

## A COMPARISON OF CERTAIN ROCKY MOUNTAIN GRASSLANDS WITH THE PRAIRIE OF ILLINOIS

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Grasslands occur at varying altitudes in mountain regions and are almost as widely distributed as the peaks and ranges themselves. Alpine and sub-alpine meadows are perhaps best known, but in them the preponderance of other herbaceous and low woody plants over the grasses is such that the fitness of the term grassland may well be questioned. At somewhat lower altitudes, particularly in the zone immediately below the sub-alpine and commonly known as the "montane," are found treeless areas that better deserve the title of grasslands. At times the transition from the forest is a gradual one, through areas of savanna in which trees are scattered at rather wide intervals over grass-grown fields. Such grasslands and savannas are a well marked feature of the eastern slopes of the Rocky Mountains in Colorado, and are also found in other neighboring states. From their open park-like planting they are popularly designated "parks." One of the best known is Estes Park, some 60 miles northwest of Denver, included within the limits of the recently created Rocky Mountain National Park.

It was the writer's privilege during the summer of 1914 to visit this Park with a class of students in field ecology and also to study for some weeks a smaller mountain grassland, known as Boulder Park, from South Boulder Creek, a small stream traversing the park from west to east. Boulder Park is 47 miles northwest from Denver upon the Moffatt Railroad, has an altitude of 8880 feet, is two and a half miles long, nearly a mile wide, and contains the little village of Tolland. On account of the richness and variety of its vegetation it was recently chosen by the University of Colorado as the site of its Summer Mountain Laboratory.

The grassland here occupies the floor of a mountain valley broadened by glacial action and partially filled with the gravels of terminal and lateral moraines. These gravels have been worked over so as to give the valley a comparatively level floor upon which South Boulder Creek meanders in broad curves, the channel often widening into shallow ponds on account of the low gradient assisted by the work of beavers. Two other shallow ponds or small lakes are drained into the creek. The stream has intrenched itself but little and the general appear-

ance of the valley floor is not unlike that of the lake plain which succeeded the ice sheet in the Chicago region and is at present partly occupied by edaphic prairie. It therefore seems that it would be interesting to compare the conditions which have produced grasslands in these two areas, situated in rather widely removed regions and differing in so many respects. It may be possible that such a comparison may so stimulate inquiry that further research along this line may contribute something to the general problem as to the factors that are efficient in producing this type of vegetation. A full analysis of the composition of the vegetation is not possible nor is it either desirable or necessary, for it has already been rather completely done by Ramaley<sup>1</sup>, Robbins<sup>2</sup>, and others connected with the Colorado Mountain Laboratory.

#### CLIMATIC CONDITIONS

As already indicated the prairies of Illinois and the mountain grasslands of Colorado now under consideration, differ rather more than 8000 feet in altitude, and this brings a corresponding difference in temperature. The mean summer temperature of Boulder Park is about 15 degrees F. lower than that of the Chicago Region, only about six weeks of midsummer are usually free from frosts and a drop in temperature below the freezing point has been known to occur during almost every week of the year. There is almost no growth before June first, and very little after the end of August, thus making a short vegetative season that almost entirely eliminates annuals from the mountain habitat. Winter temperatures also differ somewhat, but probably not enough to materially affect vegetation, at least it may be said that this mountain park is no colder than many prairie regions, such as those of the Dakotas.

In humidity the two regions are probably closely comparable, although no accurate data are available from Boulder Park, where, in spite of the light showers that are an almost daily occurrence during a considerable portion of the summer, the mountain air is quite as dry as that of Illinois during the summer months. The amount of precipitation in the two localities is of the same order of magnitude, Illinois, (about Chicago) averaging a little over 30 inches and Boulder Park a little less than that amount, per annum. Curiously enough snow never accumulates to any great depths nor does it usually remain long in this valley, probably on account of

the long slopes which lead directly down to it from the Continental Divide, here some 2500 feet above it, but less than ten miles distant.

Both localities are exposed to high winds, but the mountain habitat particularly so. During the colder months of the year in particular do westerly winds of high velocity and great desiccating power sweep down from the Continental Divide.

#### SOIL CONDITIONS

The soil conditions are very diverse. The rich agriculture of Illinois is associated with a prairie soil of almost exhaustless fertility. It is a dark, heavy loam or silt of rather fine texture, possessing, as has been shown by Harvey<sup>3</sup>, a large water holding capacity as indicated by a high wilting coefficient. On the contrary, the soil of Boulder Park is lacking in fertility and coarse in texture, consisting of glacial gravels with a very small percentage of humus. No determination of its water holding capacity nor of its wilting coefficient have been made, but they are known to be low, since investigations of actual soil moisture conditions by Ramaley<sup>4</sup> show, during July, from 1.5 to 5.5 per cent of moisture in the drier portions, and only 11 per cent of moisture in the soil of the mesophytic meadow. In and about the shallow lakes there are small accumulations of peat and in portions of the sedge-moor the accumulation of humus has been rather considerable, so that in spots the soil becomes comparable in its organic content with that of corresponding areas in Illinois.

It seems certain that during the summer season the soil of this mountain habitat, except where it is at or near the water table, is deficient in soil moisture and this deficiency is reflected in the xerophytic aspect of its vegetation. It is interesting to note in this connection that Harvey<sup>2</sup> has found that the soil moisture in the Chicago prairie falls below the wilting coefficient at midsummer.

Summarizing the comparison of climate and soil factors in the two grasslands it will be seen that they differ widely in respect to altitude, length of growing season and in soil fertility and texture, but agree in possessing conditions of relatively low atmospheric humidity, in being exposed to high winds and in having a deficiency in the supply of soil moisture at least during the weeks of midsummer. Further the precipitation in the two habitats is practically the same in amount, although a closer study would probably show that it

differs considerably in its distribution in relation to the growing season.

Both habitats have been subject to fires and it seems possible that fire may be a factor affecting to some extent at least the development and maintenance of grassland conditions. The arguments for its effectiveness in Illinois need not be discussed here and it may only be said that in the Rocky Mountains near the valley which was the site of these observations, where there had been repeated fires, the development of tree seedlings, seemed to be a slow and difficult matter.

#### THE PLANT SUCCESSIONS

In comparing the character and order of the development of the vegetation of the two grasslands the writer will limit himself to that portion of the Illinois prairie with which he is most familiar, that is, to its occurrence in the Chicago region and will also omit all but the necessary facts regarding this vegetation since they are already available in the reports of Cowles<sup>5</sup>, Harvey and others. It will be necessary, however, to give rather more details regarding the Colorado mountain grasslands.

In both there is a well marked hydrarch succession of associations proceeding, in the Chicago region, from filling of the shallow lakes which followed the recession of the glacial Lake Chicago and which still persist in the form of larger and smaller bodies of water of which Calumet and Wolf lakes are examples. Very similar shallow lakes are found in Boulder Park as exemplified by Park Lake. The culmination of these successions is, in both regions, a rather mesophytic grassland that may very conveniently be designated prairie-meadow to distinguish it from the other associations of the series. Our present knowledge seems to point to this as the only manner of origin of the prairies of the Chicago region and as the usual course of development of most of the grasslands of Illinois, but in the Colorado mountain parks there is also a xerarch succession leading from the bare glacial gravels in a well marked series of associations slowly culminating in the same or a similar more mesophytic prairie-meadow.

#### THE HYDRARCH SUCCESSION

In the mountain parks of Colorado small shallow lakes are not uncommon, some being due to "kettle hole" origin at the time of the recession of the glaciers. Two of these, known

as Park and East lakes, are found in Boulder Park and having been rather carefully studied the succession, may be taken as representative of that of this class of mountain lakes. The soil at the bottom and shores of the lake consists of the original glacial gravels with a very small amount of alluvium carried in by tributary streams, and a larger or smaller amount of peaty vegetation. The waters are nearly stagnant on account of the small amount of run-off from surrounding areas. The larger of these lakes is only about 3 to 4 feet deep, and the other but little deeper, the conditions being similar to such shallow lakes of the Chicago area as Wolf and Calumet. It would therefore be expected that the same associations would be represented in the two regions especially as no vegetation shows a wider distribution or greater uniformity than aquatic and sub-aquatic associations, and in fact the same type of succession is actually seen but with several notable differences.

The algal association in the mountain lakes instead of being abundant and varied as in Illinois, seems to be made up of a comparatively small amount of two species of *Spirogyra*, some *Chaetophora* and *Draparnaldia* and a few blue-green algae of small size. It seems safe to say that there is not more than 20 per cent of the mass or number of species of algae found as in similar shallow water in Illinois. The other submerged aquatic community may be termed the *Myriophyllum*-*Batrachium* association, from the two species *Myriophyllum spicatum* and *Batrachium trichophyllum*, its only members. The latter is the more abundant, but the mass of the two is small compared with the submerged aquatics of more eastern waters.

Separated from the associations already mentioned and occupying the shallow water near the shores is the main aquatic community, a pondweed association, characterized by plants with ribbon-like submerged and floating leaves. Its dominant member is a bur-reed, *Sparganium angustifolium*, whose leaves float on or near the surface, and *Potamogeton lonchitis* and *P. foliosus*. This paucity of forms contrasts with the conditions in Illinois where at least twice as many species and double the mass of vegetation are to be found in the corresponding habitat. The mountain lakes are also deficient in the entire absence of any association corresponding to the water lily or cat-tail associations, but the submerged and floating leaves of the pond-weed association are followed at once by the emergent sedges. Perhaps nowhere do the two regions resemble each other more closely than in this stage of the succession known as the sedge swamp, fen, or sedgemoor. It is

true that many of the species are different but the same genera are present, and, what is more important, the ecological types are the same and the association occupies the same place in the succession.

In the Colorado parks this is often one of the most extensive associations in its extent and apparently is of rather prolonged duration. Several undetermined mosses are rather abundant upon the soil, but the initial and most abundant seed plant is *Carex utriculata*, soon mixed with *C. variabilis*, *C. lanuginosa*, *Eleocharis tenuis*, and such herbs as *Caltha rotundifolia*, *Sedum rodanthum*, *Montia chamissonis* and *Spiranthes stricta*. As soil formation advances and the drainage gradually develops, bringing the soil surface well above the ordinary water table, the change is marked by the invasion of *Carex festiva*, and many of the grasses of the succeeding grassland. It is, however, a noticeable feature of the grassland that many of the pioneers of the sedgeswamp persist in the meadow, a condition not uncommon also in the low prairie of Illinois.

Following the sedges is the main grassland community, termed the meadow association in the mountains, but corresponding directly with the prairie grassland of Illinois. In aspect the two agree closely, the bulk of vegetation being rather coarse grasses mingled with many herbaceous plants of other habits of growth. In both the other herbs outnumber the grasses in species, the mountain grassland abounding in species of *Eriogonum*, *Cerastium*, *Thalictrum*, *Potentilla*, *Geum*, *Epilobium*, *Gentiana*, *Pentstemon*, *Galium*, *Astragalus*, *Carduus*, *Senecio* and *Erigeron*. In many parts of the grasslands the limits of this meadow association may be determined by the distribution of *Erigeron macranthus*, a species that seems to be a certain indicator of the degree of mesophytism characteristic of this meadow. From the evidence at present available it is impossible to decide whether such a meadow is the true climax of these mountain parks, but it is certain that it persists for long periods and occupies the most mesophytic habitats outside the forests. In it the soil has the best development of humus and possesses the best water supply and in it is seen the greatest luxuriance of plant life, including a considerable number of species from the associations immediately above and below it. From the sedge-moor come *Carex festiva* and *C. variabilis*, *Calamagrostis canadensis*, *Deschampsia flexuosa*, *Koeleria cristata* and *Beckmannia erucaeformis*, while among the more mesophytic of the dry-grass species which intrude, are *Stipa comata*, *Festuca pseudovina* and several of

the more mesophytic species of *Muhlenbergia* and *Agropyron*. Among the more abundant grasses are several species of *Poa*, *Agropyron*, *Agrostis*, *Deschampsia*, *Phleum* and *Bromus*, the last mentioned genus being particularly abundant wherever there is a contact between the forest and grassland.

#### THE XERARCH SUCCESSION

The porous condition of the glacial gravels, which form the greater portion of the soils of Boulder Park and similar montane areas, provide such excellent natural drainage that with the recession of the mountain glaciers large areas of these gravels must have been left without vegetation and with surface but little more inviting to plants than the bare rock. At present these gravels are seen upon the mountain slopes, the ridges representing lateral and medial moraines and in the irregularly placed terminal moraines. More level areas probably represent the gravel bars of glacial streams. Upon the dry surface of these soils lichens appear to have played a comparatively small part in the establishment of vegetation, probably on account of the instability of the surface particles during high winds. Still crustose and foliose lichens are fairly abundant upon the larger boulders. The most important pioneer plant appears to be *Selaginella densa* forming mats over and between the coarse soil particles. It is closely followed by the succulent *Sedum stenopetalum* and several xerophytic grasses growing as crevice plants. The mat forming habits of the *Selaginella* prepares the soil for the other pioneers, among which *Antennaria parvifolia*, *Arenaria Fendleri*, *Chrysopsis villosa*, *Orthocarpus luteus*, *Carex stenophylla* and *Commandra pallida* are conspicuous. The constant presence and predominance of the first mentioned xerophyte would make it appropriate to term this pioneer vegetation the "Selaginella association." It is characterized by low growing perennial plants, a large percentage of bare ground and very slow advance towards a less xerophytic condition. This slow advance is largely due to the low water content of the soil, due to its coarse texture and to the extreme slowness of the humus accumulation. High winds dry the dead vegetation, break it into fragments and carrying it off, leave almost nothing to form humus, while the little that may be formed is still liable to be removed by the same agency in the form of dust. The finer soil particles, resulting from the disintegration of the gravel, are often lost in the same manner. The mat forming tendency most evident in the *Selaginella* and the habits of vegetative reproduction in such plants as the *Carex* and *Commandra*

finally increase the amount of vegetation and make the entrance of new species an easier matter.

The succeeding community may be called the *Carex-Artemisia* association from the comparative abundance of *Carex stenophylla*, *C. filifolia*, *Artemisia frigida* and *A. canadensis*. Grasses also begin to be rather conspicuous, being represented by species of *Festuca*, *Muhlenbergia* and *Koeleria*. The mat-forming habits of several of these grasses is of the greatest importance because only within such mats does the formation of humus occur, and with it the advance of the association. Even in this association not more than one-half the surface is actually covered by the vegetation. About this time the invasion of other species in small communities giving a patchy character to the vegetation becomes conspicuous. Such aggregations are found of all species, but among the more conspicuous may be mentioned those of *Antennaria parvifolia*, *Campanula rotundifolia*, *Potentilla* spp., *Aragallus Lambertii*, *A. Richardsonii*, and *Achillea millefolium*.

The succeeding stage is well developed and is perhaps the most usual vegetation of the montane parks. It is characterized by the greater development of grasses in comparison with other herbaceous species and has been designated by Ramaley, who has studied it most extensively, the "dry grassland." From a study of the composition of a large number of permanent quadrats Ramaley<sup>6</sup> finds that there is still much bare ground, amounting to about 25 per cent of the whole area during the month of July. The same investigator reporting upon the composition of the vegetation finds 30 per cent of it composed of various species of grasses, species of *Muhlenbergia*, making up 8.18 per cent, and of *Festuca* 7.78 per cent. *Carex* spp. amount to 11.25 per cent and *Aragallus* spp. to 9.68 per cent, while *Selaginella densa* still covers more than 5 per cent of the whole area. Among the more common species are *Agropyron violacea*, *Festuca octoflora*, *F. pseudovina*, *Koeleria cristata*, *Poa* spp., *Muhlenbergia gracilis*, *M. Richardsonis*, *Stipa comata*, *Carex filifolia*, *Potentilla Hippiana*, *P. gracilis*, *Aragallus Lambertii*, *A. Richardsonii*, *Artemisia* spp. and *Pentstemon procerus*. Other species are rather numerous and some become locally abundant while it is to be noted that all the species of the pioneer associations persist. There can be no doubt that this dry grassland association in its various modifications is a comparatively permanent vegetation and it is even possible that it is the climax for the more exposed situations, altho a rather careful examination leads to the conclusion that it is gradually advancing in mesophytism largely through

the mat and tuft habits of many of its grasses. This is accompanied by a slow addition of humus to the soil, improving its water-holding capacity, and this in turn reacting to cause a closer stand of vegetation. This transformation seems gradually to advance this succession to a more mesophytic association differing from that described as the climax of the hydrarch succession principally in the smaller amount of such species as *Carex festiva* and other secondary species of rather decidedly hydro-mesophytic character. Most of the grass species of the dry grassland association are still to be found, but the more xerophytic in decreasing abundance. The quantity of *Poa Muhlenbergia* and *Stipa* has increased and such forms as *Deschampsia*, *Agropyron*, *Danthonia*, *Poa* and *Avena* have come in. The grasses now show a greater predominance over other herbaceous plants although several new ones appear among the latter, the most conspicuous being *Erigeron macranthus* that seems to be a rather constant indicator of mesophytism. As previously noted this prairie-meadow association has a great variety of species, many showing peculiar local abundance, but unfortunately neither the extent of our investigations nor the space at our disposal permits their discussion in this paper. No more noticeable evidence of advancing mesophytism can be given than the data of Ramaley that the bare ground in the prairie-meadow is not more than 10 per cent of the total area and that it is often entirely absent. The question of the possibility of a forest invasion of these grasslands seems quite as far from settlement as that of the relationship of grassland and forests in Illinois and can not be discussed at present further than to remark that while the Colorado mountain grasslands show much evidence of great permanency, indications are not lacking that they are areas of potential forests and show the invasion of trees at certain points.

#### SUMMARY

From the preceding rather superficial observations the following agreements and differences may be noted as existing between these Rocky Mountain grasslands and the prairies of Illinois, as seen in the Chicago region:

#### *Agreements*

1. The two regions have very similar conditions of rainfall and humidity and in both there is a midsummer deficiency in soil moisture.

2. In both there is a well marked hydrarch succession passing from the aquatics through the sedge-moor in a closely comparable series of associations.

3. Both possess a climax prairie-meadow association in which herbaceous species other than grasses are fairly abundant.

### *Differences*

1. The two regions differ much, as has been shown, in altitude, in temperature, in length of growing season and in character of soil.

2. The mountain region is distinguished by the greater paucity of aquatic species.

3. The mountain region exhibits a xerarch succession comparable to nothing found in Illinois.

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