RAUNKIAER'S "LIFE-FORMS" AND STATISTICAL METHODS

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(With Three Tables)

C. Raunkiaer, who on January 1, 1912, succeeded E. Warming as Professor of Botany in the University and Director of the Botanic Garden and Museum at Copenhagen, is one of that distinguished Danish school which has done so much to promote the study of the vegetative organs of plants in relation to their environment. His name is primarily associated with a system of so-called "biological types" or "life-forms" and its application in phytogeography. The idea underlying this interesting and valuable system was first expressed at a meeting of the Danish Botanical Society in December 1903, and a short summary was published in 1904 (**1**). In a more elaborate form it appeared in French in 1905 (**2**), and in a still more extended form in 1907 (**3**) and 1908 (**4**)—this last paper was translated into German by Tobler and so became more widely known than in the less accessible Danish periodicals. The following account will, it is hoped, convey to English readers a general impression of Raunkiaer's system, besides indicating the evolution of the concept on which it is based.

In the 1905 paper (**2**) Raunkiaer reviews the work of Humboldt, Grisebach, Schouw and Engler as representing what may be termed the floristic aspect of phytogeography, and that of Warming[1] on "growth-forms," and points out that something is still lacking to express the correlation between vegetation and climate. He proposes to circumscribe the domain of geographical botany as "that geographical science which endeavours to characterise the earth by its climate in so far as this is manifested by the adaptation of plants to the various seasons." As expressed later (**3**), he aims at finding a method of estimating the value of the climate of the various regions of the earth by some standard which has a bearing on plant-life. The usual physical methods fail to do this, because different physical factors may have the same effect on plant growth, and the influence of various combinations of factors may result in essentially the same growth-form. Thus "physiological drought" may arise from widely different combinations of physical factors—cold and drought. The plant itself must be the recorder of the biological value of any climate. Any valuation used must have a uniform standard; nothing can be gained by using cytological adaptations in one growth-form, bud protection in another, and leaf-structure in others.

The factor selected by Raunkiaer is the adaptation of plants to the critical or

[1] Warming, E., *Oecology of Plants* (Oxford, 1909), Ch. II.

rigorous season as expressed by the nature and the degree of protection possessed by the dormant perennating shoot-apices. The preliminary to this is a classification of plants according to shoot-apex or bud protection, and the biological types or life-forms form the basis of the earlier memoirs (**1, 2, 3, 4**).

Phanerophytes have their dormant buds on branches which project freely into the air; they are the trees and shrubs. Amongst these several modifications are recognised. (*a*) According to degree of protection one can distinguish evergreens with naked or with covered buds, and deciduous species with covered buds —these are fully illustrated in Raunkiaer's second and third papers (**2, 3**). (*b*) According to size, since this is determined by the relation between the plants and the humidity of the environment, one can distinguish (1) **megaphanerophytes** with a stature over 30 metres, (2) **mesophanerophytes** 8 to 30 m., (3) **microphanerophytes** 2 to 8 m., and (4) **nanophanerophytes** less than 2 m. high. Combining the groups (*a*) and (*b*), we have fifteen sub-types of phanerophytes.

Chamaephytes include plants with their buds or shoot-apices perennating on the surface of the ground or just above it (not exceeding 25 cm.), so that in countries with snow they will be protected in winter, while in other countries with a dry season some protection will be afforded by plant remains. The buds are thus better protected than in phanerophytes. The chamaephyte types include (1) active chamaephytes, with shoots diageotropic and persistent throughout their whole length—*Empetrum nigrum*, *Lysimachia Nummularia*, etc.; (2) passive chamaephytes with weak stems which lie on the ground—*Stellaria Holostea*, *Cerastium trigynum*, etc.; (3) suffruticose chamaephytes, in which the perennating parts remain on the surface of the ground after the herbaceous parts have died away on the approach of the critical season—many Mediterranean species of Labiatae, Papilionaceae, etc.; (4) cushion plants. Obviously, it is sometimes difficult to draw a sharp line between this life-form, the phanerophytes which precede it, and the next type.

Hemicryptophytes have their dormant buds in the upper crust of the soil, just below the surface; the aërial parts are herbaceous and die away in the critical period, so that they form an additional protection to the earth-buds. The perennating parts may be long or short, laterally extended or forming compact root-stocks, hence the group includes a large number of our native woodland and hedgerow species (*Lamium album*, *Mercurialis perennis*, etc.), and many rosette or half-rosette species (*Caltha palustris*, *Bellis perennis*, *Chrysanthemum Leucanthemum*, *Taraxacum*, etc.). This type may be subdivided to a considerable extent.

Cryptophytes include plants with their dormant parts subterranean in the case of **geophytes** with bulbs, rhizomes, tubers on stem and root, and root-buds (*Rumex Acetosella*, etc.). Another division is characterised by semi-aquatic dormant buds—**helophytes** and **hydrophytes.** The helophytes or marsh-plants do not include all so-called marsh species, but only such cryptophytes as have their buds at the bottom of the water or in the subjacent soil—*Typha*, *Sparganium*, *Acorus*, *Phragmites*, *Sagittaria*, etc. The hydrophytes (e.g. *Nymphaea*, *Zostera*, *Hippuris*, *Elodea*, *Potamogeton*) have either perennating rhizomes, etc., or winter-buds.

Therophytes, or plants of the favourable season, live through the unfavourable season as seeds; hence they are annual plants. They are specially characteristic of deserts and of regions under high cultivation. In temperate regions, two divisions are recognised: (*a*) summer-flowering annuals, (*b*) winter-flowering annuals—e.g. *Viola tricolor*—which pass through the winter in a vegetative condition.

Raunkiaer's papers, as well as an earlier paper by Warming in 1891, contain a wealth of observation and illustrations of the vegetative parts of many species, and form a distinguishing feature of the Danish school. Whilst the above grouping is easily enough determined in most cases, there is sometimes difficulty in deciding on the type, and—as Raunkiaer points out—a species may belong to one type in one country and to another type elsewhere. Thus, Ostenfeld (*Botany of the Faroes*, 1908) includes *Montia lamprosperma* both as an annual of the corn-fields and as a perennial helophyte in natural formations; also *Matricaria inodora* var. *phaeocephala* as an annual in the potato-fields and as a perennial hemicryptophyte in the sand-strand vegetation.

In his 1908 paper (**4**), Raunkiaer bases his analyses on the following ten life-forms:

1. **S** = Stem-succulents.
2. **E** = Epiphytes.
3. **MM** = Megaphanerophytes and Mesophanerophytes.
4. **M** = Microphanerophytes.
5. **N** = Nanophanerophytes.
6. **Ch** = Chamaephytes.
7. **H** = Hemicryptophytes.
8. **G** = Geophytes.
9. **HH** = Helophytes and Hydrophytes.
10. **Th** = Therophytes.

This list, starting from the phanerophytes, forms a series in which each type is on the whole better adapted for the rigour of the critical period than the one preceding it. The succulents and epiphytes stand apart by themselves.

The utilisation of these life-forms in plant-geography is only indicated in a general way in the earlier papers, but in the 1908 one (**4**) this aspect is elaborated. In Table I we give a few of Raunkiaer's analyses for various types of climate; the locality is indicated, also the total species actually analysed, while in the later columns the results are given as percentages according to the grouping given above. Such an analysis for any region is termed a *biological* or *phyto-climatic spectrum.* The *normal spectrum* is the base-line, and the outstanding features of the other spectra are deduced by comparison, not by the highest percentage in their own curve, but by the amount of variation from the normal spectrum. The latter is, ideally, the phyto-climatic spectrum of the whole earth; actually, it is obtained by computation, and at present is given only as approximate. It was arrived at by first selecting 1000 representative species, and then taking 400 of these which were carefully analysed. This number 400 has been carefully controlled in various ways. Thus, taking the stem-succulents, the number of species known is about 1300, while the total species of flowering-plants (Raunkiaer excludes pteridophytes) is taken as 13,000: this gives the 1 per cent. of the normal spectrum. Again, the Compositae have been estimated as one-tenth of the total flowering-plant population of the earth, and of the actual 400 plants analysed, 45 were Compositae, hence the spectrum in this respect approaches to an average. Other evidence deduced from his study of spectra leads Raunkiaer to regard the normal spectrum as a good working hypothesis.

What do the numbers signify? If the numbers for Seychelles in Table I are considered, it will be seen that every life-form is represented, hence this is a rich and varied flora, differing most from the normal spectrum in the high percentage of **MM** and **M**, and the low percentage of **H**. If Seychelles and the Danish

TABLE I

Examples of Biological Spectra

	Total No. of Species	Percentage of Species belonging to each Life-form									
		S	**E**	**MM**	**M**	**N**	**Ch**	**H**	**G**	**HH**	**Th**
Normal Spectrum ...	400	1	3	6	17	20	9	27	3	1	13
Eastern N. America (*B*)											
Baffin's Land ...	129	—	—	—	—	1	**30**	**51**	13	3	2
Labrador coast ...	246	—	—	2	1	8	**17**	**52**	9	5	6
Georgia	717	(0·1)	(0·4)	5	7	11	4	**55**	4	6	8
Danish West Indies ...	904	2	1	5	**23**	**30**	**12**	9	3	1	14
Western N. America (*C*)											
St Lawrence (Alaska)	126	—	—	—	—	—	**23**	**61**	11	4	1
Sitka	222	—	—	3	3	5	7	**60**	10	7	5
Death Valley	294	3	—	—	2	**21**	7	18	2	5	**42**
Western Europe, etc. (*C*)											
Francis Joseph Land	25	—	—	—	—	—	**32**	**60**	8	—	—
Spitzbergen	110	—	—	—	—	1	**22**	**60**	13	2	2
Iceland	329	—	—	—	—	2	**13**	**54**	10	10	11
Denmark	1084	—	(0·1)	1	3	3	3	**50**	11	11	18
Stuttgart	862	—	—	3	3	3	3	**54**	10	7	17
Madeira lowlands ...	213	—	—	—	1	14	7	24	—	3	**51**
Libyan Desert (Egypt)	194	—	—	—	3	9	**21**	20	4	1	**42**
Aden	176	1	—	—	7	**26**	**27**	19	3	—	17
Seychelles	258	1	3	**10**	**23**	24	6	12	3	2	16

West Indian islands (St Thomas and St John) be compared, the same varied flora is revealed, but the optimum point is shifted to the right, **N** and **Ch** being distinctly increased in the tropical but drier climate of the Danish West Indies. This is further emphasized if the spectrum for Aden be compared: more extreme drought conditions have raised **Ch** and **H**. The moister tropics show in this as in other cases a marked preponderance of phanerophytes—in other words, they are distinguished by a phanerophytic climate. With increasing drought the conditions become more antagonistic to plant-life, and the less protected life-forms give place to the more protected.

Raunkiaer's statistics refer as yet only to the Northern Hemisphere, and within this he recognises three principal regional climate-zones:

(*A*) a tropical area with uniform and high temperatures, but a varying humidity; passing northwards from this we have

(*B*) an area of decreasing warmth correlated with an increasing difference between summer and winter, but with a precipitation suitable at most times for plant-life—such areas distinguish the eastern parts of the continental masses (America and Europe-Asia);

(*C*) warmth decreasing from equator to pole as in *B*, but with decreasing precipitation, at least in summer (although further north the conditions do not differ much from *B*)—characteristic of the western parts of the continents.

These climate-zones are characterised as *A*, *B*, and *C* climate-series respectively, and they are limited by *biochores* or plant-climate boundaries as suggested by Köppen. As yet Raunkiaer has not attempted to lay down the biochores except in a tentative manner. On examining these climate-zones, it is seen in eastern North America (*B* series) that the southern spectra of the West Indies and Georgia have a large number of species with all the life-forms represented, and with a large proportion of phanerophytes. The series suggests three types of climate—phanerophytic, hemicryptophytic, and chamaephytic. Western North America shows a *C* series, in which desert regions are strongly represented. In the south, Death Valley corresponds to Georgia, and the better protected forms predominate, especially the stem-succulents and therophytes. Further north there is closer agreement with the *B* series. In the Old World the climate-zone *C* alone has been followed out. There is here a distinct contrast between therophytic (above 30 per cent.) and hemicryptophytic (above 40 per cent.) climates. The therophytes increase in deserts, and again in the more cultivated areas (Denmark and Stuttgart). The application of the therophyte test is shown in Paulsen's recent memoir[1]; the Transcaspian lowlands lie near the southern Russian steppes (Yekaterinoslaw) and the Pamir highlands, but the spectrum reveals close similarity with desert regions adjoining the Mediterranean (Libya, Samos, Cyrenaica), and this with other considerations leads Paulsen to place Transcaspia with the deserts rather than with the steppes.

These statistical methods are also applicable to more limited areas, and a fairly exhaustive study of the Arctic region has been made (**4**). Here the chamaephytes become important guides, and significance is attached to the biochores indicated by 10, 20, and 30 per cent. of chamaephytes. Thus in Nova Zembla the chamaephyte percentage of the whole flora is 19, but a more detailed analysis shows that in the zone 70—71° N. Lat., and in each degree-zone northwards the chamaephytes exceed 20 per cent. (75—76°, 31 per cent., 76—77°, 50 per cent.). The course of the 20 per cent. **Ch** biochore has been traced by Raunkiaer through all the circumpolar lands: it lies between Scandinavia and Spitzbergen and fringes the arctic coasts of Asia, crossing Bering Straits between St Lawrence Island and the Commander Islands and following the arctic coasts of Canada. The 30 per cent. **Ch** biochore includes Baffin Land, Francis Joseph Land, and Jan Mayen, but does not touch the arctic coasts of Asia or Alaska. The 10 per cent. **Ch** biochore lies between the Faroes and the Shetlands, in Norway it divides the lowlands from the highlands and the extreme north, while in Siberia it crosses the Yenisei about 67° N. Lat., and in America it lies between Sitka and Chilcat

[1] Paulsen, O. "Studies on the vegetation of the Transcaspian lowlands." *Second Danish Pamir Expedition Reports*, Copenhagen, 1912.

(Alaska) and through South Labrador. These biochores are regarded as significant, as they agree approximately with recognised isotherms: the 20 per cent. **Ch** biochore corresponds closely with the 4·4° C. June isotherm, and the 10 per cent. one with the 10° C. June isotherm. In order to compare different climates, Raunkiaer devised "hydrothermic figures," by representing in a single diagram the curve of the monthly averages of temperature and that of the monthly averages of rainfall; then, by determining the biological types or combinations of types corresponding with the hydrothermic figures, he obtained the "biological expressions" of the various climates. For instance, the tropical climate, constantly warm and humid, is characterised by the predominance of phanerophytes belonging to the least protected sub-types; the sub-tropical climate, with winter rains, by evergreen phanerophytes with unprotected buds. Temperate regions are distinguished by the essentially hemicryptophytic character of the vegetation; deserts by the therophytic type.

Summarising, it thus appears that from the equator northwards there is a definite series of biological spectra. The phanerophytes and therophytes develop with warmth, and northwards decrease and disappear. The cryptophytes, although widely distributed, also disappear in the north. The hemicryptophytes reach a maximum in temperate climates, where they remain constant at about double the normal spectrum. The chamaephytes increase northwards, and their biochores delimit certain phyto-climatic zones: (1) cold-temperate zone, the hemicryptophyte zone south of the 10 per cent. **Ch** biochore; (2) boreal zone of **H** and **Ch** between the 10 and the 20 per cent. **Ch** biochores; (3) arctic zone, the chamaephyte zone from 20 to 30 per cent. **Ch** biochores; (4) arctic-nival domain with over 30 per cent. **Ch**.

TABLE II

Altitudinal Distribution of Life-forms, Puschlav (Switzerland)

Altitude	Total No. of Species	Percentage of Species belonging to each Life-form									
		S	**E**	**MM**	**M**	**N**	**Ch**	**H**	**G**	**HH**	**Th**
Above 2850 metres ...	51	—	—	—	—	—	35	61	2	—	2
2550—2850 ,, ...	199	—	—	—	—	—	25	67	4	—	4
2250—2550 ,, ...	348	—	—	—	1	3	18	64	7	1	6
1900—2250 ,, ...	492	—	—	—	1	3	13	68	8	1	6
1550—1900 ,, ...	487	—	—	—	3	4	11	62	10	1	8
1200—1550 ,, ...	449	—	—	2·5	2·5	4	7	60	9	1	14
850—1200 ,, ...	604	—	(0·2)	2	3	5	5	55	9	2	19
Below 850 ,, ...	447	—	(0·2)	3	4	3	5	55	8	1	21
Normal Spectrum ...	400	1	3	6	17	20	9	27	3	1	13

The application of these methods to altitudinal zones will be seen from the details of the Puschlav valley in Switzerland, shown in Table II. At lower levels there is a complete series from the phanerophytes; passing upwards there is a marked decrease of all groups except **Ch** and **H**, and the 10, 20, and 30 per cent. **Ch** biochores are revealed. The same succession holds good for other mountains which have been investigated; the variation in **H** is slight, that of **Ch** great, but the altitudes of the biochores vary greatly. Thus in the Western Alps the 20 per cent. **Ch** biochore is at 2440 metres; on Tatra in the Carpathians at 2200 m.; in Norway between 1000 and 1200 m.; on Clova mountains in Scotland, between 700 and 800 m.; and in the Faroes somewhat below 500 m.

As Raunkiaer remarks, much remains to be done towards perfecting these phyto-climatic regions. The necessary spectra can only be constructed where the flora is completely known, and recorded much better than is usually done in floristic works. In the circumpolar lands there is thus a gap as regards the flora of northern Canada, and growth-forms are too often very imperfectly described, even in the standard British floras for instance. From such defective material Raunkiaer has worked out a system which all must admit is of the greatest interest and importance.

The system works much better in limited areas such as islands. Yet it is clear that our methods of subdividing continental areas with varying altitudes are so defective that any method such as Raunkiaer's merits careful consideration.

In 1909 (**5**) Raunkiaer applied his methods to the study of strand vegetation in the Danish West Indian islands where the soil is new, for instance in lagoons which are being formed and gradually filled up and covered with plants, and on sandy shores. He compared in detail a small peninsula of alluvial soil in Santa Cruz with a sandy peninsula on the coast of Denmark, and found that the percentage of growth-forms on the new soil in both localities depends upon the climatic and not upon the edaphic factors. The West Indian peninsula showed 69 per cent. of phanerophytes and the Danish peninsula 47 per cent. of hemicryptophytes—that is, in both localities the same type predominates as in the countries to which they belong. He gives other examples to illustrate the fact that the geological age of a flora has no influence in determining its biological spectrum, which is determined solely by climate. He then considers the question whether the biological spectrum of a country can be changed by immigration from other countries, and points out that immigrated and naturalised species belong to the same growth-forms and in the same mutual proportion as the native plants of the country.

The sixth paper cited (**6**) is a study in "Formationslaeren," or the vegetation on a given soil or substratum, in contrast to "plant-climatology," the term suggested to define the grouping within the larger domains determined by climatic factors, as dealt with in our earlier part. Raunkiaer points out that hitherto the treatment of plant formations has been largely subjective, each observer estimating the value of the species, so that different observers may estimate the same formation differently. It is true that any of the exact methods, e.g. the quadrat method of Clements, the "gridiron" of Oliver and Tansley[1], and the Rothamsted method of analysing and weighing grass herbage, need much time, and probably have revealed the difficulties rather than solved them. Raunkiaer's method does not attempt a complete analysis of any unit-area, but it is claimed that it gives a correct expression of the mass-conditions of the species in any plant community (formation) by means of mechanical enumeration, so that comparable results are obtained. The method consists in recording the species on a unit-area; each

[1] *New Phytologist*, **3**, 1904, p. 228.

species counts as one, and no attempt is made to distinguish between common or rare species. After 50, 100, or more unit-areas of a given plant community are thus recorded, the occurrences are added; the dominant species may occur in each unit-area, the rare on very few. Table III, slightly abridged by omitting species hardly represented, shows results from the analysis of a beech-wood undergrowth. *Anemone nemorosa* occurs in 5 out of every 5 areas examined, the other species are given on the same scale. The letters show that there are 7 geophytes, 10 hemicryptophytes, and 1 chamaephyte, and that *Anemone nemorosa* is to all the others as 6 : 94.

TABLE III

Analysis of the Undergrowth of a Beech Forest, from Raunkiaer (abridged)

						Shoot-count
Number of Unit-Areas examined	—	10	20	100	400	—
Size of Unit-Area in sq. m. ...	—	10	1	0·1	0·01	—
Anemone nemorosa	**G**	5	5	5	5	5
Gagea lutea	**G**	3	1·5	0·85	0·26	0·03
Ranunculus Ficaria	**H**	2	0·25	0·05	0·06	0·09
Oxalis Acetosella	**H**	1·5	0·75	0·8	0·25	0·2
Melica uniflora	**H**	1·5	0·25	0·25	0·01	0·008
Milium effusum	**H**	1·5	—	—	—	—
Corydalis intermedia	**G**	0·5	1	0·2	0·05	0·03
4 other species	**G**	0·5	0·5	0·2	0·13	—
6 ,, ,, ...	**H**	1·5	0·5	0·2	—	—
1 ,, ,, ...	**Ch**	—	—	0·05	—	—
Proportion of *Anemone nemorosa*	$\frac{6}{94}$	$\frac{29}{71}$	$\frac{51}{49}$	$\frac{66}{34}$	$\frac{85}{15}$	$\frac{94}{6}$

The number at the head of each of the first four columns gives the actual number of unit-areas examined and the size of the unit-area; the numbers are reduced to a scale with highest number 5, which Raunkiaer prefers to a decimal or percentage scale. The last column gives results by counting the number of shoots (leafy and flowering) of *Anemone nemorosa* on 1 sq. metre; 1281 were thus counted and their distribution is shown on a quadrat figure. The smaller unit-areas are obtained by means of a wooden frame of the requisite size which is thrown down and the included plants counted.

In a later paper (**7**) an improved type of apparatus is recommended. This consists of a ring to be fixed on a walking-stick; a piece of metal is fixed on the ring, with a screw-thread into which a metal rod can be screwed, and the length of this rod is equal to the radius of a circle of 0·1 sq. metre or any required unit-area. The stick is thrust into the ground at intervals, and the species occurring within the circle described by the tip of the rod are recorded and tabulated.

The importance of Raunkiaer's contribution lies in the careful examination of results obtained on unit-areas of different sizes[1]. That variable results are

[1] Pethybridge and Praeger ("Vegetation south of Dublin," *Proc. R. Irish Acad.* **25**, 1905, p. 141) used a similar method. Their lists were prepared from a number of representative areas by a mechanical process; the lists for each association were tabulated by numbers, and from this the general list for each plant association was prepared according to an example given; the method was not followed out in detail.

obtained will be seen from the table, and careful interpretation is necessary. It was found that the smaller the unit-area the more closely does the percentage of *Anemone* correspond to the actual count of shoots. The amount of time needed for a 10 sq. m. area is an objection; on the other hand, with small areas great care must be exercised to exclude (as is done) tips of shoots within the frame but not rooted in the unit-area. These and other variations are fully dealt with in a series of tables. As the result of experience, Raunkiaer regards 0·1 sq. m. as the most useful area. The number of readings is variable, but they must be carried on till a relatively fixed scale is reached so that further readings do not materially alter the averages from preceding readings; in the case of the beech-wood undergrowth dealt with, 50 readings of 0·1 sq. m. gave stability.

Referring to these variations Raunkiaer says (**5**, p. 38):

"The table (Table III of this paper) shows that by using 0·01 sq. m. as unit-area, and also with 0·1 sq. m., each species acquires the same degree of frequency as in a shoot-counting method if the frequency be expressed in whole numbers from 1 to 5; if one uses half-degrees or a decimal scale in determining frequency then *Gagea lutea* and *Oxalis Acetosella* are greater it is true by half a degree; but in considering the affairs of nature, one cannot and ought not to place any value on a variation between two formations which merely consists in one or more species of one having a frequency, e.g. 2, while in the other formation they have 2·5 or 1·5."

It seems then that this method has its limitations and, as with all other methods, a certain amount of subjective common sense must be used, and this becomes more evident when the remainder of the memoir (pp. 41–129) is considered. This takes up the examination of a number of representative types of vegetation in Denmark. Besides the statistical method just described, there is introduced the distribution of life-forms; thus, the *Anemone nemorosa* facies of the beech-wood is geophytic since the 0·1 sq. m. readings show geophytes 82 per cent., hemicryptophytes 18 per cent.

The first series of studies is on beech and conifer woods, scrub and cultivated lands on glacial clays and overlying humus soils. A second series deals with heaths, bogs, etc., on glacial sands, and a third with formations on salt soils. The types are too numerous to take up separately, but several examples may be used to examine the working of the statistical methods.

A successful application is evident in a comparison between (*a*) a grass-field one year sown, (*b*) grass-field 8 years old, (*c*) the field margins. It appears that of 110 species recorded 10 occur in all three situations, while in each case 5 or 6 species constitute over 66 per cent. of the whole vegetation. There is also a sharp distinction of the one-year grass by the preponderance of therophytes, while the 8-year grass and the field margins are mainly **H** and **Ch**. The decrease of *Rumex Acetosella* after the first year, and the increase of *Ranunculus repens* between the first and eighth years, are also revealed.

The examination of retrogressive scrub, with oak, hazel and blackthorn, destroyed by disforesting and grazing, a condition well-known in Britain, reveals some weaknesses of the mechanical method. In order to arrive at a list of the scrub vegetation, there are deducted "humus-plants" and species presumed to have come from adjoining cultivated fields; there remains a reputed flora of the mineral soil. Here the experience of the observer is called on to discriminate, and one can imagine that the results of various observers might differ considerably.

The studies of the ground-vegetation of woods show the method in one of its best aspects—the detection of variations due to soil and illumination. Thus in one table (No. 22) readings are shown from unit-areas in different parts of spruce woods; *Aira flexuosa* and *Oxalis Acetosella* were the two dominant plants, but they occur in different proportions and give rise to the following facies (each based on 50 readings of 0·1 sq. m.):

(*a*) *Aira* facies in open spruce wood—*Aira* 50, *Oxalis* 1, 6 other species varying from 1—4.

(*b*) *Aira-Oxalis* facies—*Aira* 50, *Oxalis* 50, 7 other species 1—6.

(*c*) *Oxalis* facies in denser and gloomier places—*Aira* 0, *Oxalis* 50, 5 other species 1—4.

(*d*) No flowering plants in quite dense and dark places.

(*e*) *Oxalis* facies in transition from spruce to beech with *Anemone* facies—*Oxalis* 50, *Aira* 0, 9 other species 1—4.

The contrast between spruce hemicryptophytic wood and beech geophytic wood is also revealed. These and other studies show that the method has great value in showing up differences in the plant covering; it does not claim to explain the variations. Under the author's experienced guidance the results obtained are valuable guides and enable one to follow the distribution. But in unskilled hands a mechanical method may be made, by formidable numerical lists, to prove what statistics usually prove—namely, anything the speaker wishes! It will still be possible to obscure important facts in plant distribution quite as much as any subjective method has done. Thus, in woods one frequently finds a drier type of vegetation interrupted by moist spring-flushes with an entirely different vegetation. If 50 readings are made at random and the results averaged, the existence of a flush vegetation might be masked, and another observer on the same ground but selecting only the drier vegetation would get a different set of statistics. In the same way, variations in illumination and topographical features might be slurred over by untrained observers. If, however, as Raunkiaer has shown, the divergent readings are kept apart, a considerable advance is possible in ecological studies. The heterogeneous nature of migratory formations on non-stabilised soils[1] is at once revealed, as in the salt-marsh vegetation described for Denmark. The method also works well in determining the composition of close vegetation like grassland, but it is not intended for determinations of yield per acre for agricultural purposes. In the case of uniform vegetation on stable soils, e.g. a Callunetum, the meagre floristic list and the openness of the vegetation should render elaborate statistical methods unnecessary.

Raunkiaer's work appears to have been hitherto somewhat neglected by all except Scandinavian botanists; among recent publications by the latter, containing results of general interest arising from the application of Raunkiaer's system in

[1] See C. B. Crampton: "The geological relations of stable and migratory plant formations." *Scottish Bot. Review*, **1**, 1912. (Review in this Journal, **1**, 1913, p. 47.)

the study of vegetation, mention may be made (in addition to the memoir by Paulsen already referred to) of a paper by Simmons on Swedish Lapland (reviewed in this Journal, **1**, p. 64). There can be little doubt that Raunkiaer has opened up a promising field for investigation, and it seems no less certain that when brought more prominently to the attention of botanists in all parts of the world his system will be applied extensively and with valuable results. For instance, the investigation of the floras of larger or smaller areas from the points of view here indicated would form an excellent branch of study for the field botanist, even if the immediate outcome were merely an annotated list of the species, with the determination of the "biological type" to which each belongs. Raunkiaer has himself brought out a new edition of his *Dansk Ekskursions-Flora* (1906) in which the biological type is indicated under the description of each species. The very fact that it is sometimes difficult to decide to which type a species should be assigned would doubtless lead to a more detailed investigation of the life-histories of many flowering plants—autecological studies of this kind are among the most urgently needed pieces of ecological work. On the other hand, the application of Raunkiaer's principles would also involve more thorough and detailed observation of climatic and other habitat factors than is usually made in phytogeographical study.

For further details, reference may be made to the 1908 paper, which gives tables based upon data from various parts of the world, and an extensive bibliography.

LIST OF RAUNKIAER'S MEMOIRS REFERRED TO

(**1**) "Om biologiske Typer, med Hensyn til Planternes Tilpasning til at overleve ugunstige Aarstider." *Bot. Tidsskrift*, **26**, 1904.

(**2**) "Types biologiques pour la géographie botanique." *Bull. Acad. Roy. d. Sci. de Danemark*, 1905, pp. 347—437, 41 figures.

(**3**) "Planterigets Livsformer og deres Betydning for Geografien." Kjöbenhavn, 1907, 132 pp., 1 plate, 77 figures.

(**4**) "Livsformernes Statistik som Grundlag for biologisk Plantegeografi." *Bot. Tidsskr.*, **29**, 1908, pp. 42—83, 34 tables. (Translation by G. Tobler in *Beih. Bot. Centralbl.*, **27**, Abt. 2, 1910, pp. 171—206.)

(**5**) "Livsformen hos Planter paa ny Jord." *Mem. Acad. Sci. de Danemark*, **8**, 1909, 70 pp., 29 figures.

(**6**) "Formationsundersögelse og Formationsstatistik." *Bot. Tidsskr.*, **30**, 1909, 110 pp., 20 figures.

(**7**) "Measuring apparatus for statistical investigations of plant-formations." *Ibid.*, **33**, 1912, pp. 45—48, 1 figure.