Review: Ecological Succession of Mosses, Isle Royale, Lake Superior

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volume of distilled water and adding silver nitrate drop by drop. A small portion of the plant was then washed in distilled water until no precipitate appeared with silver nitrate and the material was thoroughly dried and pulverised, and the powder extracted with 20 times its volume of distilled water; the filtered extract was clear, but gave with silver nitrate an abundant precipitate, much more copious than that obtained in the first experiments. This is taken by Okamura to indicate the absorption of sea salt by the tissues of the moss plant; a quantitative analysis showed that about 28 per cent. of salt was present in the washed and dried plant—a remarkably high result, in view of the fact that no salty taste could be detected in the fresh plant.

ECOLOGICAL SUCCESSION OF MOSSES, ISLE ROYALE, LAKE SUPERIOR

Cooper, W. S. "The ecological succession of mosses, as illustrated upon Isle Royale, Lake Superior." *Plant World*, **15**, 1912, pp. 197—213.

During his ecological work on Isle Royale, Lake Superior, the author was impressed by the importance of the mosses in the various successions leading up to the final forest vegetation. In the present paper he indicates the important part which mosses play in these successions, and suggests some of the possibilities of what he well describes as an undeveloped field of study.

For the general character of the successions on Isle Royale, reference should be made to the review in this JOURNAL (**1**, pp. 146—152) of the author's important general paper on the vegetation of this island. As there shown, the plant successions leading up to the establishment of the climax forest are divided into xerarch and hydrarch successions, having their origin in xerophytic and hydrophytic habitats respectively. The xerarch successions are divided into the rock shore and the beach successions, the latter not extensively developed on Isle Royale. In the course of the rock shore succession the pioneers on the rock shores obtain their first foothold in three sorts of successions, thus initiating three separate lines of advance, or subsuccessions: in the rock surface subsuccession a crustose lichen stage is followed successively by foliose and fruticose lichen stages, large *Cladonias* being dominant in the last; the crevice subsuccession is initiated by crevice herbs, these are followed by trailing shrubs, and even trees frequently appear; while the rock pool subsuccession originates in water-filled depressions and advances through the building of a mat after the manner of the bog succession. These separate lines unite in the formation of the heath mat, in which the elements of the rock surface and pool vegetation are bound together by the trailing shrubs from the crevices; a xerophytic forest stage, characterised by *Pinus Banksiana* and *Picea mariana* but seldom found pure, may here intervene, or the climax forest (composed mainly of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*) may follow directly the establishment of the heath mat. The hydrarch successions include the delta swamp succession, in which mosses take little part; and the bog succession, in the course of which lake basins become filled through the centripetal encroachment of vegetation, the stages being as follows—aquatics, sedge mat, shrub or shrub-sphagnum, bog forest, climax forest. In the secondary succession, which follows the burning of the forest and leads back the climax state, mosses play a subordinate part.

Rock shore succession. At a variable height above the lake level, according to degree of exposure, the three subsuccessions have their beginnings. Upon the bare rock surfaces grow crustose lichens, together with numerous tufts of *Grimmia ovata*, which is found as near the water as any of the lichens and clings as closely to the rock. It is the most abundant moss at the lower edge of the crustose lichen zone, but two other species are usually present—*Orthotrichum anomalum*, which is commonest a little higher up, and *Hedwigia albicans*. Above this zone is another in which the foliose lichens are the most conspicuous plants; *Grimmia* and *Orthotrichum* have now lost their dominance, being eliminated in the competition with the larger lichens and *Hedwigia*, which is here the commonest moss. In the third lichen zone, dominated by fruticose forms, especially the larger *Cladonias*, mosses are infrequent, being unable to compete with the comparatively tall and wide spreading lichens in the contest for space and light; *Rhacomitrium canescens* sometimes accompanies the *Cladonias*, making the mat more

coherent than where it is absent, *Hedwigia* persists to some extent, and the other two pioneer species occur in areas of incomplete invasion.

In the crevice subsuccession mosses are of little importance, *Polytrichum juniperinum* and *P. piliferum* being the commonest species occurring as crevice plants; in the late stages of the subsuccession *Thuidium abietinum* often appears; in sheltered crevices, especially on the steep cliffs facing north-west, occurs a rather numerous group of mosses of which the commonest is *Swartzia montana*, while others are *Bartramia pomiformis*, *Bryum intermedium*, *Eucalypta ciliata*, *Hylocomium triquetrum*, *Polytrichum commune*, etc.—because of the verticality of the surfaces such habitats remain much the same for a long time, and one frequently finds small cliffs in the fully developed climax forest bearing a moss flora almost identical with that here listed.

In the rock pool subsuccession mosses are frequently absent, but in some pools they are the exclusive mat formers, the depressions being more or less completely filled up with masses of *Climacium americanum*, *Polytrichum commune*, *Aulacomnium palustre*, *Amblystegium fluviatile*, etc.

In the heath mat, in the formation of which the three preceding subsuccessions unite, many of the early arrivals among the mosses persist, and numerous others appear, including those peculiarly characteristic of the climax forest. Most important at this stage are *Thuidium abietinum* and *Calliergon Schreberi*, frequently abundant in a stunted condition among the tangles of juniper and *Arctostaphylos* which form so important a part of the heath mat. Besides contributing to the supply of humus the mosses now come to aid in the conservation of soil moisture. On areas where crevices in the underlying rock are rare the large *Cladonias* (*C. rangiferina*, *C. sylvatica*, *C. alpestris*) form extensive dense growths during the late stages of the rock surface subsuccession, which frequently remain until entirely surrounded by the climax forest. Apparently the only species able to supersede the *Cladonias* in such places is *Calliergon Schreberi*; the young plants germinate among the branches of the lichen clumps and gradually spread over their surfaces, cutting off light and air and bringing about their death. Besides *Calliergon* and *Thuidium*, various forest species commonly make their first appearance with the heath mat—species of *Dicranum*, *Hylocomium*, *Hypnum*, etc.; hence the characteristic forest mosses become established notably in advance of the forest itself.

When the xerophytic forest stage intervenes, the undergrowth is practically a continuation of the heath mat, with the three forest mosses, *Calliergon Schreberi*, *Hylocomium proliferum*, and *Hypnum crista-castrensis*, gradually attaining dominance. In early stages it is common to find a ground cover composed largely of *Cladonias*, with practically no humus; in a slightly more advanced condition *Calliergon* is gaining the upper hand and the climax trees are coming in; later still *Hylocomium* and *Hypnum* are found disputing the dominance of *Calliergon*, and the climax trees increasing at the expense of the *Pinus Banksiana* and *Picea mariana*; when the climax state is attained the latter trees have disappeared and the three climax trees are in control, while the undergrowth is composed largely of *Calliergon*, *Hylocomium* and *Hypnum* in about equal proportions.

The increasing mesophytism from the heath mat stage onward is due, more than to any other factor, to the increasing abundance of the three mosses just named, with its results—continual additions to the humus accumulations, and effective conservation of moisture. Before they enter, the amount of humus on the rock surfaces is almost negligible; in the climax forest the depth is sometimes 1 metre and it is composed largely of moss remains, together with rotten wood and tree waste of various kinds.

In the course of the bog succession mosses first appear on the sedge mat, where they are of little importance, *Scorpidium scorpioides* being the only moss occurring commonly with the sedges. With the invasion of the sedge mat by the various species of *Sphagnum* a new stage begins in which the moss element is predominant. The importance of the abundance or scarcity of sphagnum in determining the line taken by the bog succession is indicated in the author's general paper on Isle Royale vegetation (see review in this JOURNAL, 1, pp. 146—152), besides the interesting contest between the sphagnum and the plants which precede and follow it. Young plants of *Polytrichum strictum*, *Aulacomnium*, and *Calliergon* (in order of their usual first appearance) start among the sphagnum heads and spread over the mass in all directions, stoppage of the upward growth of the sphagnum resulting; in some bogs *Camptothecium nitens*

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was found invading the sphagnum in a similar way, while *Hylocomium proliferum* and *Hypnum crista-castrensis*, mosses of the climax forest, often follow soon after *Calliergon*. Under some conditions the sphagnum is able to hold its own against the invading mosses and even to become an invader itself, tongues of the moss being found advancing into parts of the bog forest previously free of sphagnum, and even actually climbing a slope into the climax forest itself.

The factors which determine whether mosses or *Taxus canadensis* shall become dominant in the undergrowth of the climax forest are uncertain, but it is suggested that the development of an abundant moss vegetation requires a comparatively short time and may thus be accomplished in the brief intervals between windfalls characteristic of exposed situations, while for the *Taxus* to establish itself in sufficient abundance and luxuriance to obtain and maintain dominance requires a long time and comparatively stable conditions, obtainable only in very sheltered places. This explanation is based on the fact that mosses are more abundant in parts of the forest which are much exposed to wind, while the *Taxus* is more abundant in sheltered situations where windfalls are comparatively rare, i.e. where the trees drop one by one without seriously disturbing the lower vegetation. Of the three elements in the climax forest the mosses are weakest in the competition. The tree element is able to exclude both the *Taxus* and the mosses; the *Taxus* when abundant excludes mosses and holds its own against the trees; while the mosses are able to exclude neither. Nevertheless the mosses are immensely important to the maintenance of the climax forest because they quickly establish themselves whenever conditions permit, and through their accumulation of humus and conservation of moisture.

SOIL CONDITIONS AND PLANT GROWTH

Russell, E. J. "Soil conditions and plant growth." London (Longmans Green), 1912, 168 pages; price 5s.

Following an historical and introductory chapter, the author deals with the constitution, carbon and nitrogen cycles, and biological conditions of the soil; with the soil in relation to plant growth; and with soil analysis and its interpretation. There is also an appendix on methods of soil analysis.

The main theme of the work is the consideration of the soil from various points of view—not merely that of chemical and physical analysis—as an environmental factor of the plant. The concept of "limiting factors" is emphasised by the author, who in this connexion brings forward facts showing that the addition of mineral salts has but little effect, or none, on the yield if some other factor (e.g. water supply) is already a limiting factor. The author points out that the problem of soil fertility has been shown by recent work to be an extraordinarily complex one. There is apparently great diversity in the constitution of the soil flora and fauna in different soils and different localities, as well as in that of the various substances which accumulate in soils by decomposition of organic debris of all kinds, hence it is difficult to arrive at general conclusions regarding the delicate balance which doubtless exists, for instance, between the soil flora and fauna.

Since there is probably nothing connected with soil investigation that is without direct or indirect bearing upon ecological problems, it seems unnecessary to analyse in detail here the contents of this important publication, which should be in the hands of every student of plant ecology and physiology. The author gives a literature list with over 300 citations.