LITTORAL VEGETATION ON A HEADLAND OF MT. DESERT ISLAND, MAINE. III. ADLITTORAL OR NON–SUBMERSIBLE REGION ¹

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Belts in the Adlittoral Region

The terrain of this adlittoral region at Otter Cliffs, (from 14 to 193 feet elevation), starts with a series of rough, but usually vertical, cliffs extending from about high tide level up to 30 or 35 feet above mean low water. From the top of this cliff a sometimes smooth but elsewhere rough and broken slope extends on upward, at about a 25 per cent grade to the summit of the promontory 200 yards back from the cliff and 193 feet above mean low water. This ground, from 14 to 193 feet elevation, is occupied by four distinct vegetational belts which we have designated the supra-littoral, the extra-littoral, the upland and the summit belts.

On a shore with the severe exposure to sun, wind and waves, characteristic of much of the Otter Cliffs area, the transition from marine vegetation to the inland vegetation, typical of the soil and climate of the district lying behind the coast, (see Moore & Taylor, '27, Plate I) is rather gradual, and as one proceeds inward several belts of smaller herbs or of more or less stunted shrubs and trees must be passed through before reaching the fully developed climax formation, a "spruce forest" (Plate XXII, XXIII, Figs. 31, 34). Although the transition zone may be narrower in horizontal width than on a more protected shore, it is usually, because of the greater range of wave action, much greater in vertical extent. In the vegetation bordering quiet bodies of water, ecologists have generally recognized but a single zone of transition-commonly termed the "supra-littoral"-between the marine formations that are subjected to periodic inundation by salt water, and the inland formation higher up. Thus for example, Johnson and York ('15, p. 17) take the lower and upper limits of this belt at Cold Spring Harbor as 8 and 12 ft. respectively. Above this belt the vegetation no longer bears the impress of its nearness to the sea, and many inland plants (e. g. Acer rubrum, Robina pseudo-acacia, Fraxinus americana, to mention only a few), may get down pretty close to its lower limit. The entire transition belt extends at most to but 4.4 feet above mean high water-which at Cold Spring Harbor is at 7.6 feet—and in places this belt may be still narrower vertically.

At Otter Cliffs, however, the first rooted plant, a depauperate Plantago

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decipiens, a distinct halophyte, was first encountered at an elevation of 18 feet, i.e. at 7.6 feet above mean high water, and the first arboreal species, a stunted white spruce, Picea canadensis, only 18 inches high, grew at 25 feet above mean high water. The forest characteristic of the region begins to make its appearance, in stunted form, near the 50-foot level (Pls. XXI, XXII, Figs. 29, 31). Accordingly the complete transition region here occupies some 40 feet, vertically, beyond the mean high tide level. The plant covering of this vertically extensive transition region, between the tidal zone and the upland with its characteristic inland forest, is composed of two distinct belts The lower of these, the supra-littoral, is washed at many points by waves or by copious splash from waves and bears a very scanty covering of plants. The upper of the two, the extra-littoral belt, on the contrary, is washed by the sea only in quite exceptional storms, though it is at times wet by considerable spray. It has a pretty continuous vegetation of low, heathlike species. The two higher belts of this shore (50 to 193 feet) receive some wind-blown spray and "cyclic" salts, but their vegetation bears no special stamp of its proximity to the sea.

Supra-Littoral or Plantago-Porphyridium Belt 2

(From 14 to 30 feet)-" Spray Zone"

The supra-littoral belt is the most sparsely populated of all those to be distinguished on this rocky shore (see Pl. XXI, Fig. 29 (below), Pl. XXII, Fig. 30 (at right)). This condition seems clearly due to the fact that, while this belt is quite out of reach of the tides and even of normal waves, by which all the plants of the true intertidal zone must be wet daily, it is nevertheless subject to thorough drenching, not only in the winter but also by the waves or spray of the occasional storms of spring and summer. For example, after a storm in August 1927, water from the ocean was found in small pools at the 38-foot level, and plants on soil at 36 feet were thoroughly drenched. Therefore the only plants that can grow in this zone (in its lower parts at least) are such algae as may live in pools, or in trickles of fresh water on the cliffs, and those lichens and other terrestrial plants that can withstand drenching with salt spray even during their growing season. The number of species of algae in the first category that may grow in the latitude of Mt. Desert Island is not inconsiderable, but most of them require more fresh water than is available in this belt of our area, where pools and trickles dwindle greatly in dry summers. In fact, only 5 of the many algae that might grow at these levels have actually been distinguished in this belt within our area. The number of terrestrial plants of this coast which can withstand an occasional drenching with salt water is very considerable. The

² The authors acknowledge the aid of Professors C. C. Plitt and E. N. Transeau in the identification of the lichens and the freshwater algae, respectively, of the adlittoral region.

number of these salt-tolerant forms, however, which can at the same time endure the high cvaporation rate they would experience on these sun-baked cliffs, while subsisting on the limited fresh water supply afforded by the very scanty soil filling the narrow rock crevices, is really rather small. The upper boundary of this belt is in reality so dependent on topography that the approach to high water mark of the plants of the next higher, or extralittoral belt, is determined by the height of the top of the cliff, with its gentler slope and adhering humus. This height may range from 28 up to 40, or even 60 feet on closely neighboring parts of this shore. Protecting ledges may break the force of the waves, reduce the splash and spray on the cliffs behind them and thus may allow Empetrum and other species from the extra-littoral belt to push down several feet below the 28-foot level, which is the lowest point reached by Empetrum in our particular area. We found growing in this supra-littoral only 5 seed plants, 1 moss and 3 lichens. Of all these probably only 3 of the algae (Calothrix, Oscillatoria and Enteromorpha) and one of the seed plants (Plantago) are really confined to the immediate shore line and are hence to be thought of as essentially littoral plants. While these three algae and Porphyridium may form definite associations, the several seed plants found (except perhaps Empetrum) are so scattered that they can scarcely be said to form definite communities. The mosses may form pure associations, but over very limited areas only.

Since all the seed plants of this belt occur as widely scattered individuals or in small tufts, it is impossible to distinguish among them dominant from subordinate forms. The characteristic supra-littoral plants, approximately in the order of their relative importance, are Plantago decipiens, Aira flexuosa, Porphyridium cruentum, Enteromorpha micrococca, Moss No. 1, Mougeotia sp., Oscillatoria sp., Calothrix fasciculata, and (in the upper half of the belt only) Aster novi-belgii, Prenanthes trifoliolata, and Empetrum nigrum.

Plantago decipiens is the one seed plant that is really characteristic of this belt. It occurs nowhere below this level, though it may be found on bare ledges up to 45 or 50 feet. In all cases it is on rocks reached by salt spray. Only rarely are two plants of this species near enough to touch each other, or for the roots to come into competition underground. This Plantago grows out of the narrowest cracks in the bed rock of the cliffs, on all exposures and on both sloping and vertical walls (Pl. XXI, Fig. 29, below). The amounts of soil and water available in the rock crevice are, in most cases, evidently extremely small. The size and vigor of the individual plants seem to be determined chiefly by these amounts. This sparse sprinkling of P. decipiens here is in striking contrast with its abundance on neighboring marshy shores. The lowest individual of P. decipiens found in our area, a dwarfed and sterile one, was at the 18-foot level. The lowest flowering specimen (3 inches) was at 19 feet. The highest specimen recorded, a sterile one, was at 51 feet, on an almost bare rock at the top of a vertical cliff.

The fact that this plant grows much farther above high water level here than it does on the marshy shores of this island, or even on rocky shores where it is more protected, seems clearly due to the fact that on this exposed shore the spray saturates or washes away the soil of the rock crevices to a far greater height above the upper tide-mark than it does on quieter shores. In the more protected places, even on Otter Cliffs, the soil collects in considerable quantity and gives standing room to a goodly number of competing inland plants at a level (32 feet) far below that of the highest specimens of Plantago. This Plantago is found on the same ledge with other, quite varied plant associates, but always on the most sterile, soilless parts. It does not gain a footing in the larger soil masses among the upland plants growing there, in spite of the fact that it may grow 15 feet higher up, where the cliff is bare and well-lighted. Whether it is an actual need of salt or the lack of competition of other plants by shading that determines the occurrence of P. decipiens on these exposed and almost soilless areas, must be determined by experiment. This Plantago is perennial but its leaves are not evergreen at Otter Cliffs. Only small, young leaves were living in March, 1927.

Aira flexuosa, the second seed plant in frequency, except perhaps in the upper tenth of this belt, is a grass growing in small tufts, commonly in cracks on vertical cliffs down to 23 feet. (Pl. XXI, Fig. 29). Individuals occurring in this belt are plainly stragglers from above, which find it possible to establish themselves here on favored spots, but it evidently does not endure salt spray as well as the *Plantago*, and it needs more soil.

Aster novi-belgii and Prenanthes trifoliolata are two other seed plants occasionally found here which are not real maritime species. Both of these are restricted in our area to the upper third of this belt, where a few of each species may find sufficient soil on little shelves or in crevices. They are clearly stragglers from above, which only very rarely find a possible habitat below the 30-foot level.

A fifth seed plant, *Empetrum nigrum*, is occasionally found in this belt. The lowest clump of this species, at 28.5 feet, is evidently from the belt above, allowed to drop down by the washing away of the soil beneath a clump which grew near the edge of the cliff (Pl. XXI, Fig. 29). We at first thought that the clump might have just been lowered (in 1923) by the washing away of the soil beneath it. But the same clump was growing well in September 1926, which shows that established plants can persist at this level. On other more protected shores of Mt. Desert Island, as, e.g., near the Mt. Desert Island Biological Laboratory, at Salisbury Cove, *Empetrum* may be found flourishing year after year on rocks at the 20-foot level. Light seems the most important of the other external conditions that influence the distribution of this plant, for the densest clumps of it are found on well lighted ledges, and it never grows well in shade.

One sterile moss (probably Orthotrichum or Grimmia) is found sparingly on the horizontal faces of the cliffs near the 20-foot level (e.g., at 90 W. x

10 S.). It must often be wet with salt spray even in the growing season but it remains living and green in spite of this.

Porphyridium cruentum is as widespread vertically as any plant in this belt. While, because of its diminutive size, the individual Porphyridium is not visible, yet the thousands of plants that grow together form dark, brick red patches, yards across, which are visible from many rods away. It occurs on the smooth, vertical wall of rock behind the shingle beach from about 120 W. by 20 N. to 130 W. by 35 N. Here it is exposed to the early morning sun, but shaded from the south and west. This rock face is moistened by the seepage of water from the soil above, except during a continued dry spell, when the desiccated algae firmly encrust the granite cliff (Pl. XXI, Fig. 29). During winter much of the Porphyridium on this cliff is covered by a thick layer of ice (Pl. XXI, Fig. 30).

Enteromorpha micrococca is found in this belt ranging as high as 17.8 feet at 50 S. x 70 W. (See Johnson and Skutch '28a Chart II and Pl. XIII, Fig. 20.) Here it occurs in a recess in the cliff exposed only to the northeast, and in all but the driest weather it is moistened by a fresh water trickle issuing from a crevice in the rock, and at the same time it often receives considerable spray from the waves at high water. In winter it may be protected from spray by masses of ice formed from seepage water.

Mougeotia, of a species not determinable from the sterile threads collected, was present every summer from 1923 to 1926 in the trickle that drains into our area near 70 N. by 160 W. Here it covered the soft friable rock with a pale green film, which was well exposed to the morning sun, and where, during continued dry weather, the filaments dried until they could be powdered.

A species of *Oscillatoria* was found along the cliff extending south of Pool N, growing near the lower limit of the supra-littoral belt. The filaments formed small, densely black masses with a very smooth surface, looking like dabs of tar, always on rocks with a northern exposure, where they were kept rather moist by seepage from above.

Calothrix fasciculata, the last to be mentioned for this supra-littoral belt, occurs in flocculent, dark green masses attached to the bottom of a small pool of brackish water at 80 W. by o N., at an elevation of 15 feet.

It will be seen from this description that the plant population of this supra-littoral belt, outside of the tide-pools and the rain-water pools is, on the steep cliffs of our area, the sparsest and least varied one encountered in the whole series of belts. It is made up entirely of perennial species of seed plants, mosses and algae.

Extra-littoral or Empetrum-Cornus-Juniperus Belt

(From 30 to 50 feet)-"Transition Zone"

The most striking environmental features of the extra-littoral belt are the thin, gravelly soil and the great exposure to wind and sun. It is subject to the strong onshore winds, and the rocks probably crumble from the action of wind and frost, rather than from any direct solvent effect of the salt The cliff tops are, at most points, well out of reach of the waves of the most violent storms and any salt reaching the the soil must be wind blown or "cyclic." Judging from determinations secured elsewhere, the amounts of salt carried into this zone in this manner may be rather large (see Grabau '20, Chap. vii). However, the rainfall in this region is so abundant, and the run-off so rapid, that soluble materials are certainly washed back into the sea before they can accumulate to any extent. That there is no considerable accumulation of sea salts in the soil is attested by the pronounced acidity of the soil water, since marine salts would surely impart to it an alkaline reaction, as they do in salt meadows. But the somewhat lower acidity of the soil here, as contrasted with that of the belt above, may conceivably result from the slight residuum of salts left in the soil. Most of the plants of this belt are not halophytes, although, in its lower portion at least, they are often xeric 3 in aspect. This is a characteristic which they share in common with the entirely different flora of the supra-littoral belt of depositing shores (Kearney, '04, Johnson and York, '15). Only two so-called halophytes, Plantago decipiens and Solidago sempervirens, occur here. The ready access of seeds, and the local freedom from competition probably make possible their existence. This Solidago is certainly not an obligate halophyte, for it self-sows readily where introduced on dry soil at Baltimore, many miles inland. The occupants of this belt, taken as a whole, belong to the more hardy inland species, and form the farthest outposts of the true inland vegetation.

The general aspect of the vegetation in this belt is somewhat heath-like, (see Hill, '23, p. 336) with mats of *Empetrum* and tufts of grasses, among which are scattered, or less commonly clustered, plants of *Cornus canadensis* and *Maianthemum canadense* (Pl. XXIII, Fig. 33). Shrubs of any considerable size are infrequent in most of the belt, while trees, always dwarfed, are still more rare. The horizontal zonation within this belt is not very marked. The striking feature of the plant distribution is rather the transverse (i. e. vertical) bands of *Empetrum*, alternating with other bands composed of one or both the junipers or (nearby) of wind-blown *Thuja* (Pls. XXI, XXII, Figs. 29, 31, 32). Since practically all the species of this belt are perennial, its vegetation is far more constant in aspect from year to year than that of

³ See Cooper W. C. and Weese, A. O. A suggestion to amend certain familiar ecological terms. Ecology: 7: 389-390, 1926.

any of the lower belts. The vegetation of this belt includes several of the species that help to form the so-called heath investigated by Gates ('12) on the beach of Lake Michigan.

The edaphic conditions within this belt change considerably as we pass inward from the cliff edge. In the lowest reaches, the rock is covered by angular rubble derived from the weathering of the granite ledges above. Between these fragments, and also in the depressions in the rock, is more or less fine "rock-flour." Areas of bare granite are numerous. Humus is practically absent from this well-aerated soil. Higher up, humus begins to appear and increases in depth towards the upper edge of the belt. The principal humus-builder and soil accumulator is the crowberry, Empetrum nigrum. On gaining a foothold in a cranny or pocket in a ledge, the plant grows and sends out horizontal shoots trailing over the bare rock surface (Pls. XXI, XXII, Figs. 29, 31). The axes of the main branches become sinuous and contorted and may reach 5-8 mm. in thickness. These creeping stems bear numerous, abundantly ramifying, ascending branches, the terminal branchlets of which are less than 1 mm. in diameter. The small, strongly revolute, dark green leaves remain alive for two or more years, then gradually dry up and may remain on the stem in a decaying state for several years more. Finally the whole plant forms a low, dense, green mat (Pl. XXIII, Fig. 33), which is so thick and resistant that it makes a cushion soft to lie upon. The fallen leaves accumulate in the maze of branches resting on the surface of the rock, here to be transformed to humus. In the same manner, particles of soil and vegetable matter washed down from above are caught under the Empetrum. When sufficient humus has been gathered, the creeping stems send out fine adventive rootlets, which bind the debris firmly together. If such a crowberry plant is torn from the rocks, it carries the mat of black humus with it and so leaves quite naked the rock over which it grew. Later on, as is shown by plants higher up the hillside, a layer of rock flour accumulates beneath the humus, probably derived in part from the subjacent rock, and in part by the settling down of water-carried particles. Meanwhile, other humusinhabiting plants have sprung up among the branches of Empetrum, taking root in the soil collected by the latter. On the open hillside these invaders are not able to crowd out the crowberry, which continues dominant. It seems probable that most of the extra-littoral soil, especially that part of it which is rich in humus, was accumulated in this matter by Empetrum (see also Moore and Taylor '27, pp. 128-131).

Soil acidity determinations were made at a number of points scattered through this zone. Individual readings ranged from pH 5.0 to pH 6.1 in no orderly manner. Most samples gave a value under pH 6, and the average of 15 readings is pH 5.6. It is interesting to compare this result with that obtained for the evergreen forest just above, where the acidity ranged from pH 4.6 to 4.9 with an average from 8 stations of pH 4.8. The pronouncedly lower acidity of the seaward zone (difference of 0.8) may, as suggested

above, be due to the influence of wind blown alkaline salts, although the more rapid oxidation of humic substances in the more exposed locality, or the differences in the plant covering, may prove to be the determining factors. Acidity determinations were made with a Stirlen-Wallace double-wedge comparator (Wherry, '24).

Empetrum nigrum, the habit of which has just been described, is the most abundant and conspicuous plant of this belt. The dark green mats of this shrub cover large areas completely, and give the prevailing color to the zone. It extends downward to 28 ft., but is more abundant toward the upper limit of the zone (see Table I for vertical range, and Chart II in Johnson and Skutch '28^a for distribution of plants in this zone). In late March, 1927, the upper leaves of Empetrum were brown in color but the lower leaves of each branch were green. The upper ones had become green and active again by June. Stamens were apparently nearly mature in March.

Juniperus horizontalis is a hardy, grayish conifer, living specimens of which extend down to 35 ft. (Pl. XXI, Fig. 29), while a dead plant was found three feet lower. This juniper grows on the projecting bosses of the ledges where not covered by ice in winter (Pl. XXI, Fig. 30). The branches are closely appressed to the rocks. They may become 3 cm. or more in thickness, and are much gnarled and contorted. Where they grow out to the edge of an exposed ledge they may bend sharply back, forming an elbow. One such stem was found which had grown in the form of a "4."

J. communis depressa forms thick, rough, bristly mats (Pl. XXII, Fig. 31) which are of a conspicuous grayish, or yellowish green color due to the white bands of wax running along the middle of each needle. Neither of the junipers can compare with Empetrum as a humus builder, since they do not hug the ground so closely, and do not allow other species to get a start beneath them.

The other plants of this belt may be divided roughly into two classes, those living near the cliff edge which root in crevices in the rock or in the rubble and rock flour, and those which grow among the Empetrum farther back. The former are the more xeric in structure, and at the same time they are more scattered than the latter. The vegetation just above the 30-foot contour is sparse and the predominant color of the area is the rusty-gray of the rock. Here grow Campanula rotundifolia, Achillea millefolium, Plantago decipiens, Prenanthes trifoliolata, Solidago Randii, Aster novibelgii, Aira flexuosa, and Agrostis perennans, all herbaceous forms, most of them plants with erect stems, and narrow or finely dissected leaves. Shrubby forms occurring in somewhat similar, though usually slightly more protected situations are Spiraea latifolia, Ribes grossularia and Myrica carolinensis (Pl. XXII, Figs. 31, 32). Empetrum itself, as a pioneer plant, must be mentioned along with the plants of bare soil. Where there is a large expanse of bare rock and rock flour at 47 to 50 feet (as near o N. by 100 W.) many of these plants extend to the upper limit of the zone. Potentilla tridentata, preeminently a plant of exposed, dry rocks (Pl. XXII, Fig. 31), does not extend below 43 feet. Plantago decipiens is particularly abundant on the edge of the cliff at 47 feet, but here the plants are dwarfed. Although not happening to occur in the area under survey, Solidago sempervirens and the ubiquitous Rhus toxicodendron (infrequent on Mt. Desert) grow in this zone at nearby points, and hence should be mentioned here.

Strongly opposed in many characteristics to the foregoing group are the humus-loving plants which find shelter among the mats of Empetrum. None of the plants in this group occur below the 40 ft. contour. conspicuous are the large-leafed Maianthemum canadense, Cornus canadensis (Pl. XXIII, Fig. 33) and Trientalis americana. These plants perennate and spread by means of slender, branching rhizomes which creep through the humus. The first two forms are strongly gregarious (Pl. XXIII. Fig. 33) and their clusters of large, glossy leaves, contrasting strongly with the minute foilage of the crowberry, among the branches of which they grow, give them an aspect altogether foreign to their setting. The aerial parts die down during the winter and so at the most severe season the perennating portions are well protected by the Empetrum mats, and by a considerable thickness of soil. These three species usually occur in partially shaded habitats, and here in this belt of our area, the trees, and the hillside rising steeply to the west of them, cut off the direct sunlight early in the afternoon. Two species of heath, Vaccinium pennsylvanicum and V. Vitis-Idaea minus occur above the 40-foot contour exclusively, while a third, V. macrocarpon, extends down to 35 feet but is only sparingly represented. It is found more abundantly at 50 feet, about shallow pools of darkly stained water in the rock. Pteris aquilina occurs only in the uppermost portion of the belt above 46 feet where it forms a small brake. Danthonia compressa is also rather abundant higher up.

Of the three arboreal species scattered in this belt, *Picea canadensis* extends lowest down, being represented at 35 feet by a small tree only 18 inches high which, however, showed 22 annual rings. The small spruces stand out like sentinels of the forest among the lower-statured vegetation around them. *Abies balsamea* does not descend below 47 feet, and when growing in this belt does not reach over 18 inches in height. *Thuja occidentalis* touches the upper margin of the belt at the 50-foot contour. On neighboring cliffs, at 60 feet, this *Thuja* may form the outermost sloping fringe of vegetation (Pl. XXI, Fig. 32).

For other less important species that may occur in this belt reference should be made to Table I and to Plate XXIII, figure 32. Of the total of thirty-four vascular plants recorded for this belt, all except two, *Plantago decipiens* and *Solidago sempervirens* occur at inland stations on the island. Aside then from these two herbs, the flora of this belt is composed, not of maritime species, but rather of hardy recruits from various inland habitats. For example, 13 species, mostly of xeric and sun-loving plants, are common

both to the extra-littoral belt and to the exposed summit of the promontory (see Table I and II). In the latter habitat the conditions of existence are very severe, and as a result we find that it is the hardier plants of the first group which recur at the higher station. Thirteen species are common to the extra-littoral and to the evergreen forest (Tables I and II). These, as we should expect, are the shade-loving and less xeric types, which occur higher up in the extra-littoral belt. *Maianthemum, Cornus* and *Trientalis* are plants, typical of open spots on the forest floor, which have worked their way down into the belt below. That there is a real difference in the flora of the three belts may be seen from the fact that only 5 species are common to all, and of these only 2 (*Vaccinium pennsylvanicum* and *Juniperus communis*) are of any importance in more than two zones.

It is remarkable that so many structural modifications characteristic of xerophytes should be found in the little group of plants stationed in this extra-littoral belt. Of those structural features commonly recognized as typical of species of dry situations, the following are exemplified more or less markedly here: (1) Succulence: by Plantago and Campanula. (2) Stomata opening into enclosed spaces: by Aira and Empetrum with inrolled leaves; by Juniperus horizontalis with scale leaves appressed to the stem and the stomata on the abaxial surfaces just beneath the margin of the next overlapping leaf. (3) Resin or latex: shown by Myrica, Juniperus, Picea and Abies (resin); Prenanthes, Potentilla and Campanula, (latex). (4) Waxy or scurfy epidermis: by Solidago Randii, Juniperus communis Potentilla, Picea, Abies. (5) Schlerophyllous leaves: by Vaccinium macrocarpon and V. Vitis-Idaea, Empetrum. (6) Scale leaves: by Juniperus horizontalis.

In August, 1924, the osmotic pressures of the leaves of nine species growing in this zone were determined by the aid of plasmolyzing solutions of sucrose and potassium nitrate. The results need not be given in detail here, but three species (*Empetrum*, Aster and Myrica) gave values between 10 and 15 atmospheres, and the remaining six (Aira, Juniperus horizontalis, Plantago, Potentilla, Solidago Randii and Vaccinium Vitis-Idaea) gave between 15 and 20 atmospheres. These values, while not unusually high, are nevertheless decidedly above the average for herbs and low shrubs, and indicate a considerable degree of environmental aridity.

Mosses are inconspicuous in the extra-littoral zone. The specimens found in the more sheltered crannies of the rock are small and often sterile, so that their identification is a matter of difficulty or is impossible. The following have been identified: Aulacomnium palustre, Dicranella heteromalla, Pohlia nutans and Mnium (hornum?).

The large expanses of bare rock afford favorable habitats for encrusting lichens (Pl. XXII, Fig. 31, at right of hat). The proximity of the sea assures them an abundant, if somewhat intermittent, supply of moisture, either in the form of nightly dews, or of the fogs which are rather frequent.

In addition, several fruticose species grow among the vascular plants. The following lichens have been identified from this zone: Cladonia fimbriata (L.) Fr. v. coniocraea (Flk.) Wainio, C. furcata (Huds.) Schrad., C. pyxidata (L.) Fr. v. neglecta (Flk.) Mass., C. sylvatica (L.) Rabenh. f. laxiuscula Del., Crocynia lanuginosa (Ach.) Hue., Lecanora muralis (Schreb.) Schaer., Lecidea convexa (Fr.) Th. Fr., Parmelia conspersa (Ehrh.) Ach. v. imbricata Mass., P. conspersa f. isidiata Leight., P. physodes (L.) Ach., P. sulcata Tayl., P. saxatilis (L.) Ach. v. isidiata Anzi, Pertusaria amara (Ach.) Nyl., Rhizocarpon geographicum (L.) D C., and R. petraeum (Nyl.) Zahlbr.

Upland or Picea Belt, Evergreen Forest

(From 50 to 180 feet)

The two uppermost zones, which bear a true inland vegetation, were not studied in the same detail as the five lower ones. A brief survey was made of these two upper belts for comparison with the extra-littoral, as well as for the completion of the picture of the sequence of vegetation in passing from the water's edge on this eroding shore to the rocky summit above.

Inland from the extra-littoral lies the evergreen forest belt, which is a Piceaetum in which Picea rubra is the dominant species. However, at the lower margin of the forest, there is a narrow transition belt in which P. canadensis assumes dominance. (Pls. XXI, XXII, Figs. 31, 32.) latter has a more northerly range. As has been mentioned, it is represented in the extra-littoral belt of our area, while P. rubra does not extend that far seaward. Picea canadensis becomes more numerous toward the upper margin of that belt, and at the beginning of the next it occupies a border several trees deep, and the beautiful silver-hued trees attain considerable size. The seaward limbs of these trees are densely covered with small twigs, which lie in a horizontal plane (see Hill '23, p. 360), and have somewhat the appearance of a witch's broom. Some of the more exposed trees have branches often 21/2 inches thick springing from near the root collar; these extend along the ground and may take root in the duff. Behind the shelter formed by P. canadensis, its darker-foliaged and less beautiful congener, P. rubra, thrives well, to the almost complete exclusion of its hardier relative. Mixed with the spruce are other coniferous as well as several broadleafed species, no one of which forms an important constituent of the forest on the lower reaches of the hillside, but a number of which become more abundant higher up. Here should be mentioned Pinus strobus, Tsuga canadensis, Betula alba papyrifera, Abies balsamea and Thuja occidentalis. (Pl. XXII, Fig. 32.) On the lower portions of the hillside, especially where the ground is more level and the soil is deeper and may therefore hold an abundance of ground water, the trees of the almost pure stand of red spruce have slender, columnar trunks, and form such a close canopy

that the light penetrating through it is insufficient to support much woody undergrowth (Pl. XXIII, Fig. 34). Here the clear forest aisles are densely carpeted with dark green mosses and liverworts, among which *Bazzania trilobata* is particularly abundant. Such a stand of spruce is typical of the southern coast of Mt. Desert Island. The suppressed firs of the forest floor

Table I. Vertical range and distribution of plants of the extra-littoral belt

	v oj pra	nis of the extra-litt	oral belt
Species	Symbol	Upper Limit	Lower Limit
Abies balsamea (L.) Mill.	Ab	Forest	47 feet
Achilles millefolium L.	A	Summit	31.5 "
Agrostis perennans (Walt.) Tuckerm.	Ap		
Aira flexuosa L.	Ai	Forest & Summit	23 "
Aster novi-belgii L.	As	Summit	23 "
Campanula rotundifolia L.	Ca	50 feet	35.5 "
Cornus canadensis L.	C	Forest	41.5 "
Danthonia compressa Austin	D	50 feet	38 #
Empetrum nigrum L.	E	Forest & Summit	28 "
Fragaria virginiana Duchesne	F	Summit	41 "
Ilex verticillata (L.) Gray	I	48 feet	48. "
Juniperus communis L. var. depressa Pursh.	Jo	Forest & Summit	38 "
Juniperus horizontalis Muench.	J	50 feet	30 H
Maianthemum canadense Desf.	Me	Forest	48 11
Myrica carolinensis Mill.	M	Summit	35.5 "
Picea canadensis (Mill.) BSP	Pi	Forest & Summit	35.5 "
Plantago decipiens Barneoud.	Pl	51 feet	18 "
Potentilla tridentata Ait.	Pt	Summit	43.5 "
Prenanthes trifoliolata (Cass.) Fernald	Pr	47 feet	20 "
Pteris aquilina L.	Ps	Forest	46.5 "
Pyrus melanocarpa (Michx.) Willd.	Py	Summit.	36.5 "
Ribes grossularia L.	R	Forest	32 "
Rosa nitida Willd.	Ro		45 "
Rubus idaeus L.	Ru	Summit	40 #
Solidago Randii (Porter) Eritton	S	Summit	
Spiraca latifolia Borkh.	Sp	Cumilit	
Thuja occidentalis L.	T	Forest	31.5 1
Trientalis americana (Pers.) Pursh.	Tr	forest	50 "
Vaccinium macrocarpon Ait.	Vm		47 "
Vaccinium pennsylvanicum Lam.		50 feet	34.5 "
Vaccinium vitis-idaca L. v. minus Lodd.	٧	Forest & Summit	44 "
HILLED HOUG.		Forest	42 #

show a peculiar manner of growth. They remain low, less than shoulder high, and the lower branches have a relatively enormous spread, sometimes exceeding the height of the sapling. The weight of these branches bears them down to the ground, and they become buried by the forest litter, so that the exposed ends appear not to have any connection with the parent tree. Higher up on the hillside the soil is thin, ledges crop out, the stand of trees is more sparse, and, under the more open canopy of *Picca rubra*, shrubs and small trees become more numerous, while low bushes often form a dense covering to the ground. Most important among these shrubs are *Viburnum nudum*, *Kalmia angustifolia*, *Alnus mollis* and *Gaylussacia baccata*. This huckleberry in particular forms a low, close growth. The composition of this forest is discussed in more detail by Moore and Taylor ('27, pp. 124–127).

The herbaceous species of the forest, largely perennials, are not numerous. They are most abundant in those open spots of the *Picea* belt, where the forest floor receives most light. Here *Aira flexuosa* forms close stands. *Polypodium vulgare* creeps over ledges, or boulders as is shown in figure 34, Plate XXIII. The distinctive zig-zag stems of *Aster acuminatus* are conspicuous, and *Aralia nudicaulis* is also abundant. The patches of *Cornus*, *Maianthemum*, *Trientalis* and *Pteris* near the lower edge of the forest are often continuous with the stands of the same species in the belt below. *Clintonia borealis* first makes its appearance here in the lower edge of the evergreen forest.

Outcrops and ledges of bare rock are numerous in the forest, and on these grow *Empetrum* and *Juniperus communis depressa*, but the former does not here reach nearly the luxuriance it attains on top of the open cliff below. At a spot about half-way up the hillside, in a closed rock basin a miniature *Sphagnum* bog has developed, where grow *S. capillaceum*, a sedge (*Carex trisperma*) and a single red maple (*Acer rubrum*). Around the border of the bog *Polytrichum commune* grows luxuriantly and by another smaller bog *Osmunda cinnamomea* is found.

Throughout this belt mosses and lichens are numerous. Usnea drapes the dead limbs of the trees, and species of Cladonia, in particular C. alpina, form exquisite miniature forests on the ground. Crustose and foliose forms cover the bark of trees and the outcropping rock ledges. The fog laden winds, which during the growing season often blow in from the sea, together with the persistent shade, seem responsible for the unusual luxuriance of the cryptogamic vegetation.

A thick layer of humus, merging into duff above, covers the ground throughout this forest, and may reach a depth of 10 inches. Beneath this is a stratum of whitish, sandy loam, which seems to be almost entirely derived from the weathering of the granite bed-rock. Determinations of soil acidity made both in the superficial humus and the underlying rock-flour, give very uniform readings of pH 4.6 to 4.9, with a mean for eight samples of 4.8. The water which trickles down over the cliffs after a heavy rain has a pH

of 4.8, and thus serves as an index of the acidity of the soil through which it has seeped. The water in the *Sphagnum* bog is slightly more acid (pH 4.4).

Table II gives a complete list of plants collected in this belt:

Table II. Plants collected in the upland or Picca belt, evergreen forest Trees and Shrubs:

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Abies balsamea (L.) Mill.

Acer rubrum L.

Alnus mollis Fernald.

Amelanchier canadensis (L.) Medic.

Betula alba L. var. papyrifera (Marsh) Spach. Bibes grossularia L.

Empetrum nigrum L.

Gaylussacia baccate (Wang.) C. Koch.

Juniperus communis L. var. depressa Pursh.

Kalmla angustifolia L.

Nemopanthus mucronata (L.) Trel.

Linnaea borealis L. var. americana (Forbes) Rehder.
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Herbs:

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Aira flexuesa L.
Aralia nudicaulis L.
Aster acuminatus Michx.
Aster macrophyllus L.
Cornus canadensis L.
Cypripedium acaule Att.
Caultheria procumbens L.
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Filices:

Asplenium sp. Osmunda cinnamomea L.

Musci:

Dicranum majus Turh.
Dicranum scoparium Hedw.
Hypnum schreberi Willd.
Leucobryum glaucum (L.) Sch.
Mnium sp.
Polytrichum commune L.

Hepaticae:

0.4

Bazzania trilobata

Ptilidium ciliare (L.) Nees.

Lichens:

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Alectoria chalybeiformis (L.) Gray
Cladonia alpina
Cladonia fimbriata (L.) Fr. v. coniocraea (Flk.) Wainio
Cladonia furcata (Huds.) Schrad.
Cladonia gracilis (L.) Willd. v. elongata (Jacq.) Flk.
Cladonia gracilis (L.) Web.
Cladonia squamosa (Scop.) Hoffm. f. denticollis (Hoffm.) Flk.
Cladonia squamosa (Scop.) Hoffm. f. laxiuscula Del.
Cladonia uncialis (L.) Web.
Gyrophora Muhlenbergia Ach.
Lobaria pulmonaria (L.) Hoffm.
Parmelia pulmonaria (L.) Ach.
Parmelia saxatilis (L.) Ach.
Parmelia sulcata Tayl.
Ramalina dilacerata (Hoffm.) Arn. f. pollipariella Arn.
Umblicaria pustulata (L.) Hoffm.
Usnea dasypoga (Ach.) Nyl.
Usnea florida (L.) Hoffm.
Usnea hirta (L.) Hoffm.
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Lysimachia guadrifolia L.
Carex trisperma Dewey
Clintonia borealis (Ait.) Raf.
Maianthemum canadense Desf.
Melampyrum lineare Lam.
Trientalis americana (Pers.) Pursh.
Viola sp.

Polypodium vulgare L. Pteris aquilina L.

Sphagnum acutifolium = S. capillaceum (Weiss,) Schwank.

Stereodon cupressiformis (L.)

Brid. var. filiforme Brid.

Stereodon imponens = Hypnum imponens Hedw.

Summit or Empetrum-Potentilla Belt

(From 180 to 193 feet)

The summit of the promontory at 193 feet above mean low water is a flat table of rock 50 x 150 feet, topped by an observation tower which was used during the period of our survey as a radio compass station of the United States Navy. The granite rock often lies naked, but rock flour has accumulated in the depressions, and where vegetation has established itself, considerable humus has been formed. In the small basins of rain water in the rock grow sedges (Carex scoparia and C. atrocinctus brachypodus) and a Bidens. The strong insolation, exposure to the wind, and thinness of the soil make this an inhospitable habitat, and many hardy species which grow on the cliffs, but are absent from the intervening forest, again make their appearance here. Among these are Achillea millefolium, Aster novi-belgii, Cornus canadensis, Myrica carolinensis, Potentilla tridentata, which often marks the course of a fissure in the rock for some yards, and Solidago Randii. Empetrum forms only a few denser mats here. A few plants characteristic of the evergreen forest do, it is true, venture up on the summit, but a more important element of the flora is made up of other hardy species which we meet here for the first time, such as Epilobium spp., Rumex acetosella, Aralia spinosa, etc. The arboreal species, e.g. Picea rubra, Betula, etc., form only stunted bushes, and no real trees occur on the summit proper. The only specimen of Sambucus racemosa seen was well-developed, but this is evidently because it grew in a rather sheltered spot next to the tower.

The acidity of the sparse soil of the summit (humus, duff, and rock-flour) ranged from pH 4.0 to 5.0 with an average for 10 samples of pH 4.8, which

is the same as that for the evergreen forest.

The following is the complete list of plants collected from the summit: Trees and Shrubs: Betula populifolia, Empetrum nigrum, Gaylussacia baccata, Juniperus communis depressa, Myrica carolinensis, Nemopanthus mucronata, Picea canadensis, Picea rubra, Pyrus americana, Pyrus melanocarpa, Rubus idaeus, Sambucus racemosa, Vaccinium pennsylvanicum, and Viburnum cassinoides.

Herbs: Achillea millefolium, Agrostis hycmalis, Aira flexuosa, Aralia hispida, Aster novi-belgii, Bidens (discoidea?), Carex scoparia, Epilobium angustifolium, Epilobium sp., Festuca rubra, Fragaria virginiana, Gaultheria procumbens, Hypericum sp., Plantago major, Poa palustris, Potentilla tridentata, Rumex acetosella, Scirpus atrocinctus brachypodus, Solidago Randii, and Viola lanceolata.

Musci: Ceratodon purpureus, and Polytrichum juniperinum Willd. Lichens: Peltidea (canina?) and Gyrophora Muhlenbergia Ach.

Evaporation Rates in the Extra-Littoral Belt and the Evergreen Forest

For all belts above the supra-littoral, continuous records of the evaporating power of the air were made during July and August, 1924. The instrument employed was the Livingston porous-cup atmometer, spherical pattern, set up with a mercury valve to prevent the entrance of rain water. Readings were made once or several times weekly, according to the expected waterloss. The stations at which atmometers were located are as follows: Extralittoral; Station A on the 32-foot ledge, at 35 S. by 85 W. exposed to the morning sun but shaded in the afternoon (see Johnson & Skutch '28a, Chart II), and Station B on the top of the cliff at 5 S. by 110 W. Evergreen forest; Station C in the Picea canadensis zone just within the edge of the forest, and Station D farther inland, in a more open area in the Picea rubra. Summit; Station E, completely exposed. At one station within each zone (B, C and E) a black atmometer was operated beside the white one to serve as an index of the sunlight intensity. All of the atmometers used were restandardized in Professor Livingston's laboratory at the end of the summer, and none was found to have changed its coefficient by more than 0.03. These readings for station D may be compared with those of Moore & Taylor ('27, p. 65) for their spruce station, which is only 250 yards from station D.

Although our readings do not extend over a very long period, they do serve to indicate the intensity of those important environmental factors during the growing season, which is the season when evaporation is most critical for the plants, and they make possible a comparison between the several belts of vegetation (see Table III). From the second part of table III it will be seen that the summit and the extra-littoral belt receive practically equal amounts of sunlight and are highly insolated as compared with the intervening forest. These two zones are subjected to the highest rates of evaporation, but are not equal in this respect. The higher rate at the summit (station E) is due in part to its greater distance from the sea, and in part to the higher wind velocity which must prevail there. Station A has a lower rate of evaporation than station B, because it is protected from wind and sun by the high cliff which rises immediately to the west of it, and perhaps also because it is nearer to the sea. Station D, in an opening in the woods, farther inland and higher than C, would be expected to show a higher rate of water loss than C, which stood beneath the thick foliage of a spruce tree. Finally, when the period July 7 to 29 is compared with that of July 29 to August 23, it will be seen that in 1924 the former was the drier and sunnier, and that this difference is manifest at all stations for which there are records.

Table III. Evaporation rates and amount of sunlight in parts of July and August, 1924

	A	В	С	D	E
Mean Daily Evap. July 7 to 29 Mean Daily Evap. July 29 to Aug. 23. Mean Daily Evap. July 7 to Aug. 23 Ratio:	11.2	16.7 cc. 14.8 15.7 1.91	9.9 cc. 6.4 8.2	12.2 cc. 8.9 10.4 1.27	19.2 cc. 2.83 *

Amount	of	sunlight	(reading	of	black	sphere	minus	white	sphere)	
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	В	C	E
Mean Daily Sun. July 9 to 29 Mean Daily Sun. July 29 to Aug. 23 Mean Daily Sun. July 9 to Aug. 23 Ratio:	10.6	2.9 cc. 2.3 2.6 1	10.7 cc.

^{*} For period July 29 to Aug. 23 only.

Summary and Conclusions

- 1. The foregoing account is a report of an ecological study of the vegetation above the upper tide mark of a rocky, exposed ocean shore of Mt. Desert Island, Maine, made during the summers of 1923 to 1927, and March 1927.
- 2. For 20 feet above the upper tide mark in this adlittoral zone are found bare, vertical, granite cliffs and more rounded ledges. These are succeeded above by a zone of loose, fine rubble at the top of the cliff, and this in turn by a rough, rather steep hill rising to 193 feet at the Peak of Otter, which is clothed by an evergreen forest, except on a few larger ledges and on the wind-swept top of this granite promontory.
- 3. The main aim of this study was to determine the exact vertical and horizontal distribution of the plants found here, and to correlate these with features of the environment such as substratum, direction of exposure to light and winds and the resulting differences in evaporation rate.
- 4. Because of the vigorous and almost constant wave action and lack of soil, the lower margin of the truly terrestrial vegetation is crowded up some feet above the mean high water level, *i.e.* much above where it would be found on quiet shores.
- 5. In this addittoral, or terrestrial region four belts of vegetation are recognized: (a) The supra-littoral belt, extending from 14 to 30 feet and characterized by scattered Plantago decipiens, Aira flexuosa and yard-wide coatings of Porphyridium cruentum. (b) The extra-littoral belt, extending from 30 to 50 feet and characterized by a low, heath-like vegetation dominated by Empetrum nigrum, Cornus canadensis, and Juniperus horizontalis. (c) The upland or Picea belt—an evergreen forest, which extends from 50 to 180 feet and is dominated by Picea rubra and Abies balsamea. (d) The summit belt at 180 to 193 feet, with a very sparse and open vegetation of Empetrum and Potentilla tridentata, and with fewer, scattered specimens of other shrubs, mostly low, and of herbs.
- 6. The paucity of vegetation in the supra-littoral belt is due to the lack of soil on the nearly vertical rock faces.
- 7. In these belts measurements were made of the evaporating power of the air and the total radiation, using white and black bulb atmometers, and also of the pH of the soil. The results of these studies of evaporation and insolation are presented in Table III.

8. The prevailing high rate of evaporation in the exposed extra-littoral belt and on the summit, coupled with the dry, rocky substratum of both, ally these two belts floristically, despite their wide vertical separation.

9. The plants of the extra-littoral belt which (in the growing season at least) is beyond the reach of waves and usually of spray, are not halophytes, but are almost all hardy, more or less xeric types of herbs and low shrubs, that are common in dry situations on the mountains farther inland. Most of them occur again in openings in the evergreen forest and at the summit. Plantago decipiens and Solidago sempervirens are the only distinct halopytes found here.

10. The evergreen forest betrays its proximity to the ocean chiefly by the wind-blasted trees at its seaward margin and by the rich covering of lichens and bryophytes on its floor, which covering may be ascribed to the shade, and to the moisture from ocean fogs that frequently drift through the forest.

communities on the same area could be demonstrated in the intertidal zone, changes of this character in the plant covering of the adlittoral zone were evident. Thus at the upper edge of the extra-littoral belt, the evergreen forest may be forced to retreat by the desiccating effect of the strong wind at the seaward border and probably also by reduction of its soil water supply through crumbling of the cliff and falling away of the sparse soil just below it. There is thus, at these levels, a gradual succession from the evergreen forest to the heath-like mats of *Empetrum, Cornus*, and prostrate junipers. If any younger trees do withstand the changed conditions they become dwarfed and form prostrate mats (Pl. XXII, Fig. 31), thus simulating the normal heath-like covering of this zone. The instances observed indicate that older trees left on the edge of the cliff are very slowly killed and that in general the change in character of the vegetation comes about gradually.

12. In our area, just as differences in salinity of the seawater have no discoverable influence on the distribution of the marine algae, so the differences in hydrogen-ion content of the soil are apparently not great enough (Sphagnum bogs excepted) to affect appreciably the distribution of terrestrial plants. On the contrary, these studies of the intertidal (submersible) and the terrestrial plants of the Otter Cliffs area indicate clearly that in both types of habitat the same two factors, namely light and evaporation, are those most often critical in determining plant distribution. The factor compensating for evaporation, i.e. water supply, also plays much the same part in both land plants and intertidal species. For, just as an abundant soil water supply allows land plants to grow where the evaporation rate is high, so the supply of water by wave splash or by drainage rills from pools, allows littoral algae to live at higher intertidal levels than those at which they can survive on a well-drained substratum.

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DESCRIPTION OF PLATES XXI, XXII, XXIII 1

PLATE XXI

Fig. 29. View of cliff west of shingle beach, near 40 north x 135 west, photographed Sept. 8, 1926, showing transition from marine area to evergreen forest; in foreground *Porphyridium*; at brow of cliff *Aira* with *Plantago* at the left of it; on cliffs *Juniperus horizontalis*, *Empetrum* and *Juniperus communis depressa* form dense mats on the slope below spruce-balsam forest. Boulders 2, 3, 9 (below) are the ones so numbered in figure 30.

Fig. 30. The view shown in figure 29 photographed on March 30, 1927, by A. F. Skutch, showing the masses of fresh water ice covering some of the *Empetrum* and most of the *Porphyridium*, as is usual during the winter. The numbered rocks bear the same

numbers respectively as in figure 29.

PLATE XXII

Fig. 31. View looking north from 150 south x 100 west taken Sept. 5, 1926, showing the extra-littoral belt (transition zone) on top of cliff; levels 50 to 70-feet; the mats of *Empetrum, Potentilla tridentata, Juniperus communis depressa, Myrica carolinensis* and (dying or dead) decorticated trunks of *Picea canadensis*; evergreen forest in background; several protruding tongues of this occupy moist gullies. White hat in foreground is 10 inches across. Map near center 20 inches long.

Fig. 32. Top of bluff, at 65-foot level (near X in Fig. 31) showing wind-blown Thuja (ranging in height from 1½ foot left to 10 feet at right) Alnus, Betula, Pyrus, Myrica, Empetrum, and Pteris, in the foreground, with one-sided, wind-blown and dying

Picea canadensis and P. rubra in background. Photographed Sept. 5, 1926.

¹ The photographs are by D. S. Johnson except figure 30.

PLATE XXIII

Fig. 33. A portion of the extra-littoral, or transition belt, near 90 south x 100 west, showing mats of *Empetrum* and of *Juniperus communis depressa*, with a clump of flowering *Cornus canadensis*. New shoots of *Picea canadensis* in the background.

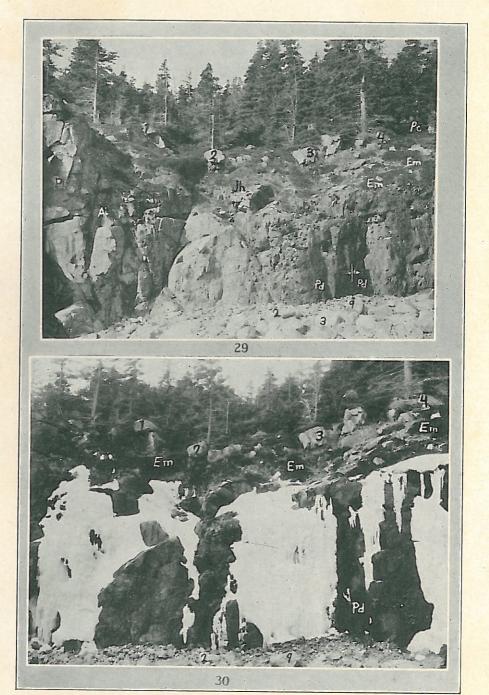
Photographed June 17, 1927.

Fig. 34. Interior of evergreen forest near 150 south x 350 west at about 90-foot level. Showing forest of *Picea rubra*, interspersed with *Abies*, *Pinus strobus* (behind boulder), Tsuga (in background), *Alnus* and *Betula*. On the forest floor are *Polypodium rulgare*, *Hypnum*, *Bazzania*, *Peltidea aphthosa*, and *Cladonia* (sp.), *Usnea* is abundant on trees. Photographed Sept. 5, 1926.

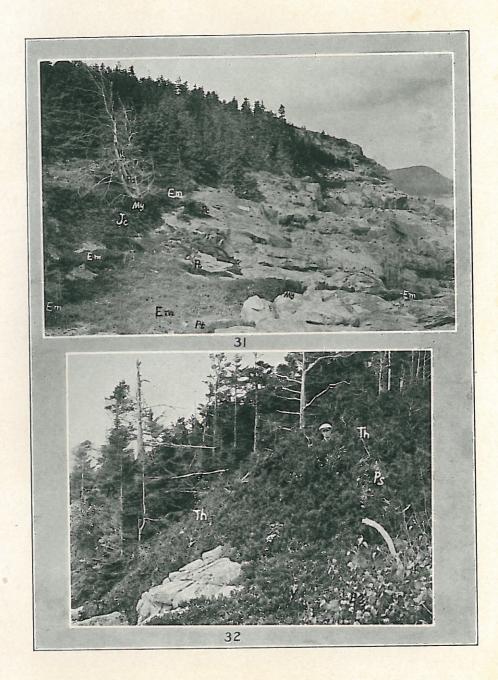
SYMBOLS USED TO INDICATE PLANTS IN PLATES XXI, XXII, XXIII

Ai = Aira flexuosa; Be = Betula alba papyrifera; Cc = Cornus canadensis; Em = Empttrum nigrum; Jc = Juniperus communis depressa; Jh = Juniperus horizontalis; My = Myrica carolinensis; Pc = Picea canadensis; Pd = Porphyridium cruentum; Pl = Plantago decipiens; Ps = Pteris aquilina; Th = Thuja occidentalis.

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