

FAIRY RING KINETICS

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(With 2 Text-figures)

The behaviour of a system of fairy rings, and in particular its condition on attaining a steady state, is studied theoretically with the help of a simple geometrical model. From the properties of this model, the proportion of the ground occupied by the mycelium is calculated and shown graphically as a function of the growth rate for different values of the reproduction rate. The consequences of interaction between fairy rings of different species, and the factors affecting the mean lifetime of the rings, are also considered.

Conclusions are drawn from these relationships regarding the adaptation of larger fungi for life in various habitats. The ring habit is very inefficient and the communities to which it gives rise very open; these conditions are likely to promote the evolution of a number of species of nearly identical ecological requirements. It is found that there is a minimum area for any species in which it can produce a stable ring system; the possible means by which Basidiomycetes can compete successfully in smaller areas are discussed.

These points, though somewhat conjectural, touch many subjects of general biological and ecological significance, and may be of value in suggesting further lines of fruitful experimental inquiry.

I. INTRODUCTION

We are so familiar with the phenomenon of fairy rings that we do not always appreciate what interesting and peculiar problems of ecology and biology they raise. Their practical importance, though it has never been accurately assessed, is no doubt considerable, seeing that with many species their effect is marked both on the growth and on the ecological succession of the herb layer, often agricultural grassland. It is therefore desirable to know as much as possible of the properties belonging to this habit, and of the kinds of fungus communities to which it can give rise.

A large grass field carrying a system of fairy rings can be visualized as like a pond in a light shower of rain. Each ring grows outwards at a constant (or irregularly fluctuating) rate, and new rings are added to the system with approximately constant frequency. When rings of the same species meet, then, unlike ring waves on water, their intersected portions are obliterated; but as between different species either or both may survive the intersection. The important thing is that no ring ever remains still, but only stops growing when it dies. However, all these processes take place with extreme slowness; in the rain-drop analogy the rings grow at a few feet per second, and new ones appear at the order of ten per square foot per second, whereas fairy rings grow at a few feet per year and appear less often than ten per hundred acres per year.

The following are the main points of interest regarding fairy ring

systems which are open to theoretical generalizations. First, the proportion of the ground occupied by the mycelium; secondly, the factors affecting interspecific competition in mixed ring systems; thirdly, the age distribution of individual rings. I propose to examine each of these questions with the help of mathematical analysis; fortunately it is possible to construct a very good geometrical model of such a system, from which its behaviour can be deduced with reasonable accuracy, using only elementary calculus.

2. GEOMETRY OF THE SYSTEM

It is assumed that the system consists of mycelia growing at a uniform and constant rate ρ , on a uniform and constant plane field of area A . If the rate is not in fact constant, but if the variations are common to the whole system, the effect is simply that of a modified time scale, so that no real loss of realism is involved here. The system has thus two spatial dimensions; we can therefore represent the age of the system as a third spatial dimension, and all the properties of the system will be inherent in the resulting solid figure. In this figure each ring is represented by a right cone; for simplicity the whole system will be regarded as enclosed in another right cone. Since we shall be largely concerned with steady state conditions, this bounding cone can be regarded as very large and the significant part of the system as concentrated near its axis. Two intersecting (and mutually obliterating) rings are represented by the *exposed* surface of two intersecting cones.

In relation to a given ring (which I shall call the *preposite*) any other ring will be called an *impingent* if it has intersected or is destined to intersect the preposite. Any ring which wholly encloses the preposite will be called an *ampectant*. If a ring A has an ampectant A' and a second ring B has no ampectant not common to both rings, then B will impinge on A' , their intersected portions will disappear, and B will thus never impinge on A . It is thus easy to see that the condition that two rings should be mutually impingent is that the number of ampectants of each which are not also ampectants of the other should be equal. In this sentence we must allow compound rings, i.e. those formed by previous intersection of two or more, to count as single ampectants; however, it will in due course appear that the probability of any preposite having a compound ampectant both of whose elements are also ampectants is so small that the results will be scarcely unchanged if we count only single rings as ampectants, which greatly simplifies the mathematics.

In the cone model, the condition that a ring should be an ampectant is evidently that the vertex of its cone should lie within the anticone of its preposite (see Fig. 1, where P represents the preposite, and $B + D$ constitutes its anticone). The condition that such an ampectant should not be also an ampectant of another ring Q is therefore that it should not lie in the intersection of the two anticones (i.e. not in D in Fig. 1). The mean numbers of ampectants peculiar to each ring are therefore proportional to the volumes B and C respectively (the number of vertices per unit volume, representing the rate of initiation of rings, being constant). For

the case where the bounding cone is very large it can be shown from elementary geometry that the approximate relations hold:

$$C = \frac{1}{2} \pi \rho^2 T^2 (t'' - t' + t), \quad (1a)$$

$$B = \frac{1}{2} \pi \rho^2 T^2 (t'' + t' - t), \quad (1b)$$

where t represents the age (i.e. height of cone) of the preposit P , t' is the age of ring Q , $t''\rho$ the distance between their centres, and $T\rho$ the mean radius of the field. If σ is the number of new rings per unit area per unit

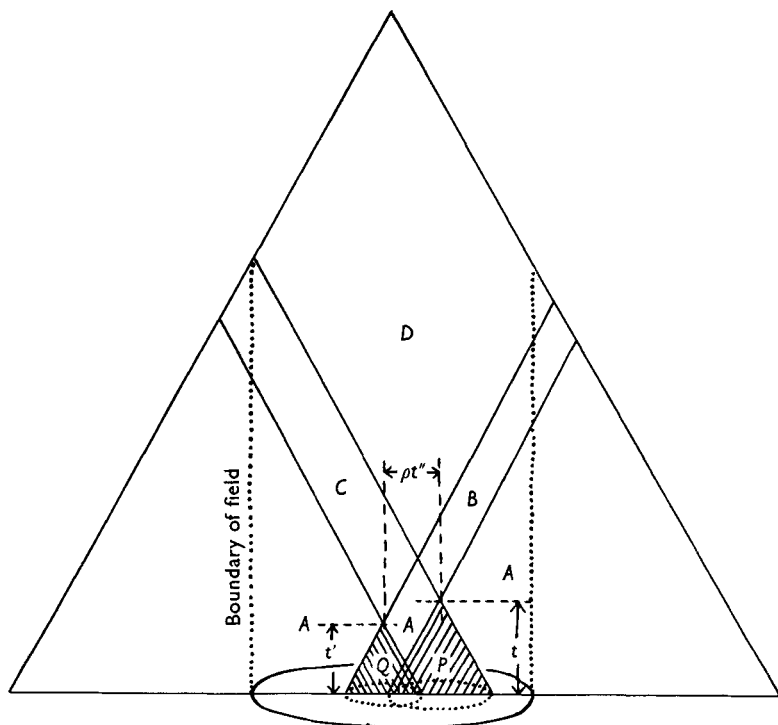


Fig. 1. The main points of the geometrical model. The diagram is not drawn to scale, in that, with the proportions shown, the approximations used in the calculations would scarcely be acceptable.

time the number of vertices within the prescribed volumes are therefore σB and σC respectively. It can be shown from the conditions postulated above that the probability that P and Q are mutually impingent is

$$p(t, t', t'') = \exp[-\sigma(B+C)] \sum_{i=0}^{\infty} \frac{(\sigma BC)^i}{i!^2}. \quad (2)$$

3. RATE OF GROWTH OF IMPINGENT GROUPS

Let us define an *impingent group* as consisting of such rings as are mutually impingent. It is evident from this definition that all the rings in the system can be classified into a set of mutually exclusive impingent groups. Every

point in the field will be traversed once and once only by the boundary of every impingent group. The mean interval between one such transit and the next may be called the *generation time* of the groups.

Suppose now that the effective radial width of the rings is r , and that the generation time is τ . Then, out of a period of time τ each point in the field will spend a mean time r/ρ within the mycelial area, so that the proportion of the ground occupied by the latter is

$$x = r/\rho\tau. \quad (3)$$

Now the volume contained within the compound figure of intersecting cones which represents an impingent group up to the moment of origin of its successor must be that containing one vertex. The height of this figure is on the average τ . If then we denote the area at time t of the group by $a'(t)$, we have

$$1 = \sigma \int_0^\tau (a'(t) - a'(0)) dt. \quad (4a)$$

Since the rings will in general overlap, the sum of the areas of all the rings a will be in general greater than a' , and elementary sampling theory shows that on the average

$$a' = A(1 - e^{-a/A}), \quad (4b)$$

where A is the area of the whole field. To find τ , and hence x , we have therefore to evaluate this integral. The working of this problem will be found in the Appendix. The result is that equation (4a) reduces approximately (near the centre of a large field, with known orders of magnitude of the quantities involved) to

$$1 \simeq \sigma \int_0^\tau A \left\{ \exp \left[-\frac{64\pi^2\rho^4}{A^6\sigma^4} \right] - \exp \left[-A^2\sigma^2 t^2 \left(\frac{\pi\rho^2}{A^3\sigma^2} + \frac{8\pi^2\rho^4}{A^6\sigma^4} \right) \right] \right\} dt, \quad (5)$$

from which we can derive the equation for τ in the form

$$\tau \simeq e^{64c^2} \left\{ \frac{1}{A\sigma} + \frac{(-\frac{1}{2})! [A^2\sigma^2\tau^2(c+8c^2)]}{2A\sigma\sqrt{(c+8c^2)}} \right\}, \quad (6)$$

where

$$c = \pi\rho^2/A^3\sigma^2.$$

This equation can be solved for τ in terms of A , ρ and σ , by successive approximation (the incomplete factorial can be obtained from tables of the normal probability integral). The results are shown graphically in Fig. 2, where the values of x are plotted against the growth rate ρ for different values of (a) σ , and (b) the product $\rho^2\sigma$.

4. INTERSPECIFIC COMPETITION

The data exhibited in Fig. 2 can be used to assess the theoretical conditions governing the competition between species of ring-forming fungi. Three separate cases have to be considered, according to what happens when rings of different species impinge. In the first case, which I shall call *indifference*, both rings continue to grow and fructify after intersecting; in the second case, of *bilateral extinction*, both rings are obliterated in the intersecting region, as if they were of the same species; in the third case

there is *unilateral extinction*, one ring being unaffected while the other is eliminated.

In unilateral extinction the species eliminated can maintain no equilibrium at all, and its occupation of the territory is dependent on the continued arrival of propagula from elsewhere (unless the reproduction rate is so great that even a very small population can produce sufficient propagula to colonize the transient vacancies). In general, however, the

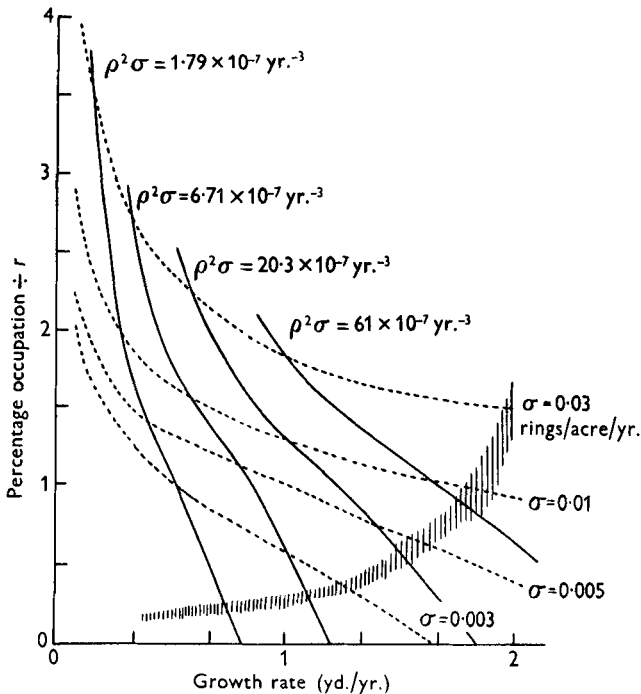


Fig. 2. The curves are drawn for a field of 10 acres; for larger fields the part of the diagram above the shaded zone is unchanged, except for the labelling of the contours, which will be governed by $A\sigma = \text{const.}$ For smaller fields the diagram rapidly becomes inapplicable as explained in the text. The quantity r is the effective width of the active zone of the rings, whose value will depend *inter alia* on the definition of 'cover' which one works to.

conditions are so unfavourable that such species will exist only in immature ring systems, or where their successful competitors are excluded by other factors.

In cases of indifference, the two ring systems will simply co-exist; they will attain a steady state in which both have a finite proportional occupation, whatever the relation between their parameters, and the only index of relative success will be their net reproductive efficiency per unit area.

In bilateral extinction (the most interesting case, since it will cover very closely related species), the one with the larger growth rate will eventually eliminate the other, though the time required will be very long unless the difference is large; we assume equal values of σ . (This may be seen by

considering the intersection of two cones with parallel axes but different vertical angles; at a sufficient distance from the vertices the cone with the larger angle will wholly enclose the other.) Likewise, if both have the same growth rate ρ , but different reproduction rates σ , the one with the greater σ will after sufficient time (again likely to be very long) eliminate the other. Application of the method of dimensions shows that the condition that both species should have a finite occupation density at the steady state is that their values of the product $\rho^2\sigma$ should be equal. It follows that of two bilaterally competing species, the one with higher $\rho^2\sigma$ will always tend to oust the one with the lower value. Thus the eventual survivors of such a competing group will tend to have the same $\rho^2\sigma$, and this the highest possible for them. Of two such, the one with higher σ and lower ρ will be able to achieve the higher proportional occupation of the ground, though this is not necessarily decisive for survival.

Inspection of Fig. 2 will now show that there will be a general tendency towards more rapid reproduction of rings and slower growth rate. Since the ring habit is itself dependent on the exhaustion or poisoning of recently occupied ground, there is likely to be a definite lower limit to the growth rate, and there is also an upper limit to the rate of reproduction. Thus we may expect a fairly definite clustering of the values of steady-state occupation about the optimum thus determined. Consideration of the order of magnitude of the actual rates observed in nature leads us to expect this to be of the order of 0.05, i.e. 5 % of the ground occupied, based on the arbitrary assumption of 2 yards for the effective thickness of the rings. Data which I have obtained on the ecology of fungi in Skokholm Island, making this same assumption, bear out this expectation fairly well (Parker-Rhodes, 1953). Any other figure for the r of equation (3) would be equally consistent if applied to the same data, though the 'observed' and 'calculated' percentages would both differ from the figures given here. Fig. 2 also shows that, despite the general tendency towards slow growth, species subject to bilateral extinction may tend to a higher growth rate, owing to the steep slope of the $\rho^2\sigma$ -contours.

There is unfortunately little direct experimental evidence to test these conclusions. There are, indeed, only a few references in the literature to what happens when two rings of different species meet. Shantz & Piemeisel (1917) report that *Agaricus campestris* is extinguished unilaterally by *Calvatia cyathiformis*, but this is the only recorded case of unilateral extinction known to me, though there must be others awaiting discovery. Indifference is no doubt much the commonest condition, but again specific confirmation is lacking; one proven instance has been given by myself (Parker-Rhodes, 1950, pl. 8) with *Lactarius rufus* and *Collybia maculata*. Bilateral extinction is presumably the rule with the most closely related species, but it may well occur in other cases also.

To some extent the long-term conclusions of this section are open to question, since, as we shall see in §7, the time required to reach a steady state may in some circumstances, especially before the coming of man broke up the primeval grasslands of temperate climates, be so long that species may become adapted specifically to existence in juvenile ring systems. But in default of further evidence speculation is idle.

5. NON-UNIFORM FIELDS

In the foregoing discussion it has been assumed that the field of the ring system was large, that is to say, boundary effects were neglected. Exact treatment of this problem is difficult, and the mathematical models required can never be very realistic; it is sufficient therefore to consider the matter qualitatively. Supposing the field to be bounded by ground uninhabitable by the mycelium, the percentage occupation will be less at the edge than near the centre, because there mycelium can only arrive from one side instead of from all round. In the ideal case of an infinite straight-edge boundary, the reduction will be exactly half; it will become negligible at distances from the boundary of the order of the distance covered by the growing mycelium in the generation time τ of an impinging system.

Similarly, any limited region of uninhabitable territory within a large field, such as an outcrop of rock, will be surrounded by a zone of similar width in which the mean proportional occupation will be reduced, though by less than half. Conversely, a narrow promontory from the field, surrounded on most sides by uninhabitable ground, will support a mean occupation of less than half the general mean.

If the field is appreciably smaller than the 10 acres assumed in Fig. 2, the mean occupation will be rather drastically curtailed. Other factors being equal, the occupation density is proportional to $A \cdot \exp[-kA^{-6}]$. With the optimum plausible figures of $\sigma = 0.1$ ring per acre per year and $\rho = 6$ in. per year, k is approximately 100, and the exponential factor falls from about $\frac{1}{2}$ to virtually zero as A falls from 2 to 1 acre; for less favourable σ and ρ the vanishing will occur for larger areas. It follows that fairy ring systems cannot permanently exist on areas appreciably less than 10 acres. It obviously does not imply that rings cannot occur on such areas, as everyone who has a lawn must know, but that such rings will be very infrequent when (if ever) a steady state is reached. These small areas can therefore play only a negligible part in the ecology of long lived ring-formers such as we have been considering.

6. FACTORS AFFECTING THE EFFECTIVE REPRODUCTION RATE

It is evident that one of the most important factors for ring-forming fungi is the effective rate of reproduction of new rings. Any means, therefore, by which this could be increased, may be of advantage to the species. Two possibilities may be considered: homothallism, and spontaneous breaching.

Obviously, if the successful germination of at least two spores of appropriate 'sex' is necessary for the establishment of a new fruiting ring, the rate of such new establishments will be less than if a single germination were effective. Since there is no reason to suspect that homothallism necessarily carries with it any important loss of growth rate, a homothallic race will usually have a larger value of $\rho^2\sigma$ than heterothallic races of the same species which will react with it in bilateral extinction. We must therefore expect to find few cases of both habits co-existing in obligately ring-forming species, unless perhaps geographical or ecological isolation

mitigates the relationship. In particular, if a homothallic strain of any heterothallic species appears, it would be expected to eliminate, in time, all the latter, unless some are saved by effective barriers. This would of course be a long-term disadvantage to the species affected, by curtailing its capacity for variation; we might therefore expect that fairy ring fungi would be exceptionally resistant to relapsing into homothallism, except in cases where the homothallism is facultative and rarely exercised. This exception may apply to gasteromycetes, such as the Lycoperdacei, several species of which are reported as homothallic, since their spores are normally distributed in relatively dense clouds so that most rings will be in practice the product of multiple germination whatever a single spore may be able to accomplish in a Petri dish.

Turning now to spontaneous breaching, let us suppose that by some means (say a lethal gene locally homozygous through caryallaxis with a new germling) a length of the perimeter of a growing ring is abolished. The subsequent growth of such a ring should ideally proceed with two in-curving horns which, when they meet, will reconstitute the closed perimeter and at the same time abstrict a Y-shaped portion from which a new ring could grow inside the parent. Such a secondary ring will belong to the next impingent group after that of its primary; the points of origin of secondaries will lie at a more or less definite distance within the effective perimeter of the primary. The effect of such spontaneous breaches on the growth of an impingent system requires a little consideration.

In the geometrical model (Fig. 1) all secondary cones of a given impingent group, having a present radius $\rho t'$, have their vertices on a circle at a height t' and of radius $\rho(T+t-t'-t_0)$ (where $T+t$ is the age of the impingent group to which the secondaries belong, and t_0 is the delay occupied in the process described above). Evidently the aggregate area b contributed to the system by the secondaries will be

$$b = \int_0^{T+t-t_0} 2\pi^2 \rho^3 \lambda_0 \cdot t'^2 (T+t-t'-t_0) \cdot dt' \\ = \frac{1}{6} \pi^2 \rho^3 \lambda_0 \{t^4 + 4T''t^3 + 6T''^2t^2 + 4T''^3t + T''^4\}, \quad (7)$$

where

$$T'' = T - t_0 \approx T$$

and λ_0 is the rate of breaching. This expression will combine additively with the a of §3; it will be seen that the coefficient of t in this polynomial will be of comparable order with that in a (see equation (13) in the Appendix), and therefore negligible in comparison with that of t^2 , only if

$$\lambda_0 \sim 63\pi^{\frac{3}{2}} \rho^4 / A^{\frac{1}{2}} (A\sigma)^3, \quad (8)$$

which, with $A = 5 \times 10^4$, $A\sigma = 10^{-1}$, $\rho = 1$, makes $\lambda_0 \sim 10^{-6}$, in which case the effect of the breaching on the effective reproduction rate would be small; if therefore the effect is to be appreciable, the new polynomial outweighs the old, and its dominant term being in t , not in t^2 , the equation for τ will become

$$\tau = \left\{ \frac{1}{A\sigma'} + \frac{1 - \exp[-2\pi^{\frac{1}{2}} \lambda_0 A^{\frac{1}{2}} \tau]}{2\pi^{\frac{1}{2}} \lambda_0 A^{\frac{1}{2}}} \right\} e^{A\lambda_0/2\rho}. \quad (9)$$

From this it is apparent that except for very small values of λ_0 the effect of spontaneous breaching followed by formation of secondary rings will be to reduce the proportional occupation of the ground at the steady state, the effect increasing rapidly with the area of the field; in fact, under these conditions, the extra rings increase the sweeping effect more effectively than they add to the number of fructifications. If we take the case where $\lambda_0 \sim 10^{-6}$, so that equation (6) is still approximately correct, the number of secondaries added within a given impingent group during the period τ will be $3\lambda_0\sqrt{(1+\rho^2)}/\rho$; with $x=0.05$ and $\rho \sim 1$ yd. per year, this quantity is $\sim 10^{-3}$ of σ , whereas for $\rho \sim 10^{-1}$ yd. per year, the two quantities are comparable. Thus spontaneous breaching could only be an appreciable factor in raising the proportion of occupied ground if the growth rate were very small and the field area not much in excess of 10 acres.

7. LONGEVITY OF FAIRY RINGS

It is commonly assumed that ring-forming fungi are among the most long-lived of all organisms. If we regard any secondaries which may be formed as above as continuations of their primaries, this may well be correct, but it is more natural to regard this as a case of vegetative reproduction, and to define longevity in terms of the geometrically continuous perimeter.

The problem can be approached by the method of dimensions. There are three parameters which may be considered relevant; the growth rate ρ , the reproduction rate σ , and the surface density of surviving rings; this last may be replaced, if we leave out the total number of rings (which is of course a dimensionless quantity), by the field area A , though care will be required in its interpretation. The first of these parameters can, paradoxically, be ruled out as a mere scale factor; for although an increase in ρ will reduce the time needed for a ring to reach a given size, it will simultaneously increase the size reached by the ring when its first successor appears, which, as is evident from §3, is what really determines the time scale of the system. It follows that, in general, the mean life is

$$\bar{t} = k/A\sigma, \quad (10)$$

where k is a numerical constant which we shall evaluate.

At first sight this equation appears paradoxical, as it implies that rings tend to live longer in a small field than in a large one. We must remember, however, that steady-state conditions are implied, and that the total number of rings does not appear in the equation. If we suppose that a given number of rings in a small field are spread out more widely, they will obviously take longer to impinge and so live longer; but if they were formerly in a steady state they will be so no longer, and the number of rings will increase until a new steady state is reached, which will not occur until equation (10) is again satisfied. Actually (though I have avoided diachronic considerations in this paper) it will take so long to reach a steady state in a large field of say more than 100 acres that under such conditions the foregoing analysis is scarcely relevant. Such large areas of uniform conditions for ring growth are rarely encountered in the presence of intensive human settlement, and are therefore of little economic

importance; but unfortunately the chief quantitative work on this question up to date, that of Shantz & Piemeisel (1917), was done in such conditions in the American prairies. Their data must therefore be taken as referring to a relatively juvenile state of the ring system. In Western Europe the rings in such aged or undisturbed vegetation as remains and is of economic interest (e.g. so-called permanent grass, marginal grazing lands, etc.) will usually be in nearly steady-state conditions.

We may rewrite equation (10) less paradoxically, by taking account of the actual number N of surviving rings in the field, and writing $A = N/\nu$ where ν is the surface density of the rings. This last at the steady state can depend only on ρ and σ , and the method of dimensions gives the result $\nu = h\sigma^{\frac{1}{3}}\rho^{-\frac{2}{3}}$; substituting this into equation (10) then gives us

$$\bar{t} = hk/N\rho^{\frac{1}{3}}\sigma^{\frac{1}{3}}, \quad (11)$$

which shows the virtual dependence of \bar{t} on ρ on the rather artificial assumption that N is fixed.

The constant k can be evaluated from the geometrical consideration that the product $A\sigma\bar{t}$ is the average ring's share of $A\sigma T$ (ρT being the mean radius of the field) and that this is 3 times the total number of rings present; since at the steady state each ring must have on the average exactly one successor, it follows that $A\sigma\bar{t} = k = 3$. The constant h in equation (11) can be found from the fact that, if we consider a single ring only, itself constituting the whole of its impingent group, its lifetime must be in general equal to the generation time of the latter. Thus, for $N = 1$ equation (11) should reduce approximately to (6), whence $h = 3^{-\frac{1}{3}} = 0.481$ approx.

The equation $\bar{t} = 3/A\sigma$ shows now that the order of magnitude of the mean lifetime of rings at a steady state should usually be from 30 to 300 years. This is broadly speaking borne out by such observations as are available. In those cases, such as very extensive fields, where steady states are not reached, lifetimes may be much greater than this, and under these conditions the supposed great longevity of fairy rings may be true. But in situations here regarded as typical they are likely to be less long lived than many species of forest trees, for example, and so, probably, less also than their mycorrhizal fungi.

Always up to now we have made the assumption that there is no intrinsic cause of death other than the mutual interference of the rings. This, obviously, is not strictly true. Though the observations of Shantz & Piemeisel indicate that some rings can live as long as the above figures predict, their maps also make clear that these old rings are always fragmentary, and the breaches which appear in them are not normally filled in the manner envisaged above, but tend to be permanent; moreover, many of their figures can only be explained on the assumption that half-rings and smaller fragments may persist for a long time without reforming themselves into complete perimeters. There are also reports in the literature suggesting the simultaneous death of a whole ring at a relatively early age; such an occurrence is recorded for example for *Aspropaxillus giganteus* by Rosenvinge (1933). If the average lifetime of a ring, in view of these hazards, is nevertheless of the same order of magnitude as the \bar{t} calculated above, our conclusions will not be much affected. But if their effect is to

reduce the average lifetime appreciably below this, the effect will not be negligible. If the expected proportion of compound rings is small, attainment of the steady state will be delayed, and the proportional occupation achieved by the system will be reduced; but if there would be a substantial proportion of compound rings if they survived long enough, premature decease will have the effect of a reduction of growth rate, and so increase occupation percentages. The modification required in Fig. 2 is unlikely to be appreciable, except for the lowest reproduction rates, whose unfavourable effects on occupation will be less than indicated in the graphs.

One important effect of premature decease may be its effects in inter-specific competition with unilateral extinction; for it may enable the weaker species to survive indefinitely, if this should have the advantage in length of life. There is, however, no evidence on this point.

8. DISCUSSION

One general conclusion which emerges from this analysis is that no species of ring-forming fungus can attain an occupation of more than a few per cent of the available ground (excluding ground occupied in the sense of being made uninhabitable by the species, the extent of which is in most cases quite unknown). This is therefore a habit of very low ecological efficiency, and it can only exist at all, one must suppose, on account of some biological impossibility of colonizing those habitats where it is best exemplified in any other manner. That such low density, and consequent open structure of the fungus communities, is a fact, is demonstrated by the results I have obtained on Skokholm Island (Parker-Rhodes, 1953). The work of Shantz and Piemeisel, as I have already mentioned, cannot be cited here since it does not refer to a steady state, whereas on Skokholm the available fields, being relatively small (up to about 25 acres), are probably already in this condition. There are in fact rather few obvious rings of any species there, which is what one would expect of a mature system. It is interesting also that the one species for which there are few ecological barriers on the island, and therefore disposes of a field of well over 100 acres, is *Lepiota procera*, which exhibits a ring system of the 'juvenile' type, similar to those described by Shantz and Piemeisel.

One must conclude, I think, that there is a fundamental property in the physiology of fungi, at least of the larger Basidiomycetes, which makes impossible the continued growth of mycelium in the same body of medium. If that were so, the only non-ring forming species would be those growing in habitats where the annual access of organic matter is sufficient for the year's needs of the fungus; here, continued growth of the fungus would be possible by successive recolonization of the annual layers without lateral spread of mycelium. Such conditions evidently obtain best in forest communities, but are neither universal in nor limited to these; Pteridieta, for example, provide a fairly considerable rate of access, as do Sphagneta and many other hygrophytic associations. In these, one may suppose, the ring habit is obligatory only on the species affecting the deepest layers of the humus, and will be a considerable handicap to the rest. There are indeed some species which often or usually form rings even in woodland leaf-

humus, such as *Craterellus tubaeformis*, but the growth of these may well depend merely on local variations in the rate of access of organic material, which may be considerable.

On this hypothesis, the ring habit would only be typical in those plant associations having a low rate of access, such as poor grassland and other low-growing vegetation. This is, of course, borne out by general experience. There remains, however, the problem of those habitats which combine a low rate of access with small areal extent, that is, with frequent intermission of the characteristic flora; such, for example, are many mountain and coastal habitats where the vegetation is much dissected by rocks, clearings and small open spaces in woods on thin soils, sand dunes, burnt ground, and most ruderal habitats. Such places are attractive to relatively few species, but intensive study generally reveals the presence of more fungi than they are usually credited with. We have seen that such small areas are unlikely to be adequate for ring-formers of the character we have been discussing, and this prompts the question of what adaptations would be needed to enable a Basidiomycete successfully to compete for them. One possibility would be to reduce the linear scale of their operations, producing scanty and restricted mycelia, small growth rates, and small basidiocarps; such a species could maintain a stable ring system in a smaller area than more expansive forms. Such a one is *Crinipellis stipitarius*, one of the commonest species of such habitats. Conversely, however, slow growth rates would be a considerable disadvantage in open competition with typical ring-fungi.

Another adaptation serving the same end would be an increased reproduction rate, which would make possible the rapid replacement of rings extinguished by having reached the boundaries of the field. This raises the question, why is the actual reproduction rate of typical ring fungi so extremely low; that it is so seems borne out by all observers (the data of Shantz and Piemeisel are relevant here). The reason is not far to seek: if the normal course of events were that a single spore should germinate to establish a uninucleate mycelium, the great majority of rings in a heterothallic species would remain sterile until their first impingement. It can, however, be shown from equation (6) that the majority of rings in a stable system with optimal parameters will be thus virgin (the compound rings are in a majority only in the bottom region of Fig. 2). Therefore a species with this habit would be supporting a large haploid population, itself a retarding factor on evolution, without the benefit of much gain in reproductive capacity. Thus, as in the analogous case of homothallism, there will be a contradiction between the short-term advantage of reproduction rate and the long-term advantage of evolutionary potential; the latter is best served by allowing only a very brief life to the uninucleate mycelium, so that at least two compatible spores must germinate together in order that a new ring be initiated, and this we may take to be the general rule among ring-fungi.

These considerations do not apply in the case of species which affect small fields, such as we have seen to be incapable of supporting stable ring systems; in these habitats the increased reproduction rate made possible by the presence of monospore uninucleate rings awaiting diploidi-

zation through a second germination may outweigh other considerations. This is perhaps the condition of such comparatively large species characteristic of ruderal habitats as *Volvaria speciosa*, which sometimes appears, seemingly for the first time, in large rings. Though such species are also found in ordinary open grassland, they may depend for ultimate survival on their more circumscribed retreats.

The most obvious remedy for a low reproduction rate would be increased spore production. In this the Lycoperdacei excel, and we might therefore expect to find these fungi especially commonly in restricted habitats; but in fact they are almost invariably typical large-field ringformers. Perhaps, however, a high rate of reproduction may enable such a species of *Calvatia cyathiformis* to survive in juvenile ring systems in the face of unilateral extinction.

Ecologically, the main conclusion from the analysis is that the communities of Basidiomycetes in poor grassland associations will be in general very open, whereas those in most associations with a rate of access of organic matter sufficient to support non-ring-forming mycelia are closed, at least when they have reached a steady state. In such open communities direct interspecific competition, other than that arising from bilateral or unilateral extinction, will be reduced to a minimum. Both these forms of interaction are certainly less frequent, probably much less so, than indifference. This opens an opportunity for the evolution of a large number of species whose niches are differentiated from each other only by such mutual adaptations as are necessary to avoid hostile interactions; for such a set of species can exploit the substrate more effectively than any one of them, not through complementary ecological specialization but in spite of identical requirements. It is of course almost impossible to adduce evidence for so negative a thesis; but it is at least significant that the number of species of Basidiomycetes in such grassland is often much greater than that of the plants, notwithstanding the simple structure and high uniformity of the habitat. In view of this conclusion it is perhaps unnecessary to expend our ingenuity in trying to apply Gauss's principle to these fungi.

APPENDIX

DERIVATION OF THE EQUATION (5)

The area of the preposite ring is $\pi\rho^2t^2$; that of any other ring of present radius t' is $\pi\rho^2t'^2$. The number of rings having a radius within the range $\rho(t' \pm \frac{1}{2}\delta t')$ and a central distance from the preposite within the range $\rho(t'' \pm \frac{1}{2}\delta t'')$ is obtained from the element of volume of the cone model in which their vertices lie, and is $2\pi\rho^2\sigma t''\delta t'\delta t''$. The chance that any one of these is an impingent on the preposite, and therefore the proportion of them which belong to the impingent group, is $p(t, t', t'')$. Therefore their aggregate area is given by the double integral

$$\begin{aligned} a &= 2\pi^2\rho^4\sigma \int_0^T \int_0^{t''+t} t'^2 t'' p(t, t', t'') dt' dt'' + \pi\rho^2 t^2 \\ &= 2\pi^2\rho^4\sigma \int_0^T t'' e^{-A\sigma t''} \int_0^{t''+t} t'^2 \left(1 + \frac{A^2\sigma^2}{4} (t''^2 - t - t'^2) + \dots \right) dt' dt'' + \pi\rho^2 t^2. \quad (12) \end{aligned}$$

Now, the quantity $A\sigma$ is equal to the absolute rate of appearance of rings over the whole field, which is in practice of order less (usually much less) than one per year; we may therefore approximate (near the centre of a large field) by ignoring further terms of the series. Moreover the limit T in the integral over dt'' is the time required by the preposite ring to grow to the size of the whole field, which we may take as infinite. With these approximations the integral can be evaluated as

$$a = \frac{2\pi^2\rho^4}{A^5\sigma^4} \left\{ 32 + 21(A\sigma t) + \left(\frac{A^3\sigma^2}{2\pi\rho^2} + 4 \right) (A\sigma t)^2 + \frac{5}{6}(A\sigma t)^3 - \frac{(A\sigma t)^5}{120} \right\}. \quad (13)$$

This expression can be further simplified, when account is taken of the orders of magnitude of the quantities involved. We know that in general $A \geq \sim 10^4$ yd.², $A\sigma < \sim 10^{-1}$ per year, and $\rho \sim 1$ yd. per year, and it can be shown that with these values the terms in t^3 and t^5 will not exceed 1/20 of that in t^2 , which contains 90% of the whole quantity in all practical cases. In that case the equation reduces to

$$\frac{a}{A} \approx \frac{64\pi^2\rho^4}{A^6\sigma^4} + \left(\frac{\pi\rho^2}{A^3\sigma^2} + \frac{8\pi^2\rho^4}{A^6\sigma^4} \right) (A\sigma t)^2, \quad (14)$$

which substituted in equation (4) gives (5) of the text.

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