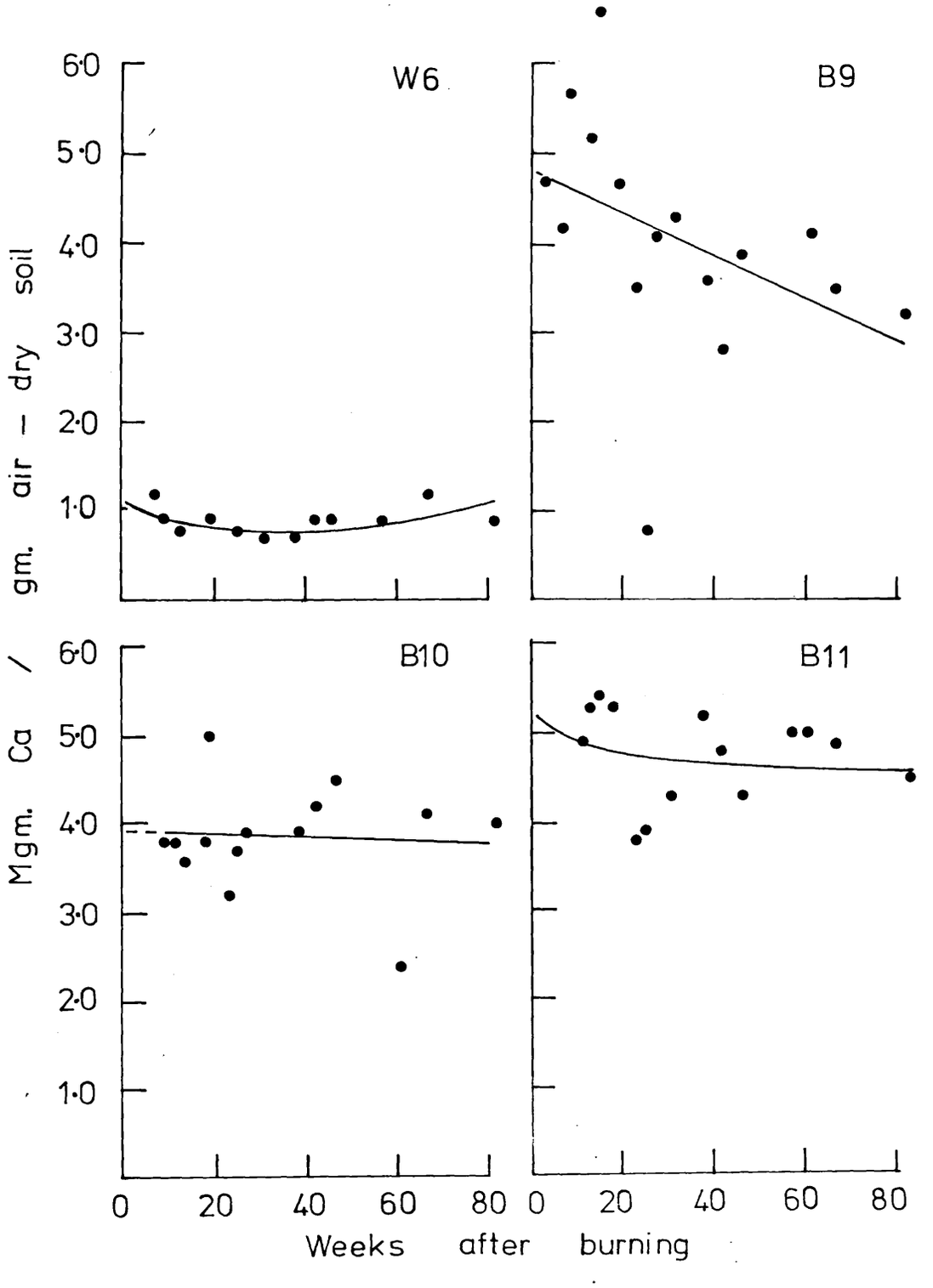


Fig. 49. Changes in the magnesium levels of soils from sites in Experiment 2.

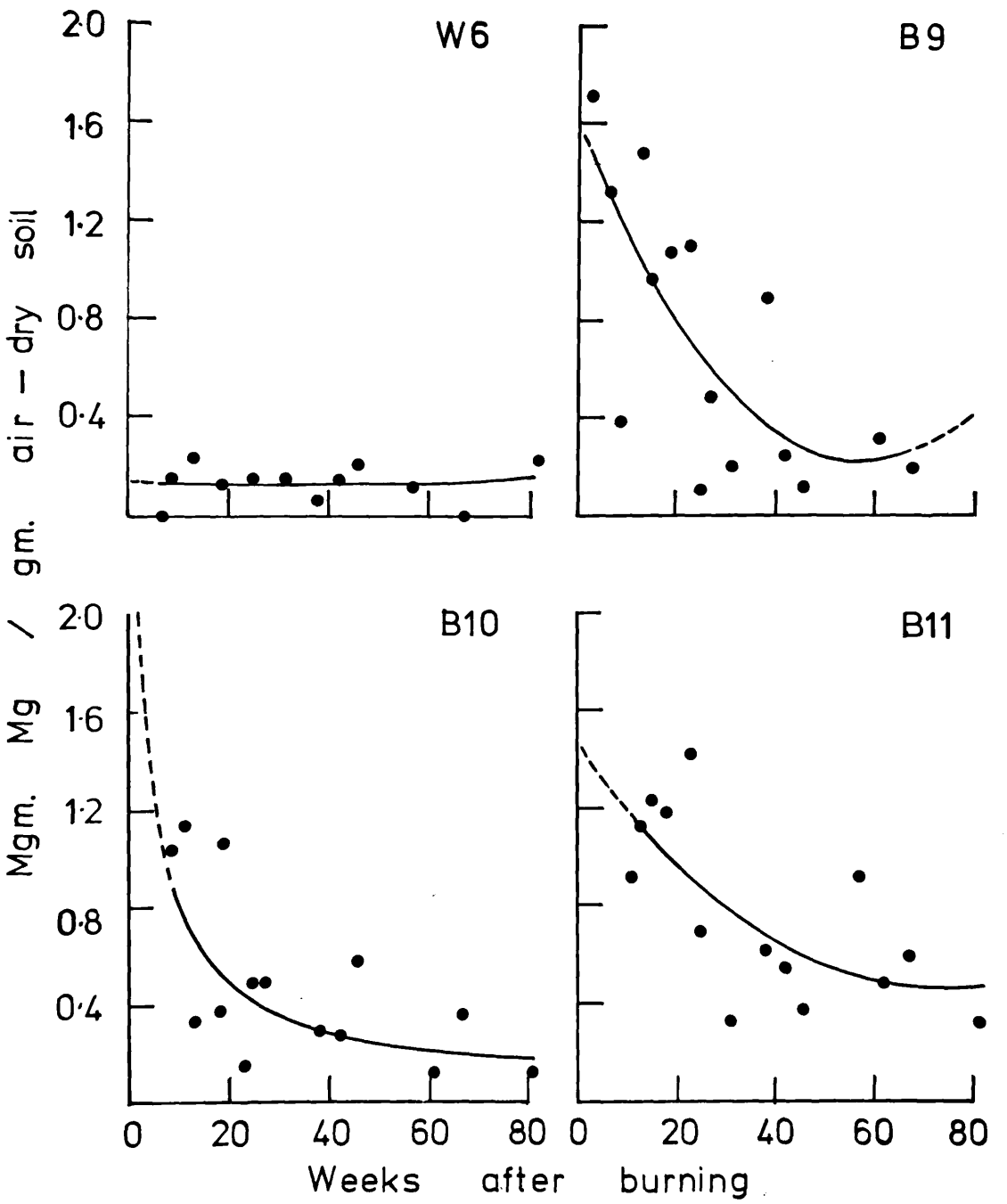


Fig. 50. Changes in the sodium levels of soils from sites in Experiment 2.

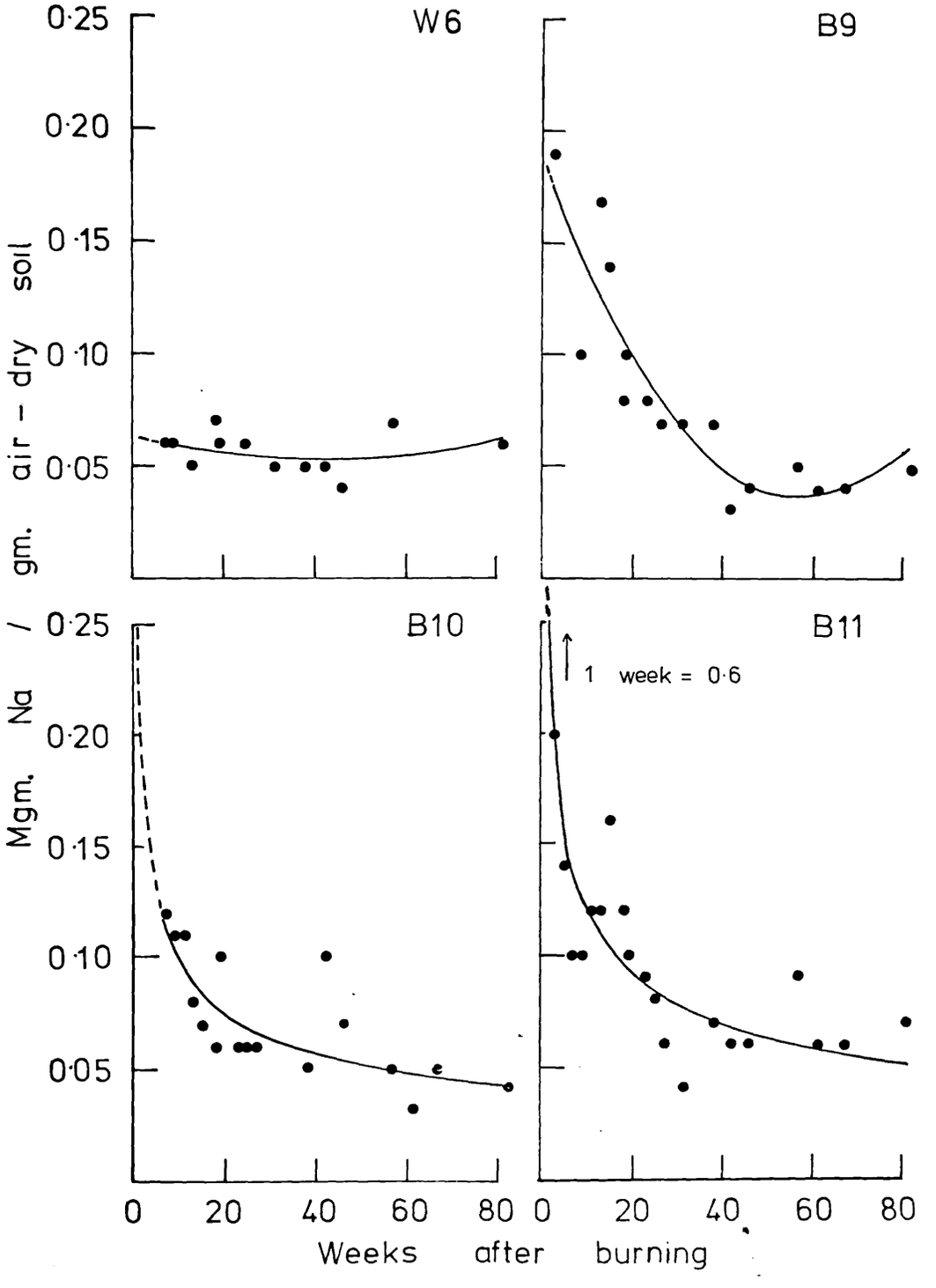
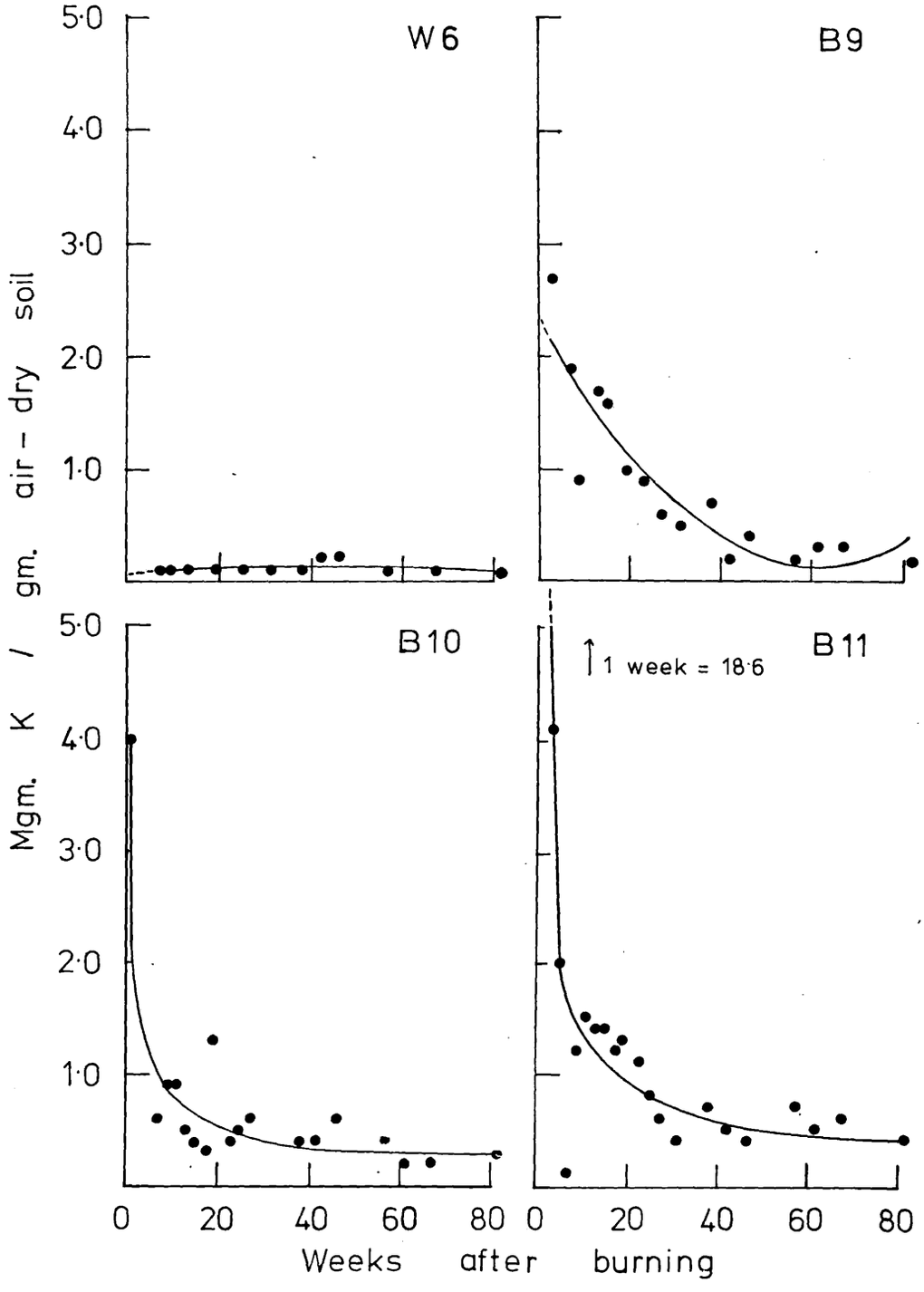


Fig. 51. Changes in the potassium levels of soils from sites in Experiment 2.



Phosphorus

The phosphorus levels in soils from bonfire sites in Experiments 1 and 2, showed a marked increase as a result of burning, as shown in tables 40 and 41. No subsequent decrease however, was found in soils of Experiment 1 (table 40) and although levels did decrease in Experiment 2 soils, they did not reach unburnt soil levels during the 18 months investigation period, although approaching it in soil from B9 (fig. 52).

Soil from sites B12 and A1 showed that most of the phosphorus found after burning, comes as expected, from ash. As shown in table 42, site A1, the weeded site to which ash had been added, had a phosphorus range of 0.75-1.63 mgm.P/gm. air-dry soil, compared with the 0.13-0.28 mgm.P/gm. air-dry soil range, of soil from B12. The level of phosphorus in soil from site B12 however, was higher than in the unburnt soil, indicating that at least some of the increase in phosphorus is due to the heating of the soil.

Table 38 shows that all the rapid fire soils and soil from bonfire site a. at South Haven Peninsula, had low phosphorus levels in comparison with those from bonfire sites even those collected 18 months after burning. It should be noted however that most of the rapid fire site soils were field-moist when analysed. Air-drying the soils, as was done with soils from other sites, may cause an increase in the phosphorus level (Jackson, 1958) and figures may therefore not be comparable. Soils from rapid fire sites R1 and R2 at Royal Holloway College however, still showed low phosphorus levels

Fig. 52. Changes in the phosphorus levels of soils from sites in Experiment 2.

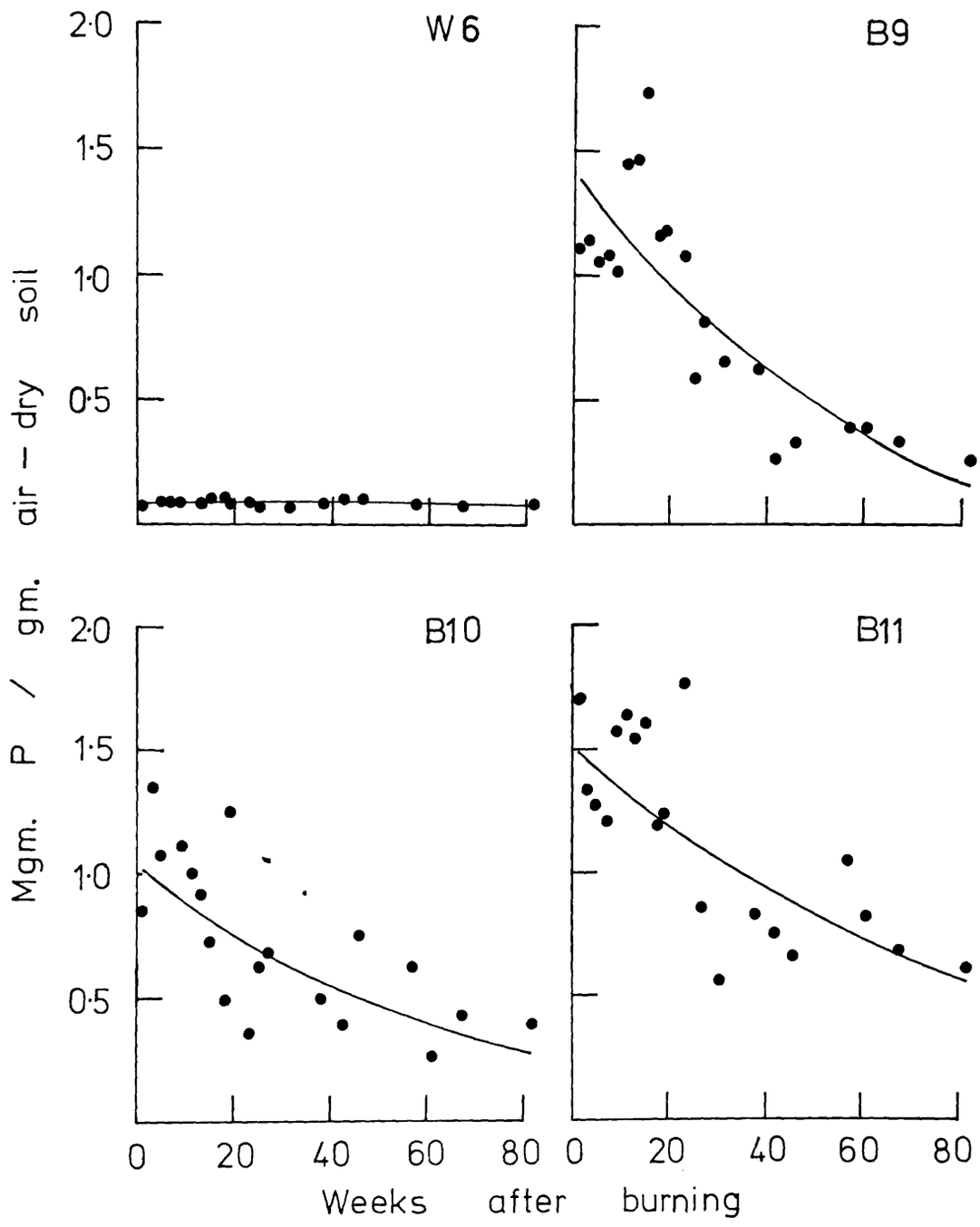


Table 42. Phosphorus levels of soils from sites B12 and A1, Experiment 2 (mgm.P/gm. air-dry soil).

Wks. after burning / Site	A1	B12
1	0.91	0.20
5	0.85	0.28
9	1.11	0.21
13	1.20	0.28
18	1.04	0.15
19	0.75	0.13
23	1.27	0.22
25	1.05	0.13
27	1.63	0.15

Table 43. Changes in total nitrogen levels of soils from sites in Experiment 2 (mgm.N/gm. oven-dry soil).

Wks. after burning / Site	B10	B11
5	3.52	3.13
7	2.89	3.55
9	3.09	3.36
14	3.32	2.66
17	3.51	2.88
19	3.44	2.76
23	2.82	3.91
27	3.15	3.44

Level in unburnt soil = 3.13

(table 38), although analyses were carried out on air-dry soil, whilst field-moist soil from the bonfire sites in Experiment 1, still had very high phosphorus levels (table 40).

In comparing figures obtained in this investigation for unburnt soil, with those which would be expected for such soil, it is seen that the figures are high. For example, Jackson (1958) states that as a general guide to crop response above 0.02 mgm.P/gm. air-dry soil is adequate to high. Whereas unburnt soil in this investigation had phosphorus contents ranging from 0.07-0.11 mgm.P/gm. air-dry soil. As already mentioned air-drying may raise the dilute acid-fluoride extractable phosphorus, but it may also have been increased as a result of the very small ratio of soil to extracting solution used i.e. 0.1:10, instead of the 1:7 ratio suggested by Bray and Kurtz (1945). These small amounts of soil were used to avoid having to make a large number of dilutions for the bonfire soils, which had a very high phosphorus content.

Nitrogen

Total nitrogen.

Table 43 shows that during the first 7 months after burning the total nitrogen level of soils from bonfire sites B10 and B11 ranged from 2.66-3.91 mgm.N/gm. oven-dry soil, whilst the nitrogen content of the unburnt soil was also of this order. These figures fell within the range expected for an unburnt arable soil. (Campbell & Lees, 1967). Total nitrogen therefore, does not appear to increase or decrease as a result of a bonfire.

Neither could any increase or decrease with time after burning be detected.

Determination of total nitrogen involved a lengthy procedure and subsequent investigation was therefore concentrated on the available forms of nitrogen.

Ammonia and nitrate nitrogen

Results of ammonia nitrogen determinations by the Nessler method were very variable and although freshly collected, moist ash from recent bonfire sites had a distinct smell of ammonia, no difference could be seen in the levels of burnt and unburnt soil from the sites in Experiment 2. There also appeared to be no decrease in ammonia nitrogen with time after burning in these soils (table 44). Nitrate nitrogen levels as determined by the ultra-violet absorption method however, as shown in table 45, initially appeared considerably higher in the bonfire soils than in the unburnt soil. Soil from bonfire sites B9 and B10 had a nitrate nitrogen content of 57.55 and 73.35 p.p.m. respectively, whilst that of the unburnt soil from site W6, ranged only from 6.75-10.35 p.p.m. over the 6 month sampling period. These high nitrate nitrogen levels progressively decreased with time, approaching unburnt soil levels within 6 months.

Although the nitrate nitrogen levels of the unburnt soil fell within the range expected for an arable soil i.e. 2-20 p.p.m. (Russel, 1961), subsequent work indicated that the ultra-violet absorption method of determination was not indicating the true nitrate

Table 44. Changes in ammonia nitrogen levels of soils from sites in Experiment 2, as determined by the Nessler method (p.p.m.N of air-dry soil).

Wks. after burning / Site	B9	B10	B11	W6
1	-	-	-	39.00
3	16.58	42.51	12.68	-
5	20.49	-	-	41.93
7	7.80	-	-	-
9	24.38	28.28	12.68	35.10
11	19.50	-	-	26.33
13	7.80	48.95	-	23.40
15	7.80	27.30	20.48	27.30
18	-	29.45	13.65	-
19	13.65	17.55	4.89	35.10
23	13.65	48.75	17.55	22.43
25	22.43	29.25	22.43	32.18
27	31.20	24.38	24.38	-
31	-	-	27.30	-
38	-	-	19.50	-
42	-	-	12.68	-
46	-	-	23.40	29.25
57	-	-	9.75	25.35
61	-	-	9.75	-
67	-	-	11.70	-
81	-	-	30.23	21.45

Table 45. Changes in nitrate nitrogen levels of soils from sites in Experiment 2, as determined by the ultra-violet absorption method (p.p.m. N of air-dry soil).

Wks. after burning / Site	B9	B10	W6
1	57.55	73.35	10.35
3	23.85	-	-
5	30.15	31.95	-
7	15.75	34.20	8.55
9	17.10	21.15	7.00
11	17.55	20.70	-
13	12.36	18.0	-
14	11.25	15.30	6.75
17	37.13	16.65	-
19	9.90	14.40	-
23	10.75	18.45	9.0
25	8.50	-	-
27	10.80	-	-

nitrogen levels particularly with regard to the burnt and heated soils. A sample of soil heated to 150°C for 3 hours, which contained 19.75 p.p.m. N according to the ultra-violet absorption method, was sent to the United Kingdom Atomic Energy Authority at Wantage for analysis by the double distillation technique (Piper, 1950). Results of these analyses showed the soil to contain 9.60 p.p.m. N. Some substance or substances were therefore interfering strongly with the determination by the ultra-violet absorption method. Since as is described later, soils heated to 150°C for 3 hours had very high ammonia levels, tests were carried out to find whether ammonia nitrogen interfered with the determination. Solutions containing known amounts of potassium nitrate and ammonium sulphate, were analysed for nitrate nitrogen. It was found however, that the gross interference described above, could not be accounted for by either the ammonia or sulphate ions (table 46). In addition when absorption curves for ammonium sulphate and potassium nitrate were drawn up (fig. 53), it was apparent that at 210 mμ, where absorption was read in the nitrate determination, the absorption of ammonium sulphate was low in comparison with that of potassium nitrate. It seems most likely that the major interfering substance or substances are of an organic nature. Seaver & Clark (1912), noted the dark colour of heated soil extracts and assumed that it was due to the 'large amounts of peculiar organic substances held in solution', whilst many other workers have found high levels of

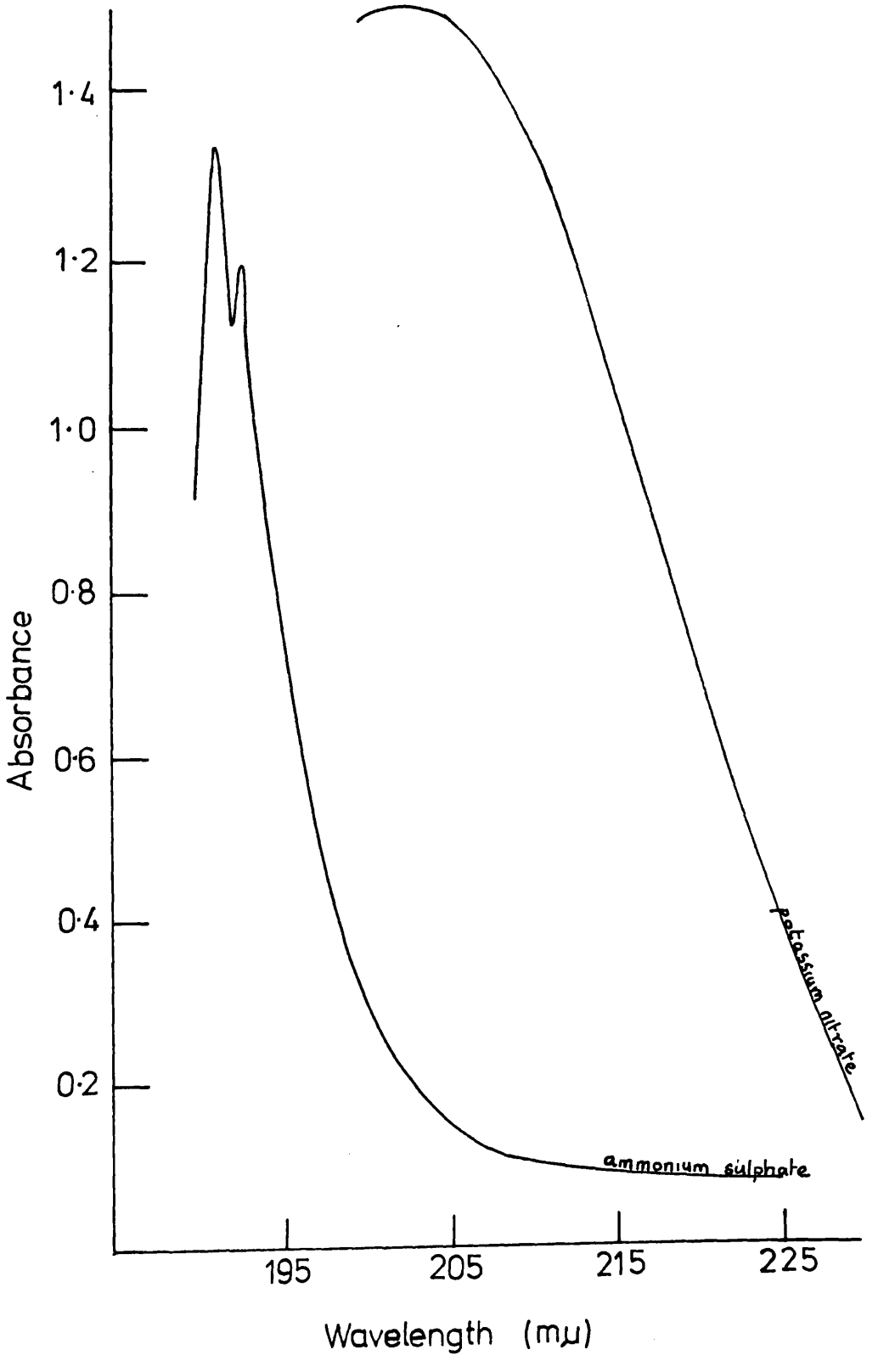
Table 46. Interference by ammonium sulphate in the determination of nitrate nitrogen by the ultra-violet absorption method.

P.p.m. added				P.p.m. NO_3-N found on analysis	Difference between NO_3-N added and NO_3-N found (p.p.m.)
NO_3-N	NH_4-N	K	SO_4		
0.23	0.40	0.63	1.37	0.25	0.02
0.23	0.80	0.63	2.74	0.26	0.03
0.00	0.80	0.00	2.74	0.01	0.01

soluble organic substances in heated soil (pp.199-200). The yellow-brown colour of extracts of many of the bonfire soils (p.204) indicated that they had a high soluble organic content and even after treatment with alumina cream, the extracts of burnt soils still had some yellow colour in them, the concentration of 'nitrate nitrogen' appearing to be closely related to the colour of the extract. For unburnt soils where the levels of these soluble organic substances would be low, interference was probably negligible, but it is very likely that for recently burnt and heated soils, figures determined by ultra-violet absorption largely represent soluble organic matter.

Insufficient soil had been collected from sites B9, B10 and B11, to allow for analysis by the double distillation method and an additional bonfire site B14, was therefore set up in September 1969 (adjacent to sites B9, B10 and B11), especially for further investigation

Fig. 53. Ultra-violet absorption curves of potassium nitrate and ammonium sulphate.



of changes in available nitrogen after burning. A grid was erected over the site and random, surface soil samples collected twice a week for 12 weeks. Air-drying and storage of the soils from sites B9, B10 and B11, probably caused considerable alteration in the available nitrogen levels, particularly in ammonia nitrogen, determinations were therefore carried out on the field-moist soil immediately after collection.

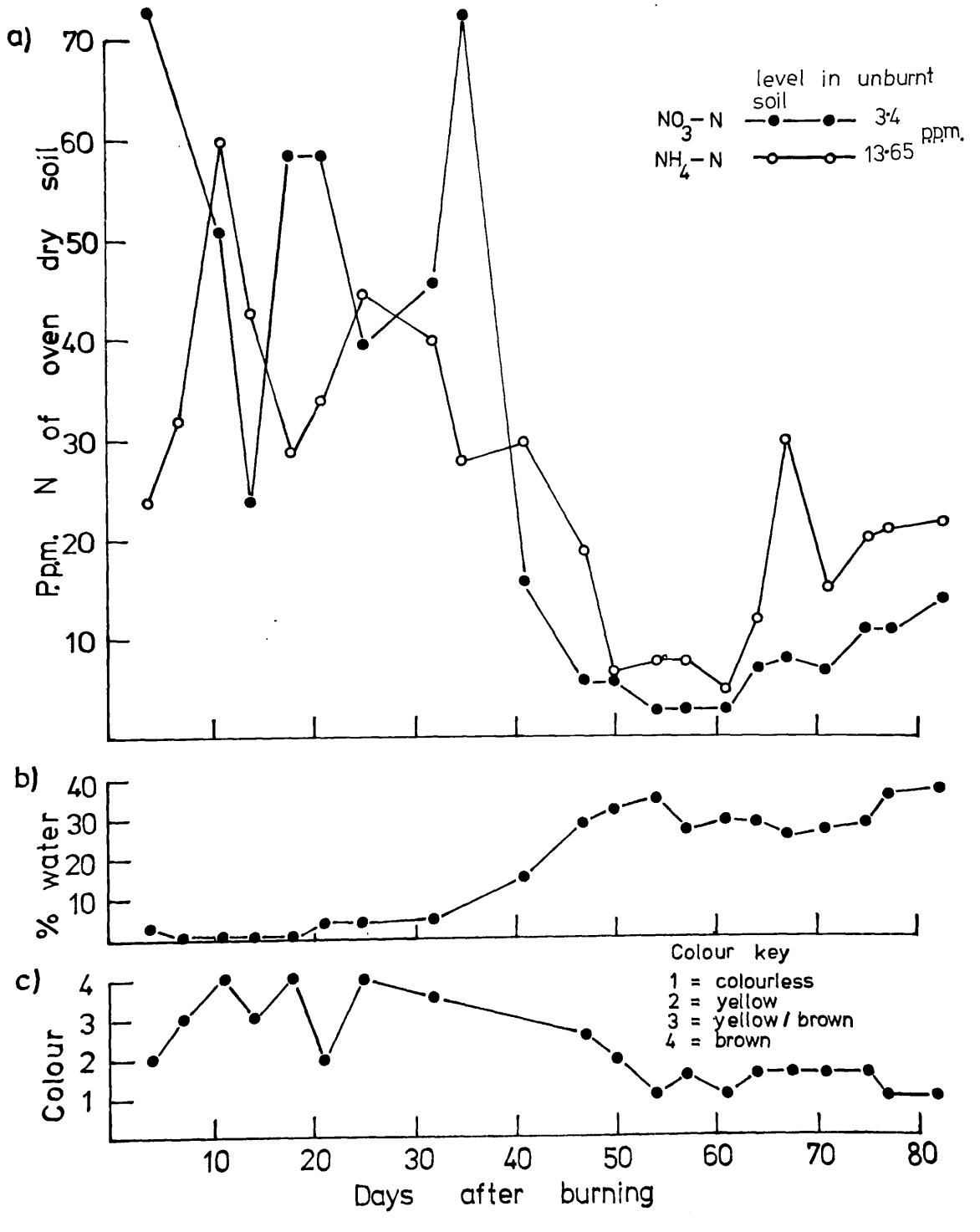
Initially, as shown in fig. 54 a, levels of nitrate and particularly ammonia nitrogen in the bonfire soil, were much higher than in the unburnt soil adjacent to the soil and during the first month showed large fluctuations in level. During the second month levels decreased, reaching those of the unburnt soil after about 7 weeks. Both forms of nitrogen however, showed a tendency to rise again in the third month, but had not reached the initial very high levels at the end of the sampling period. Time unfortunately did not allow for further sampling. Soluble organic substances as indicated by the colour of the soil extracts decreased gradually with time (fig. 54c).

IV. THE EFFECTS OF HEAT AND STERILISATION ON THE CHEMICAL NATURE OF THE SOIL

The effect of heat on the organic content and available phosphorus and nitrogen levels

The basic soil and its initial treatment was the same as that used to test germination of Funaria on heated soil (p.129)

Fig. 54. Changes in a) the levels of ammonia nitrogen and nitrate nitrogen (as determined by the double distillation method), b) the field - moisture content and c) the extract colour, of soil from site B14.

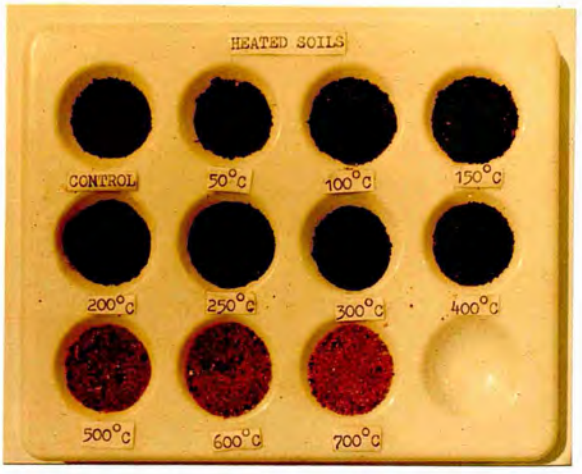


aliquots of sieved air-dry garden soil being heated for 3 hours to one of the following temperatures: 50°C, 100°C, 150°C, 200°C, 250°C, 300°C, 350°C, 400°C, 450°C, 500°C, 550°C, 600°C, 650°C and 700°C. The loss in weight of each aliquot on heating was determined, and analyses carried out for available phosphorus and nitrogen.

As shown in fig. 55, on heating the soil to temperatures above 150°C, the soil showed signs of charring, becoming progressively darker, until at 400°C the soil became orange-brown in colour and at temperatures above 400°C became orange. The extracts of soils heated to temperatures between 150°C and 300°C and most noticeably that heated to 200°C, were yellow-brown in colour, this colour however, disappearing in extracts of soils heated to above 300°C. The soil gradually decreased in weight when heated up to 150°C, but at temperatures above this decreased sharply in weight, until at temperatures above 350°C a more gradual loss in weight again occurred (fig. 56).

Phosphorus levels as shown in fig. 57, increased gradually with heating up to 150°C and then increased sharply in soils heated to temperatures between 150°C and 250°C, increases becoming gradual again on heating up between 250°C and 650°C but phosphorus levels dropping sharply in soil heated to 700°C. The concentration of ammonia nitrogen rose gradually with heating up to 100°C and then sharply, reaching a peak in soils heated between 150°C and 200°C. Above 200°C, with rise in temperature, the concentration of ammonia nitrogen decreased sharply, becoming lower than in the unheated soil in soils

Fig. 55.



The appearance of garden soil after heating to various temperatures.

Fig. 56. The weight of 1gm. of soil after heating.

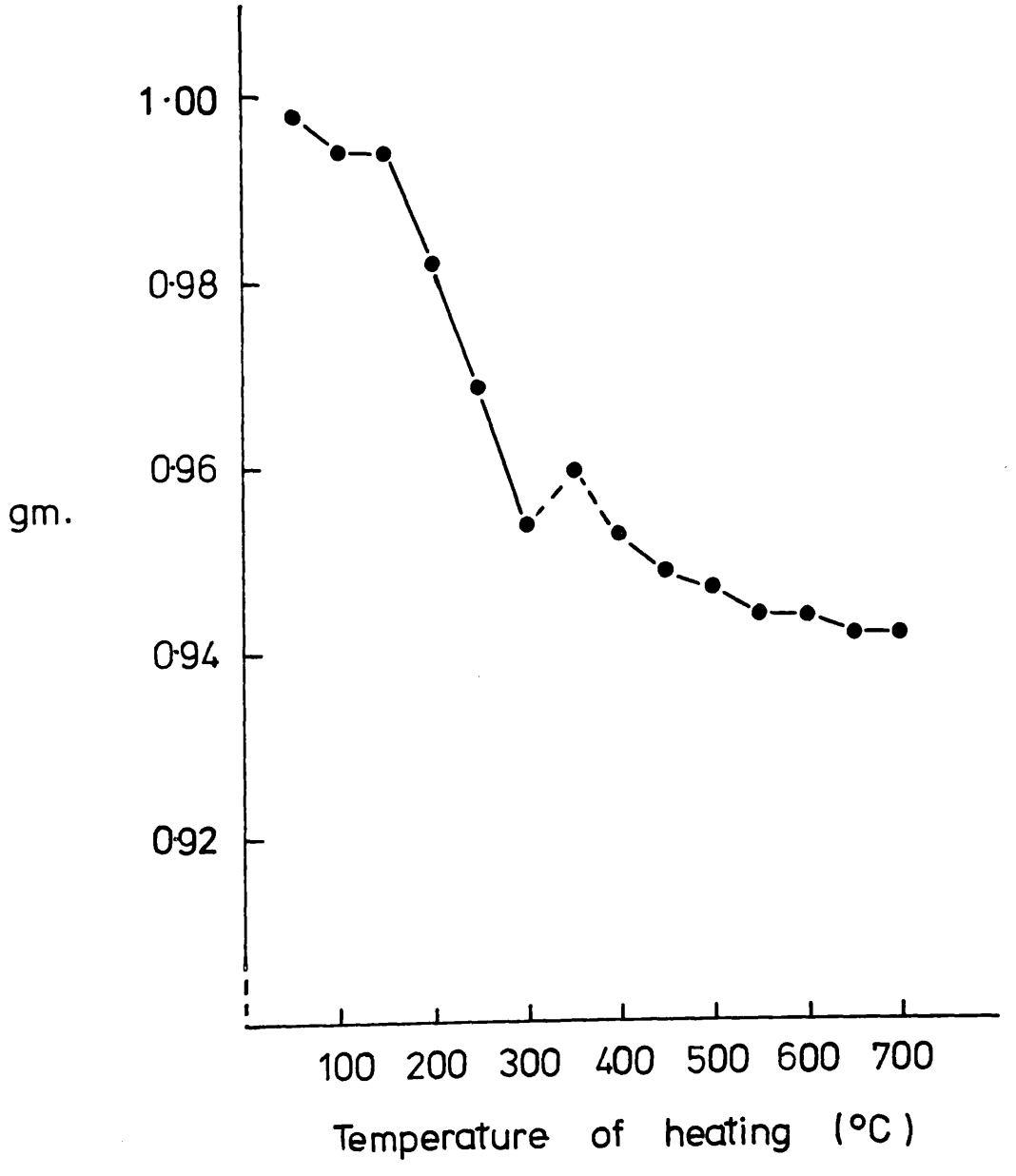
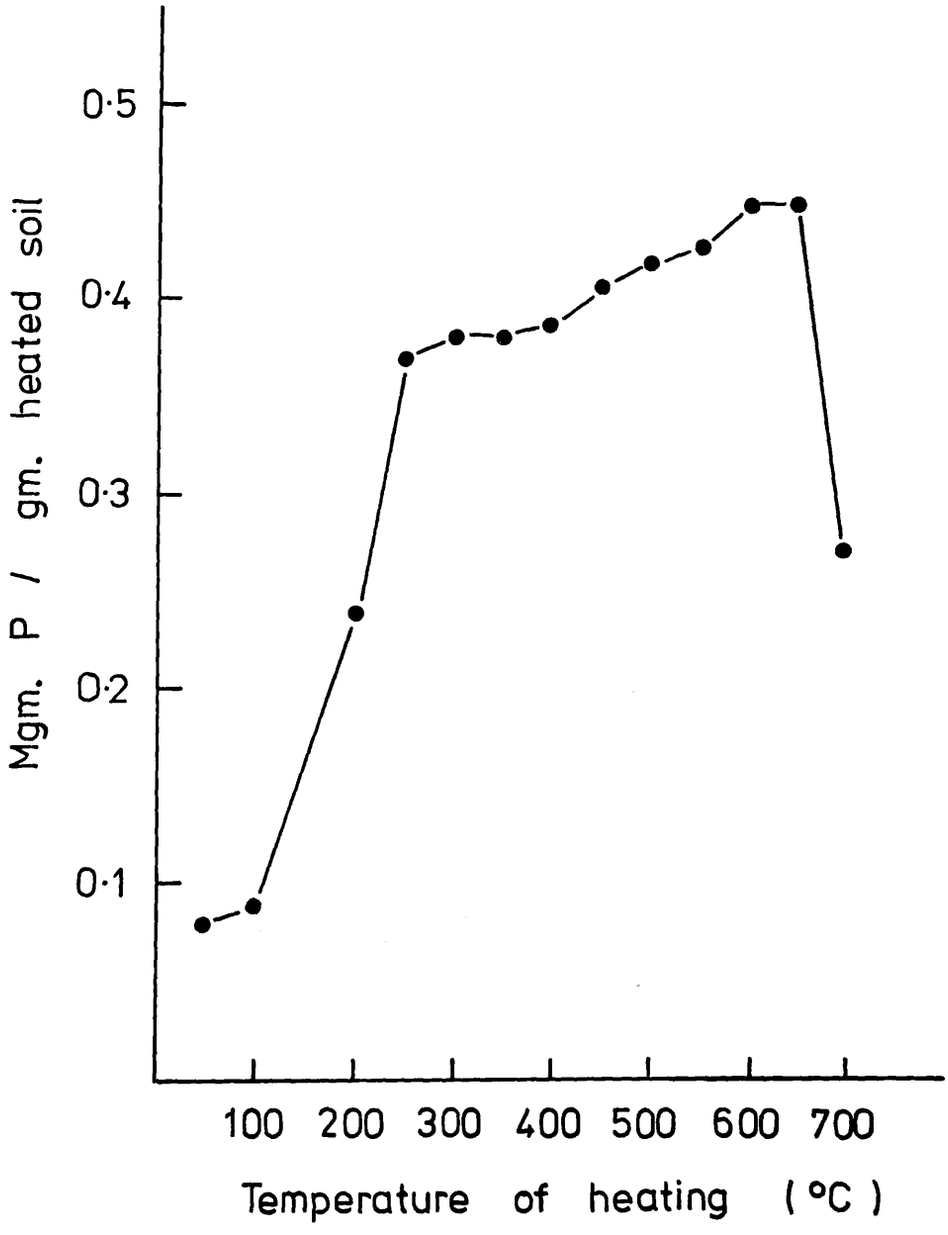


Fig. 57. The effect of heating soil on the level of phosphorus.



heated to 400°C and above (fig. 58). Nitrate nitrogen levels as shown in fig. 59, also apparently rose gradually with heating of the soil to temperatures of up to 100°C and then sharply reaching a peak in soils heated between 150°C and 250°C. On heating the soil to temperatures above this the level dropped sharply, until at temperatures above 300°C, the level decreased more gradually and finally in soils heated to above 600°C, nitrate nigrogen could not be detected. Analysis for nitrate nitrogen however was carried out by the ultra-violet absorption method, which as discussed earlier was found to be inaccurate, particularly when used for burnt and heated soils, due to interference by other substances probably of an organic nature. The figures obtained and discussed above, thus probably reflect the concentration of these soluble organic substances rather than nitrate nitrogen, although at temperatures of heating above 500°C, concentrations of both are obviously low.

The long term effects of heat and radiation sterilisation on available soil nutrients

Changes in the levels of available nutrients were followed over a period of 3 months in soil sterilised by heating to 150°C for 3 hours, some of which was allowed to become reinfected. Changes in these soils, the chemical nature of which would have been significantly altered by the heating, were compared with soils sterilised by irradiation. In addition, germination tests were carried out with Funaria to find how long it took for the expected initial toxicity (see p.183) of the heated soil, to be reduced to a

Fig. 58. The effect of heating soil on the level of ammonia nitrogen.

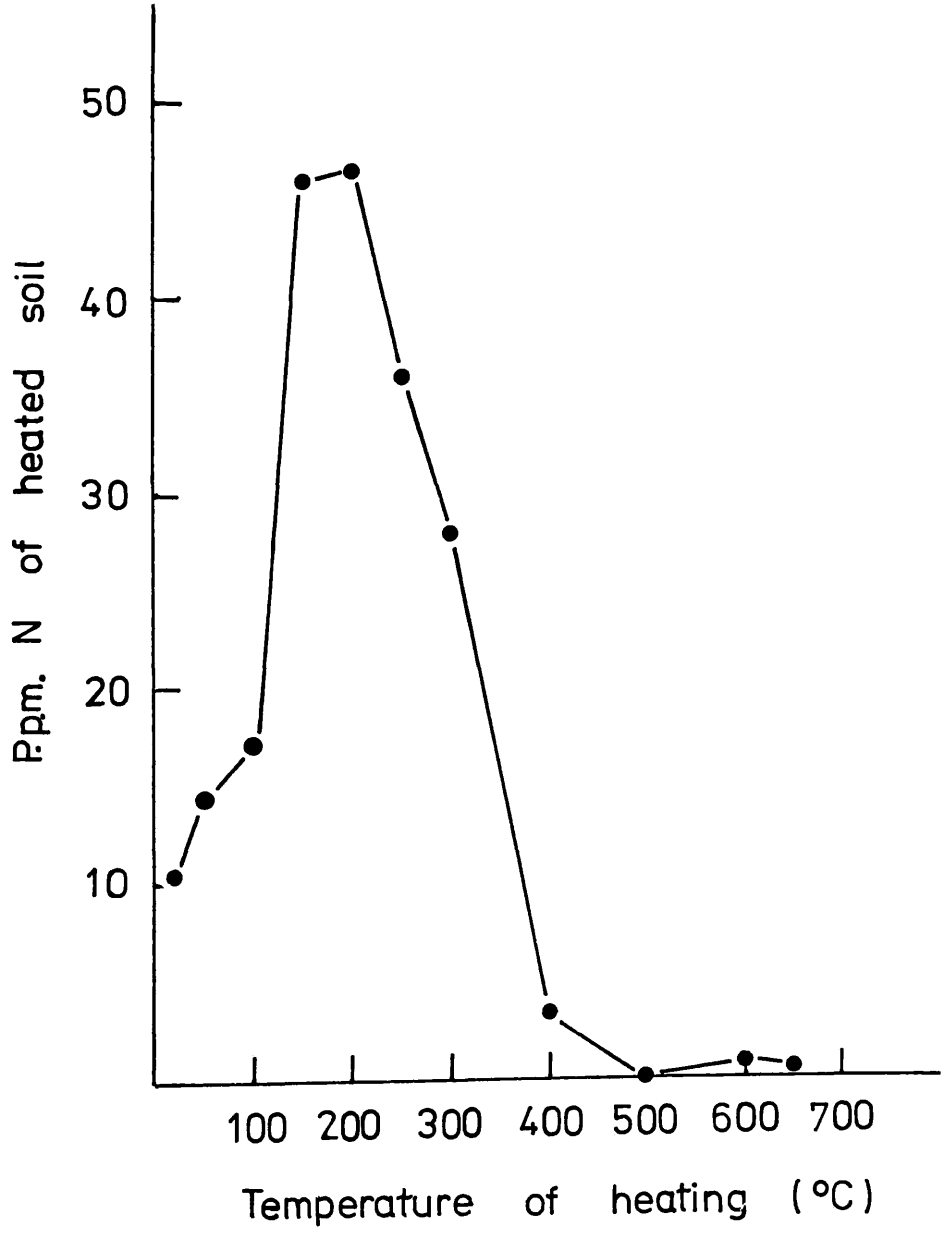
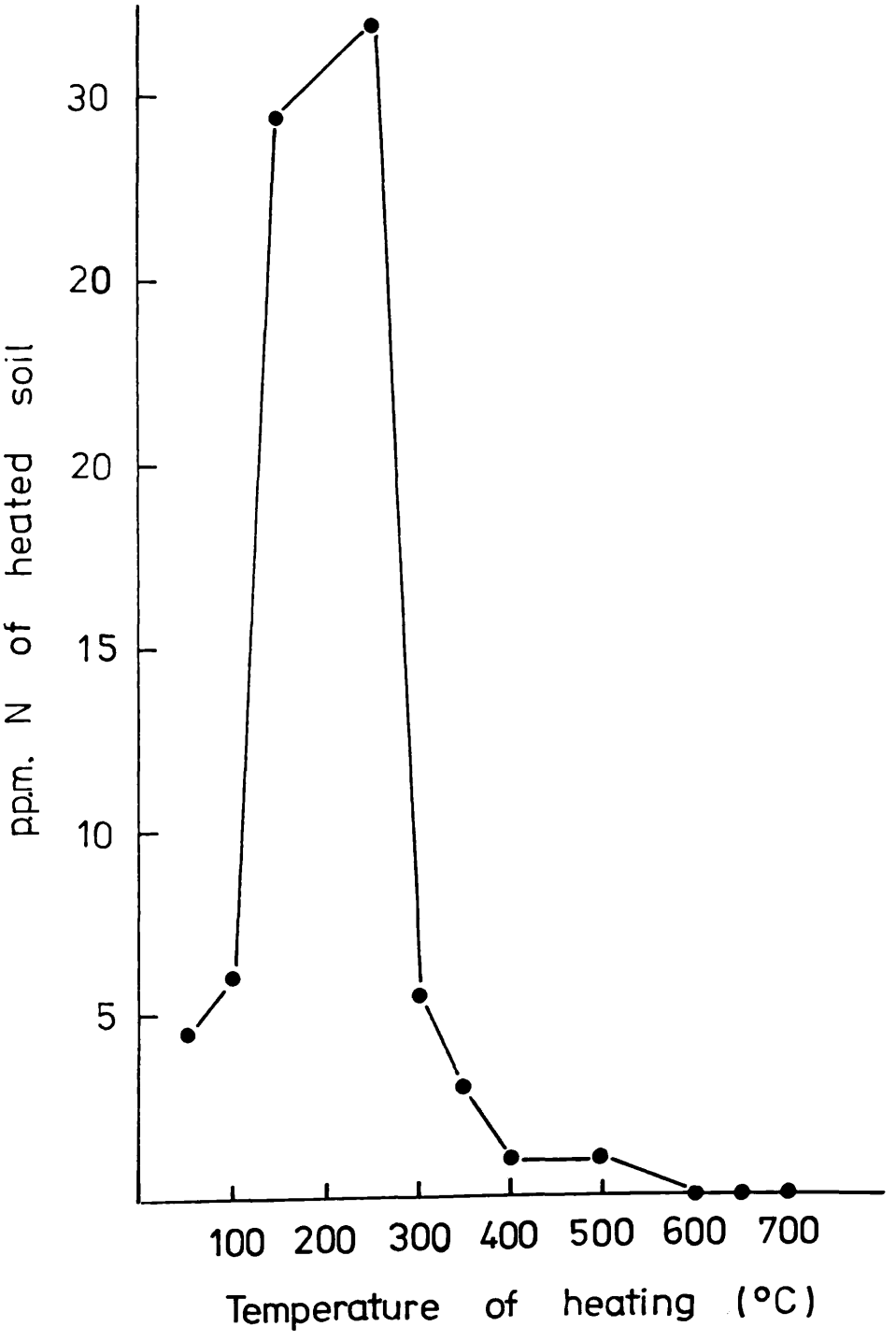


Fig. 59. The effect of heating soil on the level of nitrate nitrogen (as determined by the ultra – violet absorption method).



level which the moss could tolerate.

Garden soil from the grounds of the Botany Department, was air-dried, sieved (mesh B.S. 410 no. 5) and divided into 105 aliquots of 100 gm.. 63 aliquots were placed in 500 ml conical flasks, sealed with cotton wool plugs, 21 left as controls and the remaining 42 sterilised by heating to 150°C for 3 hours. Another 42 aliquots were sealed in heavy gauge polythene bags and sterilised by subjection to 2.5 megarads. These aliquots were then transferred to sterile 500 ml flasks and enough sterile distilled water to just moisten the soil added to each of the flasks, care being taken to ensure that 21 of the heat-sterilised and 21 of the radiation-sterilised aliquots remained sterile. Five treatments were thus set up:

a. heat-sterilised, soil kept sterile;

b. heat-sterilised, soil allowed to become reinfected;

c. radiation-sterilised, soil kept sterile;

d. radiation-sterilised, soil allowed to become reinfected;

e. untreated soil (control).

All the flasks were closed with cotton wool plugs and placed in a north-facing greenhouse. Three flasks of each treatment were removed at random from the greenhouse at regular intervals, some of the soil taken for spore germination tests and the rest used for determinations of available phosphorus, ammonia and nitrate nigrogen, total exchangeable bases and pH. As in the previous experiment

nitrate nitrogen was determined by the ultra-violet absorption method and so in the heated soils at least, figures probably represent nitrate nitrogen plus soluble organic matter. For the unheated soil and the irradiated soils where these concentrations of soluble organic matter would be low it is felt that the trends shown are due to nitrate nitrogen. Since the overall trends shown by the heated soils were similar, it seems likely that although the high initial concentrations reflected the level of soluble organic matter, the trends shown are mainly due to changes in the levels of nitrate nitrogen and in the following description the figures are referred to as those for nitrate nitrogen. A bacterial count was carried out on the soils after $9\frac{1}{2}$ weeks (for method see appendix pp.280-1). This showed none of the soils were completely sterile, but that there were obvious differences in the numbers of micro-organisms in the 'sterile' and reinfected soils (table 47). Since it was possible that the reinfecting organisms were not those normally found in soil populations, 1 gm. of fresh, garden soil was added to the reinfected flasks at this stage of the experiment. In repeating the experiment it would have been better to add the fresh soil earlier in the experiment to give a longer sampling period after its addition.

For pH and all the nutrients determined, between individual flasks of a single treatment, there was considerable variation in results. The results given therefore, are the average result for

Table 47. Bacterial populations in heat and ratiation sterilised soils, 9½ weeks after treatment.

Treatment	Soil sample no.	Plate 1	Plate 2	Plate 3	Average for 9 plates of each treatment
Untreated soil	1	1	1	1	
	2	1	1	1	1.0
	3	1	1	1	
Radiation sterilised	1	3	3	3	
	2	3	5	4	3.6
	3	4	3	4	
Radiation sterilised and reinfected	1	1	1	1	
	2	2	1	1	1.4
	3	2	2	2	
Heat sterilised	1	3	3	3	
	2	3	4	4	3.6
	3	4	4	4	
Heat sterilised and reinfected	1	3	3	2	
	2	3	3	2	2.7
	3	2	3	3	

Key: 1 = colonies abundant (covering over 50% of plate)
2 = " frequent (covering 25-50% of plate)
3 = " occasional
4 = " rare
5 = " absent

three flasks of each treatment. To enable the statistical differences between the treatments to be determined a much larger number of flasks than could have been handled in the present investigation, would have had to be set up. It is felt likely however, that the overall trends shown are correct, particularly when the same trend is shown by more than one treatment.

In the heated soil there was an obvious rise in the level of phosphorus and ammonia and nitrate nitrogen, in comparison with the unheated soil. Radiation-sterilisation however did not produce a noticeable change.

As shown in fig. 60 the level of phosphorus in all the soils fluctuated considerably during the course of the experiment, but except for the initial drop in level in the non-sterile soils all the treatments showed similar fluctuations. The addition of fresh soil to the reinfected soils appeared to have no obvious effect on the phosphorus level.

Changes in the level of ammonia and nitrate nitrogen are shown in fig. 61. Ammonia nitrogen showed an increasing trend in both the heated and irradiated soils over most of the sampling period, but decreased in the reinfected soils of both treatments soon after the addition of fresh soil. In soils kept 'sterile' however the level of ammonia nitrogen continued to increase. Changes in the level of nitrate nitrogen were less clear cut. In the reinfected soils levels increased after the addition of fresh soil in the irradiated soil, but although fluctuating considerably, showed little overall

Fig. 60. Changes in the level of phosphorus in garden soil after sterilisation.

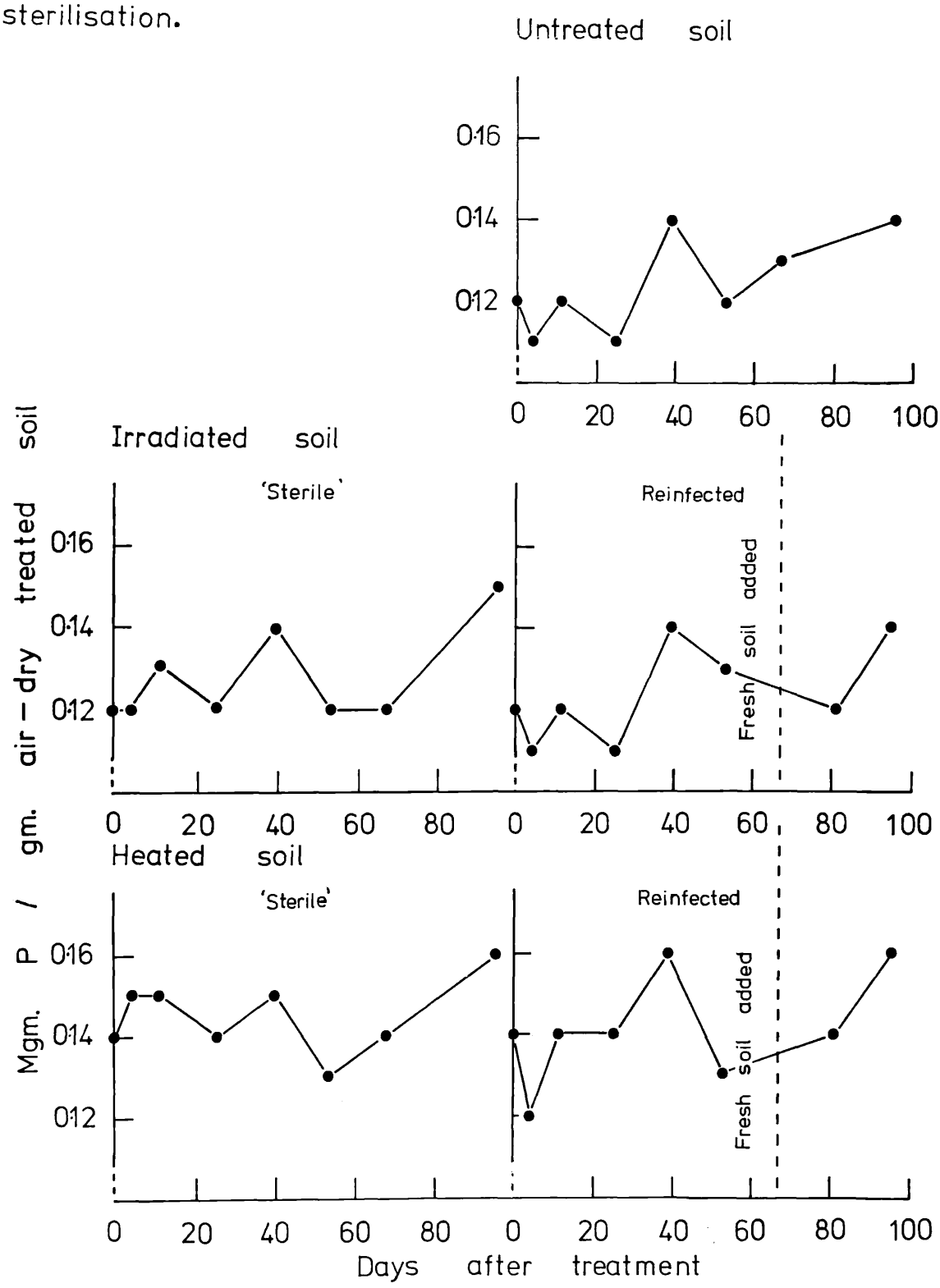
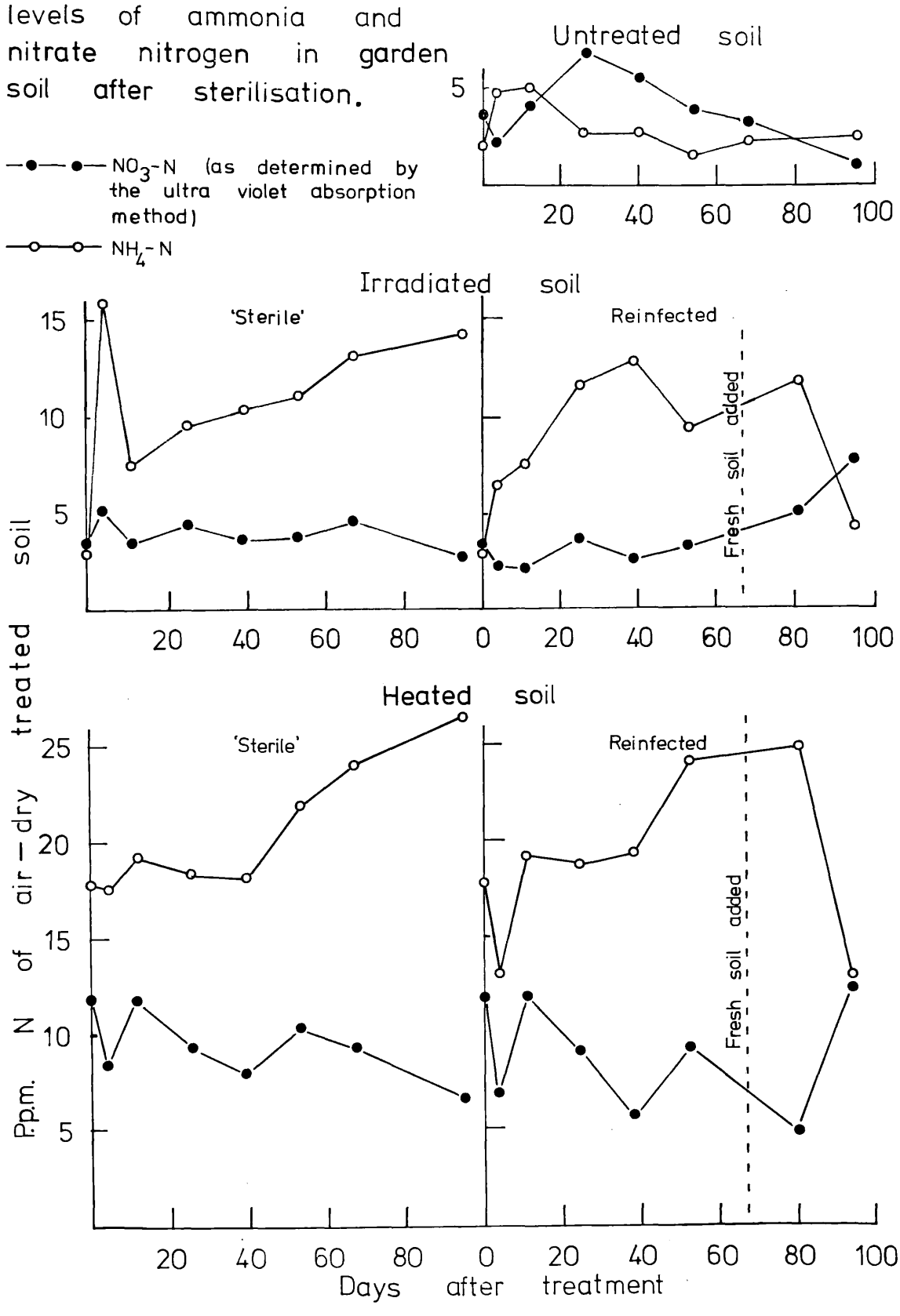


Fig. 61. Changes in the levels of ammonia and nitrate nitrogen in garden soil after sterilisation.



change in the heated soil, whilst in the 'sterile' soils they showed little change in the irradiated soil, but tended to decrease in the heated soil. After remoistening the control soil, there was an initial rise in the level of ammonia nitrogen over the first 11 days, levels then falling off again. Nitrate nitrogen levels reached their peak after 25 days and then parallel with the appearance and increase in number of angiosperm seedlings, showed a downward trend.

The trend in pH was similar in all the treatments as shown in fig. 62. Initially in the first 4 days it rose sharply. By the 11th day it had dropped, but then continued to rise until levels began to decrease again, towards the end of the sampling period. Both the 'sterile' heated and the 'sterile' irradiated soils, showed a sharp drop in pH in the 39th day samples.

Germination tests were discontinued after 4 days as Funaria was found to germinate on all the soils (table 48), the heated soil therefore not being toxic. Determination of total exchangeable bases was also discontinued after a short while (25 days), since no obvious differences were shown between treatments (table 49) and it was felt that the method was not sensitive enough to show true differences.

Fig. 62. Changes in the pH of garden soil after sterilisation.

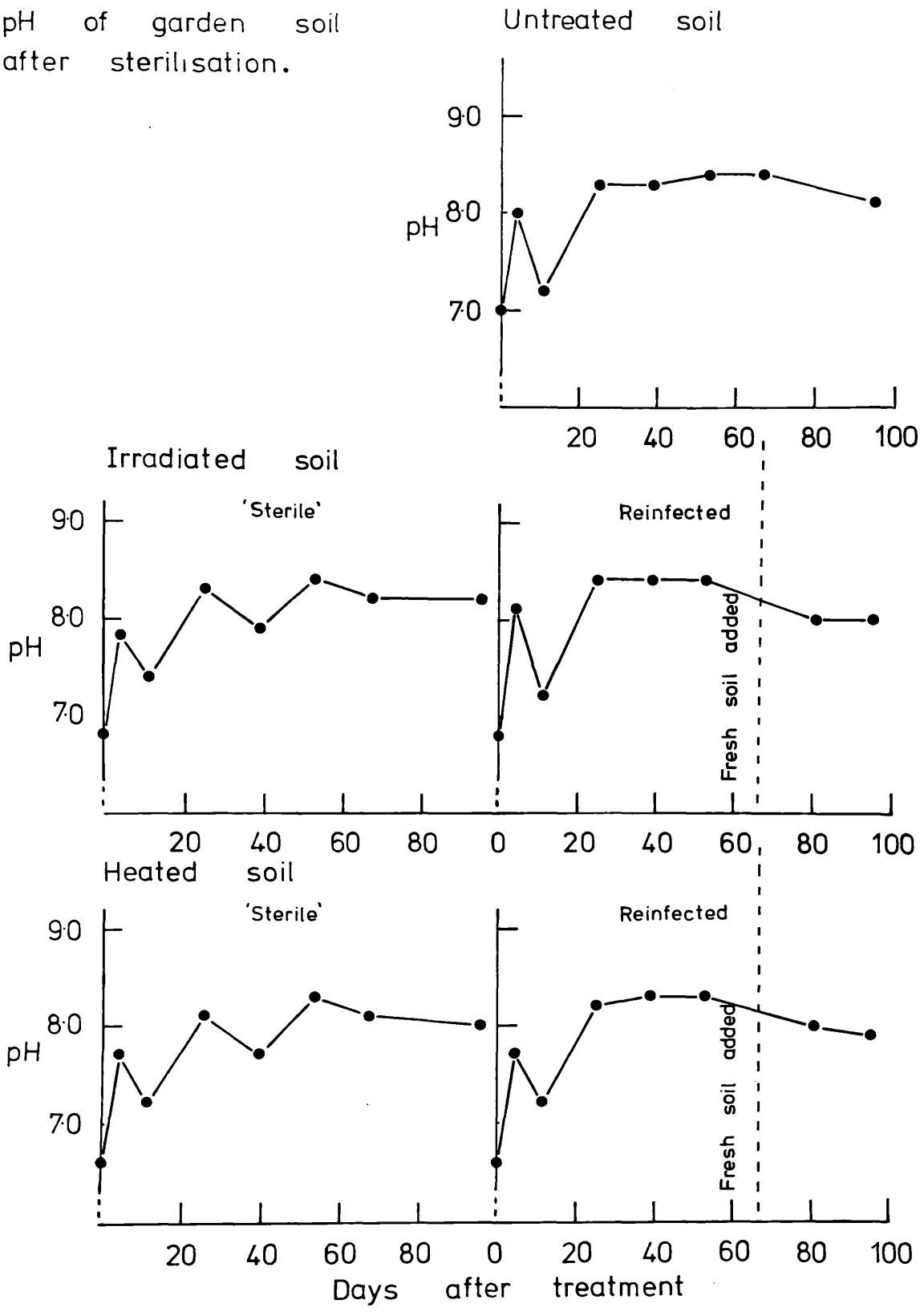


Table 48. Germination of Funaria spores on heat and radiation sterilised soils (% spores germinated).

Treatment	Days after treatment	
	0	4
Untreated soil	96.26	89.26
Radiation sterilised	95.02	74.47
Radiation sterilised and reinfected	95.02	98.33
Heat sterilised	97.97	57.25
Heat sterilised and reinfected	97.97	98.50

Table 49. Changes in total exchangeable bases in heat and radiation sterilised soils (millequivalents/100 gm. air-dry soil).

Treatment	Days after treatment			
	0	4	11	25
Untreated soil	10.33	12.57	8.43	10.47
Radiation sterilised	10.33	12.33	9.33	10.77
Radiation sterilised and reinfected	10.33	12.87	10.33	11.13
Heat sterilised	11.27	12.33	8.93	10.57
Heat sterilised and reinfected	11.27	11.80	10.30	10.10

V. DISCUSSION

Results of the present investigation dealing with the effect of burning on the surface soil alone, were largely in agreement with the findings of other workers concerned with greater depths of soil.

Bonfire soils

High concentrations of available mineral nutrients were found in bonfire soils collected immediately after burning and for some time afterwards and correlated with this the soils had a very high pH. None of the bonfires was severe enough to cause a major decrease in total organic matter, but the dark brown colour of extracts of young bonfire soils indicated a high soluble organic content, some of which must have resulted from breakdown of insoluble soil organic matter. More soluble organic matter was probably derived from the ash together with the little altered remains of plants and animals. Thus, although some organic matter is undoubtedly lost, the overall picture as shown here may be of a slight increase, together with an alteration in the proportions of the different organic fractions. As with the organic content, a decrease in the level of total nitrogen was not found after a bonfire, but an alteration in the levels of available nitrogen was found. High levels of both ammonia and nitrate nitrogen were found in bonfire soils immediately after burning, when analyses were made on field-moist soil by the double distillation technique.

As expected, together with decreasing pH, the high initial levels of nutrients in most cases decreased fairly rapidly after burning, probably mainly due to leaching. Individual nutrients however, differed in their rate of decrease. Sodium and potassium were characterised by a very sharp decrease in level in the first few months after burning, followed by a more gradual decrease. In soils from the bonfire sites in Experiments 1 and 2, sodium levels had reached those of the unburnt soil after 12 months, whilst levels of magnesium, potassium, and phosphorus had reached, or were approaching, unburnt soil levels in at least some sites after 18 months. Calcium levels rather unexpectedly showed little decrease over the sampling period. Soil from bonfire site a, at South Haven Peninsula (which showed little colonisation by either bryophytes or angiosperms during the observation period), even allowing for the decrease which would have occurred with time, had a low pH, phosphorus and calcium content, compared with other bonfire soils of similar age. The total organic content showed a slight decrease during the sampling period, as indicated by the decrease in colour of the soil extracts and the sharp decrease in nitrate nitrogen figures, as determined by the ultra-violet absorption method. This probably reflected a loss in soluble organic matter. Nitrate and ammonia nitrogen as determined by double distillation, both decreased in concentration in the second month after burning, reaching levels in the adjacent unburnt soil after 7 weeks, although levels of both began to rise again in the third month.

Most of the available nutrients found in bonfire soils, must have been derived from the ash, as shown for phosphorus. In fact the top 2 cm. of soil for the first 1-2 months after burning, was largely composed of ash and charcoal and although no mechanical analyses were carried out, these soils had a visible high small particle fraction for at least 12 months after burning. Such soils were light and easily shifted by wind and rain and as a result of animal disturbance. It is probable that the large fluctuations in levels of nutrients, which were found in soils from the bonfire sites in Experiment 2, were due to an irregular distribution of nutrients over the site surface as a result of movement of the surface soil. The likelihood of this movement occurring, would be increased by the lack of a protective vegetation covering or litter layer. The exposure of the surface soil to climatic influences, would also lead to wider fluctuations in temperature and moisture content, which would have contributed to the fluctuations in nutrient levels. Results of analyses of the more stable and sheltered unburnt soil, showed considerably smaller fluctuations. Collection of small samples from a large number of places on each site, as was done for the sites under less detailed study, instead of collecting one large sample, would probably have reduced much of the fluctuation.

The rapid removal of ash from the exposed sites B17 and B20 on Coombe Hill and Cronkley Fell respectively, must have led to a more rapid decrease in the level of available nutrients, but the

removal of ash cannot explain the low nutrient content of bonfire site a, at South Haven Peninsula, as the ash layer on this site was still several inches deep after 18 months.

Rapid fire site soils

Relatively few analyses were made of soils from rapid fire sites. As expected however due to the small amount of ash deposited during such fires, the pH and total level of available nutrients were never as high as in the bonfire soils, even in soils collected in the first month after burning. With the exception of soils collected from young bonfire sites, levels of magnesium, sodium and potassium, in some cases were as high as those of the bonfire soils, but levels of calcium and phosphorus were always lower. No analyses were made for nitrogen, but the low pH of most of the rapid fire site soils, would not have favoured nitrification.

The effects of heat and sterilisation

The results of investigations into the effect of heat on soil, were also in close agreement with those of other workers. An alteration to the forces holding the water film round the soil particles, due to evaporation and partial dehydration of the soil colloids, together with some breakdown of organic matter, would as suggested by Mukerjee (1954) account for the slight rise in the level of available nutrients found in soils heated up to 100°C. As found by other workers however, the most significant changes in the

levels of nutrients occurred in soils heated to temperatures between 100°C and 300°C. Sharp increases were found in the levels of nitrate nitrogen plus soluble organic substances, ammonia nitrogen and available phosphorus. This release of available nutrients, coincided with the major breakdown of soil organic matter, as indicated by the charred appearance of the soil, its smell and sharp loss in weight. On heating the soil to temperatures above 300°C, disappearance of the dark soil colour and the yellow-brown colour of the soil extracts, together with a progressively more gradual loss in weight, indicated that decomposition of both soluble and insoluble organic matter was approaching completion. At temperatures above 500°C, with complete absence of soil organic matter, the orange colour caused by formation of iron sesquioxides became apparent. Levels of ammonia nitrogen and nitrate nitrogen plus soluble organic matter, were found to decrease sharply at temperatures of heating above 250°C, as the organic matter decomposed and volatilisation occurred. Some available phosphorus however, was still released at temperatures above which all organic matter must have decomposed and must therefore have been derived from inorganic sources. At temperatures of heating above 650°C a drop in the level of available phosphorus occurred, probably due to the formation of insoluble pyrophosphate salts.

Germination tests (see p.126) indicated that in general the absence or presence of Funaria on a particular site was reflected in the negative or positive germination respectively, of spores on

soil from that site. Tests, however, were carried out before the full significance of heating soil on its chemical nature was realised, some of the soils in the tests being heat-sterilised. The explanation of results is therefore not so straightforward as would at first appear. For young bonfire soils where high concentrations of soluble matter would already be present as a result of burning, inhibition of germination was seen even in unsterilised soils and heating would just complement the effect by releasing more soluble matter. Heating however was not strong enough to cause further breakdown of soluble substances and so reduce the toxicity. With older bonfire soils where the bulk of soluble matter resulting from burning will have been removed it might be expected that heating would cause further breakdown of organic matter and render the soil toxic again. This however, was not found and it is possible therefore, that there was insufficient of the heat-decomposable, organic fraction, left in the soil to produce the toxic effect. The heating of soil from rapid fire sites where burning had little effect on chemical composition, must have caused a significant rise in the level of soluble matter and thus rendered these soils toxic. Germination may have been able to take place in these soils if they had not been heated. Spores were able to germinate on heat-sterilised soil from unburnt areas of Coombe Hill, suggesting that the initial organic content of this soil was low.

In the investigation into the long term effects of heat on the soil chemical nature, the soil unexpectedly, did not prove toxic to Funaria spores when heated to 150°C for 3 hours. It was

found that the original soil had a low organic content in comparison with soils used for earlier germination tests and the soil heating experiment (p.129), and since most of the substances released on heating are derived from breakdown of the organic matter, the levels of nitrate nitrogen plus soluble organic matter, ammonia nitrogen and probably other substances released on heating were low.

Changes in the concentrations of ammonia and nitrate nitrogen were as expected, largely dependent on the micro-organism population, different trends being found in the control unsterilised soil and the sterilised soils and in the 'sterile' and reinfected soils, after the addition of fresh garden soil to the reinfected soil. After remoistening the control unsterilised soil, a flush of ammonification occurred, as found by other workers on remoistening air-dry soil. Levels of nitrate nitrogen began to increase a little later, reaching a peak after the level of ammonia had fallen, presumably oxidised by the nitrifying bacteria. The fall in level of nitrate nitrogen, coincided with the appearance of angiosperm seedlings suggesting its utilisation. The build-up of ammonia nitrogen and its subsequent decrease, together with the rise in level of nitrate nitrogen, after the addition of garden soil and presumably nitrifying bacteria to the irradiated soil, confirmed the observations of other workers on the effect of sterilising, or partially sterilising soil (p.201). The increase and subsequent decrease in ammonia nitrogen

level, was also seen in the heated soil and although the nitrate nitrogen level showed no overall increase, at least it did not decrease as in the heated 'sterile' soil. This effect was expected to be seen in bonfire soils, where the heat of the fire would have been sufficient to at least partially sterilise the surface soil. It seems however, that with the increase in rainfall (as indicated by the increased soil moisture fig. 54b) in the second month after burning, both the ammonia and nitrate nitrogen of site B14 were rapidly leached from the soil, ammonia nitrogen also being lost as ammonia gas from the very alkaline soil, and it was not until the third month, that micro-organism activity was sufficiently restored to overcome the leaching effect and show an increase in available nitrogen. Both ammonia and nitrate nitrogen levels however, began to rise at the same time, but it is possible that nitrate nitrogen formation was still partially inhibited. With reference to the pH of other bonfire sites, the pH of soils on which the available nitrogen determinations were made, must still have been very high, even 3 months after burning and according to the suggestion of Campbell & Lees (1967), Black (1968) and Buckman & Brady (1969), Nitrosomonas activity may have been greater than that of Nitrobacter, so that there was an accumulation of nitrite nitrogen rather than nitrate nitrogen. As the level of pH continued to fall and to become more favourable to Nitrobacter, the level of nitrate nitrogen may eventually have superseded levels of ammonia nitrogen. The scarcity of plant growth on young bonfire sites would also have favoured nitrification (Russel,

1961), as would the high level of exchangeable bases (Buckman & Brady, 1969).

Microbial activity did not appear to be very important in determining the fate of available phosphorus. Both the 'sterile' and reinfected soils and the control soil showed similar fluctuations. Also the addition of fresh soil to the reinfected soil, made no difference to the phosphorus levels. Fluctuations may bave been largely influenced by soil temperature, which was not controlled. Similarly it was difficult to correlate the major changes in pH with microbial activity.

The initial high levels of nutrients found in the heated soils, did not appear to affect the subsequent fate of these nutrients, soils sterilised either by heating or irradiation showing very similar trends.

GENERAL CONCLUSIONS

Bryophyte recolonisation of burnt ground varies according to the sort of fire. Rapid fire sites, where the ground has only been lightly scorched and little ash deposited, are recolonised largely by the pre-burn species and only where angiosperm recolonisation is slow, as after heathland and moorland fires, do the bryophytes become abundant and form a distinct stage in the succession. On bonfire sites where the effect of the fire has been more severe, high temperatures being prolonged and much ash deposited, both angiosperm and bryophyte recolonisation are at first delayed. Eventually however, Funaria characteristically becomes abundant, Ceratodon purpureus Bryum argenteum and tuberous species of Bryum occurring as scattered shoots amongst the Funaria. These species are eventually replaced by the pre-burn species, as the angiosperm cover increases.

All the bryophytes found on the bonfire sites were those which would have been expected from a review of the literature. In view of the widely reported occurrence of Marchantia polymorpha however, it was rather surprising that this species was only found on nine of the sixty-four sites examined, particularly as on three of these sites it was the most abundant species. Several authors including Summerhayes & Williams (1926), Skutch (1929), Doignon (1949) and Remezov & Pogrebnyak (1969) have reported its occurrence in moist areas of burnt sites and it is possible therefore that, as suggested by Graff (1935) and Cremer & Mount (1965), this species requires a wetter habitat than the other bonfire species of bryophytes. Although all nine sites on which

Marchantia was found, were sheltered and would have a fairly high constant humidity, there were several other moist sites (e.g. those on Thursley Common see table 9) where this species was not found. Thus moisture cannot be the only factor controlling the appearance of Marchantia. This species was never found in fruit though gemmae were usually abundant. It seems likely that gemmae do not provide such an efficient dispersal mechanism as spores and this together with a requirement for a moist habitat may explain its absence from many of the sites. From the results of culture work by other authors e.g. Voth (1943) and the frequent occurrence of Marchantia on a wide variety of non-burnt sites, it does not seem to have very specialised nutrient requirements.

Of the bryophytes colonising bonfire sites Funaria appears to be the only one with a distinct preference for this habitat. Although a fairly tolerant species, being able to show at least some growth on a wide range of nutrient media and on unburnt soils, under natural conditions in the present investigation, dense turves were only found on bonfire sites. Ceratodon purpureus and Bryum argenteum on the other hand, were found equally commonly, and often in greater abundance, on unburnt soil. Being very tolerant species, they must be able to cope with the extreme conditions found on bonfire sites. It is likely that they are mainly taking advantage of the open conditions produced by burning, though it is also possible that Bryum argenteum has nitrophilous tendencies, which as is discussed later, would be

important in determining its occurrence on bonfire sites. It is interesting that tuberous species of Bryum often occur on bonfire sites, since it has been suggested by Whitehouse (1966), that the primary function of the tubers is to provide a means of surviving unfavourable conditions e.g. in an open habitat liable to desiccation and disturbance, a description which could be well applied to burnt ground.

The tolerance of the bonfire species to conditions adverse to most other bryophytes is illustrated by their ability to colonise brick and stonework in industrially polluted areas. Growth of all the species however, was generally poor, although Funaria showed good growth on one site where burning had possibly taken place. Funaria was not found growing on brick and stonework in less polluted areas and it is probably a poor competitor in such a habitat, when the more characteristic wall species, which may include Bryum argenteum and Ceratodon purpureus, form a more luxuriant growth.

The present investigation has confirmed the widely held view that edaphic conditions are of primary importance in determining the success of the pioneer mosses on burnt ground. It is clear from field experiments that the deposition of ash is the most important factor in rendering soil conditions suitable for growth of Funaria, but it was also shown, both in the field and in culture, that the heating effect of the fire on the soil is of some importance. Growth of Funaria on soil heated to temperatures between 100°C and 300°C (i.e.

of the same order as the surface soil is subjected to during a bonfire) was eventually stimulated in spite of the initial inhibition of spore germination on this soil. These effects of heating soil were not restricted to Funaria, Spore germination of Bryum argenteum and a non-bonfire species Eurhynchium praelongum were found to be initially inhibited on soil heated to temperatures of this order, whilst the growth of higher plants has been shown to be stimulated on heated soil by several workers (e.g. Mukerjee, 1954 and Pryor, 1963) and the initial inhibiting effect has also been noted (e.g. Pickering, 1910; Seaver & Clark, 1912; Russel, 1961 and Pryor, 1963).

It is possible that as suggested for higher plants (Fletcher, 1911 cited by Seaver & Clark, 1912) stimulation of growth of Funaria is due to the destruction of an inhibitor present in the unheated soil. A heat-labile toxin has been found in soil under certain plants (Muller, Hanawalt & McPherson, 1968), but it seems unlikely that such toxins are of widespread occurrence. Thus whilst it is difficult to discount their presence completely as is mentioned later, it is easier to link the pattern of colonisation by Funaria with the changing nutrient levels in soils.

In spite of distinct preferences for burnt ground, Funaria is a tolerant species and thus if soil is collected from every site on which it is recorded, it would be difficult as found by Hoffman, to establish a common characteristic for the soil on which it grows. A correlation can however be found between the nutrient requirements of Funaria as determined by culture experiments, and conditions in burnt and heated soil. It is difficult though, to compare directly the amounts

of nutrients in the soil with those in the culture media, because of the effects of air-drying soil samples before analysis and the uncertainty as to which soil nutrients are available. Nor can one be certain the response of Funaria will be the same on artificial media as in the field.

The initial inhibition of both bryophyte and angiosperm growth on bonfire and heated soils was undoubtedly due to the very high concentrations of soluble substances resulting from the breakdown of insoluble organic matter. The toxicity probably arose both as a result of excess concentration of plant nutrients, including micronutrients and the presence of soluble organic substances which are directly toxic to growth. For example the high concentration of ammonia nitrogen found in recently burnt soil, would alone, be sufficient to inhibit growth of Funaria. In addition, the pH of bonfire soils, immediately after burning is excessively high and may contribute to their toxicity, whilst the high osmotic potential of such soils may also have some effect on growth, though this was not confirmed in culture work with Funaria.

By the time protonemata appeared on the bonfire sites the levels of soluble substances were considerably reduced through leaching, thus the soils were no longer toxic to the growth of Funaria. As concentrations continued to change, levels would eventually be reached when growth was stimulated. Some change in the nutrient concentration would also occur as a result of the activity of micro-organisms, particularly changes in the available forms of nitrogen. It is very

probable that the initial high concentrations of ammonia nitrogen would eventually be reduced and exceeded by nitrate nitrogen levels, as the numbers of the nitrifying bacteria was restored and their activities stimulated by the high levels of pH and other nutrients. Stimulation of nitrification following burning has been shown by some authors (see Ahlgren & Ahlgren, 1960) to continue for several years.

Raising the level of nitrate nitrogen, in the presence of adequate amounts of potassium and phosphorus which would certainly exist in young bonfire soils, was shown to stimulate growth of Funaria in culture. Hoffman has also indicated that the balance between nitrogen and phosphorus is important to growth. In direct contrast to the finding of Cremer & Mount (1965), addition of nitrogen and phosphorus in the form of dried blood and bone fertiliser to unburnt but weeded plots, did not promote growth of Funaria. However, about 80 percent of the nitrogen released from dried blood is in the form of ammonia nitrogen (Russel, 1961) and this may have been leached from the soil before it could be oxidised. Moreover the very high concentration of ammonia nitrogen would itself inhibit nitrification (Black, 1968 and Buckman & Brady, 1969), whilst changes in pH may have affected the availability of other nutrients. It is likely that in Cremer & Mount's experiment differences in the amount of fertiliser added, together with different soil and other environmental conditions, resulted in a more significant rise in the level of nitrate nitrogen, which together with the increased level of phosphorus and an adequate supply of potassium, was sufficient to stimulate growth.

Good growth of Funaria is sometimes found on soil in greenhouse flower pots, but this is not unexpected because of the common horticultural practice of heat-sterilising soil, whilst watering pot plants with nutrient solutions may also encourage growth. As with the experiment described above however, it was surprising that the addition of calcium, potassium, nitrogen and phosphorus to the heated soil caused little further stimulation of growth, whilst the poor growth on unheated soil, with these added nutrients is even more difficult to explain. Nutrients may not have been added in the correct proportions whilst, without having analysed the soils it is not possible to be certain of the fate of the added nutrients. The luxuriant growth of algae and fungi which soon appeared on the fertilised soils, may have taken up most of the added nutrients before Funaria could colonise the soil, but the results of this experiment and the one discussed above, lend support to the theory that, nutrients other than calcium, potassium, nitrogen and phosphorus are important to growth. Organic nutrients although not needed by laboratory cultures may be essential under natural conditions, whilst levels of micro-nutrients may be too low in unburnt soils. In addition as mentioned earlier, it is difficult to discount completely the possibility that stimulation is due to thermal destruction of an inhibitor in the pre-burn soil.

After 18 months (by which time angiosperm colonisation was nearly complete) pH, calcium and probably nitrate nitrogen levels were still high in the bonfire soils, but levels of potassium, phosphorus

and other nutrients had reached or were approaching those of unburnt soil. In the face of angiosperm competition for nutrients and other factors, of which light and space were probably the most important, nutrient conditions were no longer adequate for growth of Funaria and therefore it disappeared from most bonfire sites in the second year after burning. On sites where the angiosperm recolonisation was slow or prevented, Funaria was still very abundant in the second year after burning. No analyses were made of soils from these sites and thus it is possible that in the absence of angiosperms, levels of nutrients are not so depleted.

There was no replacement of Funaria by the other bonfire species, the latter also disappearing as angiosperm recolonisation approached completion. It is probable that had angiosperm recolonisation been delayed for a long enough period, soil conditions would eventually have become so unsuitable for Funaria that another species would supersede it in abundance. Thus species of Polytrichum did not generally replace the pioneer bryophytes although this might have been expected from ther reports of other workers. Species of Polytrichum were only recorded from burnt sites on moorland, heathland and woodland where they form part of the pre-burn vegetation, and since such sites are those most commonly described by other authors, the frequency with which Polytrichum species are mentioned in the literature is not surprising. If colonisation by Funaria is for some reason delayed, it is possible that other species, as found by Doignon (1949), may initially be more abundant.

The optimal growth of many species of bryophytes including Funaria, occurs on more dilute culture solutions than those suitable for the growth of angiosperms. The question thus arises as to why bryophytes occur on bonfire sites before higher plants. The answer may lie in the possibility that levels of soluble organic substances, as well as concentrations of specific nutrients such as manganese, may still be toxic to angiosperms at the bryophyte stage of the succession, so that although the concentrations of inorganic macronutrients may be suitable for growth, angiosperm colonisation is still delayed.

Compared with bonfires, rapid fires resulted in little rise in the levels of pH, soluble organic matter, phosphorus and probably nitrogen and thus no initial inhibition of plant growth and subsequent stimulation of growth of Funaria is to be expected. The type of colonisation on sites resulting from fires intermediate in nature between rapid fires and bonfires, will obviously depend on the amount of ash deposited and the duration of high temperatures.

APPENDIX ONE

Methods

Examination of the surface soil for protonemata and algae

Collection of samples

A spatula full of surface soil was removed from alternate squares of the quadrat grids fifty small samples thus being collected from each site. The samples were placed in sealed specimen tubes which on return to the laboratory were wrapped in silver foil to exclude light and placed in a refrigerator 1-5^{0}C until examined. No samples were stored for longer than 48 hours.

Examination of the samples

5 ml. of 0.5% agar (Oxoid no. 3) was added to the sample in the tube, the lid replaced and the tube well shaken. The agar plus soil when poured into a 9 cm. petri dish forming a thin transparent layer, which when set was examined with a binocular microscope, magnification x 40, and the presence or absence of protonemata and algae on each plate noted. Protonemata could be recognised by the presence of rhizoid filaments with obliquely divided cells and pigmented walls and in addition buds were sometimes present. Nearly all the algae found were unicellular, coccoid members of the Clorophyceae.

The results are expressed as the percentage number of samples per site containing protonemata and the percentage number containing algae.

2. Preparation of spore suspensions and inoculation of nutrient agar

Two ripe capsules i.e. orange-yellow with the calyptra still in position, were collected from stock cultures in the greenhouse just before required and surface-sterilised by rinsing briefly in 95 percent alcohol. The alcohol was removed by rinsing in sterile detergent water (50 ml. sterile distilled water plus one drop of concentrated 'Teepol') and the capsules then immediately crushed again the side of a sterile narrow ended centrifuge tube. The released spores were washed to the bottom of the tube with sterile detergent water, the tube shaken gently to ensure that all the spores were wetted and then centrifuged at 1500 r.p.m. for 3 minutes, after which the supernatant liquid was poured away. To wash the spores this procedure was repeated three more times using sterile distilled water, spores finally being suspended in 1 ml. of sterile distilled water.

Inoculation was carried out using a wire loop, one loopful of spore suspension being placed in the centre of each medium. In order to prevent the spore suspension from running over the surface of the agar slope, the surface of the medium was kept in a horizontal position for 24 hours after inoculation to allow excess water to evaporate.

Both techniques were carried out under conditions as sterile as possible, the usual microbiological procedures being followed.

3. Methods of soil analysis

Glass distilled water and wherever possible analar chemicals, were used throughout. In experiments to find the effect of heat on soil and to determine the long term effects of heat and radiation sterilisation, soil analysis results equal the mean of two and in most cases three analyses, but on all other soils only one analysis was carried out.

a) pH

For most soils determinations were made with a bench pH meter using a 1:5 air-dry soil to water ratio. Results from determinations carried out on field-moist soil are indicated in the tables and figures. The second series of determinations made on soils from Cronkley Fell (table 39) were carried out on field-moist soil, 6 hours after collection using a portable pH meter.

b) Loss on ignition

Soils dried at 105°C overnight were ignited at 600°C for

12 hours, the loss in weight calculated and then expressed as a percentage of the oven-dry weight.

The loss in weight will represent the total soil organic matter, but will also include, bound water, the carbon dioxide of carbonates and some other salts. In the calcareous soils the carbon dioxide may have formed a significant part of the weight loss.

c) Exchangeable metallic cations

Calcium, magnesium, potassium and sodium were determined on aliquots of an ammonium acetate soil extract.

Ammonium acetate is commonly used as an extracting agent in the determination of exchangeable metallic cations, even though results are only approximate since several factors tend to raise the concentration of ammonium acetate extracted ions over the amounts truly exchangeable. These include the water soluble salts present and dissolution of some of the carbonates of calcium and magnesium (Piper 1950; Jackson, 1958). Results, however, are probably still a good indicator of soil fertility, except for the calcareous soils where very large amounts of calcium and magnesium are dissolved from the

basic rock, well beyond the true plant availability values. Time did not allow for the development of a special method for the chalk soil (Coombe Hill) and determinations were therefore not made on this soil.

The extraction procedure was an adaptation of the rapid centrifugation procedure described by Jackson (1958). The 1N neutral ammonium acetate was prepared from crystals and the pH of the solution adjusted if necessary, using 2N acetic acid or 2N ammonia solution. 5 gm of air-dry soil (except for soils with a low metallic cation status when larger amounts of soil were used) was weighed out into a 50 ml narrow necked, centrifuge tube. Approximately 20 ml of ammonium acetate was added and the stoppered tube shaken on a mechanical shaker for 5 minutes. The stopper was then removed and the tube centrifuged for 5 minutes at 4,500 r.p.m., after which the supernatant liquid was immediately filtered through Whatman's filter paper no. 1 to remove any small light particles present. This was particularly necessary when extracting 'peaty' soils. The filtrate was collected in a 100 ml volumetric flask, the sample extracted two additional times with 20 ml of the extracting solution and the filtrates collected in the volumetric flask. Finally the extract was made up to volume.

i. Calcium and magnesium

Reagents were as follows:

1N sodium hydroxide

N/200 E.D.T.A. (di-sodium ethylenediaminetetra-acetate), 1 ml = 0.1002 mgm. calcium and 0.0608 mgm. magnesium.

Calcium titration indicator, 0.20 gm. of ammonium purpurate ($C_8H_4N_5O_6.NH_4$) was ground up with 100 gm. of potassium chloride. The mixture was stored dry in a stoppered bottle since solutions of this dye are unstable.

Total hardness titration indicator, 1.0 gm. of eriochrome black T was dissolved in 100 ml. of triethanolamine.

Buffer solution for total hardness titration, 10.0 gm. of sodium hydroxide and 5.0 gm. of sodium monosulphide ($Na_2S.9H_2O$) were dissolved in 100 ml. of water and 40 gm. of borex dissolved in 800ml. of water. The two solutions were then mixed and diluted to 1L.

1-5 ml. (depending on the soil type) of the ammonium acetate soil extract was pipetted into a titrator cuvette and placed in an oven at 90°C to evaporate the ammonium acetate which interfered with the titration. When nearly dry the sides of the cuvette were washed down with a few ml. of water and the solution evaporated to dryness. The dry sample was then taken up in 20 ml of water added to the cuvette and titrated against E.D.T.A. As the end points of both the calcium and total hardness titrations were difficult to determine an 'EEL' electric titrator (filter 607) was used.

ii. Sodium and potassium

Reagents were as follows:

Standard sodium solution, 0.2542 gm. of sodium chloride was dissolved in 100 ml. of 1N neutral ammonium acetate solution. 1 ml. $\equiv$ 1 mgm. sodium.

Standard potassium solution, 0.1907 gm. of potassium chloride was dissolved on 100 ml. of 1N neutral ammonium acetate. 1 ml. = 1 mgm. potassium.

Analyses were carried out by flame photometry. Solutions containing 0.5 mgm. sodium and 0.5 mgm. potassium were used to give full scale deflection on the flame photometer. Aliquots of soil were diluted as necessary with 1N neutral ammonium acetate.

e) Total exchangeable bases

Determinations were carried out according to Brown's method (Brown, 1943), by pH determinations of a buffer-soil mixture. 2.0 gm. of air-dry soil was shaken for 1 hour with 20 ml. of 1N acetic acid, using a mechanical shaker. The pH of the mixture was then determined and compared with a standard graph.

f) Phosphorus

The extraction procedure was based on the dilute acid-fluoride method of Bray & Kurtz (1945), described by Jackson (1958). This method is believed to give results that are highly correlated with crop response to phosphate fertilisation (Jackson, 1958; Russel, 1961). The phosphorus content of the extract was determined colorimetrically using an ammonium molybdate, stannous chloride method (American Public Health Association, 1955).

Reagents were as follows:

Extracting solution, 1.11 gm. of ammonium fluoride (NH_4F) was dissolved in 4.16 ml. of 6N hydrochloric acid and diluted to 1L. with water.

Stannous chloride solution, 2.5 gm. of stannous chloride ($SnCl_2.2H_2O$) was dissolved in 10 ml. of concentrated hydrochloric acid and then diluted to 100 ml. with water. The turbid solution was then filtered through three layers of filter paper (Whatman's No. 1) and the clear filtrate stored in a separating funnel with a layer of pure mineral oil on top to prevent oxidation.

Ammonium molybdate solution, 25 gm. of ammonium molybdate ($(NH_4)_6Mo_7O_{24}.4H_2O$) was dissolved in 175 ml. of water and 310 ml. of concentrated sulphuric acid, cautiously added to 400 ml. of water. The two solutions were cooled, mixed with care and diluted to 1L. with water.

Standard phosphorus solution, 0.716 gm. of potassium dihydrogen orthophosphate (KH_2PO_4) was dissolved in 1L. of water. 10 ml. of this stock solution diluted to 100 ml. gave a solution containing 0.05 mgm. PO_4 per ml., this dilute phosphorus solution being made up freshly for each new set of analyses.

0.1 gm. air-dry soil (in a few cases field-moist soil as indicated on tables and figures) was weighed out directly into a 100 ml. conical flask, 10 ml. of the extracting solution added and the flask stoppered and shaken with a mechanical shaker for 1 minute. The mixture was immediately filtered through a moist filter paper (Whatman's no. 1) and the clear filtrate collected in a 100 ml. volumetric flask. For unburnt soils it was not usually necessary to dilute the soil extract and analyses were carried out directly on the filtrate. For burnt soils the filtrate was made up to volume with water and the analyses carried out on an aliquot. The aliquot or whole extract, was diluted to

approximately 75 ml. with water, 4 ml. of ammonium molybdate solution added and after mixing, 5 drops of stannous chloride solution. The sample was then made up to volume. 15 minutes exactly were allowed for the colour to develop and the colour then compared with that of standard solutions using an 'EEL' portable colorimeter (filter 608).

g) Total nitrogen

Determinations were carried out on Kjeldahl digests using a modification of the direct Nessler test method of Williams (1964).

Reagents were as follows:

Acid for digestion, concentrated sulphuric acid, sp. gr. 1.84, nitrogen free.

Digestion catalyst, Selenium catalyst tablets as supplied by B.D.H. Ltd., Copper tablets could not be used because of copper interference with the Nessler test (Williams, 1964).

Nessler reagent, 55 gm. of red mercuric iodide (HgI_2) and 41.25 gm. of potassium iodide (KI) were dissolved in 250 ml. of water and 144 gm. of sodium hydroxide pellets dissolved in 500 ml. of water. When cool, the sodium hydroxide solution was stirred into the iodide solution and the volume made up to 1L. The solution was stored in a dark-coloured bottle.

Sodium hexametaphosphate salt.

2N Sodium hydroxide.

Standard nitrogen solution, 4.7162 gm. of ammonium sulphate ($(NH_4)_2SO_4$) was dissolved in water and the solution made up to 1L. 1 ml. $\equiv$ 1 mgm. N.

An electric manifold and 100 ml. Kjeldahl flasks were used for the digestion. 1.0 gm. of field-moist soil was digested with 10 ml. of concentrated sulphuric acid plus one third of a catalyst tablet. Digestion was continued slowly for $3\frac{1}{2}$ hours, the flasks being shaken gently from time to time. A further 5 ml. of sulphuric acid was then washed down the side of the flask and digestion continued until the mixture was clear, this usually taking $\frac{1}{2}$ hour. When cool the mixture was carefully diluted with water to approximately 75 ml., recooled and filtered through a Whatman's no. 42 filter paper into a 100 ml. volumetric flask. Samples were made up to volume and analysis then carried out on an aliquot of the digest, 2 ml. being sufficient for most soils. The digest aliquot was placed in a 50 ml. volumetric flask and diluted to nearly 40 ml. The pH was adjusted by adding 5 ml. of 2N sodium hydroxide and to prevent turbidity, approximately 1 gm. of sodium hexametaphosphate. The flask was well shaken, 4 ml. of Nessler reagent added and the sample made up to volume. The sample was allowed to stand for 20 minutes for the colour to develop and its absorption then read at 430 mμ using an 'EEL' long cell absorptiometer, readings being compared with a standard graph.

h) Ammonia nitrogen using Nessler reagent

Ammonia nitrogen was determined by a Nessler test using a modification of the method described by Jackson (1958) for exchangeable ammonia nitrogen.

Reagents were as follows:

Extracting solution, 100 gm. of sodium chloride was dissolved in water, made up to 1L. and then acidified to pH 3.0 with 2-3 drops of concentrated hydrochloric acid.

Nessler reagent, see determination of total nitrogen, p.

10% sodium tartrate solution, $((CH(OH).COONa)_2.2H_2O)$

Standard ammonia nitrogen solution, 0.3663 gm. of ammonium sulphate $((NH_4)_2SO_4)$ was dissolved in water and made up to 1 L. 1 ml. = 0.078 mgm.N

5 gm. of air-dry soil was weighed out into a 100 ml. conical flask and 10 ml. of acidified sodium chloride solution added. The flask was stoppered and shaken for 10 minutes using a mechanical shaker and the sample then transferred to a 50 ml. centrifuge tube and centrifuged at 4000 r.p.m. for 5 minutes. A 2 ml. aliquot of the supernatant liquid was added to a 50 ml. conical flask containing 6.5 ml. of water and 1 ml. of 10% sodium tartrate solution. The flask was well shaken and 0.5 ml. of Nessler reagent then added. After exactly 5 minutes the colour of the sample was compared with that of standard solutions using an 'EEL' portable colorimeter.

i) Nitrate nitrogen by the ultra-violet absorption method

Determination was based on the method described by Cawse (1967). In this method perchloric acid is used to prevent bacterial activity in the samples, which can therefore be accumulated for up to a week. Interference from iron and nitrites is also reduced, but nitrite nitrogen interference, is additionally reduced by treatment

with sulphamic acid. Treatment with alumina cream further reduces interference from iron and also organic matter.

Reagents were as follows:

Extracting solution, 1N potassium chloride.

Alumina cream, 30 gm. of aluminium potassium sulphate ($Al_2(SO_4)_3K_2SO_4 \cdot 24H_2O$) was dissolved in 1L. water, the solution filtered and the filtrate added to a mixture of 225 ml. of water and 25 ml. of 15N ammonia solution. The aluminium hydroxide precipitate was freed from the sulphate by decanting the supernatant liquid and washing the precipitate with water, this being repeated three times. Finally a suspension of the precipitate was made up to 1L. with water.

5% perchloric acid ($HClO_4$), 41.67 ml. of 60% perchloric acid was made up to 500 ml. with water.

2% sulphamic acid ($NH_2.SO_3H$).

Standard nitrate nitrogen solution, 3.6090 gm. of potassium nitrate (KNO_3) was dissolved in water and made up to 1L. A second dilute standard solution was freshly prepared for each run of analyses, by diluting 10 ml. of the concentrated solution to 100 ml. 1 ml. $\equiv$ 0.05 mgm.N

10 gm. of soil was weighed into a 50 ml. narrow neck, centrifuge tube and 5 ml. of 1N potassium chloride solution added. The tube was stoppered and shaken for 1½ hours with a mechanical shaker, the sample then being centrifuged for 5 mins. at 4000 r.p.m. and the supernatant liquid decanted into a specimen tube. 1 ml. of the supernatant liquid was added to a 10 ml. centrifuge tube, together with 4 ml. of alumina cream. The tube was well shaken and the sample then

centrifuged at 5000 r.p.m. for 5 minutes. 1 ml. of the supernatant liquid was added to a 50 ml. conical flask together with 2 ml. of sulphamic acid and 7 ml. of perchloric acid and the absorption of the sample then read at 210 mμ using a Unicam S.P. 500 spectrophotometer. Readings were compared with a standard graph.

j) Ammonia and nitrate nitrogen by double distillation

Determinations were carried out on field-moist soil immediately after its collection. The distillation procedure and subsequent methods of determining ammonia and nitrate nitrogen levels, were the same as those described by Piper (1950). A few modifications however were made to the extracting procedure.

100 gm. of sieved field-moist soil was placed in a 500 ml. conical flask and 200 ml. of acidified sodium chloride solution (see determination of ammonia nitrogen using Nessler reagent) added. The flask was stoppered and shaken for 1 hour using a mechanical shaker and the sample then filtered under suction using a Buchner funnel and flask and Whatman's filter paper no. 42. 5 drops of toluene were added to the filtrate and the whole filtrate then transferred to the distillation flask.

4. Estimation of the abundance of bacteria in soils

A few drops of sterile distilled water were added to a sterile Petri dish and a loopful (loop diameter $\frac{1}{8}$ in.) of soil transferred to the water. Sterile Oxoid 'Nutrient agar', cooled until

just liquid, was poured into the Petri dish and the plate rotated gently to mix the soil well in with the agar. Three plates were prepared for each soil and the plates incubated for 48 hours at 25°C. Large numbers of colonies were present on some plates and therefore no attempt was made to count them, but their abundance recorded using the following scale:

1 = abundant

2 = frequent

3 = occasional

4 = rare

5 = absent

APPENDIX TWO

Tables

1. Sites studied

LOCATION	PRE-BURN SOIL AND VEGETATION	SITES STUDIED * = in detail
Bucks. Coombe Hill	Rendzina. Chalk grassland invaded by scrub.	*1 bonfire 3 bonfire 1 ? *1 ash pile
Dorset. Morden Bog	Podsolized sand and peat where drainage impeded by a layer of clay. Wet lowland Calluna heath.	1 rapid fire 1 bonfire
South Haven Peninsula	a. Podsolized sand and peat where drainage impeded by a layer of clay. Dune/heathland and wet lowland Calluna heath.	*2 rapid fire 1 bonfire
	b. Podsolized sand overlying limestone blocks. Roadside verges, calcicole species merging with heathland species.	4 bonfire
Essex. Stour Wood	Clay loam. Deciduous woodland dominated by Castanea sativa.	13 bonfire
Oxford. Waterperry Wood	Clay loam. Mixed deciduous wood with glades cleared of trees and shrubs.	*2 bonfire 4 bonfire

(cont.)

LOCATION	PRE-BURN SOIL AND VEGETATION	SITES STUDIED * = in detail
Northumb. Newcastle upon Tyne	City centre.	10 brick and stone walls 1 demolition site
Surrey. Boxhill	Rendzina. Chalk grassland encroached by scrub.	3 bonfire
Chobham Common	Podsolized sand. Lowland Calluna heath.	5 rapid fire
Royal Holloway College	Arable soil overlying Bagshot sand and gravel. Most sites on neglected lawn, but some in areas of orchard and kitchen garden disturbed by builders. Fallow ground and rough pasture.	*16 bonfire + controls *1 ash pile 5 bonfire 1 ?(possibly bonfire) *3 rapid fire *2 fertilised plots + controls
Thursley Common	a. Podsolized sand and peat where drainage impeded. Wet and dry lowland. Calluna heath.	14 bonfire 1 rapid fire
	b. Podsolized sand. Pinewood.	1 bonfire
Thursley Village and Farnham	Village and town centre.	11 stone and brick walls

(cont.)

LOCATION	PRE-BURN SOIL AND VEGETATION	SITES STUDIED * = in detail
Yorks./Durham Barnard Castle	Arable soil. Rough grassland	1 bonfire
Yorks. Cronkley Fell	a. Blanket peat. Upland heather moor.	*1 bonfire *1 ash pile *4 rapid fire
	b. Arable soil. Lowland pasture.	1 bonfire

2. Site numbers (only sites subjected to detailed study numbered)

SITE	NO
Experiment 1	
Bonfire, recolonisation recorded, soil samples collected.	B1
" " "	B2
" " "	B3
" soil samples collected.	B4
" " " "	B5
Weeded, recolonisation recorded, soil samples collected.	W1
" " "	W2
" " "	W3
" soil samples collected.	W4
" " " "	W5
Experiment 2	
Bonfire, recolonisation recorded.	B6
" " "	B7
" " "	B8
" soil samples collected.	B9
" " " "	B10
" " " "	B11
Weeded, recolonisation recorded, soil samples collected.	W6
Bonfire, ash removed, recolonisation recorded, occasional soil samples collected.	B12
Weeded, ash added (ash pile), recolonisation recorded, occasional soil samples collected.	A1
Bonfire, kept free of angiosperms, recolonisation recorded.	B13
Weeded, kept free of angiosperms, recolonisation recorded.	W7
Bonfire, soil samples collected for available N determination.	B14

(cont.)

SITE	NO
Experiment 3	
Bonfire, recolonisation recorded.	B15
Experiment 4	
Rapid fire, recolonisation recorded.	R1
" " " "	R2
" " vegetation removed before burning, recolonisation recorded.	R3
Experiment 5	
Weeded and fertilised, recolonisation recorded.	F1
" " " " "	F2
Weeded, recolonisation recorded.	W8
" " "	W9
Bonfire, recolonisation recorded.	B16
Coombe Hill	
Bonfire, recolonisation recorded, occasional soil samples collected.	B17
Ash pile, recolonisation recorded, occasional soil samples collected.	A2
Waterperry Wood	
Bonfire, protected by cage, recolonisation recorded, occasional soil samples collected.	B18
Bonfire, recolonisation recorded, occasional soil samples collected.	B19

(cont.)

SITE	NO
South Haven Peninsula	
Rapid fire, recolonisation recorded, occasional soil samples collected.	R4
Rapid fire, recolonisation recorded, occasional soil samples collected.	R5
Cronkley Fell	
Rapid fire, burnt 1963, recolonisation recorded, occasional soil samples collected.	R6
Rapid fire, burnt 1964, recolonisation recorded, occasional soil samples collected.	R7
Rapid fire, burnt 1965, recolonisation recorded, occasional soil samples collected.	R8
Rapid fire, burnt 1966, recolonisation recorded, occasional soil samples collected.	R9
Bonfire, recolonisation recorded, occasional soil samples collected.	B20
Ash pile, recolonisation recorded, occasional soil samples collected.	A3

3. Key to Fig. 3, 4, 5, 9, 10, 11, 12, 13 and 14.

X	=	Bryum argenteum
▲	=	Brachythecium rutabulum
o	=	Ceratodon purpureus
•	=	Funaria hygrometrica
■	=	Tuberous species of Bryum
Δ	=	Other bryophytes
A	=	Achillea millefolium
C	=	Compositae
H	=	Glechoma hederacea
G	=	Gramineae
P	=	Plantago lanceolata
B	=	Ranunculus spp.
R	=	Rumex acetosa
T	=	Trifolium spp.
S	=	Veronica chamaedrys
V	=	Vicia sativa
Su	=	Unidentifiable seedlings
----	=	Animal disturbance

4. Bryophyte Domin ratings for sites in Experiment 2

Date	Weeks after burning	B6	B7	B8	B12	A1	B13	W7	W6
4.4.67	1	0	0	0	0	0	0	0	0
19.4.67	3	0	0	0	0	0	0	0	0
5.5.67	5	0	0	0	0	0	0	0	0
19.5.67	7	-	-	-	-	0	-	-	0
2.6.67	9	0	0	0	0	0	0	3	0
17.6.67	11	-	-	-	-	0	-	3	1
30.6.67	13	0	0	0	0	2	1	3	3
31.7.67	18	1	2	2	2	3	2	3	3
11.8.67	19	2	3	2	2	3	2	3	3
25.8.67	21	4	5	4	3	4	3	3	3
7.9.67	23	4	5	4	3	5	3	4	4
22.9.67	25	5	6	4	4	5	5	5	4
6.10.67	27	5	6	4	4	5	7	6	-
19.10.67	29	6	7	5	4	5	7	6	4
2.11.67	31	6	7	5	-	-	-	-	-
19.11.67	33	6	7	5	4	5	7	5	3
19.12.67	38	6	7	6	5	5	8	5	3
18.1.68	42	7	8	6	5	5	8	5	3
15.2.68	46	7	8	6	5	5	8	5	-
16.3.68	50	7	8	6	5	5	8	4	3
4.5.68	57	6	7	6	5	5	8	4	3
13.7.68	67	6	7	6	3	4	8	5	2
16.10.67	81	1	1	1	1	3	8	6	0

5. Angiosperm Domin ratings for sites in Experiment 2

Date	Weeks after burning	B6	B7	B8	B12	A1	B13	W7	W6
4.4.67	1.	0	0	0	0	3	-	-	4
19.4.67	3	0	0	0	0	4	-	-	5
5.5.67	5	1	1	1	0	6	-	-	7
19.5.67	7	-	-	-	-	6	-	-	8
2.6.67	9	2	3	2	2	8	-	-	8
17.6.67	11	-	-	-	-	8	-	-	9
30.6.67	13	5	5	6	2	9	-	-	9
31.7.67	18	6	6	8	6	9	-	-	9
11.8.67	19	7	7	8	6	9	-	-	9
25.8.67	21	7	7	8	7	9	-	-	9
7.9.67	23	8	8	8	8	9	-	-	9
22.9.67	25	7	7	8	9	9	-	-	9
6.10.67	27	8	7	8	9	9	-	-	-
19.10.67	29	7	7	8	9	9	-	-	9
2.11.67	31	7	7	8	-	-	-	-	-
19.11.67	33	8	8	8	9	9	-	-	9
19.12.67	38	7	8	8	9	9	-	-	9
18.1.68	42	8	8	8	9	9	-	-	9
15.2.68	46	8	7	8	8	9	-	-	-
16.3.68	50	8	7	8	8	9	-	-	9
4.5.68	57	8	8	8	9	9	-	-	9
13.7.68	67	9	9	10	10	9	-	-	9
16.10.68	81	10	10	10	10	9	-	-	10

6. Bryophyte species lists for sites R6, R7, R8 and R9 on Cronkley Fell

Site R6 (burnt 1963)

Campylopus brevipilus
C. flexuosus
C. fragilis
C. introflexus
Dicranella heteromalla
Dicranum scoparium
Hypnum cupressiforme
Orthodontium lineare
Plagiothecium undulatum
Pohlia nutans
Polytrichum commune
P. gracile
P. juniperinum

Cephaloziella hampeana
Gymnocolea inflata
Lophocolea bidentata

Site R7 (burnt 1964)

Campylopus flexuosus
C. fragilis
C. pyriformis
Ceratodon purpureus
Dicranella heteromalla
Dicranum scoparium
Hypnum cupressiforme (new shoots from scorched colony)
Plagiothecium undulatum
Pohlia nutans
Polytrichum gracile
Rhytidiadelphus loreus
Sphagnum plumulosum
S. nemoreum

Lophozia atlantica
Orthocaulis floerkii
Ptilidium ciliare

Site R8 (burnt 1965)

Aulacomnium palustre
Campylopus flexuosus
C. introflexus
Dicranum scoparium
Hypnum cupressiforme
Mnium hornum
Plagiothecium undulatum
Pleurozium schreberi
Pohlia nutans
Polytrichum commune
Sphagnum sp.

Calypogeia trichomanis
Lophocolea bidentata
Lophozia ventricosa
Orthocaulis floerkii

Site R9 (burnt 1966)

Campylopus brevipilus
Eurhynchium praelongum
Hypnum cupressiforme
Mnium hornum
Plagiothecium undulatum
Pohlia nutans
Polytrichum commune
P. juniperinum
Orthodontium lineare

Calypogeia trichomanis
Gymnocolea inflata

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REFERENCES

AHLGREN, I.F. & AHLGREN, C.E. (1960). Ecological effects of forest fires. Bot. Rev. 26, 483-533.

ALLSOPP, A. & MITRA, G.C. (1958). The morphology of protonema and bud formation in the Bryales. Ann. Bot. N.S. 22, 95-115.

ALVIN, K.L. (1960). Observations on the lichen ecology of South Haven Peninsula, Studland Heath, Dorset. J. Ecol. 48 331-339.

AMERICAN PUBLIC HEALTH ASSOCIATION (1955). Standard methods for the examination of water, sewage and industrial wastes. Colorimetric stannous chloride method for orthophosphate. American Public Health Ass., Inc., 169.

BECQUEREL, P. (1906). Germination des spores et morphologie des protonémas d'Atrichum undulatum et d'Hypnum velutinum en milieux stérilisés. Revue gén. Bot. 18, 49-68.

BENSON, M. & BLACKWELL, E. (1926). Observations on a lumbered area in Surrey from 1917 to 1925. J. Ecol. 14, 120-137.

BENSON-EVANS, K. & BROUGH, M.C. (1966). The maturation cycles of some mosses from Fforest Ganol, Glamorgan. Trans. Cardiff Nat. Soc. 92, 4-23.

BIRD, C.D. (1962). Mosses of the Prairies of West-Central Canada. Can. J. Bot. 40, 35-47.

BLACK, C.A. (1968). Soil-plant relationships ch. 7. Nitrogen. 405-557. Wiley, London.

BOPP, M. (1963). Development of the protonemata and bud formation in mosses. J. Linn. Soc. (Bot.) 58, 305-309.

BRADSHAW, R.V. (1962). The mosses of Stanford University and vicinity. Bryologist 29, 33-36.

BRAY, R.H. & KURTZ, L.T. (1945). Soil Sci., 59, 39.

BROWN, I.C. (1943). A rapid method of determining exchangeable hydrogen and total exchangeable bases of soils. Soil Sci. 56, 353-357.

BROWN, M.M. (1919). The development of the gametophyte and the distribution of sexual characters in Funaria hygrometrica (L.) Schreb. Am. J. Bot. 6, 387-400. 1 pl.

BUCKMAN, H.O. & BRADY, N.C. (1969). The nature and property of soils ch. 16. The nitrogen and sulphur economy of soils, 437-472. 7th ed. Collier-Macmillan, London.

BURKHOLDER, P.R. (1959). Organic nutrition of some mosses growing in pure culture. Bryologist 62, 6-15.

BURREL, W.H. (1917). The mosses and liverworts of an industrial city. Resume of Presidential address to Leeds Nat. Club and Sci. Ass., 119-124.

CAMPBELL, N.E.R. & LEES, H. (1967). Soil biochemistry. Ch. 8. The nitrogen cycle, 194-215. Edited by Mclaren, A.D. & Peterson, G.H. Edward Arnold (Publishers) Ltd., London.

CAWSE, P.A. (1967). The determination of nitrate in soil solutions by ultraviolet spectrophotometry. Analyst. London, 92, 311-315.

CLARKE, C.H. (1904). Curbstone mosses. Bryologist 7, 74.

CREMER, K.W. & MOUNT, A.B. (1965). Early stages of plant succession following the complete felling and burning of Eucalyptus regnans forest in the Florentine Valley, Tasmania. Aust. J. Bot. 13, 303-322. 4 pls.

CRUNDWELL, A.C. & NYHOLM, E. (1964). The European species of the Bryum erythrocarpum complex. Trans. Br. bryol. Soc. 4, 597-637.

DAWSON, J.R., JOHNSON, R.A.H., ADAMS, S.P. & LAST, F.T. (1965). Influence of steam/air mixtures, when used for heating soil, on biological and chemical properties that affect seedling growth. Ann. appl. Biol. 56, 243-251.

DOIGNON, P. (1949). La régéneration naturelle du peuplement muscinal dans les parcelles brûlees de la Forêt de Fontainebleau. Revue bryol. lichen. 10, 160-168.

DUNCAN, U.K. (1966). A bryophyte flora of Angus. Trans. Br. bryol. Soc. 5, 1-82.

EDEN, T. (1924). Edaphic factors accompanying the succession after burning on Harpenden Common. J. Ecol. 12, 267-286.

ELLIOT, R.J. (1953). Heather burning. Ph.D. Thesis, University of Sheffield.

FLETCHER, F. (1910). Effects of previous heating of the soil on the growth of plants and the germination of seeds. Cairo scient. J. 4, 81-86.

FLORENCE, R.G. & CROCKER, R.L. (1962). Analysis of blackbutt (Eucalyptus pilularis (SM.) seedling growth in a blackbutt forest soil. Ecology 43, 670-679.

FLOWERS, S. (1933). Mosses of the Great Salt Lake Region. Bryologist 36, 34-43.

FRITSCH, F.E. (1927). The heath association on Hindhead Common, 1910-1926. J. Ecol. 15, 344-372.

FRITSCH, F.E. & SALISBURY, E.J. (1915). Further observations on the heath association on Hindhead Common. New Phytol. 14, 116-138, 1 pl.

FUNKE, B.R. & HARRIS, J.O. (1968). Early respiratory responses of soil treated by heat or drying. Pl. Soil 28, 38-48.

GARJEANNE, A.J.M. (1932). Manual of bryology ch. 8. Physiology, 207-232. Ed. by Fr. Verdoorn. Martinus Nujhoff, The Hague.

GIESY, R.M. & RICHARDS, P.W. (1959). A collection of bryophytes from Thailand (Siam.). Trans. Br. bryol. Soc. 3, 575-581.

GILBERT, O.L. (1968). Bryophytes as indicators of air pollution in the Tyne Valley. New Phytol. 67, 15-30.

GOOD, R. (1935). Contributions towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. II. General ecology of the flowering plants and ferns. J. Ecol. 23, 361-405.

GRAFF, P.W. (1935). Plant invasion following fires. Torreya 35, 137-141.

GRAFF, P.W. (1936). Invasion by Marchantia polymorpha following forest fires. Bull. Torrey Bot. Club 63, 67-74.

GRIGGS, R.F. & READY, D. (1934). Growth of liverworts from Katmai in nitrogen-free media. Am. J. Bot. 21, 265-277.

GURLITT, L. (1918). Ueber den einfluss der konzentration der nährlösung auf einige pflanzen. Beih. bot. Zbl. 35, 279-341.

HALE, L.J. (1958). Biological laboratory data. Methuen, London.

HEWITT, E.J. (1966). Sand and water culture methods used in the study of plant nutrition. Revised 2nd ed., tech. comm. no. 22. C'wealth Agric. Bureaux, Farnham Royal.

HILL, A.J. (1911). Notes on some of the principal mosses of the coast region of British Columbia. Bryologist 14, 103-106.

HOFFMAN, G.R. (1962). The ecology of Funaria hygrometrica Hedw. Washington State University, Ph.D., Botany.

HOFFMAN, G.R. (1966a). Ecological studies of Funaria hygrometrica Hedw. in Eastern Washington and Northern Idaho. Ecol. Monogr. 36, 157-180.

HOFFMAN, G.R. (1966b). Observations on the mineral nutrition of Funaria hygrometrica Hedw. Bryologist 69, 182-192.

HUMPHREYS, F.R. & LAMBERT, M.J. (1965). Soil temperature profiles under slash and log fires of various intensities. Aust. For. Res. 1, 23-39.

JACKSON, M.L. (1958). Soil chemical analysis. Constable, London.

JONES, E.W. (1952). A bryophyte flora of Berkshire and Oxfordshire II Musci. Trans. Br. bryol. Soc. 2, 220-277.

KATZ, N.J. (1926). Sphagnum bogs of Central Russia: Phyto-sociology, ecology and succession. J. Ecol. 14, 177-202.

KAYLL, A.J. & GIMMINGHAM, C.H. (1965). Vegetative regeneration of Calluna vulgaris after fire. J. Ecol. 53, 729-734.

KENWORTHY, J.B. (1963). Temperatures in heather burning. Nature, Lond., 200 (4912), 1226.

KOFLER, L. (1959). Contribution à l'etude biologique des Mousses cultivées in vitro: germination des spores, croissance et développement du protonéma chez Funaria hygrometrica. Revue bryol. lichen. 28, 1-202.

KRUPA, J. (1964). Studies on the physiology of germination of spores of Funaria hygrometrica (Sibth.). I. The influence of light on germination with respect to water balance and respiratory processes. Acta Soc. Bot. Pol. 33, 179-192.

LLOYD, P.S. (1968). The ecological significance of fire in limestone grassland communities of the Derbyshire Dales. J. Ecol. 56, 811-826.

LUTZ, H.J. (1956). Ecological effects of forest fires in the interior of Alaska. Tech. Bull. U.S. Dept. Agric. 1133, 121pp.

MCVEAN, D.N. & RATCLIFFE, D.A. (1962). Plant communities of the Scottish Highlands ch. 1. Phytosociological methods and terminology, 5-9. Monographs of the Nature Conservancy no. 1., H.M.S.O., London.

MEYER, S.L. (1940). Physiological studies on mosses I. The development of leafy gametophytes in liquid media. Am. J. Bot. 27, 221-225.

MEYER, S.L. & FORD, C.H. (1943). Influence of the hydrogen-ion concentration of the substrate on the development of leafy moss plants. Pl. Physiol., Lancaster, 18, 530-533.

MILES, J. (1967). Invasion by Bryum bornholmense Winkelm. and Ruthe of heathland treated with calcium carbonate. Trans. Br. bryol. Soc. 5, 587.

MITRA, G.C. & ALLSOPP, A. (1959). II. The effects of sugar concentration on the development of the protonema and bud formation in Pohlia nutans (Hedw.) Lindb. Phytomorphology 9, 55-63.

MUKERJEE, H.N. (1954). Improvement of soil fertility by the application of heat. Proc. Bihar Acad. Sci. 2 1-30.

MULLER, C.H., HANAWALT, R.B. & MCPHERSON, J.K. (1968). Allelopathic control of herb growth in the fire cycle of California chaparral. Bull. Torrey bot. Club. 95, 225-231.

PARKER, M.A. (1931). Mosses of the campus of Cold Spring Harbor Biological Laboratory. Bryologist 34, 83-85.

PATON, J.A. (1968). A bryophyte flora of Cornwall. Trans. Br. bryol. Soc. 5, 669-756.

PATSCHOVSHY, N. (1928). Der Einfluss der Ernährung auf die formbildung und den Entwicklungsrhythmus von Funaria hygrometrica (L.) Sibth. Z. indukt. Abstamm. u. VererbLehre, 46, 112-187.

PETTERSSON, B. (1931). Notes on the first stages of flora on burnt ground. Memo. Soc. Fauna Flora fenn. 7, 119-139.

PICKERING, S.U. (1910). Studies of the changes occurring in heated soils. J. agric. Sci., Camb., 3, 258-276.

PIPER, C.S. (1950). Soil and plant analysis. The University of Adelaide, Adelaide.

PORTER, C.L. (1935). A method of growing moss protonema for demonstration. Bryologist 38, 50-51.

PRINGSHEIM, E. (1921). Physiologische studien an moosen I. Reinkulturen von Leptobryum pyriforme. Jb. wiss. Bot. 60, 499-530.

PROCTOR, M.C.F. (1956). A bryophyte flora of Cambridgeshire. Trans. Br. bryol. Soc. 3, 1-49.

PRYOR, L.C. (1963). Ash bed growth response as a key to plantation establishment on poor sites. Aust. For. 27, 48-51.

REMEZOV, N.P. & POGREBNYAK, P.S. (1965). Forest soil science ch. 9. The effect of forest fires on soil and the soil-forming process, 195-204. Translated by A. Gourevitch, Israel Programme for Scientific Transations Herusalem, 1969.

RICHARDS, P.W. (1932). Manual of bryology ch. 13. Ecology, 367-395. Ed. by Fr. Verdoorn. Martinus Nijhoff, The Hague.

RICHARDS, P.W. (1963a). Ecological notes on West African vegetation III. The upland forests of Cameroons Mountain. J. Ecol. 51, 529-554.

RICHARDS, P.W. (1963b). Campylopus introflexus (Hedw.) Brid. and C. polytrichoides De Not. in the British Isles; a preliminary account. Trans. Br. bryol. Soc. 4, 404-417.

RUSSEL, E.W. (1961). Soil conditions and plant growth. 9th ed., Longmans, London.

SCHOENE, K. (1906). Beiträge zur kenntnis der keimung der laubmoossporen und zur biologie der laubmoosrhizoiden. Flora, Jena 96, 276-321.

SCHULER, J.F., DILLER, V.M., FULFORD, M. & KERSTEN, H.J. (1955). Culture studies on Sphaerocarpos III. The utilisation of nitrogen by Sphaerocarpos Texanus. Pl. Physiol. Lancaster, 30, 478-482.

SCHWEIZER, G. (1930). Physiologisch-morphologische studien über Funaria hygrometrica L. in Reinkulturen. Ber. dt. bot. Ges. 48, 75-84.

SEAVER, F.J. & CLARK, E.D. (1912). Biochemical studies on soils subjected to dry heat. Biochem. Bull. 1, 413-427.

SERVETTAZ, C. (1913). Recherches expérimentales sur le développement et la nutrition des Mousses en milieux stérilisés. Annls. Sci. nat. (Bot.) 17, 111-223.

SHELDON, J.L. (1907). Species of Hepaticae known to occur in West Virginia. Bryologist 10, 80-84.

SIRONVAL, C. (1947). Expériences sur les stades de développement de la forme filamenteuse en culture de Funaria hygrometrica L. Bull. Soc. r. Bot. Belg. 79, 48-78.

SKUTCH, A.F. (1929). Early stages of plant succession following forest fires. Ecology 10., 177-190, 1 pl.

SMITH, A.J.E. (1964). A bryophyte flora of Glamorgan. Trans. Br. bryol. Soc. 4, 539-596.

STEVENSON, I.L. (1956). Some observations on the microbial activity in remoistened air-dried soils. Pl. Soil 8, 170-182.

STREET, H.E. & SHEAT, D.E.G. (1958). Encyclopaedia of plant physiology vol. 8. The absorption and availability of nitrate and ammonia, 150-165. Ed. by W. Ruhland, Springer-Verlag, Berlin.

SUMMERHAYES, V.S. & WILLIAMS, P.H. (1926). Studies on the ecology of English heath II. Early stages in the recolonisation of felled pinewood at Oxshot Heath and Esher Common, Surrey. J. Ecol. 14, 203-243.

SVIHLA, R.D. (1936). Collecting mosses in the Clympic Mountains of Washington. Bryologist 39, 67-69.

VALANNE, N. (1966). The germination phases of moss spores and their control by light. Ann. Bot. Fenn. 3, 1-60.

VON UBISCH, G. (1913). Sterile mooskulturen. Ber. dt. bot. Ges. 31, 543-552.

VOTH, P.D. (1943). Effects of nutrient-solution concentration on the growth of Marchantia polymorpha. Bot. Gaz. 104, 591-601.

WARD, M. (1960). Some techniques in the culture of mosses. Bryologist 63, 213-217.

WATSON, E.V. (1967). The structure and life of bryophytes. 2nd ed. Hutchinson, London.

WATSON, E.V. (1968). British mosses and liverworts. 2nd ed. Cambridge U.P.

WHITEHOUSE, H.L.K. (1966). The occurrence of tubers in European mosses. Trans. Br. bryol. Soc. 5, 103-116.

WHITTAKER, E. (1961). Temperatures in heath fires. J. Ecol. 49, 709-715.

WILLIAMS, P.C. (1964). The colorimetric determination of total nitrogen in feeding stuffs. Analyst. London, 89, 276-281.

WILSON, K. (1960). The time factor in the development of dune soils at South Haven Peninsula, Dorset. J. Ecol. 48, 341-359.

WOLCOTT, A.R., FANG HUI LIAO & KIRKWOOD, J.I. (1967). Effects of fumigation, temperature, and level of nitrate on microbial numbers, CO_2 production, and N. transformations in an organic soil. Soil Sci. 103, 131-138.

WOLFE, K.A. (1924). A list of Nebraska mosses. Bryologist 27, 26-31.