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ON THE MACROECOLOGY OF SOME RUST FUNGI*

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I. INTRODUCTION

The effects of environmental conditions on plant pathogenic fungi have been thoroughly studied in many instances by plant pathologists (see, e.g., WALKER 1957, p. 544; STAKMAN & HARRAR 1957, p. 301; COLHOUN 1964). It is well known that many of the epidemics caused by parasitic fungi are correlated with favourable climatic conditions. In particular, much attention has been devoted to the economically important phycomycetes, to *Puccinia graminis,* and to *Erysiphe graminis.*

In natural populations the ecology of parasitic fungi has been much less studied. The purpose of this paper is not to present a review of the subject; it only aims to point out some general features in the ecology of parasitic fungi, with some examples mainly from the rust flora of Lapland. These will reveal that the ecological responses of parasitic fungi are much more delicate and complicated than a simple host-parasite relationship suggests, and that these responses can also be studied in the field. At least in Fennoscandia, very few studies exist on this problem; apparently LAGERHEIM (1909) was the first to draw attention to the climatic requirements of parasitic fungi (he stated that *Uromyces sommerfeltii (U. solidaginis)* and *Puccinia virgae-aureae* on *Solidago virgaurea* mainly occur on arctic-alpine areas). Many excellent ideas about the ecology of fungi are to be found in the review of HINTIKKA (1931), which, however, is written only in Finnish.

II. DEFINITIONS

The ecological response of a parasitic fungus can be divided into two parts: we can speak about *microecology* and *macroecology*. By microecology I mean the relationship between the parasite and its immediate surrounding, that is the host plant (or animal), while macroecology means the response of the fungus to the immediate influence of the environment upon the parasite, without the host acting as a mediator.

III. MICROECOLOGY

It is well known that, for instance, suitable moisture conditions of the host are often of great importance for succesful infection, growth, and spore production. Especially the powdery mildews *(Erysiphaceae)* and various phycomycetes offer many good examples of this. In these cases it is usually a question of a climatic affect where the host acts as a mediator, but the effect can also be caused by the soil conditions or by some other physical or chemical factor. E.g., a soil reaction which is too acidic or alkaline restricts the growth of many parasitic fungi (CHUPP 1928). It is also possible that the local soil nutrients affect the growth of the parasite, even if the experiments performed with *Puccinia graminis* have given ambiguous results. An interesting example is that of the common powdery mildew of grasses, *Erysiphe graminis,* which is strongly nitro-philous, and mainly occurs only in places where the host plants have a rich supply of nitrogen from the soil. In Lapland, for instance, it is presumably totally absent, or at least very rare on natural habitats, although common around houses. In this region *Erysiphe graminis* is a good indicator for even very sporadic places with waste; it can indeed be said that even the hygienic conditions of the Lapp houses can largely be determined on the basis of the occurrence of *Erysiphe graminis* along the walls. It should also be remembered that this species might possibly also be able to use superficial nitrogen, absorbing it directly into the mycelium; this is thus a macroecological reaction. CRAINGER (1947) experimentally confirmed the requirements of *Erysiphe graminis* for nitrogen and potassium; these were not correlated with the nitrogen content of the host.

We can also speak about microecology when studying the genetical relationships between the parasite and the host — I mean for instance the many hundreds of various races of *Puccinia graminis,* and of many other economically important micromycetes. In all these cases it is a matter about the relationship between the parasite and the host.

A good example is also provided by a Lappish rust, *Puccinia gigantea* on *Chamaenerion angustifolium* (Fig. 1). The host is very common all over Fin-
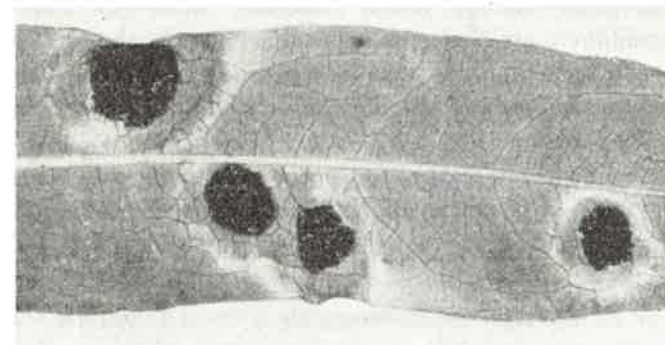
Fig. 1. Puccinia gigantea on lower side of a *Chamaenerion angustifolium* leaf (Utsjoki, Tshuoggajoki, 7. 8. 1963 Y.M.). 2.8 x.

land, but the rust is very rare, as it also is in other countries. It should now be realised that there are two races of the host. One is native and occurs especially in the north; the second is introduced, and it has long stolones and a very abundant seed production. Consequently, it has very quickly spread over the whole of Finland, although no studies have been made in this respect. Especially roads and railways have enormously contributed to spread this race. It now appears that *Puccinia gigantea* infects only the native race, not the introduced one. On the other hand, *Pucciniastrum epilobii* is very common in southern Finland on *Chamaenerion,* but rare in Lapland, and has probably never been collected on the native race of this host, at least not in Lapland. A third fungus, *Ramularia punctiformis,* seems to infect both races. If we look at the RAUHALA's (1959) distribution map of *Puccinia gigantea* in Finland, we see that in southern Finland it has been collected only in the 19th century; all the new records are from northern parts. This is probably explainable by the fact that still in the 19th century the native race of *Chamaenerion* was common also in southern Finland, and likewise the rust occurred in some places here, whereas later the native race was displaced by the anthropochorous race on which *Puccinia gigantea* does not occur.

IV. MACROECOLOGY

By macroecology I mean mainly the immediate climatic effect on the parasite; the immediate influence of the soil is naturally only possible if the parasite lives on underground parts of the host, or e.g. on leaves lying on ground. In addition, there are a few occasions in which environment or conditions other than climate or soil, act directly on the parasite (see above *Erysiphe graminis;* effects of fungicides spraying, etc.). It should now be remembered that when I speak about immediate effects on the parasite, I mean that no observable or known changes occur in the host which could affect the growth of the parasite; in each case it

should be separately studied how far the effects really are "immediate", and how far the climatic conditions act "microecologically", through changes in the physiology of the host. It seems, anyway, that *most parasitic fungi have their own macroecological requirements which have nothing or little to do with the physiology of the host.*

In speaking about climatic macroecology we make a distinction between two different aspects: the effect of macroclimate, and the effect of microclimate.

1. Effect of macroclimate

The effect of macroclimate is well visible in those cases in which the distribution area of the parasite does not cover the whole range of the host. I only mention some few cases from the Finnish flora; many good examples are provided in JØRSTAD's recent paper (1964). It should be observed that in some instances a distribution of this kind may also point to the occurrence of different host races with different distribution areas. These races do not need to be morphologically specialized; for the parasitic fungi, the physiology of the host is far more important than its morphology. It is naturally a question of microecology if the physiology of the host restricts the distribution of the parasite. Still in some cases the lack of a parasite in some area may simply be due to the fact that — perhaps owing to the geographical isolation of the host — it has not yet spread to that area.

Trichophorum caespitosum ssp. *caespitosum* is common over most of Finland, but its smut, *Anthracoidea scirpi,* only occurs in the north; in Fennoscandia it has never been found south of approximately 68°. This is explained by KUKKONEN (1964) as being caused by the more favourable local climatic conditions in the north for the germination of the spores. Another good example is provided by the easily detectable *Ustilago grandis* on *Phragmites communis:* the host is common everywhere in southern and central Finland, and even extedns north of lake Inari, but the smut has been collected only in southernmost Finland (cf. HINTIKKA 1931, p. 15).

Also among the rusts there are many good examples. *Potentilla erecta* occurs throughout all of Finland, but its rust, *Frommea obtusa,* has been found only up to about 62° (in fact, this rust is fairly inconspicuous, and new finds certainly will somewhat extend its range). FALCK (1920) presented distribution maps for three rusts parasitizing *Geranium silvaticum,* and found that of these, *Uromyces geranii* was southern, *Puccinia morthieri* northern, and *Puccinia leveillei* alpine-maritime. Later, much additional information has accumulated on the distribution of these species, but the overall picture remains the same. For instance in Inari Lapland, where the two *Puccinias* occur in many places

(MÄKINEN 1964), *Uromyces geranii* was not found until the summer of 1965 on the luxurious riverbanks of Kietsimäjoki and Inarinjoki, where many southern vascular plants (e.g., *Maianthemum bifolium, Melampyrum silvaticum,* and *Lactuca sibirica*) extend to their northernmost outposts in western Inari Lapland.

FALCK (1920) also mentions *Puccinia rubefacies* on *Galium boreale* as a rust which does not always follow its host; especially in all of southern Fennoscandia it is very rare (cf. MÄKINEN 1962, no. 833). Many other rusts are also northern, although their hosts occur throughout the whole of Finland.

An example of a different vertical distribution is provided by two rusts parasitising *Epilobium* species in Fennoscandia. Of them, *Puccinia scandica* is more arctic, occurring only in the upper parts of the alpine region, whereas *P. epilobii* commonly occurs also in the lowlands. This might partly be due to the different temperature requirements of these species. In fact, in this case there is also a difference between the main hosts, as *P. scandica* mainly lives on *Epilobium anagallidifolium,* and *P. epilobii* on *E. hornemannii.* In its distribution, the former host is clearly more alpine than *E. hornemannii* which commonly grows also in the coniferous zone. It remains to be experimentally studied whether the main host of *P.scandica* is *E. anagallidifolium* because this host is most readily available in upper alpine zones, or whether *P. scandica* is more alpine because it is mainly bound to its alpine host.

In some cases, experimental studies have established which climatic factor is the main one in restricting the distribution of a parasitic fungus. Thus the distribution of *Erysiphe cichoracearum* on lettuce is mainly determined by the temperature, while the humidity restricts the distribution of *Bremia lactucae* on the same host (SCHNATHORST 1962). Greater humidity and relatively low temperature favours the development of *Albugo candida* (MÄKINEN & HIETAJÄRVI 1965).

2. Effect of microclimate

There is yet another macroecological effect: the effect of microclimate, and mainly to this point I would like to draw attention. It is obvious that even in their distribution area the parasitic fungi do not always follow their hosts, but are sometimes restricted to certain places with favourable microlimatic conditions.

Obviously the first to pay attention to the effect of microclimate was ROUSSAKOV (1923), who studied the influence of the microclimatic temperature and humidity on the growth of cereal rusts. YARWOOD's (1959) review on the microclimatic effects on parasitic fungi is one of the few recent papers on the subject, but it mainly considers only the microclimatic effects on infection.

The processes of germination, infection, growth, and sporulation do not always have the same requirements; e.g. CROSIER (1934) found that the humidity required by *Phytophthora infestans* varies widely at the various developmental stages. Unfortunately, however, only after the last stage of development, mycologists (who always need spores!) become interested. They may thus easily arrive at wrong or at least incomplete conclusions, studying only the conditions during the spore production and omitting the conditions which perhaps have had much more influence on the occurrence of the parasite. It should also be remembered that in the species with a complicated life cycle (like the host-alternating rusts) the climatic requirements of different stages may be different.

In the following are described some examples mainly on the rust flora of Lapland.

a. Temperature

We first return to *Puccinia gigantea* on *Chamaenerion angustifolium*. The host is still common as a native race in Lapland, but all the six or seven localities of *Puccinia gigantea* are at the foot of steep cliffs facing west, or on the cliffs themselves. These cliffs clearly deviate from the surrounding areas in being microclimatically typical south bluffs (Südbergen) often with southern vascular plants. Apparently we have here a typical south bluff rust which requires the optimal warm conditions of the sunny cliffs. RAUHALA's (1959) distribution map further indicates that likewise all the other localities in N. Finland are in places where such steep cliffs occur, although naturally nothing certain can be said about the habitat on the basis of the very incomplete herbarium labels — it is very regrettable indeed that mycologists often completely ignore to give any kind of description of the locality; one is gladly surprised to find sometimes more than only the names of the province and commune.

There are several experimental records on the effect of temperature on the spore production of the rusts. MELANDER (1935) found that higher temperatures markedly reduced the time required to produce urediospores in *Puccinia graminis* on wheat. Low winter temperatures severely restrict the range of some parasites, as that of *Phymatotrichum omnivorum* which causes the root-rot disease of cotton and of some other plants. The parasite does not tolerate temperatures under freezing for longer than 1—2 days; this corresponds to about —23° C atmospheric temperature (EZEKIEL 1945). High temperatures can also naturally have a deleterious effect on the growth of the parasite; DELP (1954) showed that *Uncinula necator* may be absent on the lowermost grape leaves because of the excessively high temperature at soil surface. — In evaluating the results of the microclimatic temperature measurements, it should be kept in mind that the leaf temperature may be 9—10° C higher than the microclimatic air temperature in its immediate vicinity (CAMPBELL & DIMOCK 1955).

b. Light

A good example of a response to the sunniness of the habitat is provided by the extremely common rust on birches, *Melampsoridium betulinum*. It lives in Lapland both on *Betula pubescens* (incl. *B. tortuosa*) and *B. nana*, and is found almost everywhere. However, it is common and abundant only in open places: especially in the alpine region the rust is frequent and often causes very heavy infections (see MÄKINEN 1964). However, the rust is by no means alpine; it is also common along roadsides and in inhabited places where most of the trees have been cut down. Especially the young birch seedlings along the roads suffer badly from severe attacks by the fungus. In closed birch forests the rust normally occurs only very sparsely. These observations seem to indicate that this is a rust which even in Lapland has strong light requirements. For a related rust, *Melampsora lini*, HART (1926) experimentally determined that both enhanced and reduced light decreased the growth rate of the fungus, compared with normal light. It would be worth while studying whether the responses of *Melampsoridium betulinum* to light are similar in northern and southern Finland; probably the light requirements change as in a cline.

There are also several other rusts in Lapland favouring open habitats. For example, *Melampsora epitea* on at least *Salix hastata* and *S. phylicifolia*, and *Coleosporium campanulae* on *Campanula rotundifolia* occur mainly on shores of big rivers but are very rare or absent in closed communities.

In August, 1965, the Norwegian spruce *(Picea abies)* suffered badly in all of northern Finland from an attack of *Chrysomyxa ledi*. In many areas the infection was so severe that large areas covered by spruce were shining golden yellow instead of dark green. On the road leading from Rovaniemi to Utsjoki the infection began about 50 kilometres north of Rovaniemi and continued up to the southern part of Inari. It was most striking even for a very casual observer that the greatest damage was always on the southern side of the trees, and green colour of healthy needles advanced upwards much more on the northern side. The very tops were generally badly infested on all sides. Whether this peculiar occurrence was mainly caused by the light or temperature requirements of the parasite, or by both, should be experimentally studied. Some similar cases have been reported previously; e.g., onion downy mildew grows best on the northern side of onion stems (YARWOOD 1943); YARWOOD (1959) cites some further examples.

For a review on the effects of light on the morphogenesis and reproduction of fungi, see CARLILE (1965).

In 'the studies BEVER (1934), light decreased the incubation period of *Puccinia glumarum* on barley; however, high light intensity seemed to inhibit the growth of the parasite (cf. also HART & ZALESKI 1935, *P. graminis* on wheat). Even the powdery mildews which generally prefer shady habitats germinate more readily in light than in darkness (YARWOOD 1957). Similarly the coffee rust, *Hemileia vastatrix*, develops better in light than in shade (FERNANDO 1940).

c. Humidity

Moisture determines at least partly the geographic distribution of some plant parasitic fungi (STAKMAN & HARRAR 1957, p. 313). Although it is essential mainly for germination, in this way it becomes a limiting factor for the whole developmental cycle, and thus naturally may determine geographic distribution. High humidity, or even liquid water is often necessary for successful germination of many spores (ARENS 1929, SCHULTZ 1937, FOISTER 1946, p. 566), but the subsequent stages may be fairly independent of atmospheric humidity. As a rule, the conidia of the powdery mildews are not so sensitive to low humidity as those of phycomycetes (TAPKE 1951, YARWOOD 1957). The distribution of *Bremia lactucae* is determined both by humidity and temperature (SCHNATHORST 1962).

VAN ARSDEL (1965, VAN ARSDEL & al. 1956) demonstrated how local topographic conditions clearly affected the distribution of *Cronartium ribicola* on white pine. The rust was concentrated especially around small openings. This was explained as being due to the condensation of water on super-cooled needles, which condition is most favourable to rust infection.

Convincing evidence of the effect of humidity was recently reported by NANNFELDT & LINDEBERG (1965) who found a marked difference in the distribution of *Anthracoidea heterospora* and *A. liroi*, parasitizing many distigmaticeous sedges, e.g. *C. nigra*, *C. nigra* ssp. *juncella*, and *C. caespitosa*. In Fennoscandia, *A. liroi* mainly occurs in the north and on the mountains, while *A. heterospora* is common elsewhere. In Abisko, N. Sweden, both of these smuts occur close together, but *A. heterospora* is almost only restricted to the areas with continental climate (mean annual precipitation less than 300 mm), whereas *A. liroi* occurs in wet oceanic areas (mean annual precipitation more than 900 mm).

d. Local airflows

The distribution of the parasitic fungi, like that of higher plats, is not only determined by the habitat, but is also a result of its spreading. In this, the local airflows, determined by the topography of the area, often play an important role (VAN ARSDEL 1965). More attention to this point should be paid in mycological field studies.

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OBSERVATIONS ON THE LICHENS OF LABRADOR AND UNGAVA

PAAVO KALLIO and LAURI KÄRENLAMPI

I. INTRODUCTION

In 1963 the author Kallio had an opportunity to visit the central part of Labrador-Ungava (Map 1). The main purpose was to become acquinted with the nature of this part of Canada, which has so many features in common with the northernmost part of Finland (Hustich 1962, 1963). Particularly the fact that a new subartic field laboratory is being erected in Finnish Lapland (at 69° 45' N latitude) by the University of Turku led the authors to seek a wider background for studying analogies in different parts of the circumpolar subarctic zone.

As a special biological program was undertaken the collection of larger fungi about whose distribution in subarctic Labrador— Ungava and subarctic Finland very little is known (Savile 1963, Kallio & Kankainen 1964). During the excursions also phanerogams were collected, mostly by the fellow traveller, Prof. Ilmari Hustich. Also a few bryophytes were collected (Crum & Kallio 1967).

The collected lichens — 107 taxa in all — are listed here. The list is based on an unsystematical collection and cannot provide any detailed information on the characteristic features of the lichen flora of the area. Because, however, the lichens of Labrador and Ungava are imperfectly known (Dahl 1954, p. 470, Dix 1956, Hale 1961) the list may give some information. The identifications were made by the younger author, and Dr. Teuvo Ahti (Helsinki) has kindly placed his experience at our disposal.

The collections were made between June 24 and August 20, 1963. The chief collection area comprised the surroundings of Knob Lake/Schefferville, where the Subartic Laboratory of McGill University is situated. This laboratory was the main base for the excursions.

The area belongs to a zone of sedimentary rocks with iron ore and basic outcrops, which have left their imprint on the vegatation and the economic life. Muskeg forests as well as dry lichen—spruce forests on sandy soil are typical of the area (Hustich 1949, Ahti 1959). Close by there are, however, also ridges