Review: Behaviour of Plant Species at the Edges of Their Ranges
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changes in light intensity leads to the production of protonemal branched prothalli or attenuated outgrowths, either of which may lead to vegetative increase and formation of independent plants; the prothalli show marked individual differences in reaction to light changes and in the power to survive exposure to conditions of extreme desiccation, and there is a variation of a few weeks in the time required for the germination of spores.

BEHAVIOUR OF PLANT SPECIES AT THE EDGES OF THEIR RANGES

- (I) **Griggs, R. F.** "Observations on the geographical composition of the Sugar Grove flora." *Bull. Torrey Bot. Club*, **40**, 1913, pp. 487—499, 10 text-figures.
- (II) **Griggs, R. F.** "Observations on the behaviour of some species at the edges of their ranges." *Bull. Torrey Bot. Club*, **41**, 1914, pp. 25—49.

The subject dealt with by the author of these two papers is of great general interest, and although the first paper is devoted to the vegetation of a special area it forms the basis upon which are founded the general considerations presented in the second; hence both may be summarised under the same heading.

(I) The Sugar Grove area, a narrow strip of rugged sandstone country in south-eastern Ohio, is one of those localities where the botanical interest of a large region may be said to come to a focus. Here the plant associations, upland and lowland, characteristic of eastern Ohio reach their climax as nowhere else, while about one plant in eight of the native flora reaches here the edge of its range—this group of species includes forms which stretch away in every direction of the compass, and a study of their ranges shows that the area is the key to the understanding of the plant geography of Ohio.

The author is dissatisfied with the ordinary means of mapping vegetation, since he desires to record the distribution of groups of plants of diverse affinities. The adequate representation of these, he considers, requires not one but many maps, each portraying a typical range, and in the present paper an attempt is made to treat the Sugar Grove flora in this fashion. He indicates the various difficulties encountered in obtaining adequate data for a study of this kind, and emphasises the importance of careful and intensive work on the part of local botanists whose records must largely be taken as the basis for such study.

Contrary to general expectation regarding plant distribution as controlled by climate, most of the termini of the ranges in Ohio do not follow the parallels of latitude in a general way but run in north and south lines. The author gives lists of Alleghanian plants on the south-western edges of their ranges, Appalachian and New England species on the western edges of their ranges, Appalachian plants ranging from southern New York or Connecticut to Ohio and south through the mountains, Carolinian plants on the northern edges of their ranges, Mississippian plants on the eastern edges of their ranges, and finally a miscellaneous aggregation of plants on the southern edges of their ranges—these last have little similarity in range except that they are northern but not mountain plants.

(II) The author points out that though various writers on ecology and plant geography have discussed the behaviour of species at the edges of their ranges—the habitats they affect, their reproduction, their abundance, etc.—there are but few extensive records of detailed observations on these matters; that a knowledge of the causes which set limits to the distribution of species is of fundamental importance in plant geography and can obviously be studied only at the termini of the ranges; and that an understanding of the matter can be attained only after the collection of a large amount of detailed evidence from numerous regions.

The area studied by the author seems unusually favourable for this object, since 122 species (13% of the native flora) reach their range limits in one direction or another in the Sugar Grove region. Moreover, the high cliffs and narrow ravines formed in the weathering of the sandstone impart a ruggedness to the country which is largely responsible for its botanical

interest, providing suitable habitats for many rare plants and also making the land unsuitable for agricultural purposes, thus in a measure ensuring their preservation; hence it is wilder and more nearly in its aboriginal condition than the less rugged country around, and has long been known to Ohio botanists as one of the richest collecting grounds in the state—records made over seventy years ago provide a valuable basis for comparison of present with past conditions. Although the Sugar Grove area lies at the end of the long lobe of the Alleghanian Floral Area shown in Merriam's map ("Life zones and crop zones of the United States," *U.S. Dept. Agr. Biol. Survey Bull.* **10**, 1898) as stretching into north-eastern Ohio, the plants which terminate here are by no means all Alleghanian but include species of varied geographical affinity stretching away from the area in all directions.

Owing to the difficulty of determining whether species appearing to reach their limits in a given region really do so, the author has sought to illustrate his points as far as possible with well-known and conspicuous species—*Kalmia latifolia*, *Rhododendron maximum*, etc.

The first question concerning the behaviour of a species at the edge of its range is as to its abundance—do the individual plants become gradually scarcer until finally the species fails altogether, or is it common close up to the edge where it suddenly stops? The species whose ranges end in the area studied are classified from this point of view in a series of lists, which show that in the majority of these species the individuals are abundant in their respective stations up to the very edge of their ranges. The study of species-ranges in a broad way rather than in a restricted area, however, gives the impression that these ranges are usually bordered by a fringe of outlying stations at considerable distances from each other, and some of the most interesting species of the Sugar Grove region are such outliers, which are plants of diverse geographical affinity belonging to two definite groups—Alleghanian species here on the western edge of their ranges, and southern species limited to the poor soils of the uplands.

In attempting to analyse the factors which cause the termination of the ranges, the first inquiry is naturally concerned with the reproductive functions of the plants under discussion. It has been somewhat generally supposed that the reproductive power of many species fails at the northern or southern edges of their ranges, the failure occurring at any one of several points in the life-cycle—a plant may not produce sufficiently numerous flowers to maintain its place in plant society, it may flower freely but fruit sparingly either because of faulty fertilisation or because of a short season, or conditions adequate for adult plants may be unfavourable for seedlings. To determine how far these possibilities restrict the spread of the species under consideration, the author classifies the latter according to the apparent success of the reproductive system under the following headings: flowering scantily, 8 species; fruiting sparingly although flowering freely, 10; flowering freely, fruiting not observed, 22; fruiting freely, 35; fruiting freely, seedlings also abundant, 20; pteridophytes, prothalli not observed, 7; species abundant by vegetative propagation (scattered through the foregoing groups), 7; in the remainder the fruiting behaviour was not observed. Even after allowing for changes in the classification as the result of more intensive study, the author concludes that failure of the reproductive functions is an unimportant factor in the termination of ranges in this region, most of the plants producing such a quantity of surplus seed that even a considerable falling-off in seed production would not necessarily affect the abundance of the species; that the success of seedlings is much more important than the number of seeds; and that vegetative propagation plays an important part in various cases where the species would hardly maintain themselves but for their stolons, etc. On the other hand, it seems safe to assign failure of the reproductive mechanism as the limiting factor in those species which do not fruit well and at the same time are uncommon, being without means of vegetative propagation.

The author then discusses Blytt's view that whereas a species may be ubiquitous in the centre of its range, occurring in all sorts of habitats because highly favoured by climate, at its areal boundaries it will be closely limited to those conditions which are most favourable to it. On this view we should be best able to determine the conditions most favourable to any given species by observing its behaviour on the edges of its range, but the author gives examples which lead him to the conclusion that this view cannot be maintained.

The author considers that little progress has been made in the determination of the causes of the termination of ranges. It has been generally supposed that climatic influences are the most important factors, and by appropriate manipulation of climatic data one can draw striking

parallels with vegetational zones. Merriam constructed maps from temperature data which conform remarkably closely with the life zones of North America; Transeau plotted the ratio of evaporation to rainfall, and made a map conforming with the forest areas of eastern North America in a striking fashion. Though dealing with factors to a large extent unrelated to each other, the correspondence of each of these maps with biogeography is striking enough to lead one to conclude that each of them represents the causative factor.

The author points out that if climate were the principal factor restricting the spread of plants, the edges of their ranges should show one of two conditions. (1) Since climate changes vary gradually from place to place, the controlling conditions should appear very gradually, and the plants in response, finding the life conditions more and more difficult, should become scarcer and scarcer, and finally fail—but this happens comparatively seldom in the region studied here. (2) The range should be fringed with outliers occupying habitats where the climatic conditions are locally favourable—this is the case with perhaps 7 of the 25 outliers listed by the author. For many of the plants terminating in the region studied, the author remarks that the easiest explanation of his inability to fix upon the reason for the location of their termini is that there is no reason, that they do not occupy ranges fixed by climatic conditions but are in course of adjustment, and that competition with other plant species is apparently more important than climate in fixing the limits of their ranges.

In many cases the historical factor is important. For instance, the hemlock fir (*Tsuga canadensis*) occupies its present range because this particular species, and not some other analogous conifer like the Norway spruce (*Picea excelsa*), was present in eastern North America during the Glacial Period and because it has not yet been completely displaced by the post-glacial flora; it occupies its present habitat in the area studied, not because it is better suited for that situation than any other plant of the region, but simply because the invading hardwood forest has not had so good an opportunity to gain a foothold there as elsewhere.

There are thus apparently tension zones between different species somewhat similar to the tension zones between plant societies, in these zones some species are advancing while others are being beaten back, and just as one can determine the course of ecological succession from the behaviour of plant societies in the tension zones, so one can determine the trend of geographical movements by a study of the tension zones at the edge of plant ranges.

The author draws a parallel between the spread of plants and geological erosion: plants tend to spread, and would finally come to occupy ranges as large as their adaptability to climate would permit, just as erosion would reduce all regions to base-level. Under such conditions competition between species would cease to be a factor, for that battle would have been finished and the weaker species eliminated, and with competition would disappear the historical factor which is largely a record of the state of the struggle. At best, however, such conditions obtain only for part of the plants—there are always many species which are driven out of the favourable habitats by more aggressive plants, but find a place in unfavourable situations where their competitors cannot follow them but which they can endure. Accordingly we may find a species dominant at one edge of its range but outcast at the other, and as we pass from zone to zone into more and more severe conditions, we may find the outcast species of one region becoming the dominant ones of the next, giving an appearance of complete adjustment to climatic conditions, whereas in reality only half the vegetation is controlled by climate. Where conditions have remained stable such adjustment should be found everywhere, but as species approach the limits of their adaptability to climatic conditions their progress may be expected to be increasingly retarded, so that as in base-levelling the last stages of the process are exceedingly slow. With our present limited knowledge of plant ranges it would be rash to suppose that complete climatic adjustment of vegetation is as rare as the completion of a cycle of erosion, but it is evident that various factors may intervene to disturb the process before completion—minor changes due to shifting physiography might affect the distribution of such plants as require peculiar habitats, the whole vegetation may be thrown out of adjustment whenever and wherever new types of plants or animals are evolved, and by entering into the struggle for existence introduce an entirely different set of conditions, and finally climatic revolutions are doubtless still proceeding as in the past.

While broad conclusions regarding the shifting of plant ranges cannot be drawn from the study of a single area, the behaviour of the species reaching the edges of their ranges in the area

studied seems, according to the author, to indicate clearly that the ranges terminating there, and doubtless in other areas, are not fixed but are changing, these changes falling into line with the biotic changes known to have occurred since the Glacial Period, and that the conditions of the tension zones between the species terminating in this area find their most rational interpretation as a present-day continuation of the floristic movements following that period.

AN INTENSIVE STUDY OF HABITAT VARIATION

Kraus, G. "Boden und Klima auf kleinstem Raum. Versuch einer exakten Behandlung des Standorts auf dem Wellenkalk." Jena (G. Fischer), 1911.

There are few phenomena in ecology which present so obvious a problem, or the importance of which has been so clearly recognised, as that of the distribution of vegetation on soils rich or poor in calcium carbonate. It is all the more surprising therefore that Dr Kraus's book should have received so little notice during the three years that have elapsed since its publication.

The work in question presents the results of a study, extending over eleven years, of an area in which are developed a calcareous rock (*Wellenkalk*); a sandstone (*Buntsandstein*) almost free from calcium carbonate; and *Löss*, a fine dust-like yellow deposit usually only 10–20 cm. thick, though occasionally much thicker, probably formed by the continuous leaching out of the calcium carbonate from the upper layers of the limestone. The area thus presents soils varying greatly as regards their calcium carbonate content.

By analysing numerous samples of the rock and the soil taken at different depths, Kraus shows that in the progressive disintegration of the rock by weathering, etc., the soil becomes gradually depleted of its carbonate. The highest percentages found in the soil are about equal to the lowest present in the mother rock. Where magnesium carbonate is present in the rock, this is also dissolved and carried away, but much more slowly than the calcium carbonate. Thus the same rock furnishes soils with the most various chalk percentages. If a plant is suited for a soil with a certain definite calcium carbonate percentage and occupies such a soil, the spot would not be a lasting abode for it, as owing to the continuance of the disintegration processes in the soil the calcium carbonate content rapidly changes, so that on the smallest area one could have a continuous migration and succession of different species. In this connection Kraus points out that as the percentage of carbonate changes, so does that also of other soil constituents—sand, clay, and also substances which have a more direct significance in the life of the plant—particularly magnesium, which as we know plays an important part in regard to chlorophyll. Another factor helping to bring about the great diversity of soils as regards carbonate content is the mixing of different soils which takes place in various places.

It results from this diversity of carbonate content that over the smallest area there may be considerable variations, so that plants growing apparently in the same habitat actually have their roots in soils with very different proportions of carbonate. The same differences hold also with regard to the roots of plants at different levels, as the carbonate content of different layers of soil in the same place may be very different. Kraus thus emphasises the necessity of a knowledge of what he calls the "soil profile."

As the result of analysing the soils from the roots of a large number of single plants the author comes to the conclusion that none of the plants examined occur exclusively on one soil of approximately constant calcium carbonate content; in all cases the carbonate content varies within very wide limits. Yet it is clear that some plants prefer a higher and others a lower calcium carbonate percentage.

A study was made of heterotopic plants—that is, calcareous plants growing apparently on non-calcareous soils, and vice versa. As regards chalk plants occurring among siliceous species, it was shown that in many cases their presence is due to a sporadic occurrence of calcium carbonate in the soil, but the heterotopic plants are satisfied with less carbonate than they enjoy on their normal soil, while species requiring a very high percentage do not occur as heterotopes. In addition there are cases in which limestone plants occur on areas indubitably very poor in calcium carbonate. On the other hand non-calcareous plants occur on soils containing so much calcium carbonate that they bear a calcicole flora.