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CAUSAL PLANT-GEOGRAPHY

BY

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Let us suppose that on a map of Scandinavia we mark down a point in Denmark. In the place of the point we shall probably find a higher plant, e. g. a beech-tree or an oat plant. If we ask why these plants are growing there, it is apparently easy to give an answer: the cause is that men have determined that these plants shall grow in this place. If on the other hand we mark down the point in a territory in Sweden or Norway where culture has not yet been able to impress the natural plant distribution to any essential degree, we shall probably again find a higher plant in the place of the point. In this case it is very difficult to answer the question why this plant is growing there. We are here confronted with the central problem of causal plant-geography, namely that of elucidating why this plant grows in this place at this moment.

This problem cannot be solved in an absolute way, but it is possible to a certain degree to approach the solution of the problem. We shall begin by limiting the task somewhat by not regarding the place as a point, because in that case chance will play a very large part for the plant distribution, but rather as a narrow, homogeneous territory, a locality.

We shall begin by mentioning some previous attempts at solving the problem of plant distribution in nature.

It has sometimes been thought that this problem might be solved statistically. From the correct idea that it is the climate which plays the greatest part as to the distribution of the plants, it has been attempted to find the connection between climate and vegetation by examining the percentage distribution of the species within the growth-forms in a definite geographical territory. In Denmark the following percentage distribution of the species has for instance been found: (MM + M are mega-, meso-, and micro-phanerophytes, N nanophanerophytes, Ch chamaephytes, H hemicryptophytes, G geophytes, HH helo- and hydrophytes, and Th therophytes).

Number of species:	MM+M	N	CH	H	HH	G	TH
1084	4	3	3	50	11	11	18

The conclusion has been drawn that, the hemicryptophytes having by far the largest number of species, the climate of Denmark is a hemicryptophytic climate (Raunkiær 1907).

Against this method and the results obtained with it the objection may be raised that the same weight is attached to the different species of plants; thus no greater importance is attached to a plant as for instance the beech, growing in large parts of Denmark and in large numbers, than for instance to *Oenothera ammophila*, which grows in few localities only. It is this procedure which causes the hemicryptophytes, the species of which are very numerous, to have been regarded as the plants characterizing vegetation in Denmark and which makes the four per cent. MM+M, i. e. the trees and bushes, in Denmark disappear, although if the vegetation were left to itself they are those which would characterize the whole vegetation of Denmark. Therefore the climate of Denmark is not, as it has been deduced from the said figures, a hemicryptophytic climate, it is a forest climate, the climate being of such condition that the growth-form which has the greatest demands, but at the same time the one best equipped for the struggle for existence, namely the tree, can grow there. Hence it appears that the statistical method described above is unserviceable.

Or it has been tried to find climatic lines, for instance isotherms, coinciding with certain boundaries of vegetation. Now it cannot be denied that such coincidences may be found. Plants, for instance, which cannot bear freezing can only grow in places where the temperature does not drop so far that they freeze. But the attempt of connecting the plant distribution with a single climatic or edaphic factor is wrong in principle, as will be shown below.

When we shall try now to solve the problem of the distribution of plants in nature, we must begin with some preliminary remarks. What is immediately given in nature is the individual plants, not plant-communities. What is called plant-communities is not entities in the same sense as insect states, or human societies. There is nothing binding together the individual plants of a community, on the contrary they live in a merciless struggle with each other. Definite kinds of plants grow together only because they make about the same demands to surrounding conditions.

Hence it is concrete plants which must be the starting-point in our investigations and as it is impossible to investigate all plants we must limit ourselves to the characteristic ones; all rarities must be disregarded, at any rate to begin with; but when we really get hold of the representative plants the investigations at the same time take on a universal character, as they will hold good not only of the species examined, but also of a number of species of the same type.

As mentioned above, it is in general wrong to connect the distribution of a plant with a single climatic or edaphic factor. The fact is that every single plant is built into a definite environment, that is to say that by means of its morphological and physiological qualities it is able to maintain its existence under a definite combination of external conditions, light, temperature, precipitation, various qualities of the soil, and so on, which interact in determining the growth and development of the plant, and it is therefore necessary, if we want to understand its growth and development and also its distribution in nature, to see it in relation to all the said factors. It is difficult, but it can be done, and we thereby gain an understanding which the statistical investigation would never be able to provide. All this is best obtained when we try to imagine the demands of the plant on the basis of our knowledge of its manifestations of life. Its presence in a given locality is dependent on its demands being satisfied in the locality in question.

The main point, therefore, is not to investigate the dependence of many plants on a single factor, but the dependence of a few plants on all significant factors, both climatic and edaphic factors and other living organisms.

The starting-point of our investigation was the question: why does this plant grow in this locality at this moment? This problem may be subdivided into two:

(a) What plants can grow in the locality in question?
(b) Which of the plants able to grow there is really found there?

(a) The Potential Area of Distribution.

To begin with we suppose that we have only a single higher plant, for instance the birch, *Betula verrucosa* (or perhaps better a definite race of this plant), on the surface of the earth; unhampered by the competition with other plants it would be able to occupy the whole territory, where it is able to grow. If we marked down the distribution of the said plant on a map, we should get its potential area of distribution; however, this area will not generally be a continuous one. Within the area localities may be found where it cannot grow and which will then lie as islands within the area of distribution; nor is there anything to prevent the potential area of distribution from consisting of several, mutually separated areas (fig. 1).

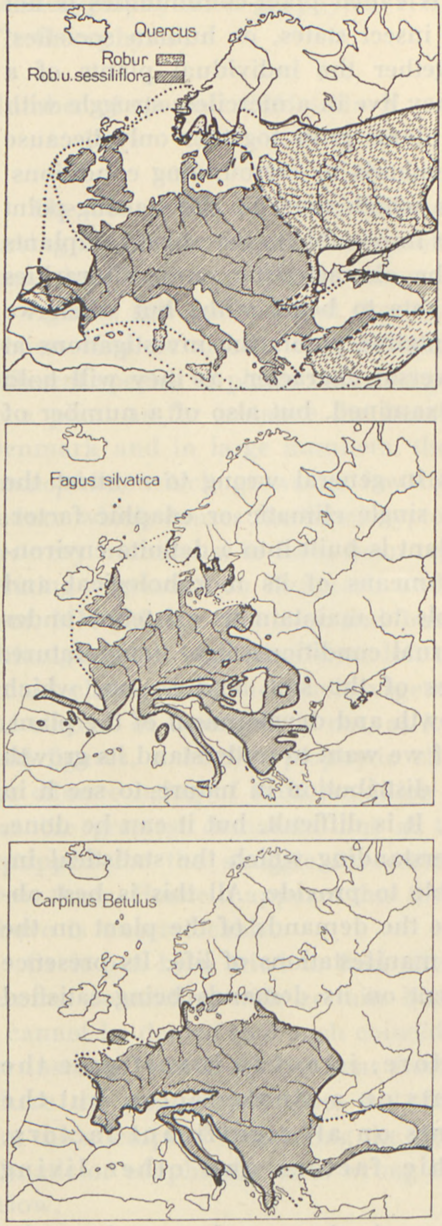

Fig. 1. The actual area of distribution of *Quercus pedunculata*, *Fagus silvatica* and *Carpinus betulus* (Rübner). Some of the boundaries of the actual area of distribution are identical with the boundaries of the potential area of distribution.

In order to explain the causal connection between the morphological and physiological qualities of the plant and its area of distribution, it would now be expedient to suppose that the places where the plant in question is not found are places where it cannot grow. A causal explanation of its potential area of distribution must therefore consist in attempting to carry out an estimation of the limits for the possibilities of existence of the plant in question.

There seem to be three main groups of conditions which must be fulfilled in order that a plant shall be able to exist.

(1) The yield of the production of matter must be positive; during the period of vegetation so much organic matter must be produced that it does not only cover the various forms of loss of dry matter during the year, but also that a surplus is left over for growth and for the reproductive organs.

(2) The plant must be able to maintain itself in the locality for an unlimited period, it must consequently be able to propagate, either vegetatively or by sexual propagation.

(3) The plant must be able to survive the unfavourable season, should such a one exist.

The said possibilities of existence will now be dealt with individually.

1. The Production of Matter as a Limiting Factor.

The production of dry matter in a plant is composed of the following items:

Gain of dry matter by assimilation of carbon dioxide
in the leaves (gross production)....................................
— Loss of dry matter by respiration in the leaves.........................
— Dry matter, used in the formation of leaves............................

Net production of dry matter of the leaves................................

Loss of dry matter by respiration in	Dry matter produced in
Axial organs......................	Axial organs......................
Roots..........................	Roots..........................
Reproductive Organs..............	Reproductive Organs (flowers, seeds)

It is expressed in the equation:

Gross production—leaf respiration—consumption of dry matter by the formation of leaves = production of dry matter in axial organs, roots and reproductive organs + loss of dry matter by respiration in axial organs, roots and reproductive organs.

As explained elsewhere, each individual quantity is influenced by a number of different factors, by the length of the period of vegetation, by climatic and edaphic factors and so on.

We are now able to estimate all the quantities entering in the equation of production at a given combination of conditions.

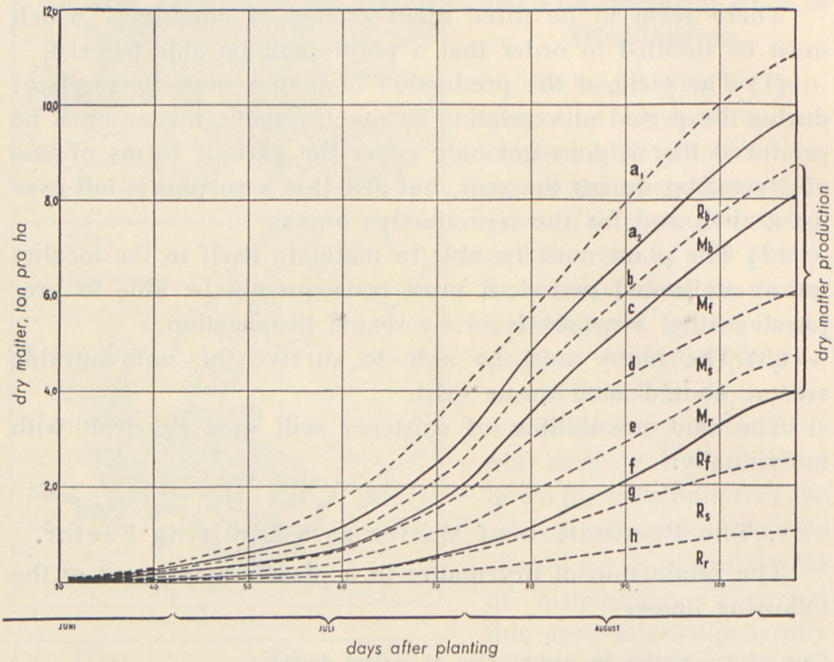

Fig. 2. The course of the individual quantities determinative of the production of matter in a stock of *Solanum nodiflorum*. All the quantities expressed as ton dry matter per ha. M_b, M_f, M_s, and M_r represent the mass of leaves, reproductive organs, stems, and roots, respectively. R_b, R_f, R_s, and R_r represent the loss of dry matter by respiration in the same organs. For further particulars see the text. (According to Poul Larsen).

As a proof hereof an investigation made by Poul Larsen (1941) of a stock of an annual plant *Solanum nodiflorum*, may be quoted. The result of this investigation is rendered in fig. 2. It appears from the figure that the quantity of matter produced and its distribution over the individual items in the equation of production can be determined at any time of the period of vegetation, and that the gross production (a_1) found agrees rather well with a_2, the production of dry matter measured directly + the loss of dry matter.

As far as forest trees are concerned, Carl Mar: Møller (1945) has made an examination of the beech, the result of which is rendered in fig. 3. From the diagram is seen the magnitude of the gross assimilation less the leaf respiration in each individual year during the whole development of the beech and further how the said quantity is distributed over the individual items of the equation of production.

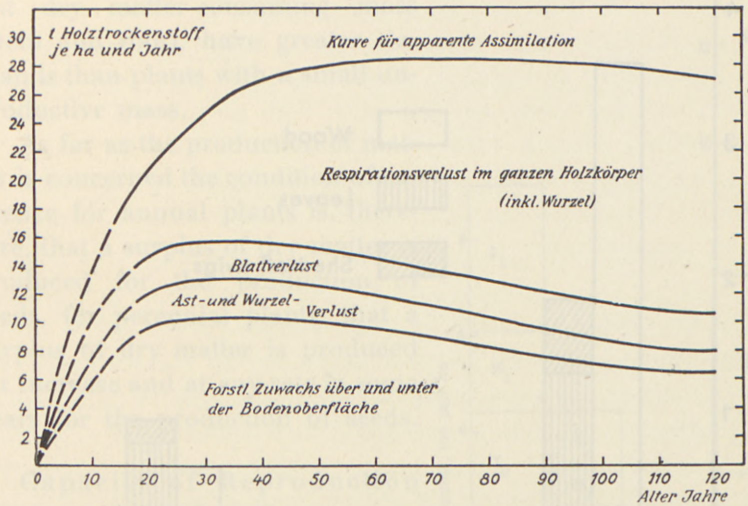

Fig. 3. Diagram showing the production of matter and its distribution in various ages in the beech, Bon. II. (Carl Mar: Møller).

In this way we are also able to determine how the production of matter changes with the surrounding conditions and to estimate when it decreases to zero, i. e. to estimate the boundaries of the potential area of distribution of the said plant as far as they are determined by the production of matter. As an example we may quote investigations made by Mork (1942) on the production of wood and leaves (+ twigs) in the birch, partly in the lowlands, and partly at an altitude of 800 m. (fig. 4). The main difference between the two localities is the length of the period of vegetation. The diagram on the left in fig. 4 shows the lowland birch with the long period of vegetation and the large production of dry matter, two thirds of which become wood, and one third only leaves and shed-off twigs. The diagram on the right shows the mountain birch with the brief period of vegetation and the low production of matter, half of which is used for the productive organs, the leaves, so that only 40 per cent. is left for wood. From the said investigations we may extrapolate the

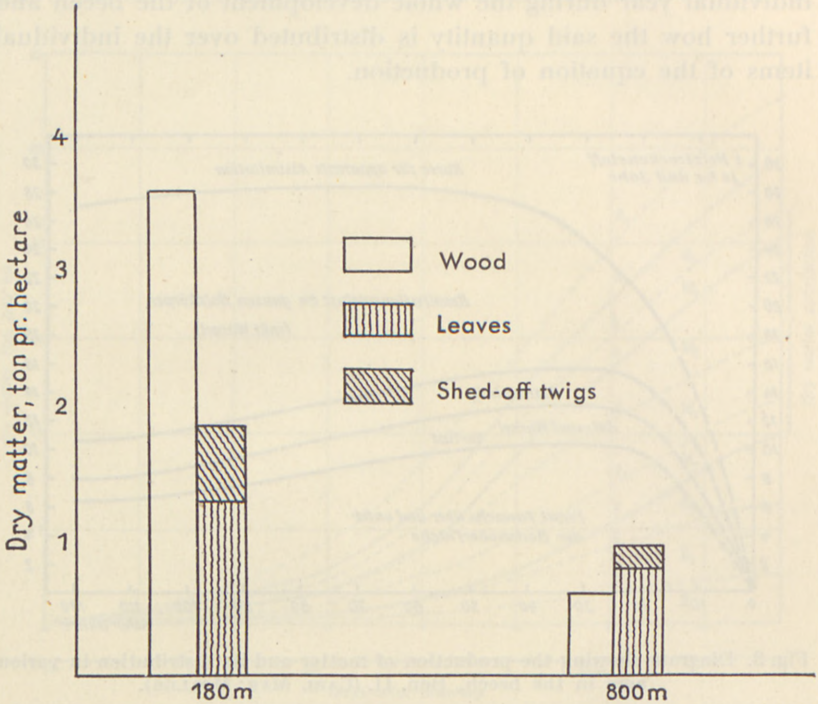

Fig. 4. Annual production of wood, leaves and shed-off branches in the birch from the lowlands and at an altitude of 800 m. (According to MORK; the production of wood corrected according to MØLLER 1945 p. 96.)

approximate altitude, where practically the whole annual production of matter must be used for leaves (and for covering the loss of respiration in the axial organs), so that the production of wood ceases. Thus we have reached the timber-line.

Parallel observations may be made when young tree plants growing in different intensities of light are examined (fig. 5). When the intensity of light has dropped to a certain limit, dependent on the kind and size of the tree, all the dry matter produced is used for production of leaves and loss by respiration, the production of wood ceases, and the tree dies (fig. 5, Kl. III).

There is some relation between the growth-form of the plant and the demands it makes to the external conditions during the period of vegetation, a fact which is especially seen when the light intensity is slight during the period of vegetation, e. g. in forests, or when the period of vegetation is brief, e. g. in arctic territories. Annual plants have greater demands than perennial weeds; trees, having a large unproductive, but dry matter-consuming mass (stem and root), have greater demands than plants with a small unproductive mass.

As far as the production of matter is concerned the condition of existence for annual plants is, therefore, that a surplus of dry matter is produced for the production of seeds, for perennial plants, that a surplus of dry matter is produced for increase and at any rate in some years for the production of seeds.

2. Capacity of Reproduction as a Limiting Factor.

In so far as the plant is able indefinitely to reproduce in a vegetative way, the reproduction will be conditioned only by an annual surplus production of dry matter.

The sexual reproduction is of a more complicated nature. It is especially dependent on the following conditions.

(1) Formation and development of flower buds. The formation of flowers is dependent on a number of different factors, the most important among which is a suitable length of the day, a suitable tem-

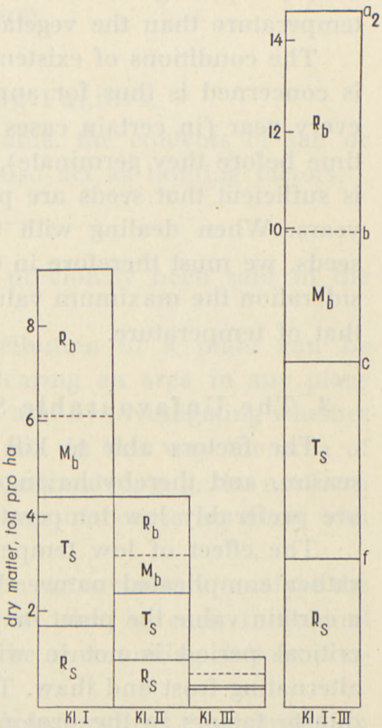

Fig. 5. The various quantities decisive of the production of matter in an unthinned 12 year old stock of ash, partly for the different classes of trees, for dominating trees (KL. I) middle-class trees (KL. II) and suppressed trees (KL. III) and partly for the whole growth (Kl. I—III). All the quantities expressed as ton dry matter per ha. The height of the columns is the gross production, M_b means mass of leaves, R_b and R_s mean loss of dry matter by respiration in leaves and axial organs, T_s means increase in the stem. As for the meaning of the letters a_2—f see fig. 2.

perature, and sometimes a certain age. Pathogenic factors, e. g. a heavy drought, may contribute to accelerate the formation of flowers.

(2) Pollination, which frequently occurs with the collaboration of definite insects.

(3) Ripening of seeds and fruit sometimes demands a higher temperature than the vegetative functions.

The conditions of existence as far as the sexual reproduction is concerned is thus for annual plants that seeds are produced every year (in certain cases seeds may, however, lie for a long time before they germinate), whereas for the perennial plants it is sufficient that seeds are produced with an interval of several years. When dealing with the conditions of the formation of seeds, we must therefore in the latter case take into special consideration the maximum values of the climatic factors, especially that of temperature.

3. The Unfavourable Season as a Limiting Factor.

The factors able to kill the plant during the unfavourable season, and thereby having a limiting effect on its distribution are preferably low temperature and lack of water.

The effect of low temperatures on the plants may be of a rather complicated nature. When the temperature drops below a certain value the plant may die. To many plants, however, the critical period is not in winter, but in the early spring with alternating frost and thaw. The resistance to low temperatures is due to factors in the protoplasm, and cannot be obtained only by alterations in the form of the plant[1]; on the whole no relation is therefore found between the growth-form of the plant and its resistance to cold. When estimating the significance of the low winter temperatures to the distribution of the plant, consideration must preferably be given to the absolute minimum temperatures, which often occur with an interval of many years only.

Not only during the favourable, but also during the unfavourable seasons a balance of water must be kept up, and lack of water may therefore frequently have a limiting effect on the distribution of the plants. The maintenance of the balance of

[1] However, a thickening of the cell wall may be supposed frequently to be of importance to the cold resistance of the plants.

water is to a very high degree dependent on the morphological properties of the plants, partly on the form and size of the root system, and partly on the anatomical structure of the leaves. There is a strong relation between the water supply and the morphological and anatomical properties. Plants throwing off the transpiring system, the leaves, are especially resistant to lack of water during the unfavourable season.

4. Other Limiting Factors.

Edaphic factors, e. g. the pH value, the contents of salt or other substances in the soil, may also act as limiting factors.

We may summarize what has previously been said in the following way:

(1) The potential area of distribution of a plant can be determined quite empirically, by clearing an area in any place of the surface of the earth whatever, and by investigating whether the plant is able to grow there or not. In this way the area of distribution of our cultural plants is estimated, e. g. the northern limit of the cereals, but the same can of course be done with regard to all other plants.

(2) Within the area of distribution we are able to analyse the production of matter, to estimate its size in each individual place, and to give an account of the surrounding factors conditioning the said size.

(3) We are able to ascertain which factors limit the distribution of the plant. The limiting factor may be (1) the surplus of the production of matter being too small (in the said case the plant may be able to produce ripe seeds right up to the limit of vegetation, compare fig. 6 *a*)[1] or (2) lack of the capacity of producing ripe seeds (in this case the plant will be able to grow vegetatively outside its area of distribution, e. g. the chestnut in Denmark, compare fig. 6 *b*) or (3) incapacity of surviving the unfavourable season (in this case the plant may grow vegetatively and produce seeds capable of germinating when protected from the unfavour-

[1] The production of matter may be a limiting factor on the outer boundary of the area of distribution. On level country it is always a limiting factor on all inner boundaries (towards all the holes) within the area of distribution.

able season, e. g. plants which are able to produce seeds in the open, but must be hibernated in green-houses, compare fig. 6 *c*).

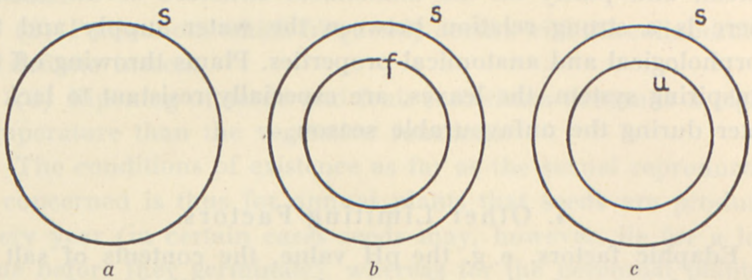

Fig. 6. Limiting factors, s production of matter, f propagation, u unfavourable season. The innermost circle marks the limit of the potential area of distribution.

Consequently we are generally able to explain the potential area of distribution of a plant, and to account for the connection between the latter and the morphological-physiological properties of the plant.

b. The Actual Area of Distribution.

For plants growing in open communities where no competition between the plants exists the potential area of distribution is identical with the actual area of distribution, i. e. the area where a given plant grows.

When on the other hand a competition exists, it is this factor that determines which of the plants able to grow on a locality is found there at the present moment. Due to this factor the actual area of distribution is in general lesser than the potential area of distribution.

We shall now try to solve the problem how to determine the actual area of distribution for a given plant if a competition with other plants exists. In order to deal with this problem we shall choose a concrete instance, namely the vegetation of Denmark.

We have in Denmark about 1100 species, the potential area of distribution of which in general comprises the greater part of the country; there is reason to suppose that, besides those, there is a number of other plants which might likewise grow in

Denmark, but which are not found here, because they have not yet arrived here on their migrations. The latter question will be disregarded here; we shall consider only the plants which are actually found in this country.

Among the plants growing in Denmark, a great number would spread over the larger part of the country if there were no other plants. The reason why they do not do so is that they are kept down in the competition with such other plants.

When, therefore, we return to the question forming the starting-point of this paper: why does this plant grow in this locality at this moment?—the answer must be: because among those whose potential area of distribution comprises the locality in question the said plant is superior to the others.

The factor being of decisive importance to the result of the struggle for existence, is generally the height of the plant. The taller plants will take away the light from the lower ones, thereby keeping them away, unless they are able to grow in the shade of the taller plants; but in that case they are only accompanying plants; they will not be able to threaten the existence of the taller plants.

When we therefore ask which growth-form will occur in a definite place in Denmark, when culture does not interfere, and vegetation is in equilibrium, the answer will be that it is the tallest growth-form able to grow in the locality in question, and that will generally be a forest tree. It is the forest trees, and not the hemicryptophytes, which, as already mentioned, will be dominating in a Denmark untouched by culture.

Among the forest trees we have again two rather different biological types, the light-trees and the shadow-trees. The difference between them is caused partly by the architecture of the assimilatory system, partly by the size of the maximum intensity of assimilation per area of leaf surface. The shadow-trees, beech, lime, and elm, have leaves placed in two rows, and a perfect architecture for utilizing the light, having a number of horizontal, almost coherent leaf planes lying above each other, the light-trees, ash, birch, and oak, have opposite leaves or $\frac{1}{3}$ or $\frac{2}{5}$ position of the leaves, which does not make it possible to build up a system of leaves able to utilize the light in a rational way. On the other hand the light-trees, at any rate ash, have a maximum intensity of assimilation which is considerably larger than that of the shadow-trees. The latter condition causes young isolated light-trees to grow faster than the shadow-trees, but the imperfect architecture of the assimilatory system causes them to be able to endure shadow to a far slighter degree than the shadow-trees. As is well-known it is the latter fact which is decisive in the competition between the trees; as the shadow-trees are able to grow up in the shadow of the light-trees, they are therefore able to displace the latter.

The shadow-trees, above all the beech, are therefore the first choosers when it is a question of covering the soil of Denmark with vegetation. The beech will therefore claim all the territories they like, i. e. light, not too meagre, mould-covered ground, preferably with a hilly surface. Under natural conditions we shall not generally get a pure beech wood in such localities, but a mixed wood, consisting mainly of beeches, especially intermingled with ashes, which, thanks to their rapid growth when young, are able to outdistance the beeches, and by means of the said quality they are to a certain degree able to assert themselves in the competition. In the beech wood an interspersion of limes and especially of elms will also appear.

In low, moist localities with stiff clay and on meagre sand beeches will not thrive and the next chooser, the oak, will get its chance here. In the said localities the oak will have superiority in the struggle with the beech, and these localities will therefore be covered mainly with oak wood. In localities with a nutritious soil, rich in mould, the oak wood will be strongly mixed with ashes, in very moist localities with running water also with alders.

Both beech and oak avoid the sour and peaty soil, whereas birches thrive on such a soil, and it will therefore be this tree which claims the latter areas.

At the bottom of the said tree communities accompanying plants will grow which are fitted for growing in their shade. In woods consisting of shadow-trees the ground vegetation is slight and, as is well known, consists partly of a spring flora, the vegetative development and flowering of which takes place before the sprouting of the trees, and which is at rest during summer. In the oak wood the light is sufficient for a development of a lower flora of ligneous plants, namely of bushes, *Corylus*, *Crataegus*, *Rhamnus*, and several others. In the birch woods an undervegetation of under-shrubs, *Calluna*, *Vaccinium* species and the like will appear.

The forest having occupied all the parts of Denmark where it is able to grow, there are still some localities left over. Those areas are the beach, the dunes, and the grey dunes behind them, which are all occupied by plants able to grow in such localities, owing to a strong specialization of their morphological and physiological properties. Further there are the fresh and the salt waters. Here we may also observe that it is the height of the flora which is the decisive factor in the struggle for the locality. In freshwaters we have closest to the beach, i. e. in low water, a bog vegetation, the assimilatory system of which lies above the surface of the water and which, if being sufficiently dense, is able to keep out other plants. Where the depth is too large for the latter vegetation, a belt of aquatic plants, fixed to the bottom and with floating leaves, will often appear, especially *Nymphaea* and *Nuphar*, which are also able to keep out other aquatic plants, and outside the latter again a belt of submerged aquatic plants.

Summary.

The central problem of causal plant-geography is this: Why does a given plant grow in this locality at this moment? This problem may again be subdivided into two: (a) what plants are able to grow in the locality in question, and (b) which of the plants able to grow there is found there at the present moment.

In order to solve the first problem, the determination of the potential area of distribution of the plants, we must investigate the conditions of existence of the plants. These seem to be the following:

(1) The yield of the production of matter must be positive; during the period of vegetation so much organic matter must be produced that it does not only cover the various forms of losses of dry matter during the year, but that a surplus is also left over for increase and (or) for the formation of reproductive organs.

(2) The plant must be able to maintain itself in the locality for an unlimited time; it must therefore be able to propagate, either vegetatively, or by sexual propagation.

(3) The plant must be able to survive the unfavourable season, should such a one exist.

The second problem, the determination of the actual area of dispersion of a plant, is solved by investigating which of the plants able to grow in the locality in question is superior to the others in the struggle for existence. The factor decisive of the result of the competition will generally be the height of the plant. The forest will therefore be the first to claim the areas, where it is able to grow, then will come lower ligneous plants, bushes, and at last the herbs.

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