THE BIOLOGICAL EQUIPMENT OF SPECIES
IN RELATION TO COMPETITION

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(WITH PLATES XIV-XVI AND SIX FIGURES IN THE TEXT.)

Darwin in The Origin of Species stated that “probably in no one case could we precisely say why one species has been victorious over another in the great battle of life,” and Yapp (48) in his Address to this Society in 1925, after quoting this passage, added “we have not progressed very far even to-day.”

Whilst only too conscious of the risk attendant upon my task I make no apology for an attempt to consider how far it is possible to analyse some of the factors of competition and replace vague generalisations by observation and measurement.

No student of field ecology can doubt the paramount importance of the competition factor and the need for replacing qualitative by quantitative data. But the question at once arises as to how far the factors involved are capable of measurement with our present knowledge and technique. Although primarily concerned here with the higher plants a reference to the causes of dominance amongst Bacteria will be helpful in this connection.

Endemic bacterial diseases which become epidemic are a particular manifestation of the assumption of dominance by cryptogamous plants which, though normally present, abruptly assume an aggressive condition. The periodicity of some diseases due to these plants is a phenomenon well known to epidemiologists. The manifestation of such periodicity is clearly dependent on the relation existing between parasite and host. Its relevancy to the relation between higher plants and their environment may be questioned on the ground that though the host is merely a particular type of environment yet a complication is introduced by the capacity of the host to develop anti-bodies to the toxins produced by the infecting organism. This objection is, however, not so fundamental as would at first sight appear, for the experiments of Pickering (25) have shown that the by-products of higher plants depress their own vigour as well as the vigour of other individuals associated with them, and, for the purpose of our comparison, it is immaterial whether the depression in fertility of the habitat be due directly to the products of the organism or to indirect auto-intoxication through the reaction of a host. In either case the environment is rendered less favourable; the difference of method does not concern us.

1 Presidential Address to the British Ecological Society delivered at the Annual Meeting on January 5, 1929.
The epidemic outbreak may clearly be due to a variety of causes such as the development of an especially virulent strain or the increased suitability of the habitat. In human diseases after a period of virulence the next epidemic phase may await the presence in the community of a sufficient proportion of non-immune individuals; a condition that may be paralleled by the epidemics of certain weeds in growing suburban areas where the ruderal habitats are plentifully provided. Another explanation is based on the assumption of a periodicity in the vigour of the organism such as Pallis (24) believed to be exhibited in Phragmites, and it may be relevant that, like the bacteria, the reed mainly multiplies by vegetative means. Such an explanation, however, demands a regular periodicity and in the case of measles, for example, would appear to be ruled out on this ground alone. But in epidemics of higher plants the phenomenon of great aggression and sometimes almost complete dominance is, as in epidemic diseases, usually followed by a diminution in frequency till the species involved becomes a normal member of the habitat. Such a history is familiar in the classical case of Elodea canadensis, and instances of the same sequence of events in the author's own experience have been exhibited by Mimulus Langsdorffii and Bidens cernua.

The epidemic nature of introductions of higher plants into new areas is too well known to need emphasis. The data furnished by Thomson (41) for New Zealand should be studied by all who are interested in these questions. One feature, however, which has occasionally been remarked upon calls for special mention in view of its importance as shedding light on possible causes. This is the fact that after the infecting organism, such as Elodea, for example, has passed its period of maximum frequency the introduction of fresh material of the same species into the pond or stream has sometimes resulted in an exacerbation which would appear to rule out the hypothesis of auto-intoxication and suggests that the presence of virgin conditions provides a stimulus sufficient to render the species vigorous enough to become dominant. Such an explanation is at least feasible and is moreover in harmony with the experience of those who cultivate plants.

The work of Greenwood and Topley (14) is important from this viewpoint. Working with considerable populations of mice under carefully controlled conditions these investigators studied the mortality from Pasteurella muris in populations to which uninfected mice were added at regular and also at irregular intervals. Their results appear to bear out fully the contention that the death rate in the population as a whole was markedly correlated with the numbers of uninfected individuals added. Similar results were obtained by Price-Jones (26) employing rats fed on Gärtner's bacillus. He found that the survivors from one epidemic infected clean rats which were introduced, whilst the previous survivors themselves fell victims to reinfection from the newcomers.

The analogous phenomenon exhibited by certain water plants justifies us
in drawing the conclusion that the vigour of a species and its consequent capacity for dominance may depend on apparently quite small and insignificant changes in the environment and provides a salutory warning against neglecting such as unimportant. But though minute differences, perhaps too small for the present crudity of our ecological technique, may be the master factors in certain cases, yet there are many features connected with the biology of the higher plants, which manifestly play an important part in determining their relative frequency, and which though remarkably neglected are yet capable of exact measurement.

We are all familiar with the fact that it is a comparatively simple matter to cultivate many species of terrestrial plants in a much wider range of conditions as regards water content, hydrogen-ion concentration, supply of nutrient salts, etc. than these species are associated with in the wild state. In the artificially protected conditions of cultures many species will withstand conditions that they cannot tolerate in nature except where by some fortuitous circumstance the pressure of competition is relieved. Under such conditions we are struck by the remarkable tolerance of species for extremes of drought and moisture, acidity or poverty of nutrient supply. With appropriately controlled conditions there is usually found to be an optimum with respect to such factors, peculiar to each species, at which the maximum vigour is attained. More rarely, as in the case of the relation of some species to soil reaction, the growth curve is bimodal.

The wide range in “water requirements” of different species and the marked diversity in this respect even between different strains of the same species, as demonstrated by Shantz and Piemeisel (37), sufficiently emphasise the importance of such optima. Often, perhaps most commonly, it is in conditions corresponding to the greatest aggregate of these optima that a particular species is best able to withstand competition. But this is by no means invariably true since some halophytes, for example, actually attain greater vigour when growing in non-saline soil, but the conditions of salinity where they normally occur depress their own vigour less than that of their chief competitors. *Rumex acetosa* affords a striking example of such selective depression from a less extreme type of habitat. This species is familiar alike to the ecologist and the agriculturalist as attaining a high frequency under acid conditions. On neutral and alkaline soils or those of low acidity the plant is normally absent or present only in a minor rôle. Yet the data obtained by Sprecher (Fig. 1), when studying the sex ratios in this species, show quite clearly (38) that for both male and female plants the vigour as indicated by the height frequency curve is appreciably greater on limed than on unlimed soil. Similar results have been obtained by other investigators, and it is pertinent to note that McIntire (21) obtained good growths of *Rumex acetosella*, in markedly alkaline soil, when not subject to the competition of lime-loving species.
Dominance may then be the consequence of unfavourable conditions acting by selective depression or to favourable conditions acting as a selective stimulus, but in either case the dominance is determined by the relative vigour of the species and its competitors. It is a natural corollary that a species in the wild state may occur under conditions that are most unfavourable to its growth as indicated by culture under conditions immune from competition. This is probably true of many annual species confined to habitats where the rigour of the conditions ensures the open character of the community in which alone they can survive. As I have elsewhere suggested the preponderance of annuals in deserts is probably due to this cause rather than to the climatic conditions. *Ranunculus parviflorus* in this country only occurs in natural habitats where the soil is very dry, as for instance on very shallow soil overlying rock. Here the plant is of low growth and small area, rarely producing more than 250 achenes and sometimes as few as 54. In cultivated ground, even when unmanured, a single plant will form winter rosettes nearly four times their normal area and produce a crop of over 2000 achenes. Again, *Lotus angustissimus*...
found on dry banks in Cornwall, where it forms quite small rosettes, will on good sandy loam without any added nutrient form a plant up to a foot in diameter. Such examples, which might be greatly amplified, sufficiently illustrate the fact that plants grow not where they would but rather where they must. It is scarcely surprising therefore that where the inhibiting effect of competition is temporarily removed by artificial conditions, as on arable land, such annuals may become pernicious weeds, as for example Salsola tragus, which is a noxious weed over a large area in the central states of America where it has been estimated that in some seasons it causes a loss of between three and five million dollars (49).

The importance for distribution of various factors such as soil reaction has been called in question on no more adequate grounds than that high acidity is not lethal to the particular species, from which it is evident that the principle here enunciated had not been apprehended. In the particular example of soil reaction the effect of competition can be demonstrated by growing an oxyphobe such as Mercurialis perennis in soils having a wide range of reaction both with and without acid-tolerant competitors, when the depression in vigour of the oxyphobe on the more acid soils becomes at once apparent. It is possible to cultivate Butomus umbellatus for several years on comparatively dry garden soil, Spartina Townsendii for an even longer period, whilst Alisma Plantago under similar conditions will produce both flowers and fruit. No one would, however, suggest that the halophytic habitat did not favour the development of the one or an aquatic condition that of the others. Such culture of plants in conditions far removed from those of their natural habitats is possible with a large number of species provided always that the surrounding soil is kept sedulously weeded. Such facts emphasise how delicate is the balance between species in the struggle for supremacy and how an adverse condition even far removed from the lethal point may weight the scale in one direction or the other.

It is not my purpose to treat here of the relation of species to the external factors of the habitat, though it is obvious that before we are in a position to assess the contributory causes of dominance or subordination of species their optimal requirements as regards light, water supply, soil reaction, supply of essential nutrients, etc. will have to be determined. The more nearly the habitat conditions simultaneously approach the optimum requirements for a given species in these several respects the less susceptible will it be to suppression by its competitors unless these same conditions bring about a corresponding increase in their vigour also. When our knowledge of such optima, and especially of their differential effects, is far more extensive than at present it may be possible to give precision to the meaning of dominance, constancy, and exclusiveness.

That many soil preferences are to be explained by their effect on relative vigour is highly probable and was admirably demonstrated by Tansley in
the particular case of the calcicole *Galium sylvestre* and the calcifuge *Galium saxatile* (40). The relation of the segregates of *Sesleria caerulea* to soil conditions has been exhaustively studied by Zlatnik in a recently published monograph (50). Under experimental conditions he finds that both the varieties *calcarea* and *uliginosa* exhibit the bimodal form of growth curve in respect to reaction to which I called attention (28) in relation to the incidence of other oxyphobe species characteristic of soils having a low hydrogen-ion concentration. From the occurrence of these segregates in nature and their behaviour in cultures Zlatnik concludes that they are restricted to special types of soil by the pressure of competition.

The shadowing of one species by another is the commonest and most obvious means of its suppression. The method is dependent for its success upon the shadowed species being incapable of growing above the aggressor and insufficiently adapted to shade conditions to tolerate them or even benefit thereby. Hence it follows that potential height and density of canopy must be considered together. Of the two trees *Betula tomentosa* and *Sorbus aucuparia*, which tend to increase towards the upper climatic limit of woodland in this country, each may reduce the light intensity beneath its shade to 12 per cent. or even 11 per cent. of that in the open, but the greater height potentiality of *Betula* which is nearly double that of *Sorbus aucuparia* is perhaps the chief factor which ensures dominance of the birch in the upland climatic birchwood, though its more efficient dispersal and consequent priority of occupation accelerates its assumption of the dominant state.

By contrast the translucent canopy of *Fraxinus excelsior* seldom reduces the light intensity to under 17 per cent., and in consequence, despite its potential height, which is comparable with that of the beech and oak, the ash-tree must endure the root competition of the dense shrub layer so characteristic of ashwoods.

Dominance in the herbaceous carpet beneath deciduous trees is largely dependent on light relations but these are complicated by the alternation between light-phase and shade-phase. Elsewhere evidence has been adduced that the difference in density of species beneath the canopies of oakwoods and beechwoods respectively is not so much due to the reduced illumination during the shade-phase, since in the *Quercetum Roboris*, with the richer ground-flora, the shade in summer is often as intense as or even more intense than in the *Fagetum*, but is dependent on the character of the branch system of *Fagus sylvatica* in which the twigs are so orientated as to cast a much greater shade than those of the oak when devoid of leaves (29). In correspondence with this feature the *Fagetum* is usually devoid of a prevernal flora, whereas that of the *Quercetum* may be rich both in species and individuals. Here the phenological relations become of primary importance in determining which are the combatants in the struggle for supremacy. A species of very low stature but producing its foliage very early in the light-phase may pre-
dominate over taller species of later development. *Ficaria verna*, of which the leaves usually begin to expand by the middle of January, thus comes to form a Society in the oakwood where the soil is moist and the shade-phase intensity low. In this Society *Mercurialis perennis*, whose foliage, unlike that of *Ficaria*, persists throughout the shade-phase, is a rare species, whereas in the areas of higher light intensity during the shade-phase the relative frequencies are reversed. So too with the frequently associated *Adoxa moschatellina* and the much taller *Circaea lutetiana*. The assimilatory period of the former usually extends from the 18th to the 166th day whereas that of *Circaea* extends from about the 59th day of the year to the 180th. *Adoxa* is thus assimilating for some 6 weeks before *Circaea* although their assimilatory periods overlap for a subsequent 15 weeks (35). This would seem to be the explanation of the fact that in the *Adoxa*-Society *Circaea lutetiana*, though present, occupies a quite subordinate rôle whereas their relations are reversed in the better-illuminated areas.

An excellent example of shading effect as a factor in competition is afforded by *Pteridium aquilinum*. The new fronds expand about the end of April or early in May and persist in the green state till November. Throughout the greater part of this period the diffuse light intensity beneath the canopy of fully-developed fronds is under 8 per cent., though the character of the foliage permits of numerous sun-flecks which somewhat mitigate the conditions beneath. Here, however, it is not merely the shading effect of the green fronds but also of the relatively persistent bracken litter which retards the growth of potential competitors (15). In the bracken Society of the Quercetum sessiflorae the prevernal species do not flourish since owing to the dead fronds they are unable to benefit greatly by the light-phase. The potential height of the bracken is very considerable. Indeed, H. S. Thompson records a specimen (42) the frond of which attained a length of 12½ ft., but this was definitely etiolated with only small pinnae, and in this country fronds rarely attain more than 2 metres without a considerable diminution of their effective assimilating and shading capacity. The value of this foliage screen as a weapon in competition cannot be better illustrated than by the struggle between *Ulex europaeus* and *Pteridium* on Harpenden Common to which attention was called in 1911 (30). *Ulex europaeus* when allowed to grow uninterruptedly there formed at one time almost pure stands from 2 to 3 metres in height. Some 24 years ago certain areas of Harpenden Common were occupied by such communities of *Ulex* in which *Pteridium* was present in small amount. The tall gorse bushes did not form a completely closed canopy so that though the bracken failed to grow above the evergreen the two species were able to persist together in an apparently balanced condition with the *Pteridium* in only small amount. During the last 20 years, however, the incidence of heath fires has progressively increased. Such fires, whilst doing little if any injury to the bracken, which together with the gorse probably benefits by the manurial
action of the ashes, result in a lapse of some seven or more years before the Ulex again attains a stature at which it can compete for light with the bracken. During the greater part of this period of years the bracken exercises a marked shading effect and materially delays the growth of the Ulex. The frequent recurrence of such fires on the areas referred to so reduced the height of the gorse that it was rapidly killed out by the bracken fronds, but the persistence of a few conspicuously tall individual bushes even in the heart of what had become a Pteridetum (Pl. XIV, Phot. 2) showed the phenomenon to be a shading effect dependent on relative height. This was further emphasised by the persistence of the Ulex as a natural hedge on the southern margin of some of these bracken areas (Pl. XIV, Phot. 1).

The persistent character of the bracken fronds renders their shading capacity almost equal to that of an evergreen, and similar importance must be attached to the persistence of the dead leaves of the beech during its juvenile stages or the mat of old foliage formed by Luzula maxima which is probably an important factor in maintaining the comparative purity of the societies of the last-named species.

In the struggle for supremacy between beech and oak the former is the victor on favourable soils because of its greater potential height, but the observations of D. Müller (23) have shown that with differences of aspect the positions may be reversed and the dominance of the oak may similarly be ensured by edaphic conditions. Hence, because we have evidence pointing to the beech as the climax phase in one locality, it is by no means safe to assume that it is equally the climax dominant throughout the area unless climatic and edaphic conditions are strictly uniform.

It is obvious that, ceteris paribus, the evergreen is better equipped in competition for light than a deciduous tree or herb since its potentiality both for assimilation and for diminishing the light intensity beneath is uninterrupted. It is this which renders the spruce fir so formidable a competitor, but the susceptibility of this species to diminishing water supply sets a lower limit to its altitudinal extension in the south of France. Deficiency in height potentiality of Taxus baccata and Buxus sempervirens may be held responsible for the usually subordinate status of these otherwise well-equipped species. But where the canopy they form is sufficiently continuous they may ultimately constitute pure societies as the taller and deciduous dominants die out.

What may be termed the "law of height," according to which in perennial communities the dominants of successive seres usually exhibit a progressive increase in stature, is in itself sufficient emphasis upon the important rôle of height alone. But the almost entire absence of data respecting the average height of the vegetative organs of species, or of the variation in this respect according to soil and situation, is sufficient evidence if such were needed that the importance of this biological feature in the competitive struggle has at the most been accorded no more than a theoretical recognition.
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The importance of the leaf-mosaic for assimilation has been stressed almost ad nauseam, but it is perhaps not improbable that this may have an equally important rôle as a screen interposed between the light and possible competitors. Indeed the small interpolated leaves of extreme examples, which appear to fill in the gaps between the better developed laminae, can add but little to the total assimilatory surface though biologically important as diminishing the sun-flecks upon which the herbage beneath in part relies for its radiant energy. The continuous social leaf-mosaics formed by the numerous shoots of *Mercurialis perennis* or *Aemone nemorosa* are as effective in this respect for the herbaceous vegetation as the mosaic of *Corylus* or *Carpinus* in the canopy of shrubs.

The work of Willstätter and Stoll (47), Lubimenko (19 and 20) and others has sufficiently demonstrated that shade species, like the shade leaves of the more plastic species, have a higher chlorophyll content with a different ratio of the assimilatory pigments compared with sun species or the corresponding sun-leaves. The shade species can not only assimilate in a lower intensity of light but find there the optimum conditions for photosynthesis. It is moreover true in general even of light-demanding species that their tolerance for shade is appreciably greater in the juvenile state. Such adaptations, whether of the juvenile or the adult, clearly militate against the efficacy of suppression by shading. The drawbacks of the habitat are further evaded by the differences in phenology already referred to and exemplified by the "prevernal," summer-green, winter-green and evergreen types of our deciduous woodlands (31).

Such physiological and phenological adjustments permit of the existence of complementary societies as defined by Woodhead (46). Despite the difference in time and spatial relations between the constituents of such societies there is probably, however, always some measure of mutual interference and competition.

The advantage of early development of new foliage in the competitive struggle has recently been emphasised by Stapledon and Davies (39), who concluded that this is one of the chief factors responsible for the aggressiveness of *Lolium italicum* when grown in various hay mixtures in competition with clovers and other grasses.

The importance of stature is seen where there is natural or artificial limitation of the growth of a closed community (cf. 8 and 18). The aggressiveness of *Bellis perennis* and *Plantago media* upon lawns and cricket-pitches derived from natural grassland is possible by reason of the artificial limitation of height of the grass, as is well shown by the quite subordinate and non-aggressive condition of these species where there is natural grassland adjoining both untended and ungrazed. Even annuals under these conditions may successfully compete with the perennial carpet, and cases are known where *Trifolium filiforme* and *Poa annua* have become dominant in lawns. It should, however, be noted that in both these species the continual removal
of their inflorescences may induce a perennial condition. This has been recorded by Henslow for *Poa annua* (13) and by the author for *Trifolium filiforme*. This change of duration is paralleled by the assumption of the perennial habit by * Arenaria serpyllifolia* at high altitudes where flower and fruit production are limited by climatic conditions.

The frequency of many low-growing species of the chalk-down is similarly dependent upon its utilisation as pasturage by sheep and rabbits. But important though relative height capacity be, and though it is essential that data of this character should be collected and recorded, yet the part played by height can easily be over-emphasised, and it is clear that height is not even the major factor in all cases between species of different height potentialities, whilst in species of approximately the same stature or having very different light requirements height is of little if any importance in competition.

Just as height and density of canopy become important by reason of the essential nature of radiant energy, so too other features become important by virtue of the necessity of water. As yet we know comparatively little respecting the effect of one root system upon another, but that there is here a considerable field for investigation is shown by comparison of the root systems of *Hypericum perforatum* and *Rumex acetosa* when grown on the same soil with and without competitors. In the presence of competitors the root system is far less richly branched so that the competition for water by other species is accentuated by a diminution of the absorbing surface (Pl. XV, Photos. 5 and 6). Further, the experiments carried out by J. W. Leather (17) seem to indicate that the water requirement of a plant increases when the volume of soil available for its exploitation diminishes.

V. T. Altonen (1) has brought forward evidence to show that it is the root competition rather than the competition for light which determines the space relations of trees in forests on poorer types of soil, and recently Ludwig Fabricus (9), by growing tree seedlings on plots in woods, with and without surrounding ditches, has demonstrated the importance of root competition between the root systems of parent trees and their offspring. The relative depths of penetration of the root systems of two species and the volume of soil they exploit may obviously be a decisive biological factor. Such differences are not only marked but may manifest themselves at a very early stage of development. For example, young seedlings of *Rumex acetosa* had rooting depths ranging from 32–79 mm. with an average of 55-4 mm. Seedlings of its common associate and rival * Arrhenatherum avenaceum* of the same age and under the same conditions had roots from 45–144 mm. in length with an average of 82-1 mm. At maturity * Arrhenatherum* still maintains this advantage, and whilst in damp pastures both attain high frequencies, with increasing aridity of the habitat * Arrhenatherum* becomes relatively more abundant.
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The rapidity of the development of the root system of many plants of dry habitats is sufficiently familiar, *Suaeda fruticosa* seedlings growing on shingle have roots 17 cm. in length when the shoot is only 7 cm. high. These differences are not only characteristic of species, but Modestov (22) found that the length and weight of the root system was even characteristic for different races of the same species. That the depth of penetration is profoundly modified by soil texture, water content, constitution of the soil atmosphere, etc. is well established. Further that different species react differently to such factors has been adequately demonstrated for the water content and the partial pressure of CO₂.

An important feature in relation to water supply is the nature of the litter produced by certain species which forms a peaty sponge as it decays at the surface of the soil. This superficial organically rich layer (31) has so high a water capacity as to retain most of the rain which falls upon it (32). As a consequence the shallow rooting species benefit whilst the deeper rooted trees and shrubs suffer from want of water. In this manner a dwarf shade-enduring peat-former such as *Vaccinium myrtillus* may bring about the suppression of the tree-layer. Similarly the sterility of the floor of a beech-wood where there is adequate illumination is probably an outcome of the imbrication of the relatively flat dead leaves which retain a considerable proportion of the incident precipitation in the capillary chambers between them.

But of all the biological features that influence frequency, capacity for propagation and dispersal must obviously be of prime consequence. Despite their obvious importance there are unfortunately surprisingly few available data respecting the vital statistics of plants, and the desirability of remedying this deficiency cannot be over-emphasised.

Since many species produce offspring both from seed and by vegetative means the question arises as to their respective merits. The strikingly successful species of *Taraxacum*, *Alchemilla*, *Hieracium*, etc. which exhibit pseudo-apogamy or the equally successful vegetative multiplication of *Elodea canadensis*, not to mention entire groups of lower plants such as the Myxophyceae and Bacteria, are sufficient indication that whatever merits the sexual process may have for the provision of variations which will enable the race to survive major vicissitudes of the environment, its absence does not preclude efficiency so long as conditions remain relatively uniform. The pseudo-apogamously produced offspring of *Citrus paradisi* have been shown to be in no way inferior in vigour to the sexually-produced offspring of the same parent. From the point of view of competition the two methods are probably to be regarded as of potentially equal value once establishment has been effected. The sexual method, except in these pseudo-apogamous species, is especially associated with the means of dispersal that promote colonisation of new areas and diminish the risk of rivalry between the parent and its offspring and between the seedlings themselves. On the other hand, vege-
tative propagation is usually associated with a better and more prolonged provision for the daughter individuals so that, whereas reproduction by means of seeds is particularly effective in the colonisation of unoccupied ground, vegetative multiplication is manifestly advantageous in closed communities.

The importance of vegetative propagation in leading to dominance is sufficiently familiar in aquatics such as Elodea canadensis in this country or Eichhornia crassipes in the waters of Florida. Similarly the extension of Opuntia inermis almost entirely by means of detached fragments at the rate of nearly a million acres a year in South Australia, illustrates the same phenomenon on land already occupied by other vegetation. A little known example but one particularly pertinent to our present consideration is that of the Japanese honeysuckle (Lonicera japonica) introduced into the south-eastern United States, where it now ranges from Texas to Massachusetts. Though rarely flowering it spreads very rapidly by means of runners and smothers out the surrounding vegetation (2).

Kerner (16) and Warming (44) are amongst the few who have furnished data respecting the rate of vegetative spread. The paucity of such data is doubtless in part due to an appreciation of the variable extent of the annual increments on the same individual or on different plants, and it is here especially evident that the familiar arithmetic mean is from the very variable character of the data more than usually unsatisfactory when no indication of either the dispersion or the probable error of the mean is furnished.

Examination of 100 stolons of Stachys sylvatica, from 20 plants growing in leaf-mould at the foot of a hedge, showed a range in length of from 5 cm. to 33 cm., the average length being 13-7 cm. Examination of the histogram of these data (Fig. 2) shows that this mean is misleading since the mode is 12 cm., whilst 50 per cent. of the stolons are 12 cm. or less in length. But the capacity to occasionally produce stolons of over 30 cm. renders the species more aggressive than if the dispersion were less marked.

Examination of the mode of growth of a typical example (Fig. 2) from this population shows several features of present interest. The length of the increments is at first short and increases with age, so that for comparison of the rate of spread in different species individuals of the same age class should be utilised. This example further shows the typically radiating trend of the majority of the new increments, from which it follows that as an implement of aggression we must know not only the length of the new increments but the duration of the old. The potential age of an increment is usually characteristic of the species and roughly exhibits a negative correlation with the diameter. But this duration is subject to modification accompanying differences in texture and water content of the soil. In general the damper the habitat the shorter the duration. Some species, such as Circaea lutetiana, and Adoxa moschatellina, are pseudo-annual: as Warming pointed out this
condition is frequently accompanied by unbranched aerial shoots. The rhizomes of *Oxalis acetosella* though slender may persist for 2 to 3 years, whilst those of *Anemone nemorosa* live 3–5 years in clay and 4–6 years in loam.

*Stachys sylvatica* is especially interesting as it forms aerial shoots comparable to the stolons just above the surface of the ground which are often

**Fig. 2.** Length of stolons in *Stachys sylvatica*. The Roman numerals indicate buds of successive seasons.
nearly twice the length of the stolons proper. It is obvious that the length of the stolon is not merely determined by the amount of material available for its construction but also by the work required to penetrate a certain distance through the soil. Hence we find that not only are the overground laterals longer than the subterranean but that the average length of the stolons diminishes with the density of the soil. I have elsewhere furnished data (31) showing that in woodland soils there is a very marked vertical gradient in the horizontal penetrability of the soil. Associated with this the thinner and more delicate rhizomes such as those of Oxalis acetosella and Adoxa moschatellina are relatively superficial, whilst deeply situated rhizomes such as those of Arum maculatum and Pteridium aquilinum are in general robust. Oxalis acetosella growing in the loose-textured humus soil of a beechwood produced rhizomes which showed annual increments ranging from 3 to 22 cm. in length with an average of 10.5 cm. and a coefficient of variation of 41 per cent. Plants growing in a wood on loam showed increments of from 2.4 to 12 cm. and an average of 7.2 cm. with a coefficient of variation of 32.3 per cent. The difference in the arithmetic means for the two types of soil was thus 3.3 cm., whilst the standard error of this difference is only 0.71. Three times this standard error is about two-thirds the difference of the means, so that the difference is almost certainly a real one and not due to errors of sampling. It might, however, reasonably be urged that in this instance we have little indication, except the general growth of the plants, which appeared to be of comparable vigour, that the observed difference in rate of spread was not largely an outcome of differences in nutrition. A more critical instance is therefore afforded by Stachys sylvatica since it is possible to compare here the relative growth of the overground “runners” and “subterranean” stolons. In so far as the length of the lateral shoots is affected by nutrition this may be expected to influence the aerial and subterranean laterals on the same plant to the same degree. Examination of a number of plants growing respectively in leaf-mould on loam and in stiff clay showed that there was no significant difference in the lengths of the overground laterals, though laterals of both types were produced in fewer numbers from the plants on clay. The stolons of the plants growing in clay ranged from 1 cm. to 30 cm. in length with a mean value of 10-24 cm. and a standard error of 0.556. The mean for the plants growing in loose-textured soil was 13.7 cm. with a standard error of 0.69. The difference of the means is thus 3.4 cm. and the standard error of difference 0.88 (cf. Fig. 3). The difference here is not only marked and “significant” but must clearly be attributed to the decreased resistance to be overcome in the lighter soil. If as seems probable the observed differences in Oxalis acetosella were similarly due to soil texture then we have the striking fact that decrease in soil density may result in an increased rate of spread amounting to 33 per cent. in the case of Stachys sylvatica and as much as 46 per cent. in the case of Oxalis acetosella. The more pronounced effect of
soil texture in the latter species can probably be correlated with the slender character of its rhizomes. Since species with slender rhizomes such as Oxalis acetosella, Adoxa moschatellina, Asperula odorata, etc. will flourish on comparatively dense soils, though their rate of growth is slow, it is not improbable that their comparative abundance in suitable locations where the soil is loose in texture is correlated with the increased rate of spread.

The species producing overground plagiotropic shoots would therefore appear to be at an advantage, and it is of course true that the rate of spread by means of runners is in many species very great. The runners of Glechoma hederacea are frequently over 73 cm. in length whilst those of Galeobdolon luteum are commonly over half a metre and sometimes attain a length of over three times that figure. But though on some light soils, as in parts of the Forest of Dean, Galeobdolon may be dominant over considerable areas the efficiency of this means of spread is considerably diminished by the fact that the adventitious roots have to penetrate the surface litter and traverse a layer of soil, perhaps already fully exploited by other roots, and certainly containing toxic substances, before becoming effective as a means of support. Lotus uliginosus can spread over 360 sq. cm. in one year (Fig. 4) and root at

![Figure 3. Length of stolons of Stachys sylvatica in relation to soil texture.](image-url)
Fig. 4. Mode of spread by rooting from nodes of prostrate shoots in *Lotus uliginosus*.

Each node, but is rarely dominant. The effectiveness of vegetative multiplication as a means of aggression results however mainly from the junction with the parent plant of which all the food resources are at the disposal of the new shoot. The shoot of *Epilobium angustifolium* or *Achillea millefolium* may
develop in the midst of a closed community where the shade is too intense for the germination or growth of seedlings, but with the reserves of the parent available the new shoot can continue its growth, even though respiration be considerably in excess of assimilation, till it has reached a level at which there is a credit balance. A common sequence of succession on the burnt areas of gravel heaths in Hertfordshire adequately illustrates the rôle of vegetative propagation. Here in the first season after burning numerous seedlings appear, amongst which the most frequent are two annuals, viz. Senecio sylvaticus and Galeopsis tetrahit, and the perennials Rumex acetosella, Holcus lanatus, Anthoxanthum odoratum and Agrostis alba. Of these Rumex acetosella, by means of its wonderful capacity for the production of adventitious shoots from its extensive and shallow root system, usually becomes a dominant at an early stage. Holcus lanatus, although capable of a greater growth in height than Rumex, does not produce stolons during the first season, but subsequently, owing to this greater height and rapid spread, quickly assumes dominance (Pl. XIV, Phot. 4), Rumex acetosella becoming relatively unimportant. Anthoxanthum odoratum, though of about the same potential height as Holcus, maintains but a slow rate of spread, so that the relative proportions of these two species are closely related to the areas they can respectively occupy before coming into contact, and the Anthoxanthum only becomes important when the number of seedlings is exceptionally high.

On general grounds it would seem that in the case of a species otherwise well equipped for the competitive struggle, even though producing few seeds or seedlings and having a slow rate of vegetative increase, there would be a steady if slow spread till dominance is attained. This would, however, only be true if the perennial species had potential immortality or at least a very prolonged life. Data on this point are hard to seek. That some plants have a definite length of life would appear from the simultaneous flowering and decease of certain bamboos over large stretches of country and comparable phenomena in relation to the talipot palm and Chusquea abietifolia (36). According to Hackel cuttings or layerings of bamboos give rise to individuals that flower at the same time as do the parents from which they are taken. The interesting experiments of Priestley and Woofenden with Stellaria media certainly appear to indicate a definite senescence in that species (27). We know that trees die of old age, but the span of life of any species is rarely noted except where it is very short as in some species of Dianthus, or where as with the bamboos the phenomenon is catastrophic in its incidence. For species with a long span of life the standard deviation would be expected to be high. In the case of annuals of the same species growing together under identical conditions the span of life for different individuals may vary by 2 months. Assuming the mean length of life to be 12 months there is a possible difference of 15 per cent. An equivalent degree of variation in a tree with a normal span of 500 years would mean a range of 75 years. Such a
degree of variation would easily obscure the fundamental fact and lead to the erroneous supposition that length-of-life has no significance in relation to plants. *Linaria vulgaris* is interesting from this point of view. The primary stem is entirely vegetative. From the main tap-root and from most of the laterals numerous adventitious shoots are produced. A typical specimen had by its second year of growth produced no less than 193 adventitious shoots. Of these most, as shown by the frequency diagram (Fig. 5), were borne on the main root, or on laterals at between 14 and 28 cm. from the parent plant. The maximum distance at which an adventitious shoot was observed was 46 cm. This same plant produced about 29,000 seeds, of which, however, the percentage germination was as usual in this species very low. Since *L. vulgaris* can attain a height of from 2 to 3 ft. it is not ill equipped in that respect; nevertheless, despite its active vegetative propagation, its slow rate of spread and low output of viable seeds must be held mainly responsible for its extremely local dominance. But these would scarcely suffice unless the average duration of life of the individual is relatively short.

Here it may not be inappropriate to refer to the well-known vigour of
hybrids which by their increased vegetative vigour may compensate for their frequent sterility. The natural hybrid between *Medicago sativa* and *Medicago falcata*, known as *Medicago sylvestris*, was estimated by Waldron to possess 47.5 per cent. greater weight than either parent (43), whilst Blaringhem (4) found that not only was the dry weight of the hybrid between *Digitalis purpurea* and *D. lutea* from 200 to 275 gm. as compared with 150 gm. for *D. purpurea* and 50 gm. for *D. lutea*, but whereas the common foxglove is frequently biennial and the yellow foxglove triennial the hybrid between them survives for a number of years. Leaving on one side the very debatable question of the origin of new species by hybridisation, it is clear that this may be the means of providing types that fulfil a different biological rôle.

How far duration of life is important cannot be estimated until we possess far more data than at present, in the collection of which Botanical Gardens and private cultivators of wild species might materially assist. Our knowledge of reproduction by means of seeds is much more extensive than of vegetative multiplication, nevertheless for no single community either British or foreign could the reproductive capacities of even the chief constituents be fully stated. (For data regarding some woodland species cf. (34).)

The number of seeds produced by an individual under suitable illumination bears a direct relation to the size of the plant, but whilst the lower limit has little if any significance, since quite depauperate plants will develop a few fertile seeds, the average seed output of a particular species in a given habitat may largely determine the frequency of occurrence, as for example *Anthoxanthum odoratum* on the burnt areas already referred to.

Actually, though the coefficient of variation with respect to seed production is high, the modes and maxima for different species are often widely separated. For example, amongst the shingle plants at Blakeney Point *Rumex crispus* v. *trigranulatus* will produce from 4000 to 25,000 seeds, *Glaucium luteum* of average size will ripen 24,000 seeds and a large plant will produce nearly 70,000, whilst *Beta maritima* will form up to 130,000 seeds. In contrast to these high numbers, a large-sized *Statice binervosa* forms less than 1000 seeds, whilst an average plant only produces about 400. The annual *Desmarestia loliacea* commonly produces between 150 and 800 fruits, whilst *Lepturus filiformis* rarely has an output of more than 90.

Having regard to the strain that seed production imposes upon the species no one can doubt that natural selection will tend to eliminate species or strains of species in which seed production exceeds the necessary minimum. So that we are confronted with the question as to whether large seed output is correlated with high frequency or high mortality. In other words, are we to regard the potential seed production as primarily an instrument of aggression or as in the nature of a life insurance premium for the survival of the species?

It is a familiar statement that most parasites have a high seed output, which is generally held to be a necessary concomitant of their very restricted...
environment, entailing a low percentage survival. Actually, however, there seems to be little data to support this. It is true that Orobanche minor has according to Wentz (45) about 1500 seeds in each capsule, but as the entire plant bears only 70–90 capsules the total number of seeds is less than 150,000, an output comparable to that of a large plant of Scrophularia nodosa, but small in comparison with a full-grown Verbascum thapsus with up to half a million seeds, or a large plant of Digitalis purpurea with three-quarters of a million, both with high germinative capacity. (It should, however, be noted that O. minor can grow on a variety of hosts. O. elatior, confined to Centaurea scabiosa, probably has a much larger seed output.)

That a high rate of mortality necessitates a large seed output is obvious, but is the number produced more than adequate for the maintenance of the species? Despite the enormous number of seeds ripened by the foxglove or mullein their number in any particular locality remains on the average remarkably constant. Occasionally after a woodland area has been felled or coppiced these two species may occur in great profusion, under which circumstances the number of seeds shed must be prodigious. Nevertheless in a few years' time the foxgloves and mulleins have resumed their normal frequency. The advantage of numerous seeds over and above the demands of normal mortality is here apparently quite temporary, an attribute of doubtful survival value unless the conditions determining such periodicity obtain in nature and the seeds lie dormant in the soil.

Actually the same phenomenon in miniature is realised under natural conditions when an old tree decays and so breaches the canopy of foliage, and there seems adequate reason for believing that dormant seeds are largely responsible for the rapid colonisation. The circumstances are paralleled by certain mud-plants (33) such as Limosella aquatica, Rumex limosus and Alopecurus fulvus, which periodically recur in such numbers as obviously to depend on dormant seeds, an assumption borne out by experiment.

Such instances emphasise the advantages of reproduction by seed as a means of rapid occupation of territory suddenly rendered available. The importance of such capacity is obviously related to the normal habitat of the species. Mercurialis perennis with its efficient and rapid vegetative increase is quite successful, although it produces but a small number of seeds of which only about 5 per cent. are viable. Ficaria verna towards its northern limit rarely produces fertile seed and multiplies almost exclusively by its rain-distributed bulbils. Both are normally associated with climax or sub-climax phases of vegetation when the capacity for rapid occupation is not so essential to success as in the earlier seres. It is perhaps true in general that the capacity for large seed output of viable seeds becomes the more important the earlier the phase of succession with which the species is associated. Conversely the more the habitat of a species approaches the climax the greater is the importance attaching to the capacity of vegetative increase.
The species of *Hypericum* form an interesting commentary upon methods of propagation. *H. perforatum* and *H. pulchrum*, both present in coppiced areas and woodland margins, are both capable of vegetative increase, but whereas *H. pulchrum* has a seed output of about 6000 and is occasional, *H. perforatum* which is often common has a normal seed output of about 8000, whilst vigorous plants may produce up to 155,000 seeds. *H. androsaemum* when well grown may easily produce 45,000 seeds but has no specialised mode of vegetative spread, and as a constituent of the climax phase is isolated in occurrence and the number of individuals few.

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The production of a large number of seeds has, however, certain drawbacks. In particular numerous seeds are usually associated with small size and consequently less food reserves to nourish the seedling in the early and more critical phases of its development. The value of large seeds in affecting just such characteristics as height and leaf canopy, which we have seen to be important in competition, is well illustrated by the experimental cultures of Eitingen (7), who grew oak seedlings from acorns of differing weights. These not only showed a striking difference in height and leaf area, but, what is perhaps more surprising, a persistence of this difference over a period of at least 8 years. From acorns of an average weight of about 2 gm. the average height in 5 years was $44.1 \pm 0.9$ cm. and the leaf area 546 sq. cm., whilst from acorns of an average weight of 7-2 gm. the average height was $82.5 \pm 1.3$ cm. and the leaf area 882 sq. cm. Acorns of intermediate weight gave more or less intermediate values. At the end of 8 years the differences, though smaller, were still very appreciable. Essential as a knowledge of seeding capacity is if our study of plant communities is to be placed on a scientific basis, yet it is valueless unless we also know the percentage germination. The range in this respect is surprising. S. K. Mukerji working with English seed of *Mercurialis perennis* found that usually under 5 per cent. were viable. Even in France, nearer the centre of its area, only about 15 per cent. appear to be viable, whereas *Mercurialis annua* even in Britain produces about 70 per cent. of viable seeds. *Clematis vitalba* with a high seed production has but a low germinative capacity, often not exceeding 2 per cent. Amongst our native forest trees *Alnus glutinosa* and *Betula alba* both exhibit great variability in this respect, but usually the germination does not exceed 25 per cent. On the other hand, over 90 per cent. commonly obtains with seed of *Fraxinus excelsior*.

Most seeds germinate best in the light, though a few such as those of *Datura stramonium* germinate best in the dark. In view of the marked fluctuations of temperature as between day and night that obtain in nature, it is interesting to note that the seeds of several species have been shown to give but low percentage germinations at constant temperatures, whereas at fluctuating temperatures germination took place freely. A striking example is furnished by *Cynodon dactylon*. Harrington (12) found that the seeds of
this species failed to germinate when grown at constant temperatures ranging from 20° to 30° C., but with alternating temperatures between 15° and 25° to 35° C. he obtained percentage germinations ranging from 15 per cent. to nearly 80 per cent. It is noteworthy that in this country, where the species is at the limit of its geographical range, Cynodon dactylon is confined to sandy shores where temperature fluctuations are accentuated.

Perhaps almost more important than the actual number of seeds which germinate is the manner in which they do so. Some idea of the incidence and magnitude of infant mortality amongst plants is furnished by the case of a large plant of Verbascum thapsus which flowered on an area of waste ground (Fig. 6). This plant produced about 700,000 seeds of which about 88 per cent. were viable. But of its potential offspring numbering over 600,000 there only remained after 6 months 108 individuals scattered at distances up to 30 ft. from the parent individual. These represented but a small fraction of the original seedlings, though in succeeding years seeds that had remained dormant subsequently germinated.

The causes of such high infant mortality are very varied, but as field observation shows it is often catastrophic in the sense that a large proportion disappear within a limited period.

It may then clearly be of paramount importance for the survival of offspring whether the seeds germinate at the same time or over a prolonged period.
Phot. 7. Seedlings of *Helianthemum Breweri* showing "discontinuous germination." Seedlings of three ages are indicated by white "daggers." These seedlings are the progeny of seeds shed simultaneously.

Phot. 8. Seedlings of *Erodium cicutarium* showing "simultaneous germination."

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I am not aware of any attempt to distinguish between the various types of germination, and as the more extreme types appear to group themselves into definite categories it will be convenient to refer to them by means of definite terms.

The first type may be termed *simultaneous germination* and is exemplified by such plants as *Salix* and *Populus* among trees and *Erodium cicutarium* or *Ranunculus parviflorus* among herbs. Here all the seeds germinate within a comparatively short period. In the case of *Salix* the seeds do not retain their vitality more than about 3 weeks after being shed and those of *Populus* only from 8–10 days (14). The vitality of *Ranunculus parviflorus* seeds is retained for some time. In nature the seeds are shed over a period in the early summer but do not germinate till September, when those which are viable do so within about a fortnight, and during a period of 8 years I have never seen seedlings at any other season. This species is a typical example of a “winter annual” (i.e. one which germinates in autumn and withers at the advent of summer or late autumn) with simultaneous germination, and this latter feature constitutes a definite danger since almost all the seedlings may be destroyed by the same adverse condition. *Veronica hederacea* affords an example of a “summer annual” with simultaneous germination. The dangers attendant upon simultaneous germination are obvious, though delay due to accidental burial may be an occasional safeguard. *Continuous germination* where the process continues over a long period without obvious interruption so long as climatic conditions are favourable is exemplified by *Lithospermum arvense*. By far the commonest type, however, is that in which the germination takes place at markedly separated intervals, *e.g.* *Helianthemum* *Breveri*, of which seedlings may be seen at one time of three very different ages (cf. Pl. XVI, Phot. 7). Of the seeds shed by the elm some germinate within about a fortnight whilst others remain dormant till the following spring. The seeds of many labiates germinate both in spring and autumn (6), whilst the germination of *Butomus*, *Alisma* and *Sagittaria* appears to take place at quite irregular intervals (10). Of the seeds of *Crataegus*, some germinate in the first spring after being shed, others not till the second spring, whilst the seeds of *Prunus avium* exhibit a periodic vernal germination that may extend over a term of four years. Such discontinuous germination may be and probably is of great importance for the survival of the species, and is dependent on a variety of causes, from variations in permeability of the testas to differences in the degree of differentiation of the contained embryos. In plants whose seeds will germinate as soon as shed a pseudo-discontinuous type may occur despite the physiological homogeneity of the seeds owing to their being shed at irregular intervals.

But though the danger of extermination of an entire crop of seedlings, due perhaps to the browsing of a slug or a sudden drought, may be circumvented by discontinuous germination, it has attendant dangers. The experiments
described by the Duke of Bedford and Spencer Pickering (3), in which a second sowing of the same species was made at intervals varying from 4 to 20 days, showed that there was a deleterious effect in respect of the total weight produced, although in the case of simultaneous germination the weight of the total crop of one species would appear to be independent of the number of individuals present. With respect to the latter feature, however, it should be noted that though the total weight of the crop may be the same the crowding probably effects a reduction in seed output, since Brenchley, when growing barley in water cultures so that the mineral food-supply was not a limiting factor, found a lower seed production in the crowded plants despite their increased vegetative vigour (5). Where the interval is long, however, the deleterious effect on the first crop of subsequent germinations is probably negligible, and owing to the need of light for germination of most seeds will not take place where the growth is already dense.

We have already emphasised the relatively greater importance of vegetative increase in closed communities and of increase by seed in the earlier and more open stages of succession. It is interesting therefore to note that in plastic species adapted to either method the conditions of greater illumination and lower water content usually associated with the earlier phases are those which tend to promote seed production. With the artificial coppicing of a woodland, for example, Galeobdolon luteum, Conopodium denudatum, etc. pass from the vegetative to the flowering condition, and Scilla nutans may exhibit an increase of nearly 24 per cent. in flower production despite the reduction in its assimilatory activity under the increased illumination (34).

Our consideration of the few biological features it has been possible to deal with in this address has sufficiently demonstrated the necessity for collecting data of this character and the possibility of their exact numerical expression. As yet it is an almost untouched field, but unless ecology is to become a battleground of polemics rather than a science it is one that we must hasten to survey. If I have succeeded in traversing some unfrequented and some untrodden paths without losing myself in the wayside tangle I owe it to the fact that I have been privileged to travel the highway under the guidance of one of the most distinguished of my predecessors in this office.

LITERATURE REFERENCES.


(8) Farrow, E. P. “Observations relating to competition between plants.” This Journal, 5, 155–172, 1917.


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(40) Tansley, A. G. “On the Competition between Galium saxatile L. and Galium sylvaticum Poll. on different types of soil.” This Journal 5, 155-172, 1917.


(45) Wentz. (Quoted from Hegi, Flora von Mitteleuropa.)


(48) Yapp, R. H. “The Concept of the Habitat.” This Journal, 10, 1-17, 1922.


POSTSCRIPT.

Since the above address was delivered the severe and prolonged frost in the early months of the year has, by its effects on various species, demonstrated the biological importance of modes of germination. Of the autumn germinating Ranunculus parviflorus in which germination is simultaneous all the seedlings in the author’s garden were destroyed. Of the seedlings of Helianthemum Breweri (discontinuous) all the earlier germinations were killed, but the species has survived by reason of the discontinuous germination, since one batch of seeds did not germinate till after the end of the severe weather. These facts moreover emphasise the great ecological importance they may attach to extreme conditions despite the infrequency of their occurrence.