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EARLY STAGES OF PLANT SUCCESSION FOLLOWING FOREST FIRES[1]

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Although foresters and plant ecologists have devoted considerable study to the regeneration of fire devastated forests and to the changes which fires cause in the composition of the forest stand, apparently few people have studied in detail the earliest stages in the revegetation of burnt forest areas, especially with regard to the pioneer cryptogamic vegetation. During the past five years, I have been interested in several burns in different portions of Maine, and have been able to study the effects of a single burn at the summit of a tropical mountain, Blue Mountain Peak in Jamaica. Unfortunately, I have not been in a position to follow continuously from season to season the revegetation of any one of these fire swept areas, but I have made a sufficient number of observations to distinguish clearly certain salient features in the succession, in which there is a marked agreement between the several areas in question. It was surprising to find that the same, or very closely related, species dominated a recent burn on the summit of a mountain 7,000 feet high in the tropics, as were most abundant on burns near sea level in New England. The displacement of the pioneer liverwort *Marchantia* by the moss *Polytrichum* with its associated lichen *Peltigera* seems to be a common sequence in many widely separated regions, and it is this widespread but apparently little recognized succession which I desire to emphasize in the present paper.

BURN OF 1924 ON MT. DESERT ISLAND, MAINE

The burnt area on which I have been able to make the largest number of observations lies on the western side of Young's Mountain and about two and a half miles south of Salisbury Cove, Mt. Desert Island, Maine, in a region in which the climax vegetation is a mixed stand of spruce and northern hardwoods. The area, about a mile long by a quarter wide, had been lumbered a decade or more prior to the fire, and was covered at the time of the conflagration by a well-advanced mixed coppice and seedling growth of hardwoods, including gray birch (*Betula populifolia*), white birch (*B. alba papyrifera*), red maple (*Acer rubrum*), red oak (*Quercus rubra*) and red cherry (*Prunus pennsylvanica*). The fire also extended, on the edge of

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the lumbered area, into older stands of red spruce (*Picea rubra*), white pine (*Pinus strobus*), and arbor vitae (*Thuja occidentalis*). In an open hardwood stand of this type the blaze is usually confined principally to the thick layer of humus and ground litter, dry herbaceous vegetation and the debris left by past lumbering operations, but where evergreens stand in the path of the fire the heat is usually sufficient to ignite the crowns, which then burn vigorously.

After helping to fight the blaze on August 3 and 4, 1924, I returned twelve days later to make observations. Although a timely shower had extinguished the fire to everybody's satisfaction, and several other heavy rains had fallen in the intervening period, it was still smouldering in the thick humus beneath the spruces along the western margin of the burn. It was striking to see how frequently the charred stump of a spruce tree stood on the top of a low outcrop of bare granite rock, its principal roots closely following the contour of the outcrop. The soil in which the tree had grown was composed almost entirely of organic matter, which had been completely consumed, leaving the large roots lying naked along the exposed rock surface. The photograph reproduced in Plate III, B, although made four years later, illustrates vividly the great destruction of humus wrought by the fire. In other cases, the burning of the humus left the collet of a birch tree propped up on its roots 15 cm. or more above the new level of the ground. It is difficult to estimate how many years of soil accumulation by the pioneer vegetation will be required before the large areas of bed rock swept clean by the fire will again support forest trees (see Plate III, A).

The only living thing at all abundant on the blackened soil, twelve days after the fire, was *Pyronema omphalodes*. The colonies of the fungus, usually not more than one or two centimeters in greatest width, were made conspicuous by their light orange color, and although in no place did they occupy a large proportion of the ground, they were scattered with a fair degree of uniformity over much of the area. The fungus seemed to thrive particularly well on beds of almost pure ash, through which the hyphae ramified. The soft, almost gelatinous, unprotected ascomycete seemed strangely out of place on this hot, dry, dusty substratum, exposed to the full intensity of the sun. By August 24, *Pyronema* had almost disappeared. It reappeared by July 17 of the following year, but now its habitat had somewhat changed. It grew only in the moister places, on the soil between mosses or liverworts, but even here the colonies were not numerous, and were much smaller than those of the previous summer. *Pyronema* is, of course, well known as an inhabitant of burnt areas both in this country and in Europe.

Although many birch trees had been killed outright, from the collets of others, the tops of which had been scorched or killed by the flames, new sprouts were already pushing forth. A peculiar and little noticed habit of the birches renders them particularly well fitted to produce new shoots quickly after injury to the crown. The base of the bole is usually greatly enlarged,

sometimes to over twice the diameter of the trunk a foot higher up (see Plate IV, B). The surface of this basal swelling is densely covered with crowded dormant buds, which readily spring into activity upon the destruction of the crown of the tree, and sometimes when the latter has suffered no apparent injury. Already, in seedlings of the gray birch in their first summer, a few buds are developed at the collet, and these continue to increase in number from year to year. The basal enlargement of the stem is very pronounced in both the white and the gray birch; in the sweet birch (*Betula lenta*) a complete swollen ring of buds is found at the collet of some trees, but its development varies greatly in different individuals, and at the base of the bole of others there are only a few scattered buds. Twelve days after the fire had raged new shoots were clustered thickly around the bases of the gray birch trunks, and the most advanced were already 6 cm. high. A few white birches had also begun to sprout from the base, but only in the case of trees which were very slightly burned; and the growth of the hitherto dormant buds was just perceptible. Neither the oak nor the maple had yet produced sprouts.

It may be of interest to record the rapidity of the growth made by the sprouts arising from the roots or stumps of hardwood trees after a fire in the late summer had destroyed their crowns. By August 24, 20 days after the fire, hardwoods of most of the species had already sprouted; the longest shoot made by each is recorded below.

Betula populifolia	24 cm.	*Rhus typhina*	11 cm.
Salix sp.	19	*Prunus pennsylvanica*	8
Betula alba papyrifera	16	*Nemopanthus mucronata*	5
Acer rubrum	14	*Populus tremuloides*	2
Quercus rubra	2 cm.		

In certain cases the difference between the amount of growth made by two species may be traced directly to the morphological habit of the tree in the production of new shoots. Thus both the gray birch and the aspen are fast growing trees, but the birch produces new shoots from already well developed buds situated above the ground, while the aspen normally forms its regenerative shoots from the root, hence the advantage of the former.

In all but the lowest regions of the burnt area, where thanks to the moister soil the rhizomes of a number of herbaceous plants had escaped destruction, very little new growth appeared during the remainder of the month in which the fire occurred. The deep-seated rhizomes of the bracken (*Pteridium aquilinum*) often survived the blaze even where the humus had been burnt away, and on August 16 a few young fronds were found pushing up through the soil, while the most advanced already stood 15 cm. high. By August 24, some had attained 50 cm. in height. The fireweed (*Epilobium angustifolium*) had by the earlier date in several instances sprouted small leaves from its subterranean portions. Regarding this conspicuous herb, which plays such an important role in the early colonization of burnt wood-

land areas in both the old and new worlds, an old observation by Irmisch, quoted by Holm ('25) is of much interest: "The primary as well as the secondary roots of the young seedlings develop buds freely, which sometimes give rise to new plants in the succeeding year. The shoots developed from old roots may grow so fast that they bloom within a month. The roots are undoubtedly capable of persisting for several years in a dormant condition until the environment changes by the clearing or burning of the woods."

My next visit to the burnt area was made on July 8 of the following year. *Marchantia polymorpha* was by this time extremely abundant throughout the area, growing on the dry, black cinders overlying the porous soil, and fully exposed to the sun. The vigorous fronds bore abundant archegonial and antheridial branches, and numerous gemma cups. Rhizoids were particularly well developed, and clung tenaciously to the charred particles and black debris. Although plants were growing even on the bare soil of the ridges, the most luxuriant groups occurred in the moister depressions and under the shade of stumps and fallen logs, where the large thalli were so crowded that they stood edgewise to the ground. *Polytrichum commune* was locally abundant in low, moist places and in the depressions between outcrops of rock, but as yet occupied only a very minor position in the vegetation of the area as a whole. By August 30, however, following a continued dry spell, the plants of *Marchantia* were dying and shedding spores freely in all but the moistest spots, and *Polytrichum* had spread until it covered densely large areas of burnt ground, particularly in the valleys.

A small gill fungus, *Flammula highlandensis,* was scattered throughout the burnt area, on bare mineral soil as well as on half-charred humus, but nowhere were there many individuals close together. Around the edges of the burn, where the fire had consumed a portion of the duff and humus without eating through to the bare mineral substratum, the discomycete *Geopyxis cupularis* grew abundantly among the needles which had recently fallen from the heat-killed but still standing spruces and firs. In the central portion of the area this fungus was very rare, and it did not occur at all on a mineral substratum. It was sought in vain in unburned areas, even right adjacent to colonies on charred ground, for these always stopped quite short at the line marking the limit of the burn. A few days later, on July 17, a larger and more conspicuous but less numerous discomycete, *Rhizinia inflata* was found growing in the zone occupied by *Geopyxis* just within the margin of the burnt area. It has already been mentioned that *Pyronema* was rare during the summer following the fire.

Among the herbaceous plants, the bracken and the fireweed, now in bloom, were the most abundant species. *Geranium Bicknellii,* seedlings of which had been found as early as August of the previous year, had already completed anthesis. This plant was widespread in the area, and appeared to be well adapted to colonize such barren ground. The repeatedly forking

branches lay prone upon the ground, radiating in all directions from the tap root. A single large plant was thus able to occupy a circle of ground 4 feet in diameter. *Anaphalis margaritacea, Aster umbellatus, A. macrophyllus, Solidago graminifolia* and *Aralia hispida* were also widespread in the burnt area. Moore and Taylor ('27) found that the last mentioned was the dominant plant in a burn on another part of Mt. Desert Island, where it constituted at least 75 per cent of all vegetation existing fourteen months after the fire. The hardwood stump sprouts had grown so rapidly the previous fall that their apical portions had not matured by the approach of cold weather, and had been winter-killed. These and other newly formed sprouts were pushing up rapidly. Seedlings of gray and white birch, principally the former, were numerous everywhere. The tallest gray birch seedling was 14 cm. high on July 17, and 49 cm. on August 30. A white birch seedling of the season's growth was 59 cm. high by the latter date. By the end of the summer, the burnt area was well covered by vegetation, and had lost much of its desolate aspect.

Almost three years elapsed before I was able to visit this area again on June 8, 1928. Seedlings of the two birches, the gray still the more abundant, now formed a very close stand. The tallest stood between 120 and 150 cm. high. *Pteridium aquilinum,* judging from the number of last season's dead fronds which covered the ground, was still an important element in the vegetation. The season's fronds were just pushing up through the soil. In places where the humus had not been completely destroyed, wild flowers of the kinds found in the neighboring woods were growing. It was principally the lower, moister regions which supported an abundance of these flowers, including *Clintonia borealis, Cornus canadensis* and *Trillium undulatum.* There was a scattering representation of *Cypripedium acaule* over much of the area examined.

Close stands of *Polytrichum commune* and *P. juniperinum* now covered considerable areas. The stands of the moss were most numerous in the valley and on the level hilltop. In neither place did they form a sward continuous for long distances, but one close-set stand, occupying a slight depression of the ground, was separated from the next by a low ridge, or by an outcrop of bare rock (see Plate IV, A). On the well drained hillsides *Polytrichum* was present only in very meagre, often widely separated stands of low plants. Here the sterile specimens proved to be *P. juniperinum,* well known for the drier habitat it often favors, while the more hygrophilous *P. commune* seemed to be the more common in the wetter depressions. On pulling up a handful of *Polytrichum* plants from one of the thrifty stands on level ground, either on the hilltop or the valley, by careful search I could almost always find traces of *Marchantia* at the base of the tuft, occasionally a living plant with the spindling thallus characteristic of the species when it grows in weak light, much more frequently the dead and partially decayed but still perfectly recognizable remains of a thallus, often of one with fertile

branches. The depauperate hillside stands of the moss did not reveal any traces of the liverwort. In certain moist and shady spots, such as were found beneath the projecting edges of rocks closely crowded by *Polytrichum,* and under the trees which stood on the boundary between the evergreen forest and the burn, *Marchantia* still grew without being hidden by the moss, and these plants were sometimes fertile. Over the considerable areas in the open which it had previously occupied, however, *Marchantia* had been completely displaced by *Polytrichum,* and only relicts of the liverwort remained to reveal the succession.

Another moss, *Ceratodon purpureus,* conspicuous by reason of the chestnut brown capsules which it bore prolifically, was abundant and important throughout the area. In the valley, where *Polytrichum* occupied all of the depressions in the rocks which had not been preempted by grasses and other flowering plants, the stands of *Ceratodon* were usually continuous with the edges of the *Polytrichum* sward, and pushed up onto the surface of the otherwise bare rock. There was abundant evidence that after this moss had formed a thin covering of soil over the rock, its stands were invaded by plants of *Polytrichum.* Thus it plays an important function in the accumulation of the humus which must cover the large areas of rock exposed by the fire before they can again support the trees which previously flourished upon them. On the drier hillside, *Ceratodon* was much more abundant than *Polytrichum,* and was here growing on soil instead of rock. It is a moss which is noted for the wide variety of substrata, including sand, soil, rock and wood, on which it can grow.

The foliose lichen *Peltigera polydactyla* was widespread in the burnt area, but nowhere abundant at this season. Although frequently growing among *Polytrichum,* it was even more plentiful among the stands of *Ceratodon.*

Burn of 1923 on Mt. Desert Island, Maine

Another lumbered area of much the same type as that just described, and situated on Mt. Desert Island about one mile west of the latter, was swept by a fire in August, 1923. The fire was fed largely by the tops, branches and other debris left by the lumbermen, which littered the ground to such an extent as to make it very difficult to penetrate the area and to fight the blaze. In its main features, the succession which followed the destruction of the young coppice growth of hardwoods with its associated herbaceous species was quite similar to that described above in more detail. On July 13 of the summer following the fire, the bracken and the fireweed dominated the scene. Seedling plants of the latter were particularly numerous. *Geranium Bicknellii, Corydalis sempervirens, Apocynum androsaemifolium,* like *Epilobium* springing from buds on roots which had survived the conflagration, and *Vaccinium pennsylvanicum,* also represented by regenerative shoots, were all abundant. Seedlings of *Myrica asplenifolia,* a shrub common on abandoned fields and pastures, were widely scattered,

and in spots covered the ground rather thickly. *Marchantia* was present in large, green patches, growing on the hot, black, dusty-dry soil. On August 12, 1925, the area was again visited. *Marchantia,* though still present and fruiting, was not so abundant as in July of the previous summer. In June, 1928, *Polytrichum* was occupying the areas previously covered by *Marchantia,* but on the site of this fire, a year older than the one which we previously considered, the relicts of the liverwort were no longer revealed among the bases of the moss tufts. *Myrica asplenifolia* now occupied a conspicuous place in the new vegetation.

Burn of 1921 near Rangeley Lake, Maine

The third burnt area on which observations were made lies in western Maine. It is situated along the eastern side of the Maine Central Railroad tracks between the stations of South Rangeley and Bemis, in the Rangeley Lakes district. Here in the summer of 1921 a very severe fire swept over several miles of second growth forest. I visited the area in early September, 1924, and again in September of the following year. The portion of the devastated land examined most carefully was a rather low, level tract, over which the destruction of the previous stand had been very thorough. Large boulders littered the ground everywhere. The dominant tree in the succession was the aspen (*Populus tremuloides*), represented chiefly by seedlings, the most advanced of which had in 1925, their fourth summer, already attained a height of 21 dm. A root sucker of the same age measured 4 m. in height. *Prunus pennsylvanica* and *Salix. sp.* were also reproducing liberally. The herbaceous vegetation closely resembled that described for the Mt. Desert Island burns, and consisted chiefly of *Epilobium angustifolium, Solidago canadensis, S. graminifolia, Anaphalis margaritacea, Aralia hispida* and *Aster acuminatus,* with *Cornus canadensis, Clintonia borealis* and *Maianthemum canadense* in the lowest stratum. Over large areas the bunchberry covered the ground with a very close stand. The bracken was poorly represented by a few depauperate fronds.

Here the struggle between *Marchantia* and *Polytrichum* was vividly portrayed in all its stages. In low, protected depressions about the bases of stumps and under the shade of boulders, *Marchantia* grew closely pressed by the moss. In these moister and more shaded spots the liverwort was growing as luxuriantly and profusely as it does over larger areas in year-old burns, and the vigorous thalli bore numerous fertile branches and gemma receptacles. Under the edges of these thalli, small, depauperate *Polytrichum* plants managed to survive. In slightly more exposed places the liverwort was not so dense, and the moss succeeded in growing above it into the light and occasionally in fruiting. In these restricted areas *Marchantia* was still the dominant plant. But over most of the tract, where the soil was not completely possessed by herbaceous plants, and not in hummocks too high and exposed to dessication, it was covered by a thick carpet of *Polytrichum*

(*P. commune* and *P. juniperinum*). In some situations, where the stand of *Polytrichum* was not very deep, the fertile branches of the liverwort, usually the archegoniophore, appeared among the moss plants, arising from a thallus hidden beneath them. Far more common was the condition in which the liverwort was not at all visible from the surface, and its presence was revealed only upon pulling up the clump of *Polytrichum,* when a few suppressed thalli, often standing vertically and not infrequently proliferating in pale, narrow, almost filamentous ribbons, would be found hidden among the bases of the moss plants, or in other cases only the decaying thalli of the liverwort remained. This was the condition over most of the burnt area where the moss formed the local facies. Fruiting plants of *Peltigera polydactyla* grew in considerable numbers among the *Polytrichum.* Thus it appears, both from the evidence of the decaying *Marchantia* among the clumps of *Polytrichum,* and by comparison with the other areas studied, that the moss had supplanted the liverwort over much of the area which it now occupied, while in the moist, shaded depressions *Marchantia,* more tolerant of these conditions than *Polytrichum,* had been able to hold its own during the four summers which followed the conflagration.

Burn on Blue Mountain Peak, Jamaica

The mass of Blue Mountain Peak, near the eastern end of the island of Jamaica, culminates in three summits, separated by saddles which are insignificant in comparison with the height of the mountain. The west or main summit is the highest, and stands 7,360 feet above sea level; it is here that the trail ends and the shelter for the accommodation of travellers is situated. To the east of this lies a slightly lower summit, the upper portion of which had been swept by a fire some years prior to my visit to the mountain in July, 1926. I was not able either by inquiry among the scattered white inhabitants of the region, or by examination of the vegetation itself, to ascertain the exact date of this fire, and can merely estimate that it occurred from three to five years earlier. The fire had covered the small area of level ground at the summit, about the uppermost 25 feet of the very steep northern face of the mountain, and on the other side had extended several hundred feet down into the saddle which separates the east peak from the southeast peak. All the trees in the region over which the fire had passed had been killed, but many remained upright, and their bleached and decorticated remains were conspicuous evidence of the disaster which had visited them. Fallen branches and charred trunks littered the ground. The forest near the summits of the mountain and on the west peak consists principally of low, often gnarled, dicotyledonous trees (see Shreve, '14), and it was apparently through a similar stand that the fire swept.

On the level summit and the burnt portion of the very steep northern or windward face of the mountain was a close sward of *Polytrichum juniperinum,* which was perhaps the most conspicuous feature of the vegetation.

The carpet of moss was particularly complete on this northern slope, where in one place it extended without break for 22 feet down the declivity. Few larger plants here grew among the moss (see Plate V, A). The moss was brown and dry at this season, but gave evidence of past fertility in the form of numerous effete sporophytes and old male "flowers." The unshaded mountain side, with its steep slope and consequently great run off, may seem a dry habitat for such a luxuriant development of *Polytrichum*, but these features are compensated by the high annual rainfall of 168 inches (4,267 mm.), and the constant cloud baths which these peaks receive. On the level summit the sward of moss was shaded by a number of ferns and flowering plants. *Pteridium arachnoideum* [2] was the dominant species, but *Histiopteris incisa* was in spots equally abundant, while *Paesia viscosa, Pityrogramma tartarea, Struthiopleris lineata, Hypolepis pulcherrima* and *Alsophila quadripinnata* occurred in greater or less numbers. *Relbunium hypocarpium*, a rubiceous plant with a weak stem depending upon the neighboring vegetation for support, or else sprawling over the ground, in habit much like a large *Galium*, was the most abundant angiosperm. The shrubby, candelabrum-like *Lobelia martagon* was prominent but not numerous, and *Manettia lygistum* climbed over the other vegetation. *Peltigera polydactyla* was frequent among the *Polytrichum* both on the summit, where it was fertile, and on the north slope, where it was sterile.

The greater portion of the area of the burn lay on the southwestern slope of the prominence, and here the ferns formed a veritable thicket which, together with the fallen trunks and tangled branches of the former forest, made progress almost impossible without the liberal use of a cutlass. The fronds of *Pteridium* became taller as one descended into the shelter of the valley, until they stood over head-high. At the lower margin of the burn fronds 2.5 meters in length were measured. Associated with the dominant *Pteridium* here were the ferns *Histiopteris, Paesia* and an occasional *Alsophila*, and the seed plants *Relbunium, Zeugites* and *Lobelia*. Here also *Polytrichum* with its associated lichen *Peltigera* covered the ground beneath the taller plants, but the shade was becoming too deep for it, and in many places the stand was composed of weak and spindling individuals, or was being invaded by other bryophytes. The large, much-branched moss *Breutelia tomentosa* was here particularly active in over-growing and covering the *Polytrichum*, as it did more sparingly on the less exposed portions of the summit. *Breutelia* is frequently found growing on the moist banks along the trails through the forested upper slopes of the mountains, and its presence was indicative of the return of shade and moisture.

As in Maine, *Marchantia polymorpha* was found here associated with *Polytrichum*. Under the shade of fallen logs and of stumps propped up by their roots, vigorous stands of the liverwort were discovered. Many of

[2] For the determination of the Jamaican ferns I am greatly indebted to Dr. William R. Maxon.

the plants were fertile and these were mostly female; only rarely were antheridiophores found, and gemma cups never. Although I pulled up handfuls of *Polytrichum* in many places with the expectation of finding it, only in a single instance did I discover direct evidence of the succession of *Marchantia* by *Polytrichum* in the form of remains of liverwort thalli beneath the moss. On the other hand, in the considerable shade beneath the bracken thicket on the southwest slope, there were many instances in which the liverwort had advanced from its retreat beneath a log or stump, and overgrown prostrate plants of *Polytrichum*. From the successional relation of these plants elsewhere, we may suppose that *Marchantia* had been the pioneer and was later supplanted by *Polytrichum*, while with the return of deeper shade, the more shade-tolerant liverwort was in places regaining some of its lost territory.

So far, mention of the occurrence of trees of species found in the neighboring unburned woods has been avoided. Most of the trees in the path of the fire were killed outright, and did not produce suckers from the stump. In general, reproduction of the arborescent species was tardy and sparse. *Clethra alexandri*, a small tree common in the higher portions of the mountains, was reproducing most rapidly; a few suckers, and a number of seedlings, the tallest 2 meters, were present. A few young trees of *Cleyera theoides*, one of *Myrsine laeta* and a single root sucker of *Eugenia alpina* were found.

Discussion

It is of interest to compare the observations reported here with those made in still other regions. Humphrey and Weaver ('15) found that following the great Idaho fire of 1910 *Marchantia polymorpha* and *Funaria hygrometrica* were among the first pioneers to grow on the charred soil of the mountain side near St. Maries. Benson and Blackwell ('26) report a study of the revegetation of an area in Surrey, England, from which the original pine forest had been lumbered in 1916. A number of charred patches were created by the burning of the branches. Two years after these fires had cooled, *Marchantia* and *Funaria* covered the whole of the burnt surfaces, and made them so much greener than the surrounding uncharred land that they suggested the term "oases" to the writers. In May, 1919, "every square inch of space was occupied; indeed, in a few places the vegetation was stratified, for *Marchantia* thalli were found actually creeping over *Funaria*, and *Peltigera* was spreading horizontally over both. The *Marchantia*, which was very abundant, showed an unusually close formation of archegoniophores and antheridiophores, and was producing gemmae. *Funaria* was beginning to die down, and was covered with ripe capsules. In the center of several of these oases, sporelings of the bracken had made considerable headway and were firmly established. The *Peltigera* to which reference is made was *canina*. By 1920, the *Marchantia* and *Funaria* had been suc-

ceeded by *Dicranum longeanum* and other mosses, but no mention of the occurrence of *Polytrichum* on the burnt spots is made. As late as 1921, the liverwort was growing well on a single oasis. Summerhayes and Williams ('26) report on another area in Surrey which, four years after being lumbered, was swept by a series of rather severe fires, which more or less completely destroyed all the invading vegetation. In dry areas, *Funaria* was followed by *Ceratodon purpureus,* which in turn was succeeded by *Polytrichum.* In moister regions, in the year following the fires, *Funaria* and *Marchantia* were abundant on the burnt areas. *Polytrichum commune* and *P. juniperinum* appeared later and displaced the pioneer bryophytes. These writers state that " Polytricha always become abundant when the last traces of the soluble salts in the ground have disappeared, and the soil returns to its former acid condition."

We have presented evidence that several species are very constantly associated on burnt areas in widely separated portions of the northern forest zone, and that either they or a very closely allied form appear again on a burnt area on a high mountain in the tropics. *Marchantia* has been observed as a pioneer in Idaho, Maine and England, and we conclude from its known behavior that when it first appeared on Blue Mountain Peak in Jamaica it was a pioneer also. *Funaria,* although very prominent on the burnt areas in Idaho and England, never assumed any importance on the areas observed in Maine, at least it certainly was not abundant on any of the scattered dates on which it was found possible to make observations. *Polytrichum,* either *P. commune, P. juniperinum,* or both, has succeeded *Marchantia* on several areas in Maine and one in Jamaica, and the form of this succession is, as has been described, highly characteristic. In Maine the stands of Polytrichum flourish only on moderately level ground, but in a region of high rainfall and frequent cloud baths like the Blue Mountains, *Polytrichum juniperinum* forms luxuriant swards even on almost precipitous soil slopes. In Maine, Jamaica and England, *Peltigera* has been found to succeed *Marchantia;* in England, Benson and Blackwell observed *P. canina* to succeed the liverwort directly, while in Maine and Jamaica, *P. Polydactyla* was constantly found growing among the *Polytrichum* which had displaced the *Marchantia. Pteridium aquilinum,* a common " fire-weed " throughout much of the north temperate zone, is replaced on Blue Mountain Peak by *P. arachnoideum,* a species so similar to the former, however, that it was formerly listed as *P. aquilinum esculentum.* Treub ('88) lists " *P. aquilinum* var." among the ferns he found growing on Krakatau three years after the eruption. Observations of the association of these cryptograms on burnt areas in other regions, particularly the tropics and the southern hemisphere, would be greatly welcomed.

While the similarity between the vegetation on the burnt summit of Blue Mountain Peak and that on burnt areas in Maine and England constitutes but another example of the well known law of plant geography that the flora of high altitudes in low latitudes finds its parallel at low altitudes in

higher latitudes, the parallel in this case seems surprisingly great. The plant associations of the neighboring unburned portions of the mountains are floristically miles away from any association in either the northern United States or the British Isles. We believe that this is the first instance in which attention has been called to the common resemblance of this particular secondary succession in the two regions in question.

The sudden appearance of *Marchantia* in such abundance as has been observed is indeed remarkable, for it is certainly not abundant in the unburned areas surrounding any of the burns reported in this paper. Underwood ('95) states that this species is " Almost universally distributed throughout our borders, as in all parts of the world. It appears to be more abundant in limestone regions, but is by no means confined to them." In three summers of field work on Mt. Desert Island, I have found the plant outside of burnt areas only once, and that a small patch of sterile individuals. In the Blue Mountains of Jamaica, a region rich in liverworts, it was not observed at all except on the burnt area, although related species, *M. paleacea* and *M. chenopoda,* were found abundantly along the trails. Benson and Blackwell ('26) remark that " while *Lunularia* and *Pellia* are extraordinarily abundant in the near neighborhood of the College, *Marchantia* has always been scarce, and no member of the college has known it to fruit in this district." Since the sudden appearance of an even-aged stand over a large area means that a large number of spores must have been carried from elsewhere, which means that a very much larger number of spores must have been liberated elsewhere, and this in turn presupposes an extensive stand of the plant, it seems probable that most of the spores falling upon a newly burnt area are derived from plants growing on an older burnt area elsewhere. Thus, in regions like Mt. Desert Island at least, where forest fires are frequent and often extensive, *Marchantia* is essentially a pioneer in burnt areas, and moves from the scene of one forest fire to that of another as the vegetation in the former becomes more crowded, the soil more acid, poorer in salts, and more deeply shaded.

Studies of the physiology of a species are always of interest when considered in relation to its habitat, and in the case of *Marchantia* they throw considerable light on its preference for burnt areas. Dachnowski ('07) and Lilienstern ('27) have demonstrated that the plant reproduces only when growing in good illumination. The high light requirement of the species was demonstrated in another manner by Wann ('25), who found that *Marchantia* is a " long-day " plant in the sense of Garner and Allard ('20.) On the unshaded ground of a recently burnt area the liverwort finds its high light requirement well satisfied. Lilienstern found also that the plants had a more normal appearance when grown in sand moistened to 40 per cent of its water capacity than when grown on a more saturated substratum, an indication of its tolerance of the aridity it must experience on bare cinders. Of interest in this connection is the statement of Wann that *Marchantia*

thrives better in the greenhouse on finely sifted cinders than on a mixture of cinders and loam. The reduction of the acidity of the soil which a forest fire brings about is probably of importance in preparing a substratum for *Marchantia*. Two factors are involved in this diminution of acidity, the direct destruction of the humus with the humic acids it contains, and the addition to the soil of the alkalis contained in wood ash. Twelve days after the extinction of the Mt. Desert Island fire of 1924, various samples of the superficial layers of the ground, containing much ash and cinder, gave pH values of 6.6 to 7.9. This was the habitat of *Pyronema*. In the similar area burnt the previous year, the alkalinity had been reduced by the leaching out of alkaline salts, and here the soil which was the direct substratum of *Marchantia* gave readings of pH 6.5 to 6.6, while a few inches deeper it stood at pH. 5.3 to 6.0. The soil of the neighboring unburnt forest had an acidity of pH. 4.5 to 5.0, a range which is typical of much of the forested portion of the Island.

Summary

1. Observations on areas devastated by forest fires in Maine and at the summit of Blue Mountain Peak, Jamaica, are recorded.

2. *Marchantia polymorpha* is an important pioneer in burnt forest areas in widely separated parts of the North Temperate Zone. It also appeared on the burnt area on Blue Mountain Peak.

3. This liverwort is gradually replaced by *Polytrichum commune* and *P. juniperinum* in the second and following years. *Polytrichum* is an important constituent in the flora of recently burned areas in the North Temperate Zone and at the summit of a tropical mountain.

4. *Peltigera polydactyla* is regularly associated with *Polytrichum* in this succession, both in Maine and in Jamaica.

5. *Pteridium aquilinum,* which is one of the most important colonizers of burnt areas in the North Temperate Zone, is replaced in Jamaica by the very closely related *P. arachnoideum.*

6. Thus there is a striking similarity between the early succession following forest fires in Maine and on the summit of a tropical peak at over 7,000 feet elevation.

7. The bud-covered, swollen base of the trunk in the birches enables them to produce shoots after a fire more rapidly than any of the other trees with which they are associated.

8. The occurrence of certain fungi typical of burnt areas is recorded.

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