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Aerial Distribution of the Root-Rot Fungus *Fomes annosus* (Fr.) Cooke in Finland

Tauno Kallio

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AERIAL DISTRIBUTION OF THE ROOT-ROT FUNGUS *FOMES ANNOSUS* (Fr.) COOKE IN FINLAND

TAUNO KALLIO

To be presented, with the permission of the Faculty of
Agriculture and Forestry of the University of Helsinki,
for public critisism in Auditorium XII on November 7,
1970, at 12 o'clock noon

HELSINKI 1970

Suomalaisen Kirjallisuuden Kirjapaino Oy Helsinki 1970

PREFACE

Numerous persons and organizations made helpful contributions towards the completion of the present study. My esteemed teacher, Dr. Peitsa Mikola, Professor of Forest Biology at the University of Helsinki, several years ago aroused my interest in problems related to the root-rot fungus. He gave me much appreciated support and guidance in writign this account of the study. Dr. Annikki Linnasalmi, acting Professor of Plant Biology and Pathology at the University of Helsinki in 1966—1969, made the institute of which she was supervisor and its facilities available for this study. Dr. Jaakko Mukula, Professor of Plant Biology and Pathology at the University of Helsinki in 1969—1970, gave me unfailing interest, advice and constructive criticism in preparing the manuscript. Dr. Aino Käärik, of the Royal College of Forestry, Stockholm, Sweden, for a number of years spared no pains to instruct me in the identifying of fungi from cultures. She also read through the manuscript and suggested many beneficial changes and modifications. Dr. Theodore Scheffer, formerly Principal Pathologist at the Forest Product Laboratory, Madison, Wisc., USA, also read the manuscript and suggested very apt amendments. The manuscript was translated into English by Mrs. Hilkka Kontiopää, M.A. (Helsinki), in good cooperation with Mrs. Barbara Rikberg. Mr. Juha Kasanen, M.Sc. (Helsinki), of the Helsinki University Computer Centre, gave me guidance in the statistical treatment of the material, and was responsible for its computer treatment. Most of the laboratory work was carried out by Mrs. Anna-Maija Hallaksela with precision and accuracy. The personnel of the University of Helsinki, Department of Plant Pathology assisted me in many ways in my work.

I received financial support from the Foundation for the Research of Natural Resources in Finland, the Agricultural Research Centre, the National Research Council for Agriculture and Forestry, the University of Helsinki, the Alfred Kordelin Foundation, the City of Helsinki, the Finnish Meteorological Institute, the Finnish National Airline »Finnair», the National Board of Navigation, the Letterstedt Association in Stockholm, and the Finnish Society of Forestry.

I wish to express my gratitude and thanks to all those mentioned above for their support and assistance.

Helsinki, September 1970

Tauno Kallio

CONTENTS

I INTRODUCTION

Fomes annosus (Fr.) Cooke, a fungus causing root and butt rot of conifers, was first described by Fries (1821, p. 373), who called it *Polyporus annosus* Fr. According to Bondartsev (1953) the fungus is also known under the following names: *Fomitopsis annosa* (Fr.) Karst., *Placodes annosa* Quél., *Heterobasidion annosum* Bref., *Ungulina annosa* Pat., *Polyporus subpileatus* Weinm., *Polyporus resinosus* Rostk., and *Trametes radiciperda* Hartig.

According to the distribution maps published (Populer 1956, Commonwealth Mycological Institute 1968, Map No. 271), *F. annosus* occurs in most parts of the world. Heikinheimo (1920) and Tikka (1934) reported *F. annosus* rot in the forests of northern Finland. According to Kangas (1952) approximately every tenth conifer in the western part of South Finland is infected by this fungus. Vaartaja (1950) has found damage caused by *F. annosus* in young seedlings of pine (*Pinus silvestris* L.) in the eastern parts of South Finland.

F. annosus is dispersed by means of diaspores (basidiospores, conidia and mycelial fragments). The basidiospores range in size from 3.5—5.0 to 3.0—4.0 μ (e.g. Overholts 1953). The conidia are subglobose to ovoid, with a size of 4.5—7.5 (—10.5) to 3.0—6.0 μ (e.g. Nobles 1948). According to Roll-Hansen (1940) there are thorn-like formations on the surface of the basidiospores whereas the conidia are smooth. Relative to their width, the conidia are longer than the basidiospores and contain a larger number of nuclei. Comparatively little is known about the occurrence of conidia in nature and their role in spreading the fungus. However, e.g. Rishbeth (1957) found conidiophores with conidia on the surface of a Douglas fir stump with an early stage of heart rot, the stump having been covered by branches after felling.

The amounts of spores produced by sporophores can be examined irrespective of the spore distribution. This method has been used e.g. by Buchwald (1938) and Hilborn (1942) in their studies of *Fomes fomentarius* (L.) Fr. and by McCracken and Toole (1969) in their studies of *Polyporus hispidus* (Bull.) Fr. According to the study Buchwald carried out in Denmark, *F. fomentarius* produced, during the season of maximum production, about 139 million spores per day per square centimeter of active sporophore surface. The spore production by the sporophores of *F. annosus* has been studied e.g. by Bjørnekaer (1938), in Denmark. He found that spores were usually produced throughout the year in 1930—1933. Spore production was stopped only by severe frost periods during the winter months.

The distribution of the fungi can be studied by trapping aerial diaspores on various sites and at different times, irrespective of where they had developed. This was the main method used in the present study. It has also been applied e.g. by Feinberg and Little (1936), Durham (1938), and Bernstein and Feinberg (1942) who studied the amounts of aerial fungal spores producing human allergy in the USA. According to their studies fungal spores in the air are definitely more abundant in the summer and autumn than at other seasons of the year. Similar results concerning the amounts of aerial spores in various seasons of the year were reported e.g. by Flensborg and Samsøe-Jensen (1948) for Denmark, Rennerfelt (1947), Nilsby (1949) and Mathiesen-Käärik (1955) for Sweden, Hyde and Williams (1946, 1953) and Richards (1954 a, b) for England.

Spores may occur at high altitudes in the atmosphere. In the USA, fungal spores in the atmosphere have been found (Stackman et al. 1923) up to an altitude of 16 500 feet (some 5 000 metres).

Frequent reports have been published on the spore population of the air at various hours of the day or night (e.g., Nilsby 1949, Gregory and Sreeramulu 1958, Harvey et al. 1969). In England, hyaline basidiospores were found to be more numerous in the air during the night and early morning than during the day (GREGORY 1952 b, HIRST 1953, GREGORY and HIRST 1957). In New York State, in a study carried out in a forest, aerial hyaline basidiospores were more numerous at night than during the day at 1 metre above the ground (DE GROOT 1968).

RISHBETH (1951 a, p. 8) proved that aerial *F. annosus* spores in England will infect freshly cut Scots pine (*P. silvestris*) stumps, and the fungus can spread from the stumps to the roots and thence to other trees. The same method of dispersal has later been verified in several countries and in stands composed of various tree species (e.g., MOLIN 1957, MILLER 1960, YDE-ANDERSEN 1961, DIMITRI 1963, SINCLAIR 1964, KALLIO 1965, REYNOLDS and WALLIS 1966, DRUMMOND and BRETZ 1967). Since the publication of RISHBETH's report, many research workers have caught aerial spores of *F. annosus* on various substrates.

A number of observations suggest that the deposition of *F. annosus* spores in cool climates is at its highest from spring to autumn (e.g. MEREDITH 1959, YDE-ANDERSEN 1961, DIMITRI 1963, SINCLAIR 1964), but in a warmer climate (e.g. the southern states of the USA), maximum deposition occurs during the winter (e.g., DRUMMOND and BRETZ 1967).

In Finland, the practice of year-round cutting is increasing. As a result, freshly exposed surfaces of stumps are present at any time of the year. Likewise, fellings and the mechanized transportation of timber cause damage to standing trees and expose the roots as well; the latter occurs especially during the snowless period when the soil is not frozen. Routes of infection are thus provided for decay fungi. Infection through the newly cut surfaces of stumps presupposes aerial dispersal of fungal diaspores, but relatively little is known about their deposition in Finland. The purpose of the present study was to investigate the aerial dispersal of the diaspores of *F. annosus*. The influence of climatic factors on diaspore deposition, and the aerial distribution of two fungi antagonistic to *F. annosus*, viz. *Peniophora gigantea* (Fr.) Massee and *Trichoderma viride* Pers., were also investigated.

II METHODS

1. Study outline

Most of the study was carried out by exposing various substrates on a given site for a set period. Aerial diaspores of *F. annosus* settled on these substrates which were then incubated in the laboratory for about 10 days. During this time the diaspores grew mycelium from which the fungus was identified. No attention was paid to the origin of the diaspores or to whether they were conidia, basidiospores, or mycelial fragments.

A preliminary study was undertaken to analyse the deposition of *F. annosus* diaspores between June 7, 1967 and May 29, 1968, by means of samples collected from different parts of Finland, mainly from airfields. In this way it was hoped to obtain a preliminary overall view of the aerial dispersal of the fungus in Finland. Preliminary information on the results of this study was published in the paper issued by the Third International Conference on *Fomes annosus* (KALLIO 1970).

The main study was concerned with the deposition of *F. annosus* diaspores in 1968. Samples were taken at regular intervals throughout the day and night from three South Finnish stands of Norway spruce (*Picea abies* (L.) Karst.) infected by *F. annosus*. Also fluctuations in the number of aerial diaspores with the time of year and the hour of day or night were studied in relation to the variations in weather elements. Both the preliminary and the main study were additionally concerned with the aerial distribution of *P. gigantea* and *T. viride*, two fungi antagonistic to *F. annosus*. In connection with the main study, the deposition of diaspores in the forest was compared with that recorded above the forest, on an open site, and over the sea. In addition, the occurrence of viable diaspores of *F. annosus* on leaves and needles in the forest and underneath the humus layer of the soil was studied. Deposition at different distances from the sporophores was also studied.

2. Growth substrates and their selection

Aerial diaspores are apparently either basidiospores or conidia. Various methods have been used to analyse the amount and kind of the aerial spores (e.g., STACKMAN et al. 1923, FEINBERG and LITTLE 1936, RENNERFELT 1947, RISHBETH 1951 a, HIRST 1952). *F. annosus* is one of the fungi whose spores cannot be identified with the methods currently available. The spores must first be made to grow a mycelium with conidiophores typical of the fungus before identification is possible. To make a culture of *F. annosus*, wood, the natural substrate of the fungus, can be used. Pine (*P. silvestris*) and spruce (*P. abies*) wood have been used as substrates by many authors (e.g. RISHBETH 1951 a, DIMITRI 1963). RISHBETH (1951 a) found that the viability of spores of *F. annosus* was maintained for relatively long periods in pine discs (in the dark with a temperature of + 15° C and humidity of 32 per cent, up to 40 weeks).

Aerial spores of many fungi usually settle on the substrates simultaneously. In the present study, the *F. annosus* diaspores were distinguished on the basis of the mycelium which grew on the substrates. In these circumstances, the mycelia of antagonistic fungi simultaneously growing on the substrate may inhibit the growth of *F. annosus* mycelium. The various substrates were simultaneously exposed to diaspore deposition so that it was possible to compare their different effects on the growth of *F. annosus* mycelium and its antagonists. The ultimate aim was to determine the deposition of *F. annosus* diaspores as accurately as possible.

In the present study, spruce discs were selected as one substrate. Another substrate selected was the agar medium developed for *F. annosus* studies by KUHLMAN and HENDRIX in 1962 (working name, K-agar), and a third the agar medium developed by KUHLMAN in 1966 (working name, H-agar). In the preliminary study these three growth substrates were exposed to aerial diaspores for periods of varying duration. In the main study, however, only spruce discs and H-agar substrates were used. Although deposition was slight, the diaspores accruing on spruce discs during a long exposure period could be measured. The agar substrates could be effectively exposed for considerably shorter periods. Consequently, by using the agar substrate it was possible to ascertain the maximum depositions during a period of profuse diaspore production, more precisely than would have been possible from spruce discs.

21. TRAP DISCS OF SPRUCE

A Norway spruce free from rot was felled weekly (in mid-winter, fortnightly) at Viikki, Helsinki. At a height of one meter from the butt, a roughly 1-meter long bolt was sawn, barked in the forest, swabbed with ethyl alcohol and transported in plastic wrapping to the laboratory where discs about 18 mm thick were cut with a power saw as aseptically as possible. The teeth in the cutting edge of this band saw blade were filed so as to be at an oblique angle to the sawn surface, in order to make the saw dust coarsely granular and thus prevent it from filling the cavities in the cells of the cross-sectioned wood. Immediately after sawing, a circular iron punch, diameter 134 mm, was used to take, again with the maximum possible degree of asepsis, equal-sized discs with a cut surface of 141 sq.cm. each, always from the same side of the stem. The discs were placed in plastic Petri dishes and inserted in plastic bags.

The trees were felled on Tuesday mornings, and the trap discs sawn from them were exposed on Wednesday or Thursday. At the time of exposure, the trap discs during the snowless and frostless period were thus 1—2 days old. RISHBETH (1959) used discs under 10 days and SINCLAIR (1964) under 14 days of age. The discs often lost moisture during the period of exposure and the subsequent laboratory phase of mycelial growth. The mean loss was about 2 per cent of the total weight in 10 days, but the variation in loss was sometimes great, depending on the weather at the time the sections were exposed. The maximum moisture losses measured were about 8 per cent, but if it happened to rain during the time of exposure the moisture content of the discs increased.

22. AGAR MEDIA

The composition of one of the two agar media used (K-agar) (KUHLMAN and HENDRIX 1962) was: 5 g peptone, 20 g agar, 0.25 g $MgSO_4$, 0.5 g KH_2PO_4, 190 ppm PCNB (pentachloronitrobenzene), 100 ppm streptomycin, 2 ml lactic acid (50 per cent), 20 ml ethyl alcohol (95 per cent), 1 000 ml water. After the medium was cooled to 41—45° C in a water bath, the acid and alcohol were added. The medium was shaken before being poured, to resuspend the relatively insoluble PCNB.

The second agar (H-agar) (KUHLMAN 1966) consisted of 5 g peptone, 20 g agar, 0.25 g $MgSO_4$, 0.5 g KH_2PO_4, 200 ppm PCNB, 50 ppm penicillin, 1.3 ml lactic acid (85 per cent), 20 ml ethyl alcohol (95 per cent), 130 ppm sodium desoxycholate, 1 000 ml water. The acid and alcohol were added as described for K-agar.

The H- and K-agar media were poured into plastic Petri dishes 88 mm in diameter (cross section surface 61 sq.cm.), and inserted into plastic bags as soon as the media had cooled down.

3. Identification of *F. annosus*

F. annosus can be identified on the substrate by its conidiophores (BREFELD 1889, p. 154). The conidiophores can be discerned by a roughly 10-fold magnification (e.g. JØRGENSEN 1954). When the fungus, by means of its aerial diaspores, has spread e.g. onto a trap disc and the disc is subsequently incubated in the laboratory at room temperature and suitable relative humidity, the fungus can be reliably identified after about 10 days (e.g. Rishbeth 1950). Evaporation of moisture in the laboratory while the mycelium is developing can be reduced by wrapping the disc in newsprint (Rishbeth 1950) or plastic (Sinclair 1964).

In the preliminary part of the present study the substrates, after being exposed as described, were incubated in plastic Petri dishes inside plastic bags at a temperature of about + 20° C for 10 days in the laboratory. At the end of this period, *F. annosus* conidiophores (Fig. 1) growing on the spruce discs were identified with a stereomicroscope, using 25-fold magnification, and were outlined with pencil on the disc surface. To facilitate systematic locating of conidiophores, an iron frame with horizontal wires at 6 mm intervals was placed on top of the disc (Fig. 2). The final result was expressed as the number of colonies of *F. annosus* conidiophores, and the total area covered by the conidiophores was determined by a planimeter. The method was similar to that used e.g. by Rishbeth (1950) and Dimitri (1963). The *F. annosus* conidiophores appearing on the agar media were identified after a 10-day incubation with an ordinary microscope and a 100-fold magnification.

In the main study, after the 24-hour observations, the exposed substrates were incubated for 10 days at + 22° C and 70 per cent relative humidity. It usually took one day for the substrates exposed outside Helsinki (Anjala and Jokioinen) to be returned; they were, therefore, 11 days old at the time they were examined. Identification of the *F. annosus* colonies and calculation of the area they covered on the spruce discs were carried out in the same way as in the preliminary study.

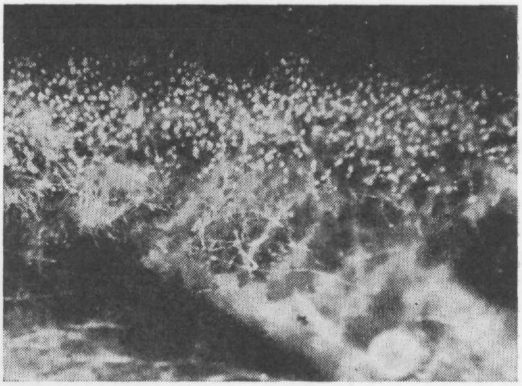

Fig. 1. Conidiophores of *F. annosus* on trap discs of spruce. × 40.

Fig. 2. Looking for *F. annosus* conidiophores by the stereomicroscope. The disc was covered by an iron frame with horizontal wires at 6 mm intervals.

4. Sites and times of trapping aerial diaspores

41. PRELIMINARY STUDY

Trap discs were placed on 6 open sites in different parts of Finland and on one forest site infected by *F. annosus* in South Finland. The open observation sites were (Fig. 3): the Ivalo airfield (68°36′ N, 27°25′ E), 145 metres above mean sea level, distance to the nearest growing tree about 50 metres, to the nearest forest about 300 metres; the Oulu airfield (64°56′ N, 25°22′ E), 14 metres above mean sea level, distance to the nearest growing tree

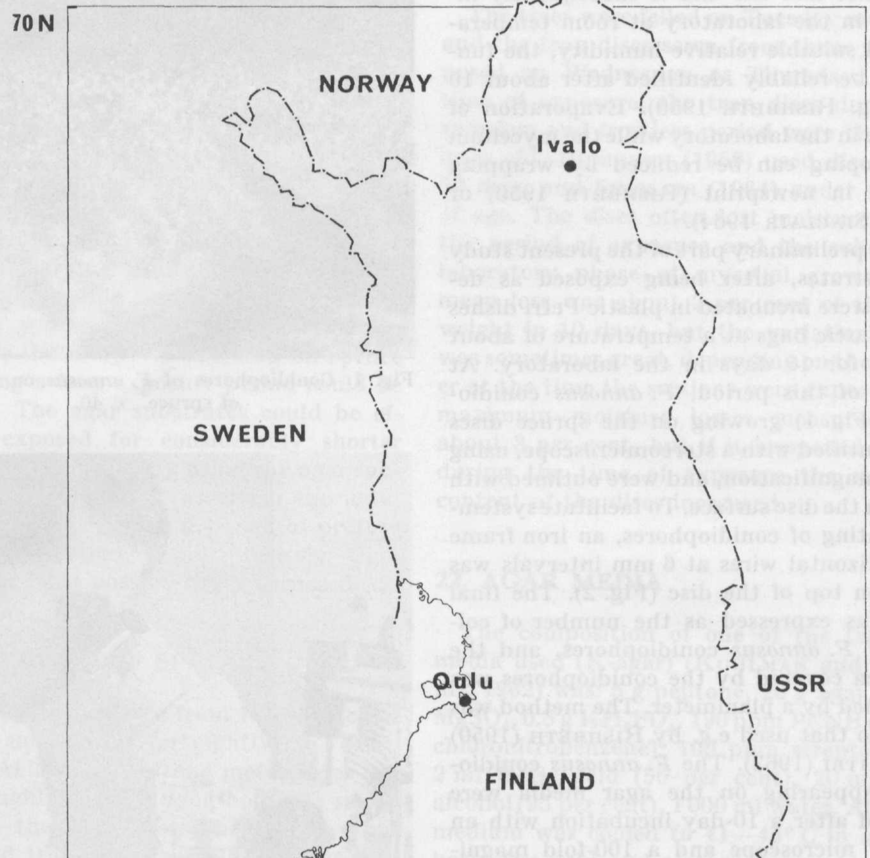

Fig. 3. Observation sites.

about 85 metres, to the nearest forest about 400 metres; the Jyväskylä airfield (62°24′ N, 25°40′ E), 140 metres above mean sea level, distance to the nearest growing tree about 10 metres, to the nearest forest about 120 metres; the Turku airfield (60°31′ N, 22°16′ E), 49 metres above mean sea level, distance to the nearest growing tree about 15 metres, to the nearest forest about 150 metres; the Lappeenranta airfield (61°03′ N, 28°09′ E), 106 metres above mean sea level, distance to the nearest growing tree about 65 metres, to the nearest forest about 200 metres; and the Viikki meteorological station in Helsinki (60°13′ N, 25°02′ E), 8 metres above mean sea level, distance to the nearest growing tree about 20 metres, to the nearest forest about 60 metres. The observation site in infected forest was also in Helsinki, Viikki (60°13′ N, 25°02′ E), about 10 metres above mean sea level. In the immediate neighbourhood of the site, there were stumps and growing trees with sporophores of *F. annosus*.

The reported exposures of trap discs to deposition of aerial *F. annosus* diaspores have ranged from 10 min. (e.g. RISHBETH 1959) to 10 hours (e.g. STAMBAUGH et al. 1962). In the present study, the growth substrates were usually exposed during daytime at hours the meteorological station personnel found to be convenient. The substrates at different observation sites were not exposed simultaneously. A few times, however, nocturnal exposures of all substrates in the country were arranged, and on these occasions no observations were recorded during the day. The spruce discs were airmailed to observation sites outside Helsinki. Each site had three discs. One served as a control and was never exposed. The lids of the plastic dishes containing the other two discs were opened simultaneously. One disc was exposed for 2 and the other for 4 hours. Each site had 3 of both the H- and the K-agar media. One served as a control in both groups. The other two dishes were opened simultaneously. One was exposed for 5 minutes and the other for 10 minutes. After the close of the observations, the substrates from the provinces were airmailed to Helsinki.

42. MAIN STUDY

The principal observation sites selected were *Picea abies* stands in Helsinki (Viikki), Anjala and Jokioinen (Fig. 3). In the Helsinki stand (60°13′ N, 25°02′ E, Fig. 4), 8 metres above mean sea level, the tree stand was about 110 years old, the dominant height about 25 metres, crown closure about 0.8, stems 180 per hectare, and the timber volume about 450 solid cu.m. per hectare including bark. The forest site type was Oxalis-Myrtillus (OMT) (CAJANDER 1949). The stand contained a large number of *F. annosus* sporophores.

Fig. 4. The observation stand in Helsinki.

At Anjala (60°43′ N, 26°48′ E), 40 metres above mean sea level, the tree stand was about 80 years old, the dominant height about 23 metres, crown closure about 0.8, stems 440 per hectare, timber volume about 260 solid cu.m. per hectare, and the forest site type was Myrtillus (MT). The stand contained a few *F. annosus* sporophores.

At Jokioinen (60°49′ N, 23°30′ E), 103 metres above mean sea level, the tree stand was about 50 years old, the dominant height about 19 metres, crown closure about 0.8, stems 530 per hectare, timber volume about 140 solid cu.m. per hectare, and the forest site type MT. The stand contained a few *F. annosus* sporophores.

On these principal observation sites the substrates were exposed on the ground. The exposure started on Wednesdays at 13.15 hours and was terminated on Thursdays at 13.15 hours. This 24-hour period constituted an observation day.

In Helsinki, during the period March 13 to December 5, 1968, there was one observation day weekly, and during the rest of the year one per fortnight. The spruce sections were exposed usually for two-hour periods from 13.15 to 15.15, 15.15 to 17.15 hours, and so on. This made twelve recording periods per 24 hours. From July 31 to September 26, the nocturnal (21.00 to 05.00 hours) recording periods lasted only one hour (from 21.15 to 22.15, 22.15 to 23.15, and so on). In the following account, the recording periods will often, for the sake of brevity, be expressed by full hours, and 13—15 will then refer to the period from 13.15 to 15.15 hours. By varying the times of exposure of the substrates, it was hoped to obtain more precise figures on the deposition of diaspores (cf. e.g. Rishbeth 1959). The H-agar substrates, during the periods from January 3 to June 20 and from October 2 to December 19, were exposed for 5 minutes each time the trap discs were changed, starting from 13.15, 15.15, 17.15 etc. hours. The durations of exposure of the agar substrates were graded from 1 to 5 minutes, according to the time of day or night, during the period from June 26 to September 26. In the middle of the night the exposure was 1 minute; during the day, 5 minutes.

At Anjala and Jokioinen there was one observation day per fortnight throughout the year, from January 3 to December 19, 1968. The trap discs were always exposed for 2-hour periods and the H-agar substrates for 5-minute periods. The substrates were exposed on identical days of the week and at the same hours as in Helsinki. Owing to a failure in transportation, the observation day at Anjala was, however, June 20—21, while in Helsinki and Jokioinen it was June 19—20. For the same reason the observation day at Jokioinen was December 19—20, but in Helsinki and Anjala December 18—19.

Each observation site had a control disc as well as an H-agar substrate serving as control. The substrates were mailed to and from Anjala and Jokioinen.

In addition to the stand in Helsinki already described, supplementary observations on the deposition of diaspores were also made in a nearby field (open site) and in the water tower during some observation days. On two observation days the deposition of diaspores was studied at the Kalbådagrund lighthouse in the Gulf of Finland.

5. Weather observations

The development, dispersal and deposition of viable diaspores is affected by numerous weather elements (e.g., Hirst 1953, Gregory 1961, Shrum and Wood 1967, Ingold 1968). Most of the diaspore catches in the preliminary study were made at or around meteorological stations so that the correlation between the variations in diaspore depositions and the weather elements could be made as easily and reliably as possible. For the same reason, the principal observation sites for the main study in Helsinki, Anjala and Jokioinen were selected in stands at the shortest possible distance from open-site weather stations of the Finnish Meteorological Institute. In addition to weather observations for the open sites, weather elements in Helsinki were also recorded in the forest in the immediate neighbourhood of the site where the trap discs and agar substrates were exposed.

51. PRELIMINARY STUDY

In Helsinki, the air temperature was measured at a weather station on an open site, at a height of 2 metres from the ground (cf. Säähavainto-opas 1951), three times a day (at 08.00, 14.00 and 20.00 hours), and the diurnal mean value was calculated by the method described by Kolkki (1966). Using a precipitation gauge with a total collection surface of 500 sq.cm., precipitation was measured at 08.00 hours in the morning, the result representing the precipitation during the preceding 24 hours (cf. Säähavainto-opas 1951). The mean air temperature and total precipitation per five-day periods in Helsinki are presented in Fig. 8, which also shows the duration of the snowy period in Helsinki.

52. MAIN STUDY

521. Open sites near observation stands

All weather observations on open sites were carried out by the Finnish Meteorological Institute. The majority of the observations in Helsinki were recorded within about 1.0 km of the site of the diaspore trapping disc, at

Anjala within about 0.1 km, and at Jokioinen within about 0.2 km.

Air temperatures were recorded as described under item 51 above. Two temperatures were used in calculating the correlation between the fall of *F. annosus* diaspores and the measured air temperature: (1) the mean temperature of the two consecutive calendar days between which the 24 hours of observation were divided, and (2) the mean temperature of the 5 calendar days preceding the 24-hour observation day. The mean temperatures of the calendar days were obtained from tables calculated by the Meteorological Institute.

The relative humidity of the air was recorded only at Jokioinen. Measurement was made at a height of 2 metres from the ground with a psychrometer installed in a Stevenson screen (cf. SÄÄHAVAINTO-OPAS 1951). Values were read from the monogram with an accuracy of 1 per cent. The value accepted as that of the observation day was the mean value of the readings taken at 14.00 and 20.00 hours on Wednesday and at 02.00 and 08.00 hours on Thursday. The correlation between air humidity and diaspore deposition of the air was calculated using the values of the observation day and the preceding 5 days, according to the principle outlined above for temperature.

Precipitation was measured in Helsinki and Anjala as described above under item 51. At Jokioinen, the precipitation was measured twice daily: at 08.00 and 20.00 hours. The diurnal precipitation was the sum of these measurements. To calculate the correlation between the deposition of *F. annosus* diaspores and the precipitation, the Meteorological Institute's records for the total precipitation, in millimetres per calendar day, were used. The precipitation values for the observation day and for the 5 preceding days were taken and their sum was calculated in the same way as described above for air temperature.

Bright sunshine was measured at Jokioinen by a Campbell-Stokes type sunshine recorder Fuess No. A 5846 and in Helsinki with a Fuess sunshine recorder No. 97 c, which recorded the sunshine conditions by 6-minute periods; i.e. tenths of an hour. The correlation between diaspore deposition and bright sunshine sum was studied on the basis of the 20 readings per recording period (from 13.15 to 15.15 hours, 15.15 to 17.15 hours, and so on). Correlations between the diaspore deposition per recording period and sunshine sum per recording period during the five days preceding the observation day were also studied.

Atmospheric pressure was recorded in Helsinki at the Malmi Aeronautical Meteorological Station (some 4 km northwest of the Viikki observation site) by means of barograph Fuess E 4398 and at Jokioinen by barograph Fuess B 3769. A fluctuation of atmospheric pressure equal to the difference between the maximum and minimum values (in millibars) of the 24-hour observation period was considered significant.

Wind velocity was recorded at the Malmi Aeronautical Meteorological Station by an anemograph Fuess E 6598 and at Jokioinen by a similar anemograph A 9246 (ANON. 1968 a). The mean wind velocity per hour obtained from the wind recordings of the Malmi Aeronautical Meteorological Station during the last ten minutes before each even hour, provided the basis for calculating mean velocity m/sec. The correlation between wind velocity and the deposition of *F. annosus* diaspores was calculated using the mean value of two of these 10-minute periods. For example, when the discs were exposed from 13.15 to 15.15 hours, the mean value of the mean wind velocities during 12.50 to 13.00 hours and 13.50 to 14.00 hours was used. At Jokioinen the diurnal wind velocity mean was used in correlation calculations.

522. Forest in Helsinki

5221. Air temperatures and relative humidities

Air temperatures and relative humidities were measured with a thermohydrograph (model Lambrecht No. 252, weekly graph), housed in a Stevenson screen (Fig. 4, cf. SÄÄHAVAINTO-OPAS 1951). The temperature and humidity values given by the recorder were compared daily with thermometer and psychrometer values. The temperature for the respective periods during which diaspores were trapped was considered to be that prevailing at the beginning of each period. For example, the temperature reading at 13.00 hours was used to correspond to the diaspore catch between 13.15 and 15.15 hours. A similar method was used for the air humidity. Temperature was measured with an accuracy of 0.1° C and relative humidity with an accuracy of 1 per cent.

5222. Temperatures of the sporophores, and air humidities in the immediate neighbourhood of sporophores

Temperatures of the *F. annosus* sporophores and the humidity of the air surrounding them have been studied e.g. by Schmidt (1966) and Schmidt and Wood (1969). Their methods were, in the main, used to measure the temperature of sporophores and the air humidity in their immediate vicinity in Helsinki. For these measurements, 6 sporophores of the *F. annosus* fungus were selected from the observation stand:

No. 1. Some 20 cm below ground level, on the under-surface of spruce roots. The white (active) surface covered about 20 sq.cm. The mean thickness of the sporophore was about 2 cm.

No. 2. (Fig. 5). Some 10 cm below ground level, on the root collar of a spruce stump. The white surface covered about 30 sq.cm., thickness about 2 cm.

Fig. 5. Sporophore No. 2 with the installed thermocouple, photographed while installation was going on and before the ground layer was repositioned. Reduced to about 0.9 × natural size.

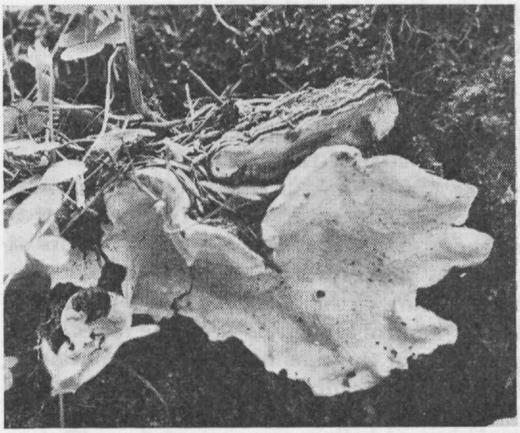

Fig. 6. Sporophore No. 6. The conductor wire of the thermocouple is visible in the upper part of the photograph. Reduced to about 0.4 × natural size.

No. 3. In the cavity of a hollow, rotted spruce stump, largely at ground level. White surface covered about 50 sq.cm. The sporophore was about 1.5 cm thick.

No. 4. In the cavity of a hollow, rotted spruce stump, about 5 cm above ground level. The white surface covered about 20 sq.cm. The sporophore was about 2 cm. thick.

No. 5. In a spruce stump about 20 cm above ground level. The white surface covered about 30 sq.cm. The sporophore was about 1 cm thick.

No. 6. (Fig. 6). In a spruce stump about 10 cm above ground level, bipartite (superimposed in a shelf-like attitude). The white surface covered some 60 sq.cm. Thickness about 1.5 cm.

The sporophores were grouped into 3 pairs. Nos. 1 and 2 formed one pair and represented the sporophores found at the greatest depth below ground surface. Nos. 3 and 4 also formed a pair and were situated in the cavities inside hollow, rotted and old spruce stumps. Nos. 5 and 6 formed the third pair, and were situated on the outer surfaces of stumps. In Finland, sporophores of *F. annosus* on the outer surfaces of spruce stumps relatively seldom occur above the forest litter layer. In this stand, however, their existence could perhaps be attributed to the immediate neighbourhood of the sea and to the rich ground vegetation.

To install the thermocouple, a hole the size of the thermocouple (model Wallace GS 3) was carefully drilled in the sporophore. Then, if necessary, soil was removed from around the stumps until the thermocouple could be inserted into the hole. The thermocouples were kept in position for a year after which they were calibrated at the Finnish Meteorological Institute. The temperatures read from them in 1968 were adjusted to agree with the calibration values. The maximum adjustment during a period of diaspore deposition was 0.6° C. The recordings were read with an accuracy of 0.1° C. The mean value of the results recorded for the sporophores of the relevant pair represented the pair concerned.

Air humidity in the immediate neighbourhood of the sporophores was measured by hygrometers (model Lambrecht KG No. 220) during the period April 24 to November 7, 1968. The hygrometers were positioned as close as possible to the spore-producing surface of the sporophores (0.5—1.0 cm) and remained in position throughout the above period.

The hygrometers were calibrated at the Meteorological Institute in the spring before they were placed in position, and again in the autumn after their removal. The relative humidities read from the meters were adjusted as indicated by the mean value curve of the initial and final calibration curves. In the hygrometer in the neighbourhood of sporophore No. 4, the difference between the adjustment curves for the spring and the autumn was so great (maximum, about 7 per cent humidity), that the humidity observations for this sporophore were excluded from the study. The maximum difference between the corresponding curves of the other hygrometers was about 2 per cent. Consequently, the relative humidity of the air in the vicinity of the surface of sporophores situated in the cavities inside hollow rotted stumps is represented by observations recorded from the hygrometer of only one sporophore (No. 3), whereas the results of the hygrometers of the other sporophore pairs (1 and 2, 5 and 6) are mean values calculated from two recordings.

The temperatures of the sporophores were recorded 5 times per 24 hours during the observation days between January 3 and April 18, 1968, and at 2-hour intervals on the observation days between April 24 and December 19, 1968, beginning at 13.00 hours and terminating at 11.00 hours the next morning. The humidities were recorded at 2-hour intervals, beginning at 13.00 hours, throughout the period. The temperature and air humidity at the beginning of each period of diaspore deposition (13.00—15.00, 15.00—17.00 hours, and so on) were used in correlation calculations to represent the relevant period.

In July 1968, the temperatures of the above 6 sporophores and the relative humidity of the air close to their spore-forming surface were recorded 4 times a day: at 02.00, 08.00, 14.00 and 20.00 hours. The records were:

Sporophore No	Mean temperature	Mean air relative humidity per cent
1	11.3 ± 0.9	100 ± 0
2	12.7 ± 1.5	96 ± 1
Mean	12.0 ± 1.1	98 ± 0
3	13.3 ± 1.6	96 ± 0
4	13.3 ± 1.0	
Mean	13.3 ± 1.8	
5	13.6 ± 2.2	95 ± 3
6	13.5 ± 2.2	94 ± 4
Mean	13.6 ± 2.2	95 ± 3

According to the t-test (e.g. Lindley and Miller 1958, Spiegel 1961) the mean temperature of sporophores 1 and 2 differed significantly, at the 0.1 per cent probability level, from the mean temperature of all the sporophores and from the mean air temperatures recorded at 2 metres from the ground both in the forest and on an open site. The differences revealed by the t-test between the mean temperatures of sporophore 1 and 2 and the mean temperatures listed above were more reliable than between the means of the other sporophore pairs and the mean temperatures of the list. The mean relative humidity of air in the immediate neighbourhood of sporophores 1 and 2 also differed, according to the t-test, at the 0.1 per cent probability level from that of all the sporophores and from the relative air humidity recorded in the forest at a height of 2 metres from the ground.

The sporophore temperatures and the relative humidity of the air in their vicinity, according to measurements made in Helsinki, varied according to the sporophores' location in the spruce stump. Schmidt (1966) reported a similar result from studies made in USA (Pa). Differences in temperature and humidity are likely to produce differences in the spore production by sporophores and also in the deposition of diaspores.

III RESULTS

1. Deposition of *F. annosus* diaspores

11. PRELIMINARY STUDY

Diaspores of *F. annosus* were found on only two occasions in North Finland: in Oulu July 29, 1967, and Ivalo May 15, 1968. These observations support the view previously advanced by several authors (e.g. Rennerfelt 1945, p. 324, Juutinen 1958, p. 36, Kallio 1964, p. 94, Eriksson and Strid 1969, p.139), that *F. annosus* is less common in northern Scandinavia than in the southern parts. Figs. 7—9 illustrate the diaspore catches recorded in South Finland. The open-site observation values of Fig. 7 are the aggregate deposition figures obtained from the airfields of Jyväskylä, Lappeenranta and Turku, and from the open area at Viikki (Helsinki). Forest observations were made in a *F. annosus* infected forest in Helsinki (Viikki). In the drawn figures, the combined results of the observations are shown bi-monthly for all those months in which *F. annosus* diaspores were met (cf. Kallio 1970, p. 67—69).

According to Fig. 7, in summer the diaspore deposition was relatively slight on open sites in South Finland during the day but considerably more profuse during the night. Daytime depositions appeared to be at their highest in the autumn. From December to mid-April no deposition of *F. annosus* diaspores was found on open sites.

This finding agrees well with results reported from England by Meredith (1959, p. 465) and from Denmark by Yde-Andersen (1961, p. 154). According to a study by Dimitri (1963, p. 357) in Germany, airborne infection of spruce stumps held practically the same level from March to November, with a minimum in July. In Poland (Orlos and Twarowska 1967, p. 216) two maxima were recorded in the spore production of *F. annosus:* one in May and the other in August or September, depending on the stand.

Fig. 8 shows the deposition of *F. annosus* diaspores from June 7, 1967 to May 29, 1968, in an infected forest and on an open field in Helsinki. The figure also lists some essential meteorological data. The diaspore depositions recorded are mainly day-time observations; observations were made during the night only four times. A comparison of the forest and open-site observations reveals that diaspore deposition was considerably greater in the forest although the range of variation was similar to that on open sites. No diaspores were trapped from December 20, 1967 to March 27, 1968. Diaspores began to fall in the spring, about 3 weeks after the mean air temperature, recorded in 5-day sequences at a height of 2 metres on an open site, had risen above zero. In the autumn, diaspores continued to fall for about 3 weeks after the temperature, measured in the same way, had fallen below zero.

Fig. 9 shows the deposition of diaspores obtained on all four dishes of the two agar substrates from the infected Helsinki forest. The figure reveals that nocturnal diaspore deposition had been considerable in the summer. The maximum recorded on August 1, 1967, between 22.15 and 22.25, amounted to 1932 viable diaspores per hour per 100 sq.cm. Sporophores were seen in the neighbourhood of the observation site. The second largest deposition was also recorded in August, viz. August 15, 1967, between 22.15 and 22.25, when 1525 diaspores per hour settled on 100 sq.cm. During the whole period from June 7 to November 20, 1967, July 5 was the only day when not a single viable diaspore of *F. annosus* was recorded from any of the observation sites. On August 30 and September 13 very few diaspores were trapped.

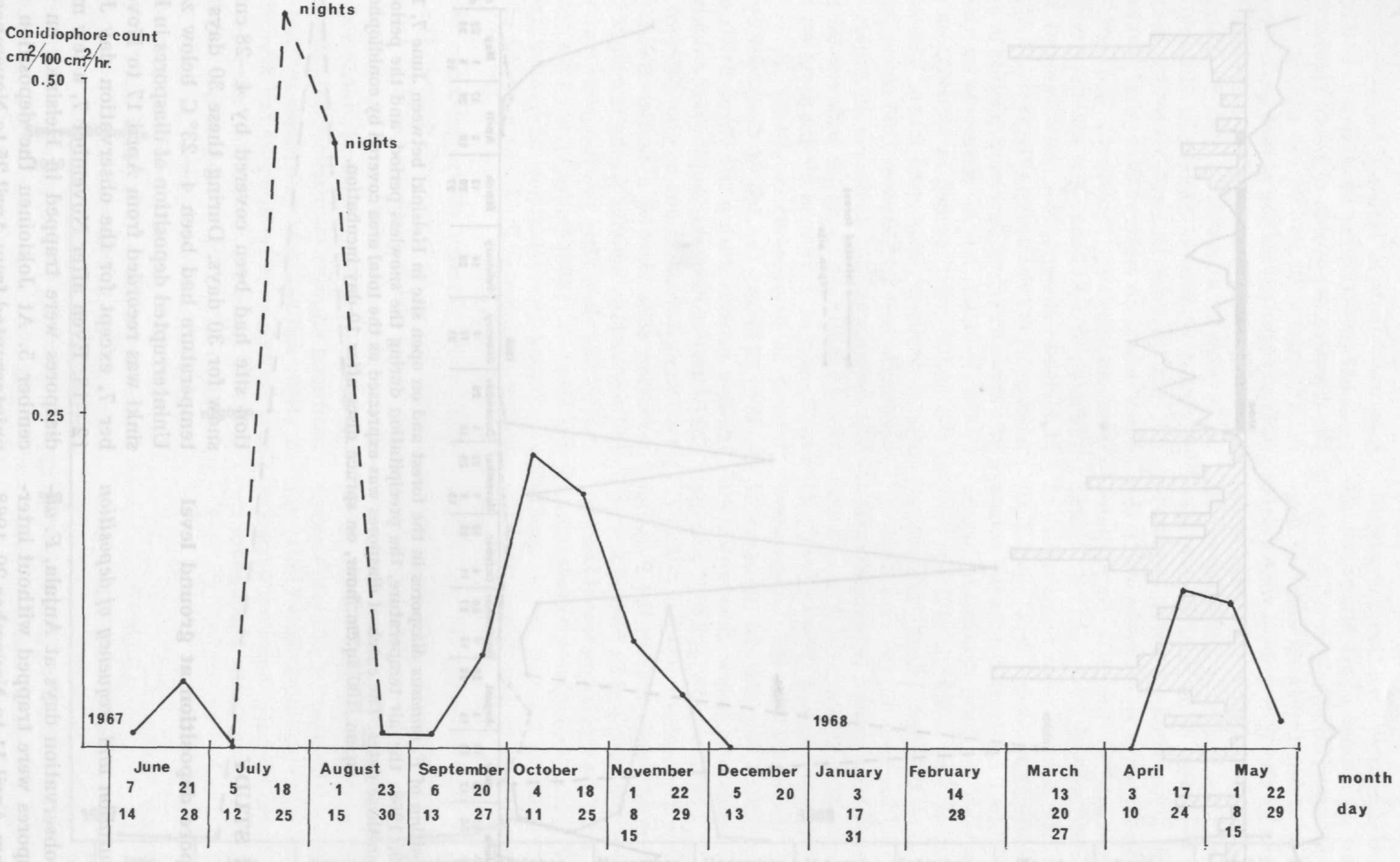

Fig. 7. Deposition of *F. annosus* diaspores on the open observation sites in South Finland between June 7, 1967 and May 29, 1968. The ordinate indicates the total surface area of all spruce discs covered by conidiophores after 10-day incubation, aggregately for all observation sites, in terms of square centimetres per 100 sq.cm of exposed trap area per hour.

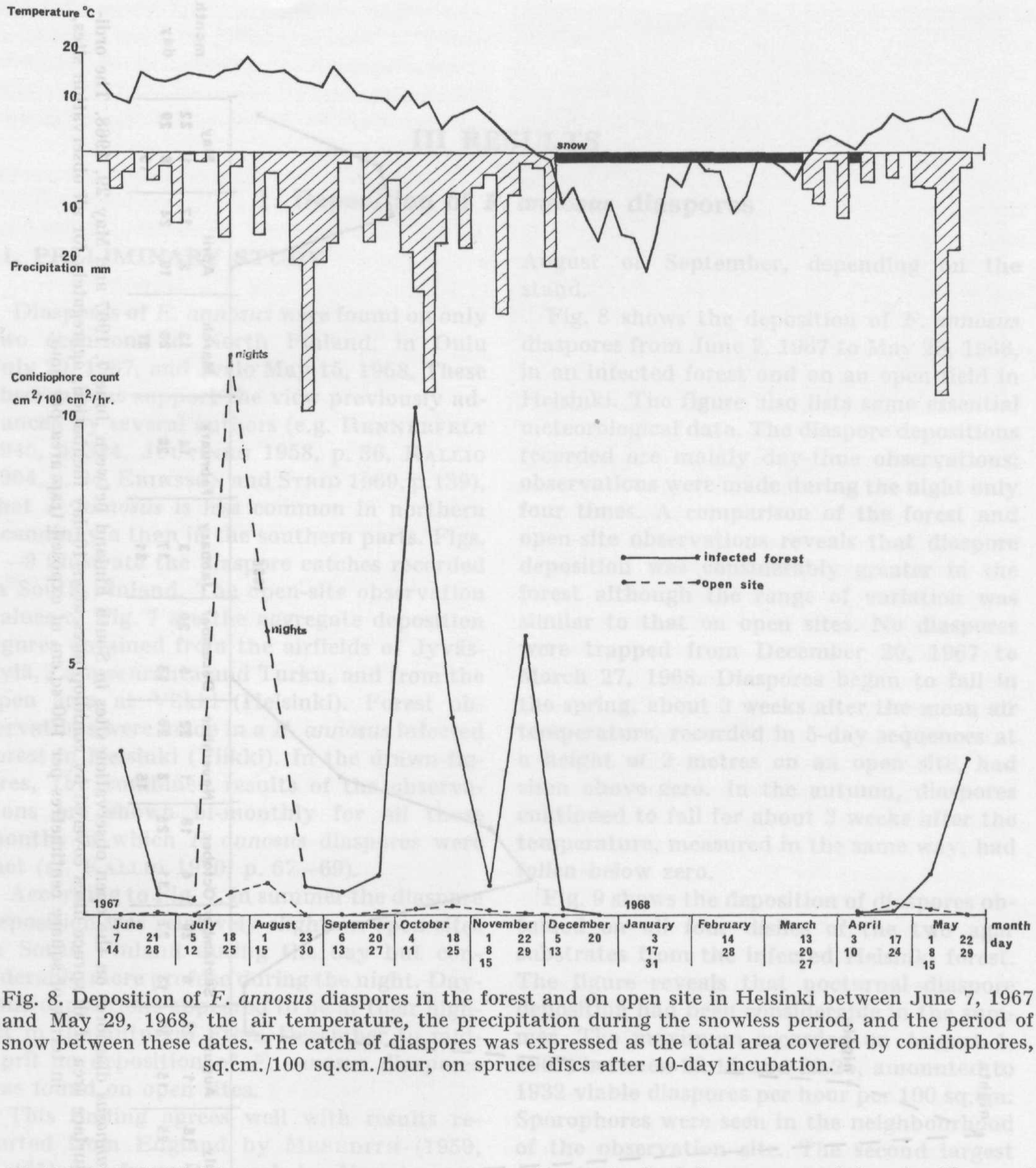

Fig. 8. Deposition of *F. annosus* diaspores in the forest and on open site in Helsinki between June 7, 1967 and May 29, 1968, the air temperature, the precipitation during the snowless period, and the period of snow between these dates. The catch of diaspores was expressed as the total area covered by conidiophores, sq.cm./100 sq.cm./hour, on spruce discs after 10-day incubation.

12. MAIN STUDY

121. Diaspore deposition at ground level in forest

1211. Duration and frequency of deposition

On the observation days at Anjala, *F. annosus* diaspores were trapped without interruption from April 11 to November 20, 1968. In Helsinki diaspores were first trapped on January 4, 1968. Before this date the observation site had been covered by 4—28 cm of snow for 30 days. During these 30 days the temperature had been 4—23° C below zero. Uninterrupted deposition of diaspores in Helsinki was recorded from April 17 to November 7, except for the observation day June 12—13. Even after November 7, a few more diaspores were trapped in Helsinki, on December 5. At Jokioinen the deposition was uninterrupted from April 25 to November 21, followed by another slight fall of diaspores on December 19. The season of uninterrupted

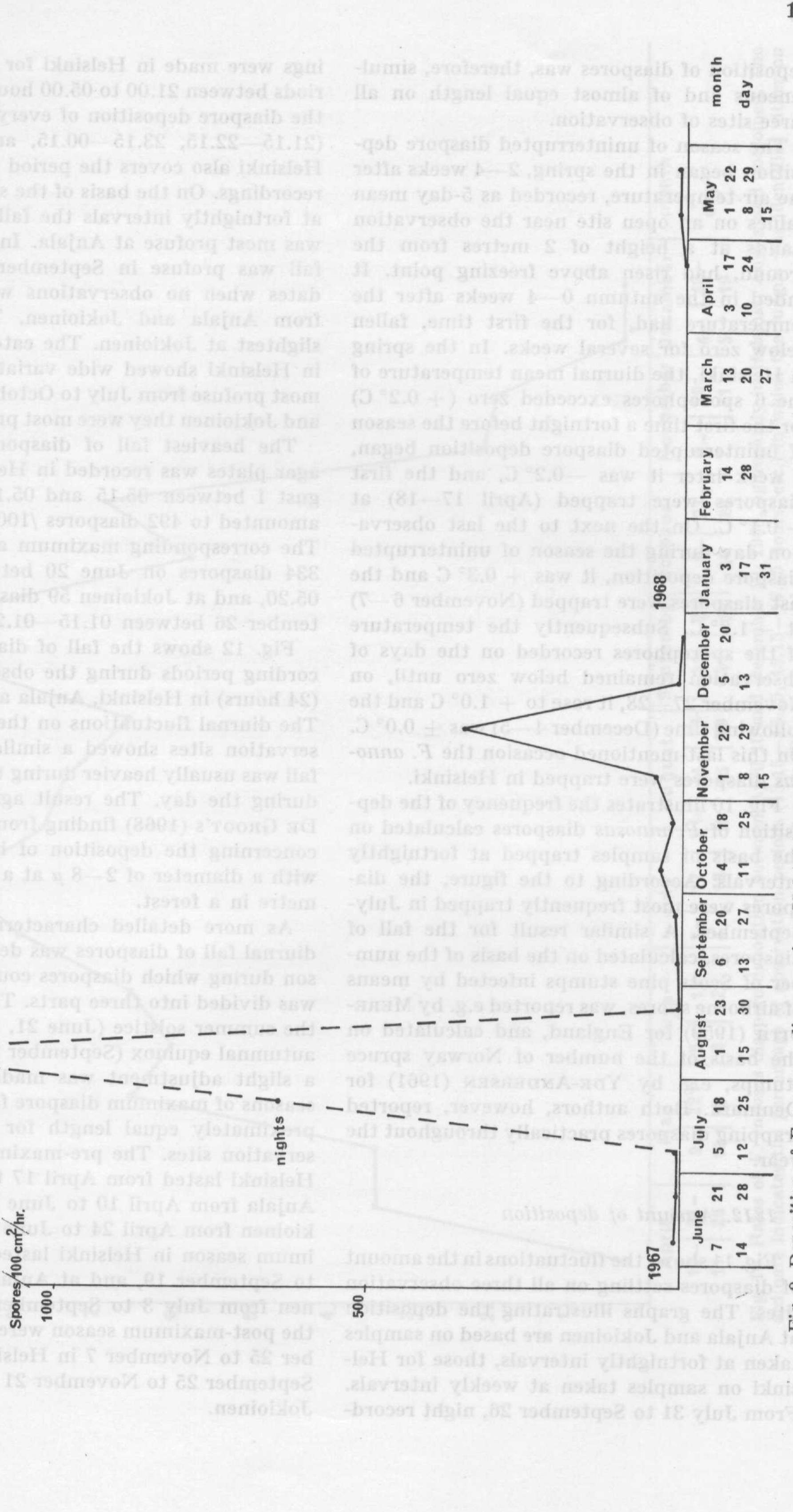

Fig. 9. Deposition of *F. annosus* diaspores in a Helsinki forest between June 7, 1967 and May 29, 1968. The spore numbers (spores/100 sq.cm./hour) were counted on agar plates.

deposition of diaspores was, therefore, simultaneous and of almost equal length on all three sites of observation.

The season of uninterrupted diaspore deposition began in the spring, 2—4 weeks after the air temperature, recorded as 5-day mean values on an open site near the observation stands at a height of 2 metres from the ground, had risen above freezing point. It ended in the autumn 0—4 weeks after the temperature had, for the first time, fallen below zero for several weeks. In the spring in Helsinki, the diurnal mean temperature of the 6 sporophores exceeded zero (+ 0.2° C) for the first time a fortnight before the season of uninterrupted diaspore deposition began, a week later it was —0.2° C, and the first diaspores were trapped (April 17—18) at + 0.1° C. On the next to the last observation day during the season of uninterrupted diaspore deposition, it was + 0.3° C and the last diaspores were trapped (November 6—7) at —1.0° C. Subsequently the temperature of the sporophores recorded on the days of observation remained below zero until, on November 27—28, it rose to + 1.0° C and the following time (December 4—5) was ± 0.0° C. On this last-mentioned occasion the *F. annosus* diaspores were trapped in Helsinki.

Fig. 10 illustrates the frequency of the deposition of *F. annosus* diaspores calculated on the basis of samples trapped at fortnightly intervals. According to the figure, the diaspores were most frequently trapped in July-September. A similar result for the fall of diaspores, calculated on the basis of the number of Scots pine stumps infected by means of airborne spores, was reported e.g. by MEREDITH (1959) for England, and calculated on the basis of the number of Norway spruce stumps, e.g. by YDE-ANDERSEN (1961) for Denmark. Both authors, however, reported trapping diaspores practically throughout the year.

1212. Amount of deposition

Fig. 11 shows the fluctuations in the amount of diaspores settling on all three observation sites. The graphs illustrating the deposition at Anjala and Jokioinen are based on samples taken at fortnightly intervals, those for Helsinki on samples taken at weekly intervals. From July 31 to September 26, night recordings were made in Helsinki for one-hour periods between 21.00 to 05.00 hours. In Fig. 11 the diaspore deposition of every second hour (21.15—22.15, 23.15—00.15, and so on) in Helsinki also covers the period of the hourly recordings. On the basis of the samples taken at fortnightly intervals the fall of diaspores was most profuse at Anjala. In Helsinki the fall was profuse in September-October, on dates when no observations were available from Anjala and Jokioinen. The fall was slightest at Jokioinen. The catches recorded in Helsinki showed wide variation but were most profuse from July to October. At Anjala and Jokioinen they were most profuse in July.

The heaviest fall of diaspores on the H-agar plates was recorded in Helsinki on August 1 between 05.15 and 05.16. The catch amounted to 492 diaspores /100 sq.cm./hour. The corresponding maximum at Anjala was 334 diaspores on June 20 between 05.15—05.20, and at Jokioinen 59 diaspores on September 26 between 01.15—01.20.

Fig. 12 shows the fall of diaspores by recording periods during the observation days (24 hours) in Helsinki, Anjala and Jokioinen. The diurnal fluctuations on the different observation sites showed a similar trend. The fall was usually heavier during the night than during the day. The result agrees e.g. with DE GROOT's (1968) finding from USA (N.Y.) concerning the deposition of hyaline spores with a diameter of 2—8 μ at a height of one metre in a forest.

As more detailed characterization of the diurnal fall of diaspores was desired, the season during which diaspores could be trapped was divided into three parts. The limits were the summer solstice (June 21, 1968) and the autumnal equinox (September 23). However, a slight adjustment was made so that the seasons of maximum diaspore fall were of approximately equal length for all three observation sites. The pre-maximum season in Helsinki lasted from April 17 to June 27, at Anjala from April 10 to June 21 and at Jokioinen from April 24 to June 20. The maximum season in Helsinki lasted from July 3 to September 19, and at Anjala and Jokioinen from July 3 to September 12. Dates of the post-maximum season were from September 25 to November 7 in Helsinki, and from September 25 to November 21 at Anjala and Jokioinen.

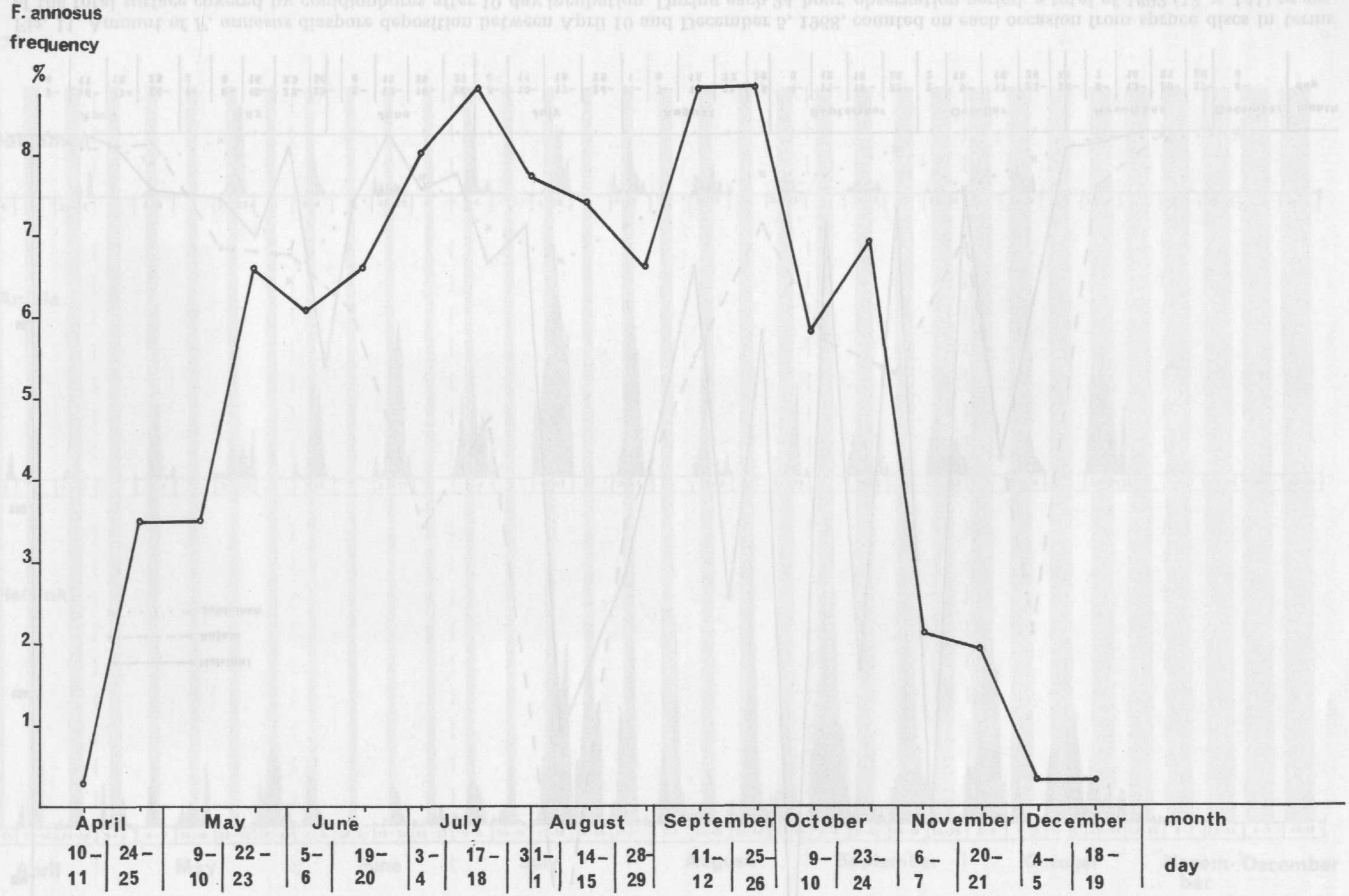

Fig. 10. Rates of *F. annosus* diaspore deposition between April 10 and December 19, 1968, aggregately in Helsinki, Anjala and Jokioinen. The ordinate indicates the percentage of observation periods (13.15—15.15, 15.15—17.15 hours, etc.) in which the fungus was identified either on spruce discs or on agar plates.

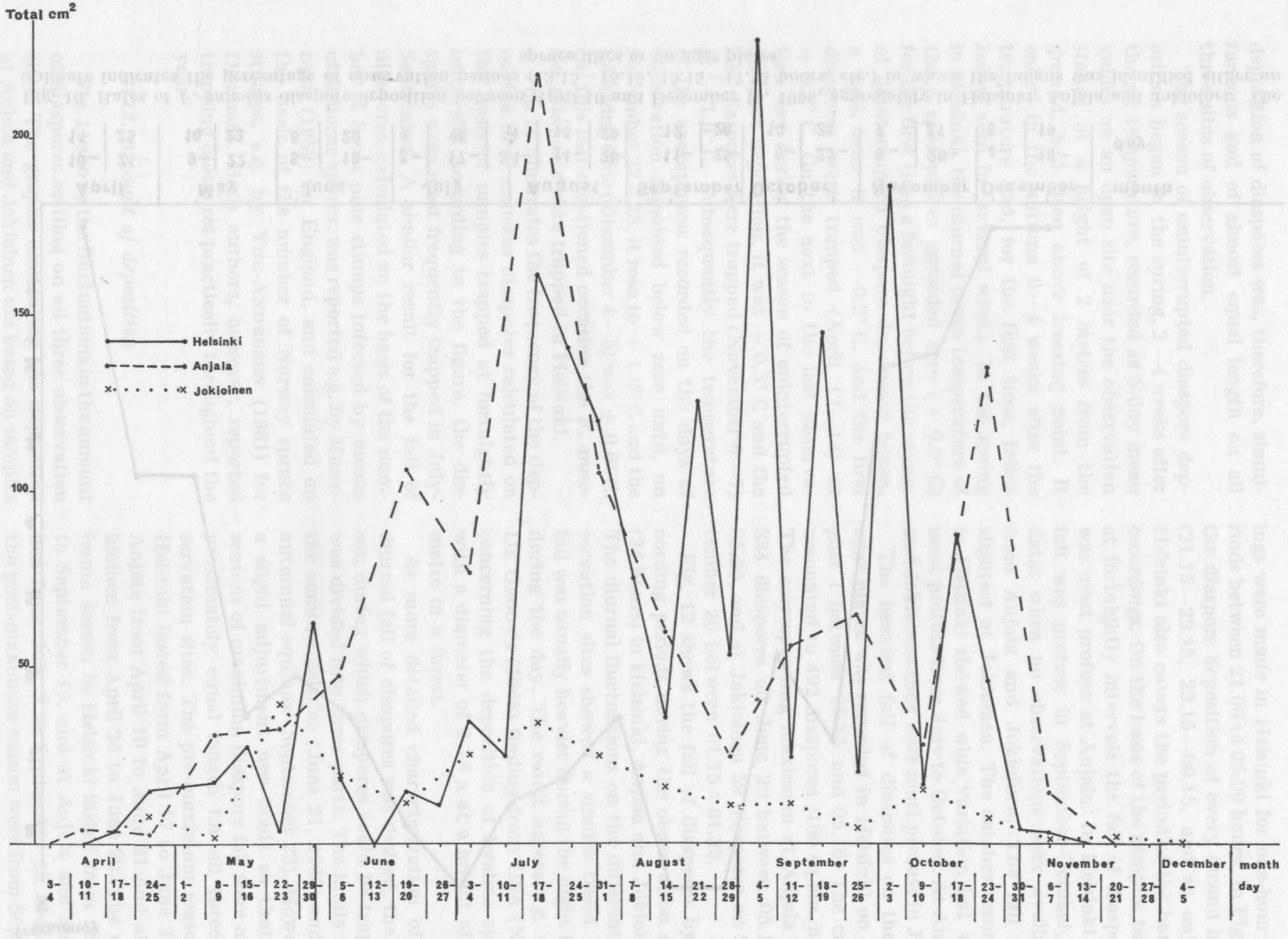

Fig. 11. Amount of *F. annosus* diaspore deposition between April 10 and December 5, 1968, counted on each occasion from spruce discs in terms of the total surface covered by conidiophores after 10 day incubation. During each 24 hour observation period, a total of 1692 (12 × 141) sq.cm. of disc surface was exposed at each observation site.

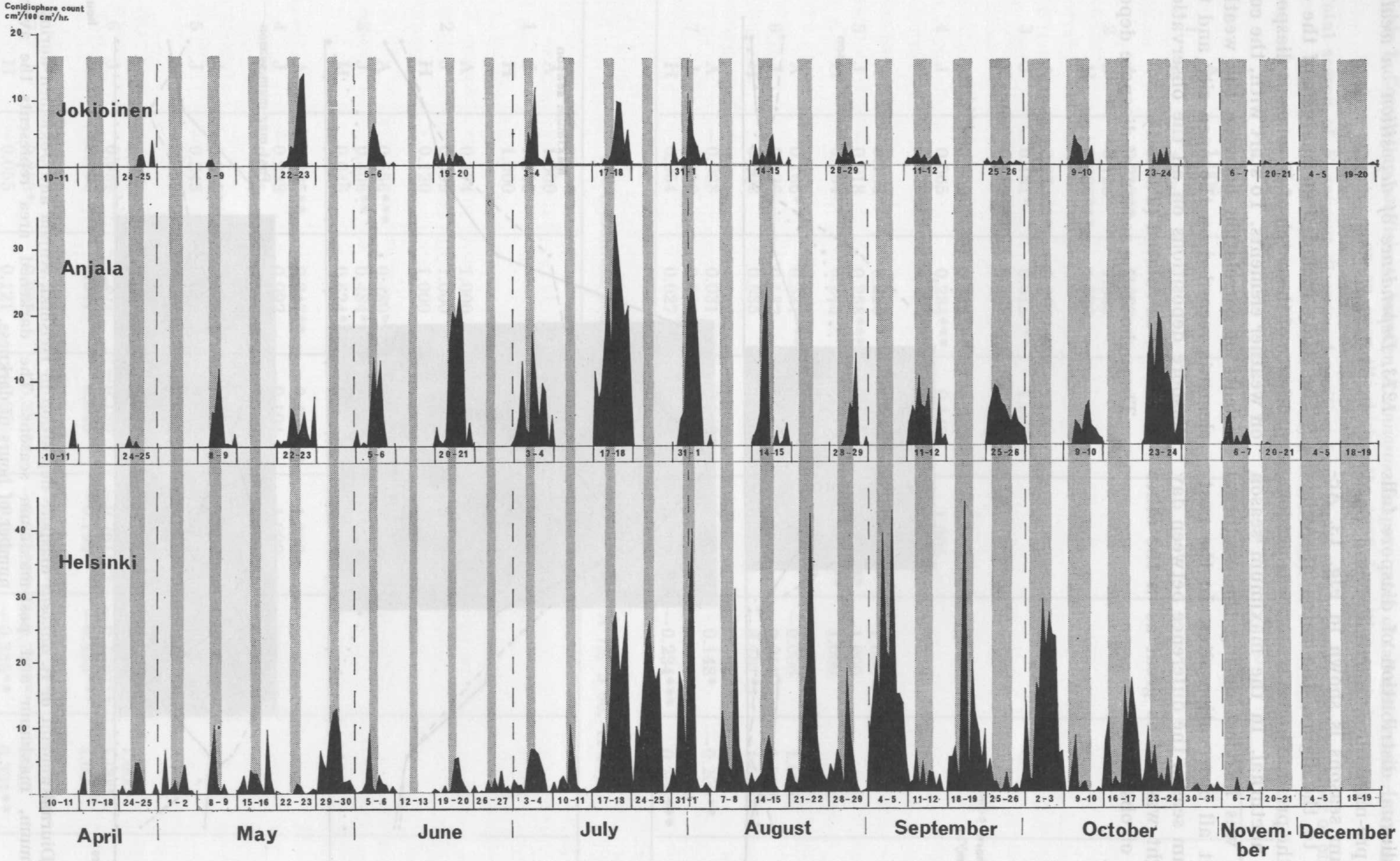

Fig. 12. Diurnal variations in the deposition of *F. annosus* diaspores on the main observation sites from April to December 1968. The darkened strip of each 24 hour observation period represents the nocturnal hours.

The diurnal distribution of diaspore falls in the pre-maximum, maximum and post-maximum seasons is shown in Fig. 13. According to the figure, the catch at Anjala during the pre-maximum season was predominantly nocturnal. In the maximum season the fall was heaviest during the nocturnal hours at all observation sites. In the post-maximum season the difference between day and night was not so great as in the other seasons of observation.

1213. Dependence of deposition on weather elements

The study included an analysis of the dependence of the catch of *F. annosus* diaspores on weather elements. To start with, the coefficients of correlation between the weather elements recorded on the open site and the diaspore depositions on all the observations sites were calculated (Table 1).

Throughout the season of diaspore deposi-

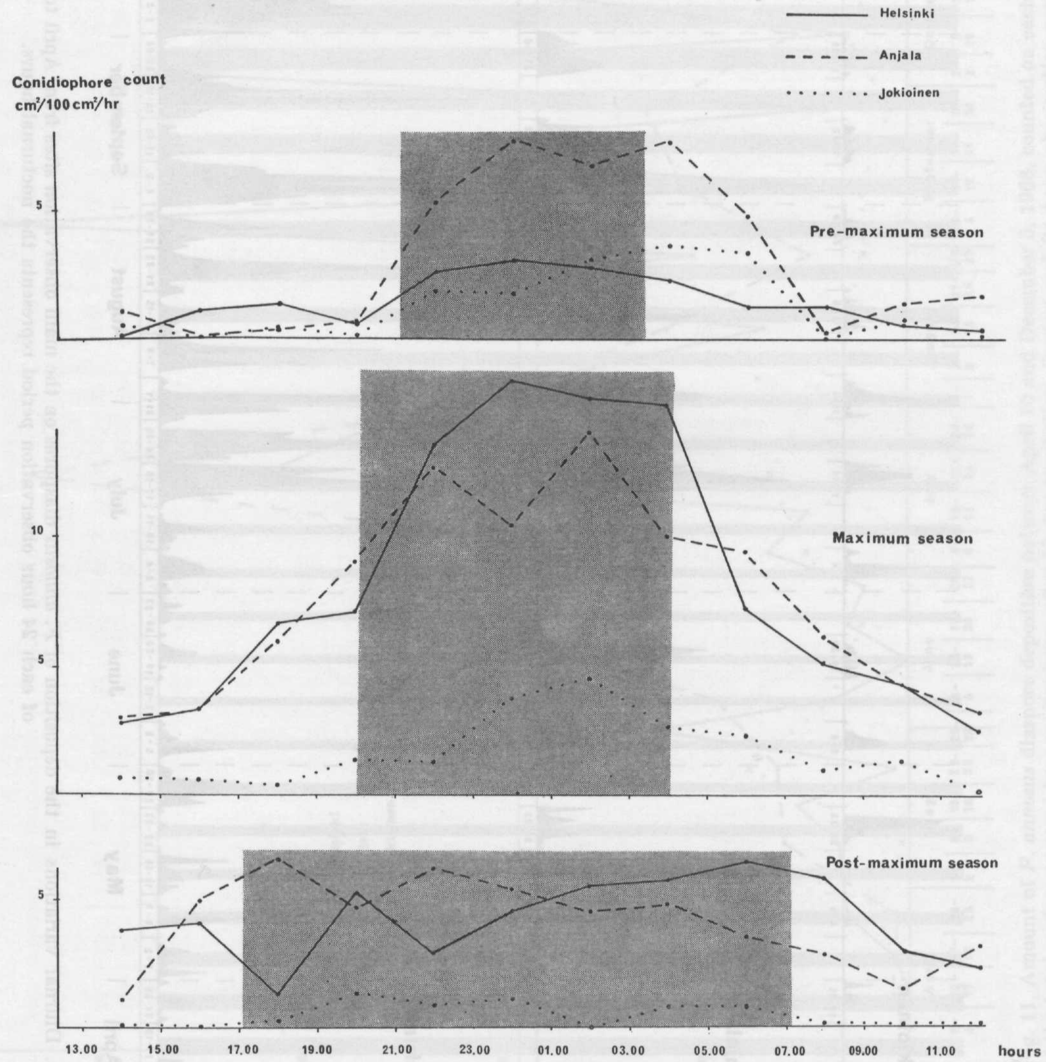

Fig. 13. Diurnal amount of *F. annosus* diaspore deposition in Helsinki, Anjala and Jokioinen during the pre-maximum, maximum and post-maximum seasons. The darkened area represents the average number of hours of darkness.

Table 1. Correlation coefficients between *F. annosus* diaspore rates of fall and weather elements recorded on an open site during the 1968 deposition period.

Total season of *F. annosus* diaspore deposition from April to December 1968 (number of observations: A 204, J 192, H 322).

		1	2	3	4	5	6	7
1	A	1.000						
	J	1.000						
	H	1.000						
2	A	0.219**	1.000					
	J	0.128	1.000					
	H	0.266***	1.000					
3	A	0.354***	0.282***	1.000				
	J	0.181*	0.515***	1.000				
	H	0.482***	0.493***	1.000				
4	A	0.202**	0.255***	0.295***	1.000			
	J	0.065	0.284***	0.140	1.000			
	H	0.179***	0.286***	0.179***	1.000			
5	A	0.168*	0.220**	0.282***	0.944***	1.000		
	J	−0.018	0.258***	0.176*	0.933***	1.000		
	H	0.154**	0.245***	0.210***	0.907***	1.000		
6	A	0.166*	0.381***	0.130	0.014	−0.006	1.000	
	J	0.126	0.132	−0.053	−0.079	−0.017	1.000	
	H	0.002	0.035	−0.040	−0.131*	−0.161**	1.000	
7	A	−0.068	0.031	−0.148*	0.269***	0.148*	−0.209**	1.000
	J	0.038	0.022	0.157*	0.108	0.009	0.060	1.000
	H	0.054	0.027	−0.082	−0.202***	−0.234***	0.264***	1.000

Pre-maximum season (number of observations: A 72, J 60, H 90).

		1	2	3	4	5	6	7
1	A	1.000						
	J	1.000						
	H	1.000						
2	A	0.174	1.000					
	J	0.099	1.000					
	H	0.120	1.000					
3	A	0.556***	0.480***	1.000				
	J	0.406**	0.484***	1.000				
	H	0.046	0.624***	1.000				
4	A	0.305**	0.347**	0.462***	1.000			
	J	−0.233	0.092	−0.104	1.000			
	H	−0.125	0.170	−0.089	1.000			
5	A	0.315**	0.321**	0.469***	0.969***	1.000		
	J	−0.243	0.088	−0.115	0.996***	1.000		
	H	−0.053	0.138	0.020	0.875***	1.000		
6	A	−0.195	−0.080	−0.256*	−0.789***	−0.789***	1.000	
	J	0.081	−0.207	−0.160	−0.761***	−0.729***	1.000	
	H	0.040	0.047	0.040	−0.190	−0.455***	1.000	
7	A	−0.177	−0.191	−0.272*	−0.453***	−0.604***	0.339**	1.000
	J	0.283*	0.087	0.333**	−0.675***	−0.702***	0.042	1.000
	H	−0.055	0.121	−0.076	0.081	−0.336**	0.331**	1.000

Table 1, continued. Maximum season (number of observations: A 72, J 72, H 144).

		1	2	3	4	5	6	7
1	A	1.000						
	J	1.000						
	H	1.000						
2	A	0.087	1.000					
	J	0.190	1.000					
	H	0.119	1.000					
3	A	0.243*	0.074	1.000				
	J	0.205	0.447***	1.000				
	H	0.453***	0.372***	1.000				
4	A	0.183	0.074	0.424***	1.000			
	J	0.116	−0.036	−0.209	1.000			
	H	−0.037	−0.087	−0.094	1.000			
5	A	0.244*	−0.056	0.017	0.408***	1.000		
	J	−0.111	−0.129	0.111	0.078	1.000		
	H	−0.045	−0.052	0.050	0.787***	1.000		
6	A	0.150	0.282*	0.117	0.410***	−0.395***	1.000	
	J	−0.149	0.195	−0.052	−0.451***	−0.135	1.000	
	H	0.000	0.046	0.023	−0.239**	0.107	1.000	
7	A	−0.096	0.021	−0.279*	−0.800***	−0.046	−0.408***	1.000
	J	−0.011	−0.187	−0.175	0.346**	−0.299*	0.175	1.000
	H	0.088	−0.080	−0.211*	−0.025	−0.280***	0.221**	1.000

Post-maximum season (number of observation: A 60, J 60, H 88).

1	A	1.000						
	J	1.000						
	H	1.000						
2	A	0.599***	1.000					
	J	0.022	1.000					
	H	0.411***	1.000					
3	A	0.265*	0.492***	1.000				
	J	−0.021	0.846***	1.000				
	H	−0.229*	0.380***	1.000				
4	A	0.556***	0.793***	0.425***	1.000			
	J	0.390**	0.224	0.126	1.000			
	H	0.322**	0.430***	0.236*	1.000			
5	A	0.552***	0.754***	0.180	0.853***	1.000		
	J	0.308*	0.403**	0.269 *	0.815***	1.000		
	H	0.400***	0.461***	0.417***	0.718***	1.000		
6	A	0.482***	0.605***	0.192	0.900***	0.695***	1.000	
	J	0.404**	0.062	−0.094	0.812***	0.475***	1.000	
	H	−0.123	−0.088	−0.441***	0.022	−0.028	1.000	
7	A	−0.084	0.046	0.647***	−0.052	−0.319*	−0.285*	1.000
	J	−0.041	−0.105	0.083	0.166	−0.012	−0.231	1.000
	H	0.054	0.298**	0.107	−0.375***	0.019	0.404***	1.000

tion, a highly significant positive correlation was noted between the air temperature recorded at a 2-metre height on an open site and the catch of diaspores at all 3 observation sites. A similar correlation has also been reported by SINCLAIR (1964) in the USA. Ross (1969) reported a corresponding negative correlation from the southern states of the USA, no correlation at all from the central states, and positive correlation from a northeastern state. During the pre-maximum and maximum seasons a highly significant positive correlation between diaspore deposition and air temperature was recorded only at Anjala. In the post-maximum season a highly significant positive correlation between air temperature and diaspore deposition was noted at Anjala and Helsinki.

Throughout the season of diaspore deposition the correlation between precipitation and diaspore deposition was generally slight. Only at Anjala was there a highly significant positive correlation in the total season and post-maximum season, and in Helsinki a highly significant negative correlation in the post-maximum season.

The correlations with regression coefficients, which on the basis of t-value were significant at a probability level of 5 per cent or less, have been selected from Table 1 and assembled in Table 2. The relations in diaspore deposition shown in Table 2 at the 0.1 per cent or lower probability level, were explained by:

1. Precipitation throughout the season of *F. annosus* diaspore deposition at Anjala.
2. Air temperatures during the pre-maximum season in Helsinki.
3. Air temperatures during the maximum season at Anjala.
4. Air temperatures and precipitations during the post-maximum season at Anjala and Helsinki.

According to Table 3, throughout the diaspore deposition season at Jokioinen, the correlation between the deposition of *F. annosus* diaspores and the bright sunshine hours of the 5 preceding days, recorded on an open site by recording periods, was negative and highly significant. The correlations between diaspore deposition and the mean temperature of the air, measured on an open site at a 2-metre height during the preceding 5 calendar days, and between the deposition and the diurnal mean of relative air humidity measured during the 24 hour observation period at a 2-metre height on an open site, were positive and significant at a probability level of 1 per cent of less. A significant negative correlation was recorded between the mean wind velocity of the preceding 5 days and the difference between the maximum and minimum atmospheric pressure readings for the observation day.

According to Table 4, on the basis of the t-test the difference between the maximum and minimum atmospheric pressure readings during the day of observation (24 hours) was the climatic factor that most reliably (probability level 0.1 per cent or less) accounted for the fluctuations in the fall of diaspores. The fluctuations were also significantly determined (5 per cent probability level) by bright sunshine during the recording periods of the 5 preceeding days, and by the mean wind velocity of the preceding 5 calendar days.

Table 5 presents correlation coefficients between weather elements measured in Helsinki and the fall of diaspores. The catch of *F. annosus* diaspores was highly significantly cor-

Explanations of Table 1.

A Anjala
J Jokioinen
H Helsinki
1 *F. annosus* on agar plate, spores/100 sq.cm./hour, by recording periods.
2 » on spruce discs, colonies/100 sq.cm./hour, by recording periods.
3 » on spruce discs, conidiophore count sq.cm./100 sq.cm./hour, by recording periods.
4 Mean air temperature (° C) of the 5 calendar days preceding the day of observation at 2 metres above ground level.
5 Mean air temperature (° C) of the 2 consecutive calendar days between which the 24 hours of the observation day were divided, at 2 metres above ground level.
6 Total precipitation (mm) during the 5 calendar days preceding the day of observation.
7 Total precipitation (mm) of the 2 consecutive calendar days between which the 24 hours of the observation day were divided.
Significant at the level: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Table 2. Relations in 1968 between the fall of *F. annosus* diaspores, temperature recorded on an open site, and precipitation.

Total season of *F. annosus* diaspore deposition

Dependent variable	Site of observation	Independent variable	t-value	Significant level
1	A	4	−3.02	**
		6	2.22	*
	J	4	2.78	**
		5	−2.69	**
2	A	4	−2.66	**
		6	6.23	***
	H	4	2.72	**
3	A	4	−2.09	*
		7	−3.05	***
	J	5	2.21	*
		7	2.57	**
	H	5	1.97	*

Maximum season

Dependent variable	Site of observation	Indepedent variable	t-value	Significant level
1	A	5	2.94	**
		6	2.68	**
2	A	6	2.02	*
	J	4	2.04	*
		6	2.74	**
		7	−3.08	**
3	A	4	5.54	***
		5	−4.30	***
		6	−3.41	**
		7	3.24	**

A Anjala
J Jokioinen
H Helsinki

1 *F. annosus* on agar plate spores/100 sq.cm./hour, by recording periods.
2 » on spruce discs, colonies/100 sq.cm./hour, by recording periods.
3 » on spruce discs, conidiophore count sq.cm./100 sq.cm./hour, by recording periods.
4 Mean air temperature (° C) of the 5 preceding calendar days at 2 metres above ground level.
5 Mean air temperature (° C) of the 2 consecutive calendar days between which the 24 hours of the observation day were divided, at 2 metres above ground level.

Table 3. Correlation coefficients between *F. annosus* diaspore deposition and certain weather

	1	2	3	4	5	6
1	1.000					
2	0.116	1.000				
3	0.172*	0.494***	1.000			
4	0.019	0.202**	0.030	1.000		
5	−0.082	0.171*	0.090	0.906***	1.000	
6	0.126	0.108	−0.090	−0.039	−0.117	1.000
7	0.019	−0.032	0.118	−0.062	−0.161*	0.023
8	−0.177*	−0.308***	−0.211**	0.372***	0.459***	−0.270***
9	−0.153*	−0.172*	0.075	−0.765***	−0.454***	−0.024
10	0.129	0.111	0.134	0.478***	0.495***	0.173*
11	0.072	0.129	0.118	0.283***	0.364***	0.510***
12	0.143	−0.151	−0.196*	−0.519***	−0.610***	0.232**
13	0.207**	0.016	−0.137	−0.241**	−0.508***	0.095

1 *F. annosus* on agar plate, spores/100 sq.cm./hour, by recording periods.
2 » on spruce discs, colonies/100 sq.cm./hour, by recording periods.
3 » on spruce discs, conidiophore count sq.cm./100 sq.cm./hour, by recording periods.
4 Mean air temperature (° C) of the 5 preceding calendar days, at 2 metres above ground level.
5 Mean air temperature of the 2 consecutive calendar days between which the 24 hours of the observation day were divided, at 2 metres above ground level.
6 Total precipitation (mm) during the 5 preceding calendar days.
7 Total precipitation (mm) of the 2 consecutive calendar days between which the 24 hours of the observation day were divided.
8 Hours of bright sunshine during the 5 preceding days, by recording periods.

Pre-maximum season

Dependent variable	Site of observation	Independent variable	t-value	Significant level
1	H	4	−2.22	*
		5	2.03	*
2	A	6	2.68	**
	H	7	2.04	*
3	H	4	−3.87	***
		5	3.81	***
		6	2.76	**
		7	2.78	**

Post-maximum season

Dependent variable	Site of observation	Independent variable	t-value	Significant level
1	A	4	−2.78	**
		6	2.20	*
2	A	4	−5.63	***
		5	6.13	***
		6	6.67	***
		7	−3.26	**
	H	4	6.70	***
		6	−5.25	***
		7	8.03	***
3	A	5	3.57	***
		6	4.93	***
		7	3.05	**
	J	4	2.25	*
		6	−2.51	*
		7	−2.13	*
	H	4	2.04	*
		6	−6.74	***
		7	4.19	***

6 Total precipitation (mm) during the 5 preceding calendar days.

7 Total precipitation of the 2 consecutive calendar days between which the 24 hours of the observation day were divided.

Significant at the level: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

elements at Jokioinen during the diaspore deposition season of 1968 (167 observations).

7	8	9	10	11	12	13
1.000						
−0.082	1.000					
−0.116	0.107	1.000				
0.293***	0.215**	0.283***	1.000			
0.275***	0.189*	0.010	0.662***	1.000		
0.158*	0.010	0.155*	0.038	0.073	1.000	
−0.022	−0.369***	−0.294***	−0.319***	−0.375***	0.326***	1.000

9 Mean wind velocity (m/sec.) of the 5 preceding calendar days.

10 Mean wind velocity (m/sec.) during the 24 hour observation day.

11 Mean value of the differences between the maximum and minimum atmospheric pressure readings of the 5 preceding days.

12 Difference between the maximum and minimum atmospheric pressure readings during the 24 hour observation day.

13 Mean value of the relative humidity of air during the 24 hour observation day, at 2 metres above ground level.

Significant at the level: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

Table 4. Relations between *F. annosus* diaspore deposition and weather elements at Jokioinen in 1968.

Dependent variable	Independent variable	t-value	Significant level
2	9	−2.15	*
	12	−2.30	*
3	8	−2.34	*
	12	−3.72	***

For further explanation of variables, see Table 3.

related with several weather elements. At a probability level of 0.1 per cent or less, it appeared to depend, according to Table 6, on the duration of bright sunshine on the observation day by recording periods (negative correlation), and the difference between the maximum and minimum atmospheric pressure readings of the observation day (negative correlation). At a probability level of one per cent or less, there was a positive correlation between diaspore fall and both air temperature and sporophore temperature.

Table 6. Relations between *F. annosus* diaspore deposition and weather elements in Helsinki in 1968.

Dependent variable	Independent variable	t-value	Significant level
2	5	2.55	*
	6	−3.50	***
	7	−2.06	*
	11	2.21	*
3	5	3.28	**
	6	−3.98	***
	7	−2.02	*
	8	−4.30	***
	10	2.33	*
	11	3.26	**
	12	−3.02	**
	13	−2.51	*
	14	−2.30	*

For further explanation of variables, see Table 5.

Multiple regression analysis (e.g. SNEDECOR

Table 5. Correlation coefficients between *F. annosus* diaspore deposition and certain weather

	1	2	3	4	5	6	7
1	1.000						
2	0.273***	1.000					
3	0.480***	0.497***	1.000				
4	0.171**	0.274***	0.166**	1.000			
5	0.141**	0.228***	0.199***	0.904***	1.000		
6	−0.149**	−0.264***	−0.253***	0.182***	0.269***	1.000	
7	−0.270***	−0.383***	−0.413***	−0.095	−0.154**	0.376***	1.000
8	−0.114*	−0.047	−0.234***	−0.439***	−0.528***	−0.162**	0.150**
9	0.169**	0.270***	0.166**	0.997***	0.914***	0.182***	−0.096
10	0.209***	0.373***	0.304***	0.003	−0.133*	−0.252***	−0.344***
11	0.192***	0.325***	0.239***	0.951***	0.921***	0.157**	−0.174**
12	0.150**	0.257***	0.187***	0.936***	0.951***	0.211***	−0.129*
13	0.244***	0.352***	0.251***	0.872***	0.780***	0.114*	−0.221***
14	−0.072	−0.095	−0.090	0.309***	0.341***	0.031	0.130*
15	0.096	0.223***	0.147**	−0.041	−0.210***	−0.361***	−0.189***

1 *F. annosus* on agar plate, spores/100 sq.cm./hour, by recording periods.
2 » on spruce discs, colonies/100 sq.cm./hour, by recording periods.
3 » on spruce discs, conidiophore count sq.cm./100 sq. cm./hour, by recording periods.
4 Mean air temperature (° C) of the 5 preceding calendar days, at 2 metres above ground level on open site.
5 Mean air temperature of the 2 consecutive calendar days between which the 24 hours of the observation day were divided, at 2 metres above ground level on open site.
6 Hours of bright sunshine during the 24 hour observation day, by recording periods, on open site.
7 Wind velocity (m/sec.) during the 24 hour observation day, by recording periods, at Malmi airfield.
8 Difference between the maximum and minimum atmospheric pressure readings on the observation day at Malmi airfield.

and COCHRAN 1968) of the weather elements and diaspore deposition measured in Helsinki gave the results shown in Table 7. The weather elements were selected on the basis of correlation analysis. According to the table, the wind, sporophore temperature, air temperature, duration of bright sunshine, air humidity and atmospheric pressure fluctuations were the variables which best explained the fluctuations in the catch of *F. annosus* diaspores. Wind velocity had the greatest and most significant effect during seasons other than the post-maximum season. In the post-maximum season, the mean temperature of the sporophores, as recorded one week earlier, was the most important and reliable independent variable to explain the catch of diaspores. In the pre-maximum season, the mean relative air humidity recorded for the 24 hours one week earlier, in the vicinity of the sporophores, was the second best independent variable, while wind velocity was the best. The same was true of the maximum season. Drought, therefore, may restrict the aerial dispersal of *F. annosus* in the spring and summer (cf. RISHBETH 1951 a).

Fig. 14 presents the diaspore catches throughout the season on agar plates and spruce discs, by recording periods, and a few weather elements which conclusively explained the variations in the catch. According to the figure, the heavier the fall of diaspores, the less the catches measured on agar plates differed from those on spruce discs. An increase of deposition in the nocturnal hours was evident. A heavy fall of diaspores occurred, however, on a few mornings with no sunshine, such as July 18 and October 3 and 17. The morning of July 18 was both cloudy and hazy. During the nocturnal hours of October 3 and 17 there had been slight rain.

elements in Helsinki during the diaspore deposition season of 1968 (322 observations).

8	9	10	11	12	13	14	15
1.000							
−0.436***	1.000						
0.196***	−0.008	1.000					
−0.467***	0.955***	0.026	1.000				
−0.488***	0.941***	−0.099	0.984***	1.000			
−0.519***	0.869***	0.130*	0.901***	0.848***	1.000		
−0.343***	0.321***	−0.142**	0.223***	0.271***	0.104	1.000	
0.054	−0.042	0.534***	−0.079	−0.183***	0.013	0.275***	1.000

9 Mean air temperature of the 5 preceding days, at 2 metres above ground level in the forest.
10 Mean air humidity of the 5 preceding days, by recording periods, at 2 metres above ground level in the forest.
11 Mean temperatures of sporophores 1 and 2 by recording periods during the 24 hour observation day.
12 Mean temperature of all sporophores by recording periods during the observation day.
13 Mean temperature of all sporophores as recorded during the observation day one week earlier.
14 Mean air humidity by recording periods in the vicinity of sporophores 1 and 2 during the observation day.
15 Mean air humidity by recording periods in the vicinity of all sporophores during the observation day.
Significant at the level: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Table 7. Combinations of the weather elements best correlated with the deposition of *F. annosus* diaspores in Helsinki 1968.

Total season of *F. annosus* diaspore deposition

Weather element or combination	Method of recording diaspore deposition	d.f.	R^2	t-value and its significance	
4	1	321	0.084		−5.43***
	2	321	0.174		−8.22***
	3	321	0.183		−8.45***
4, 5	1	321	0.116	4	−4.41***
				5	3.39***
	2	321	0.246	4	−6.80***
				5	5.52***
	3	321	0.209	4	7.40***
				5	3.28**
4, 5, 6	1	321	0.133	4	−3.12**
				5	3.74***
				6	−2.51*
	2	321	0.305	4	−4.49***
				5	6.41***
				6	−5.20***
	3	321	0.249	4	−5.38***
				5	3.90***
				6	−4.11***
4, 5, 6, 7	1	321	0.139	4	−3.36***
				5	3.97***
				6	−2.65**
				7	−1.46
	2	321	0.309	4	−4.67***
				5	6.54***
				6	−5.30***
				7	−1.27
	3	321	0.253	4	−5.54***
				5	4.09***
				6	−4.22***
				7	−1.29

Pre-maximum season

Weather element or combination	Method of recording diaspore deposition	d.f.	R^2	t-value and its significance	
4	1	89	0.059		−2.35*
	2	89	0.132		−3.66***
	3	89	0.122		−3.49***
4, 7	1	89	0.096	4	−2.87**
				7	−1.88
	2	89	0.132	4	−3.51***
				7	−0.20
	3	89	0.122	4	−3.36***
				7	−0.23
4, 7, 8	1	89	0.114	4	−3.05**
				7	−1.78
				8	1.31
	2	89	0.138	4	−3.57***
				7	−0.15
				8	0.73
	3	89	0.134	4	−3.49***
				7	−0.14
				8	1.10
4, 7, 8, 9	1	89	0.122	4	−3.13**
				7	−1.92
				8	1.58
				9	0.90
	2	89	0.163	4	−3.93***
				7	−0.45
				8	1.58
				9	1.60
	3	89	0.138	4	−2.84**
				7	−0.02
				8	0.47
				9	−0.60

1 *F. annosus* on agar plate, spores/100 sq.cm./hour, by recording periods.
2 » on spruce discs, colonies/100 sq.cm./hour, by recording periods.
3 » on spruce discs, conidiophore count sq.cm./100 sq.cm./hour, by recording periods.
4 Wind velocity (m/sec.) by recording periods during the 24 hour observation day at Malmi airfield.
5 Mean 24 hour temperature of all sporophores as recorded one week earlier.
6 Hours of bright sunshine during the 5 days preceding the 24 hour observation day, on open site, by recording periods.
7 Mean relative humidity of air in the vicinity of all sporophores as recorded one week earlier.

3

Maximum season

Weather element or combination	Method of recording diaspore deposition	d.f.	R²	t-value and its significance	
4	1	127	0.045		−2.42*
	2	127	0.093		−3.59***
	3	127	0.128		−4.29***
4, 7	1	127	0.076	4	−2.84**
				7	−2.07*
	2	127	0.095	4	−3.37***
				7	0.58
	3	127	0.134	4	−3.99***
				7	0.94
4, 7, 10	1	127	0.096	4	−2.71**
				7	−2.53*
				10	1.66
	2	127	0.107	4	−3.26**
				7	0.10
				10	1.28
	3	127	0.167	4	−3.84***
				7	0.12
				10	2.23*
4, 7, 10, 11	1	127	0.129	4	−1.09
				7	−1.83
				10	2.70**
				11	−2.14*
	2	127	0.228	4	−0.46
				7	1.38
				10	4.47***
				11	−4.39***
	3	127	0.251	4	−1.29
				7	1.20
				10	4.38***
				11	−3.71***

Post-maximum season

Weather element or combination	Method of recording diaspore deposition	d.f.	R²	t-value and its significance	
5	1	103	0.219		5.34***
	2	103	0.302		6.64***
	3	103	0.269		6.13***
5, 4	1	103	0.265	5	4.14***
				4	−2.52*
	2	103	0.326	5	5.53***
				4	−1.89
	3	103	0.340	5	4.72***
				4	−3.30***
5, 4, 6	1	103	0.280	5	4.40***
				4	−1.88
				6	−1.43
	2	103	0.335	5	5.63***
				4	−1.37
				6	−1.67
	3	103	0.345	5	4.75***
				4	−2.80**
				6	−0.84
5, 4, 6, 12	1	103	0.296	5	4.58***
				4	−1.19
				6	−1.68
				12	−1.50
	2	103	0.336	5	5.62***
				4	−1.12
				6	−1.21
				12	−0.39
	3	103	0.349	5	−4.61***
				4	−2.88**
				6	−0.70
				12	0.77

8 Difference between the maximum and minimum atmospheric pressure readings during the 24 hour observation day at Malmi airfield.
9 Air temperature at 2 metres above ground level in the forest, mean values of the 5 preceding days, by recording periods.
10 Mean temperatures of sporophores 1 and 2, by recording periods, during the 24 hour observation day.
11 Air temperature at 2 metres above ground level in the forest, mean values of the 24 hour observation day by recording periods.
12 Mean values of the relative air humidity in the vicinity of sporophores 1 and 2 during the 24 hour observation day, by recording periods.
d.f. = degrees of freedom
R² = coefficient of determination.
Significant at the level: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

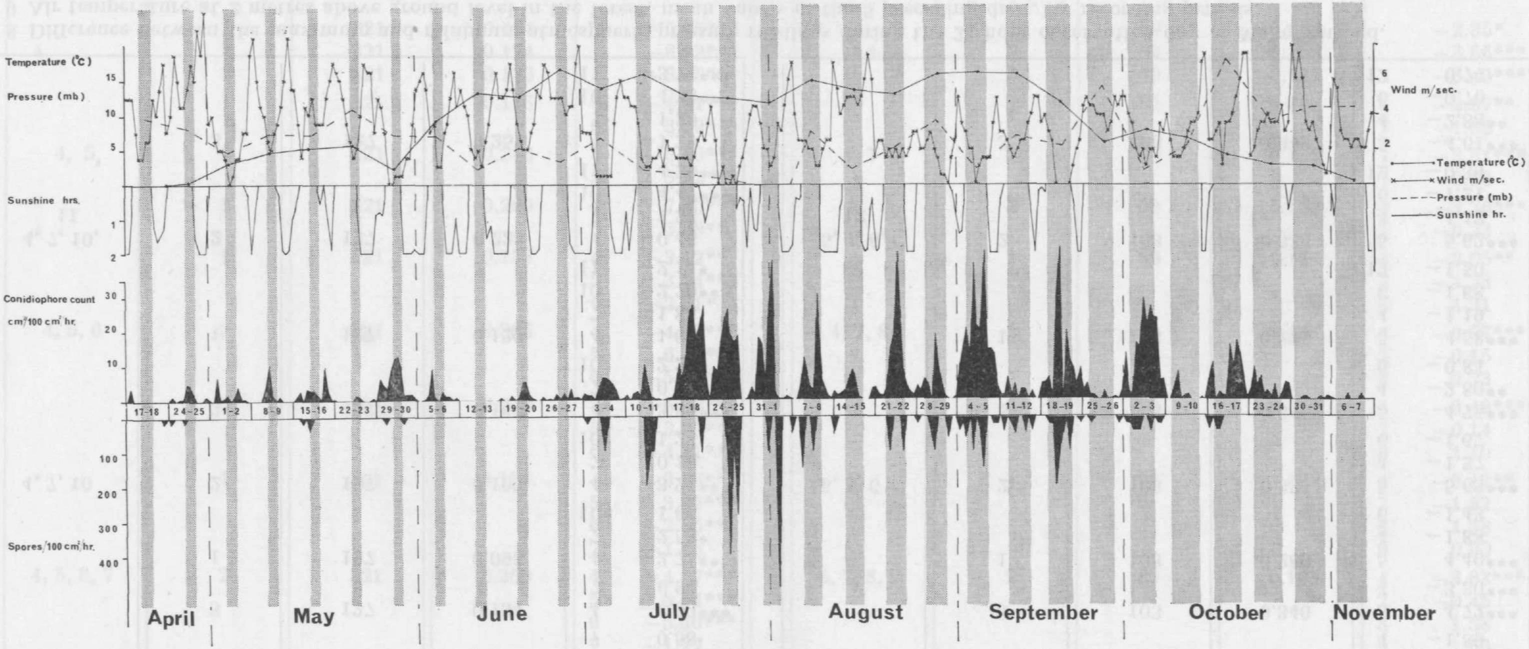

Fig. 14. Diurnal catches of *F. annosus* diaspores in Helsinki on the various observation days between April 17 and November 7, 1968. Spores/100 sq.cm./hour: catch of diaspores on agar plates by recording periods. Conidiophore count sq.cm./100 sq.cm./hour: catch of diaspores on spruce discs by recording periods. Sunshine: hours of bright sunshine during the observation day. Pressure: difference between the maximum and minimum atmospheric pressure readings during each 24 hours of observation. Temperature: diurnal mean temperature of sporophores as recorded one week earlier. Wind: mean wind velocity during each 24 hours of observation, by recording periods. The darkened strips represent the nocturnal hours in the respective 24 hour observation periods.

Table 8. Catches of *F. annosus* diaspores at different heights in the forest July 31 — Aug. 1, 1968 in Helsinki.

Time, hours	Spruce discs				Agar plates, spores/ 100 sq.cm./hour	
	at ground level		at 10 m above ground level			
	colonies/ 100 sq.cm./ hr	conidiophore count sq.cm./ 100 sq.cm./hr	colonies/ 100 sq.cm./ hr	conidiophore count sq.cm/100 sq.cm./hr	at ground level	at 10 m above ground level
13.15 – 15.15	0.7	3.7	0	0	0	0
15.15 – 17.15	1.8	1.6	0.4	2.9	0	0
17.15 – 19.15	1.1	18.3	0	0	0	0
19.15 – 21.15	1.1	16.0	0	0	0	0
21.15 – 22.15	2.1	5.3	0	0	0	0
22.15 – 23.15	5.0	8.5			0	
23.15 – 00.15	2.1	28.5	0.4	0.4	98.4	0
00.15 – 01.15	0.7	46.3			295.1	
01.15 – 02.15	0.7	40.5	0	0	0	0
02.15 – 03.15	1.4	25.8			0	
03.15 – 04.15	1.4	4.6	0	0	0	0
04.15 – 05.15	3.6	5.0			0	
05.15 – 07.15	0.7	0.4	0	0	491.8	0
07.15 – 09.15	0.7	0.4	0	0	0	0
09.15 – 11.15	1.1	1.4	0.4	0.4	0	0
11.15 – 13.15	0.4	0.6	0	0	0	0

122. Diaspore deposition at different heights in forest

The deposition of diaspores was studied during the observation day from July 31 to August 1 in Helsinki at different heights in an infected stand. On spruce discs lying on the ground the fall of diaspores was uninterrupted throughout the 24 hours (Table 8). Diaspores were found on agar plates only during the night. At a height of 10 metres above the ground, diaspores were trapped on spruce discs only during three observation periods, and there were no diaspores at all on agar plates. The wind velocity on open sites during these 24 hours ranged from 0.5 to 6.0 m/sec., from 21.00 to 03.00 in the night the range was 0.5 to 2.5 m/sec. A similar finding concerning the fall of hyaline basidiospores at different heights in the forest was reported by DE GROOT (1968). These results support the view that most *F. annosus* diaspores fall near their source.

123. Diaspore deposition on needles and leaves and in the soil

RISHBETH and MEREDITH (1957) studied the microflora on the surface of pine (*P. silvestris*) needles in England. The microflora was found to include viable diaspores of the root and butt rot fungus and its antagonist *Peniophora gigantea*. According to RISHBETH (1959), degree of exposure to sunlight is probably the major factor determining the viability of *F. annosus* spores on the needles and leaves in the forest. The prevalence of diaspores in the different stands varied greatly. A similar variation was reported by LOW and GLADMAN (1962) in the number of *F. annosus* diaspores on conifer needles in different stands in Scotland.

The method used in Helsinki was similar to that of RISHBETH and MEREDITH. The occurrence of viable *F. annosus* diaspores was examined from needle and leaf samples and samples taken from mineral soil at a depth of 10 cm beneath the humus layer. Five grams of needles (leaves, mineral soil) was shaken in 100 ml water for 30 min., after which the suspension was allowed to settle for 5 min. and then 5 ml suspension was pipetted aseptically onto spruce discs. After 10 days of laboratory incubation the discs were examined and the colonies of *F. annosus* conidiophores were identified.

During the early summer of 1968 all attempts to isolate *F. annosus* from the soil

Table 9. Diaspores of *F. annosus* in the soil and on foliage in Helsinki 1968—69.

Date	No. of samples	Discs of *P. abies* as substrate									
		Soil		*P. abies*, needles		*A. incana*, leaves		*S. aucuparia*, leaves		*E. aquilina*, leaves	
		a	b	a	b	a	b	a	b	a	b
1968											
July 5	6	0	0								
July 9	6	0	0								
July 12	1	2	0.4								
	1	0	0								
	1	1	0.8								
	1			1	0.8						
	1					1	0.2				
	1							1	0.1		
July 17	3	0	0								
	1									9	2.6
	1							12	8.2		
July 26	3	0	0								
Aug. 2	1	1	1.3								
	1	0	0								
	1	1	1.2								
	1	0	0								
	1	0	0								
	1	1	0.9								
Aug. 9	3	0	0								
	1	1	2.2								
	1	4	6.6								
1969	1	1	1.6								
Jan. 17	4	0	0								
	1	4	12.5								
	1	4	9.7								
Jan. 22	1	6	47.0								
	1	5	28.4								
	1	0	0								
Jan. 25	6			0	0						
Feb. 6	1			1	0.2						
	5			0	0						
Feb. 11	6			0	0						
Feb. 20	6			0	0						
Feb. 25	6			0	0						

a = Colonies per disc b = Total area of *F. annosus* conidiophores per disc (sq.cm.).

failed (Table 9). But on July 12, it was obtained both from soil samples and spruce needles, and also from the leaves of alder (*Alnus incana* (L.) Willd.) and rowan tree (*Sorbus aucuparia* L.). Isolation of the fungus from the 3 soil samples taken on July 17 failed, while the leaves of rowan and a bracken species (*Eupteris aquilina* (L.) Newm.) carried large numbers of diaspores. A spruce needle sample taken as late as February 6, 1969, still carried the fungus. Throughout August the fungus was found in soil samples, from which it was isolated as late as January 1969 when the forest soil in Helsinki had not yet frozen appreciably.

These results showed that viable diaspores of *F. annosus* occurred in Helsinki on needles and leaves, and in the soil. Also the findings were in agreement with those reported by MOLIN (1957), that conidia of *F. annosus* can penetrate a soil layer 20—40 cm thick.

F. annosus conidia can remain viable in the soil for a long time (KUHLMAN 1969), and so the diaspores isolated from the soil sample at the end of January 1969 may have been a few months old. Therefore the diaspores of the root and butt rot fungus in the soil can, in Finland, infect damaged tree roots at practically any time the soil is not frozen. On the other hand, with the present method of isolating *F. annosus* from a soil extract, there is the possibility that its growth may be disturbed by fungi — or their metabolic products — antagonistic to the root and butt rot fungus. It is usually difficult to isolate *Basidiomycetes* fungi from the soil, and therefore a negative result need not necessarily mean that the fungus is not present in the soil (RISHBETH 1950, cf. VAARTAJA 1969).

The diaspores of *F. annosus* on needles, leaves and twigs apparently regulate the deposition, and enable it to take place even during seasons when, owing to temperature and/or humidity, no diaspores are being produced in the stand concerned.

124. Diaspore deposition at various distances from sporophores

Observations and theory agree that, of spores liberated near the ground under normal conditions of turbulence, 99.9 per cent will be deposited within 100 m of the source (GREGORY 1952 a, cf. GREGORY 1945, DOWDING 1969). Under relatively calm conditions on clear nights perhaps only five spores in a million travel further than 100 m. However, again according to GREGORY (1952 a), the air sometimes contains a very large number of spores. On calm, clear nights when the air at ground-level is cooled by radiation, it may contain spores from a height of a few millimetres to a few metres. Gravitation causes the spores to fall. Wind blows them up into the air. GREGORY (1952 a) found that when the wind reaches a velocity of 2 m/sec. its lifting capacity begins to surmount the influence of gravity. According to his studies, precipitation greatly reduces the spore content of the air.

In Helsinki, diaspore counts were made at different distances from sporophores on the nights of July 10 and 24. The sporophores chosen for examination were in a group on the under-surface of the roots of a spruce stump partly lifted by the wind. The sporophores were about 20 cm below the soil surface. After the diaspore observations, the stump was lifted and a total of 30 separate sporophores of *F. annosus* were counted. Their white, spore-producing layer extended over something like 600 sq.cm.

The diaspore counts were made in an open field, simultaneously at distances of 0 m (directly under the sporophores), 1 m, 50 m, 100 m and 200 m from this group of sporophores. To do this five persons exposed the substrates at exactly the same moment at the five different distances. The results are presented in Table 10.

The agar plates placed underneath the group of sporophores revealed considerable fluctuations in the fall of diaspores. On July 10, at 21.27 and 23.27, with a wind of 1.5—3.5 m/sec. blowing perpendicularly against the line of observation points, the agar plates underneath the group were exposed for 30 sec. and 1 min. The catches counted on the plates apparently did not represent the true maximum deposition, for the plates were quite full of colonies, and might have been full even after a shorter exposure. Therefore, on July 24 the times of exposure were considerably shortened. The wind this time was at an approximate angle of 45° to the line of observation points and its velocity was approximately 0.0—1.0 m/sec. Three separate counts from the agar plates under the sporophore group, which were exposed for 5—10 sec., gave nearly identical results, about 200 000 diaspores/100 sq.cm./hour. At the distance of 1 m from the sporophores the diaspore catch was about 30 000 per 100 sq.cm./hour. Diaspores of the fungus were found on agar plates even at a distance of 200 m from the sporophore group. No distinct differences were apparent between the diaspore catches at distances of 50 m, 100 m and 200 m from the sporophores; this is attributed to the short exposure of the plates.

Catches on the spruce discs also showed that diaspores had drifted during both nights to these distances. The catches were much heavier on July 24 than July 10, which is in line with the observations of diaspore deposition in the infected forest nearby on the same dates, namely that many more diaspores had fallen on July 24 than on July 10.

According to the present study, the deposition of the diaspores in a labyrinthine underground cavity below the group of sporophores *in situ*, late at night in July 1968, amounted to some 200 000 diaspores/hour/100 sq.cm. At a 1-metre distance from the sporophores, the deposition was about 30 000/100 sq.cm./hour, and it declined rapidly as the distance from the sporophores increased. This observation corresponds to that reported by BONDE

Table 10. Deposition of diaspores of *F. annosus* at different distances from sporophores in Helsinki 1968.

Site	Exposure		Agar plates		Discs of *P. abies*		
	Date 1968	Time	Duration of exposure	*F. annosus* spores/100 sq.cm./hour	Duration of exposure	*F. annosus* colonies/100 sq.cm./hour	*F. annosus* conidiophore count sq.cm./100 sq.cm./hour
Under the sporophores	July 10	21.27	1 min.	11 800	5 min.	total coverage	total coverage
		23.27	30 sec.	47 200	5 min.	total coverage	total coverage
	July 24	20.55	5 sec.	453 200	1 min.	total coverage	total coverage
		20.55	10 sec.	212 500			
		21.55	5 sec.	193 600	1 min.	total coverage	total coverage
		21.55	10 sec.	236 000			
1 m distance from the sporophores	July 10	21.27	1 min.	8 300	2 hr.	total coverage	total coverage
		23.27	1 min.	10 200			
	July 24	20.55	10 sec.	28 900	5 min.	total coverage	total coverage
		21.55	10 sec.	600	5 min.	total coverage	total coverage
50 m distance from the sporophores	July 10	21.27	2 min.	49	2 hr.	total coverage	total coverage
		23.27	2 min.	0			
	July 24	20.55	1 min.	0	1 hr.	5.0	32.5
		21.55	1 min.	0			
100 m distance from the sporophores	July 10	21.27	2 min.	49	2 hr.	4.6	3.1
		23.27	2 min.	0			
	July 24	20.55	1 min.	0	1 hr.	8.5	14.5
		21.55	1 min.	0			
200 m distance from the sporophores	July 10	21.27	2 min.	49	2 hr.	1.1	1.7
		23.27	2 min.	49			
	July 24	20.55	1 min.	0	2 hr.	2.5	5.6
		21.55	1 min.	0			

and SCHULZ (1943) concerning the dispersal of the fungus *Phytophthora infestans* (Mont.) de Bary.

125. Diaspore deposition in an open place and in infected forest

The diaspore catch from a forest in Helsinki (Viikki) was compared with that from an open site (Viikki Meteorological Station). On July 3—4, diaspores of *F. annosus* were trapped in the forest almost continuously through a 24 hour period and the fall was heaviest between 21.00 and 09.00 hours (Fig. 15). Wind velocity at this time varied from 0.5 to 6.0 m/sec. On the open site, diaspores were caught only during the night from 21.00 to 05.00 hours, and the rate of deposition was much lower than in the forest. Bright sunshine during these 24 hours of observation lasted 14 hours 10 min. (sunset July 3 at 21.42 and sunrise July 4 at 03.07).

On July 24—25, diaspores of the root and butt rot fungus were trapped almost uninterruptedly in the forest, but only between 15.00—17.00 and 11.00—13.00 on the open site, and again the catch was relatively small. Wind velocity ranged from 0.0 to 4.5 m/sec. Bright sunshine during this time totalled 4 hours 36 min. (sunset July 24 at 21.08 and sunrise July 25 at 03.46). This supports the view advanced above (p. 35), that most diaspores remain near their source.

126. Diaspore deposition in and above the forest

In order to study diaspore catches in the forest, both at ground level and vertically above the same site, observations were made from the top of a water tower in an infected forest about 2.5 km east of Helsinki (Viikki). The catch at ground level in the forest near the foot of the tower was compared with that recorded on the roof of the tower at an elevation of 56 m. In the preliminary study of May

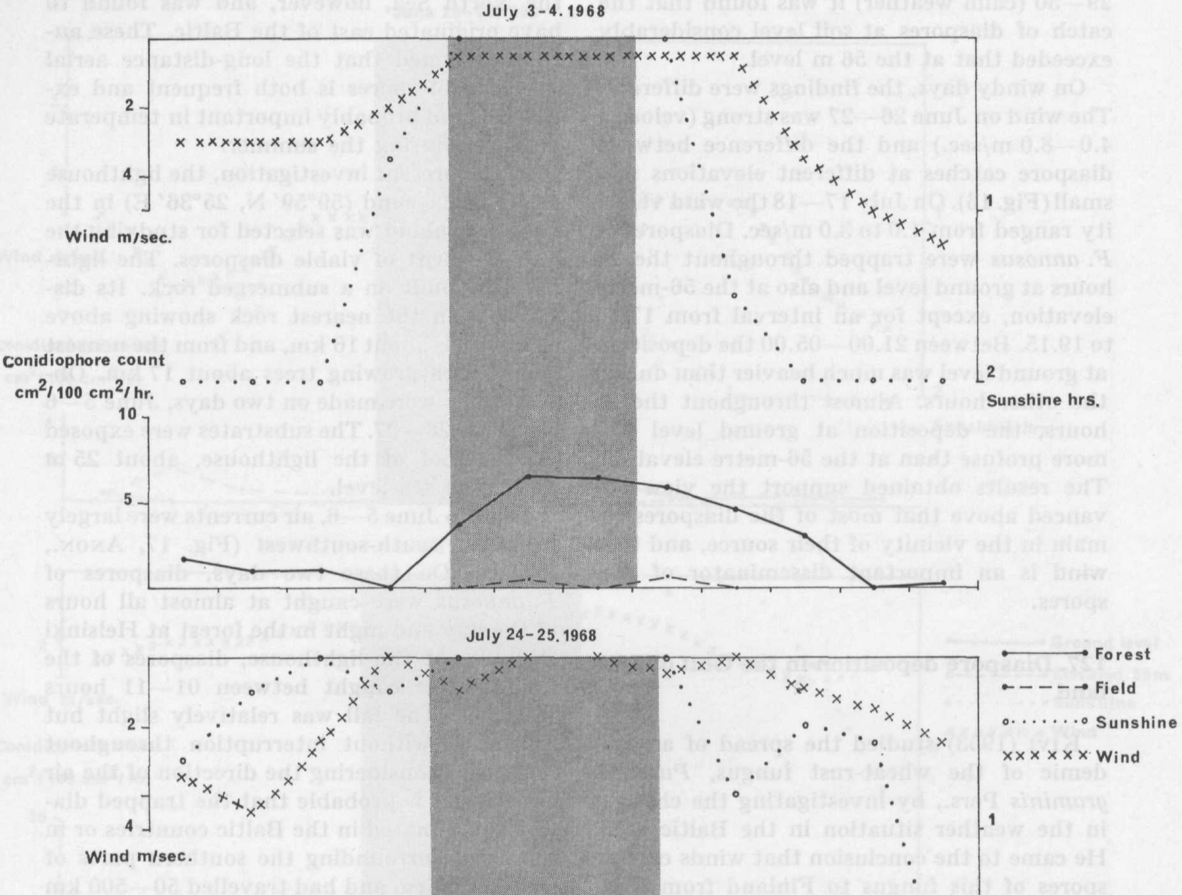

Fig. 15. Diurnal catch of *F. annosus* diaspores on spruce discs (conidiophores sq.cm./100 sq.cm./hour) on open and forest sites in Helsinki. Wind: wind velocity (m/sec.) by recording periods. Sunshine: hours of bright sunshine by recording periods. The darkened area represents the nocturnal hours.

29—30 (calm weather) it was found that the catch of diaspores at soil level considerably exceeded that at the 56 m level.

On windy days, the findings were different. The wind on June 26—27 was strong (velocity 4.0—8.0 m/sec.) and the difference between diaspore catches at different elevations was small (Fig. 16). On July 17—18 the wind velocity ranged from 1.0 to 3.0 m/sec. Diaspores of *F. annosus* were trapped throughout the 24 hours at ground level and also at the 56-metre elevation, except for an interval from 17.15 to 19.15. Between 21.00—05.00 the deposition at ground level was much heavier than during the other hours. Almost throughout the 24 hours, the deposition at ground level was more profuse than at the 56-metre elevation. The results obtained support the view advanced above that most of the diaspores remain in the vicinity of their source, and that wind is an important disseminator of diaspores.

127. Diaspore deposition in the Gulf of Finland

Kivi (1953) studied the spread of an epidemic of the wheat-rust fungus, *Puccinia graminis* Pers., by investigating the changes in the weather situation in the Baltic area. He came to the conclusion that winds carried spores of this fungus to Finland from Denmark or South Sweden. Rishbeth (1959) trapped fungal spores from the air. According to him, viable diaspores of *F. annosus* may travel across 200 miles (about 320 km) of sea.

Hirst et al. (1967 a, b) studied vertical spore clouds over the North Sea. Maximum occurrence of spores over the sea was found at altitudes of 500—1000 m, hundreds of kilometres off the coast. The spore clouds found over the North Sea were often the residue of those produced in the British Isles on the preceding days and nights. The authors were unable to identify all the fungal spores they caught. *Puccinia graminis* was identified over the North Sea, however, and was found to have originated east of the Baltic. These authors assumed that the long-distance aerial dispersal of spores is both frequent and extensive, and probably important in temperate latitudes during the summer.

In the present investigation, the lighthouse at Kalbådagrund (59°59′ N, 25°36′ E) in the Gulf of Finland was selected for studying the seaward drift of viable diaspores. The lighthouse is built on a submerged rock. Its distance from the nearest rock showing above the water is about 16 km, and from the nearest island with growing trees about 17 km. Observations were made on two days, June 5—6 and June 26—27. The substrates were exposed on the roof of the lighthouse, about 25 m above the sea level.

Prior to June 5—6, air currents were largely from the south-southwest (Fig. 17, Anon., 1968 b). On these two days, diaspores of *F. annosus* were caught at almost all hours of the day and night in the forest at Helsinki (Viikki). At the lighthouse, diaspores of the fungus were caught between 01—11 hours (Fig. 18). The fall was relatively slight but continued without interruption throughout this time. Considering the direction of the air currents, it is probable that the trapped diaspores originated in the Baltic countries or in the areas surrounding the southern parts of the Baltic Sea, and had travelled 50—500 km to reach the site of observation.

Before June 26—27, the wind had been from the west-southwest for several days. Diaspores of the root and butt rot fungus were caught between the hours of 21.00—23.00 and 01.00—07.00. Compared with the fall in the Helsinki (Viikki) forest, however, this deposition was slight. The diaspores trapped on June 26—27 probably came from the islands of the Baltic or from South Sweden, over distances of about 70—500 km. This finding supports the view that viable diaspores of *F. annosus* can be carried by the air over long distances.

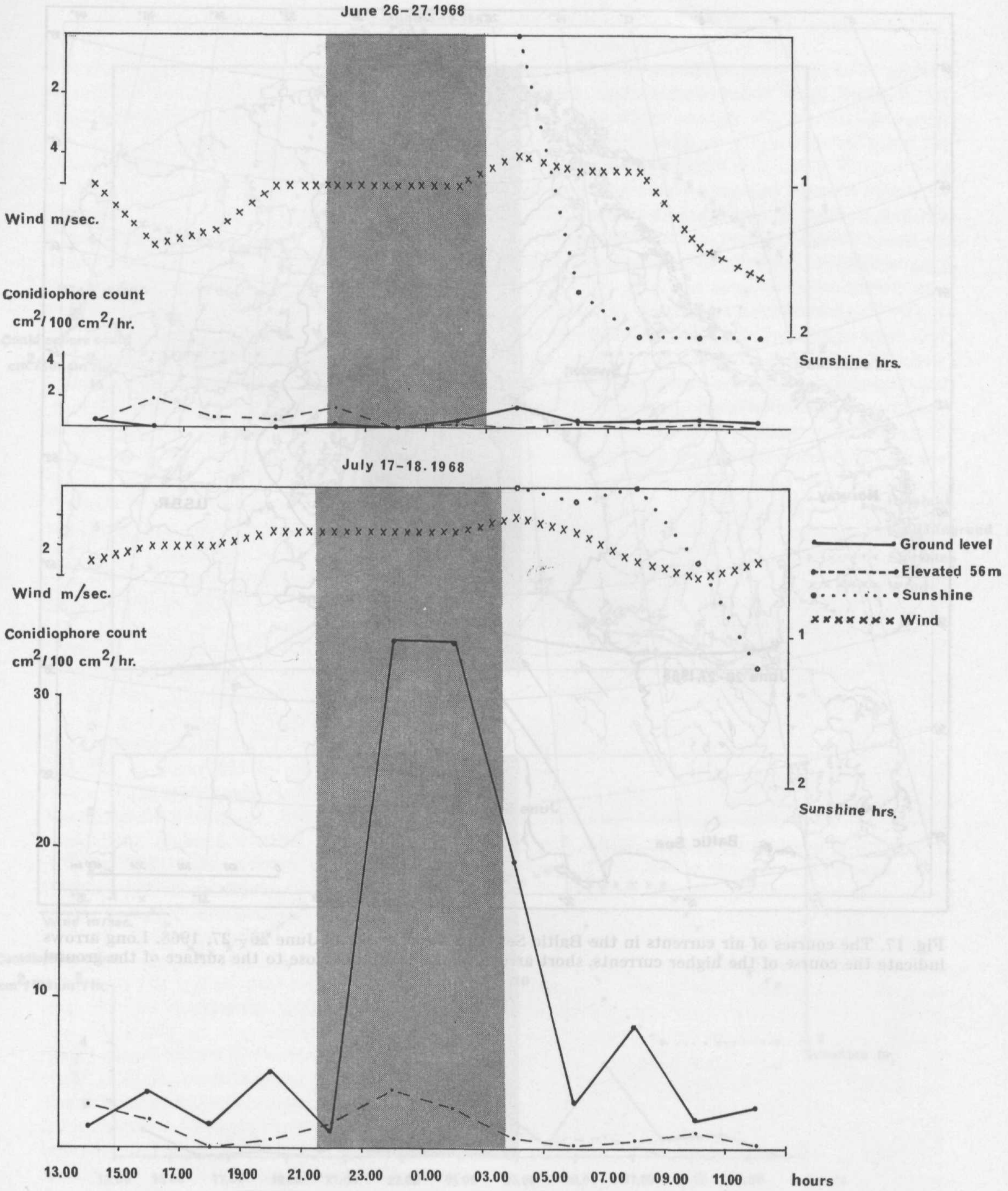

Fig. 16. Diurnal catch of *F. annosus* diaspores on spruce discs in an infected forest in Helsinki (the Myllypuro Water Tower), on the ground and at 56 metres elevation. Wind: wind velocity (m/sec.) by recording periods. Sunshine: hours of bright sunshine by recording periods. The darkened area represents the nocturnal hours.

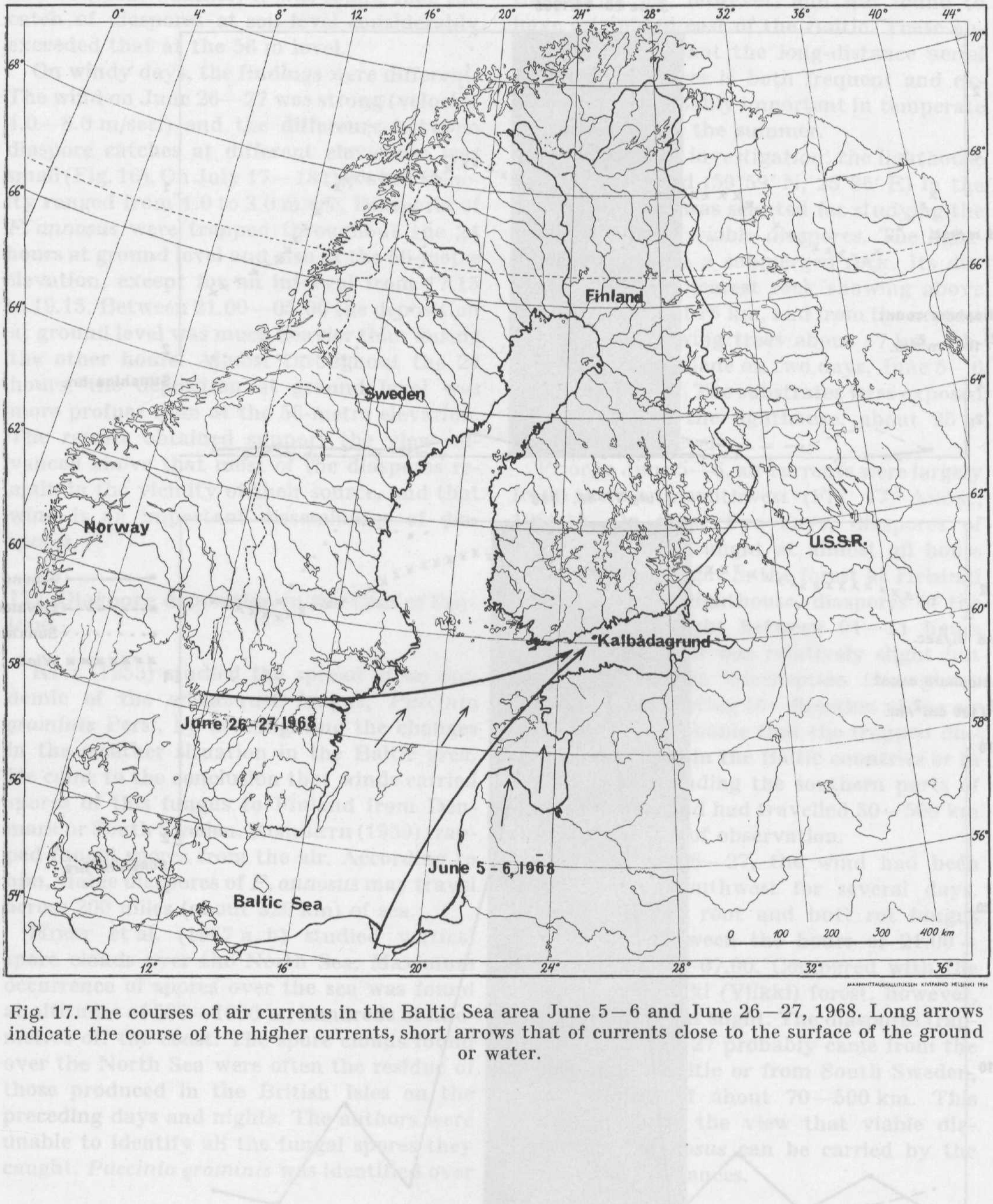

Fig. 17. The courses of air currents in the Baltic Sea area June 5–6 and June 26–27, 1968. Long arrows indicate the course of the higher currents, short arrows that of currents close to the surface of the ground or water.

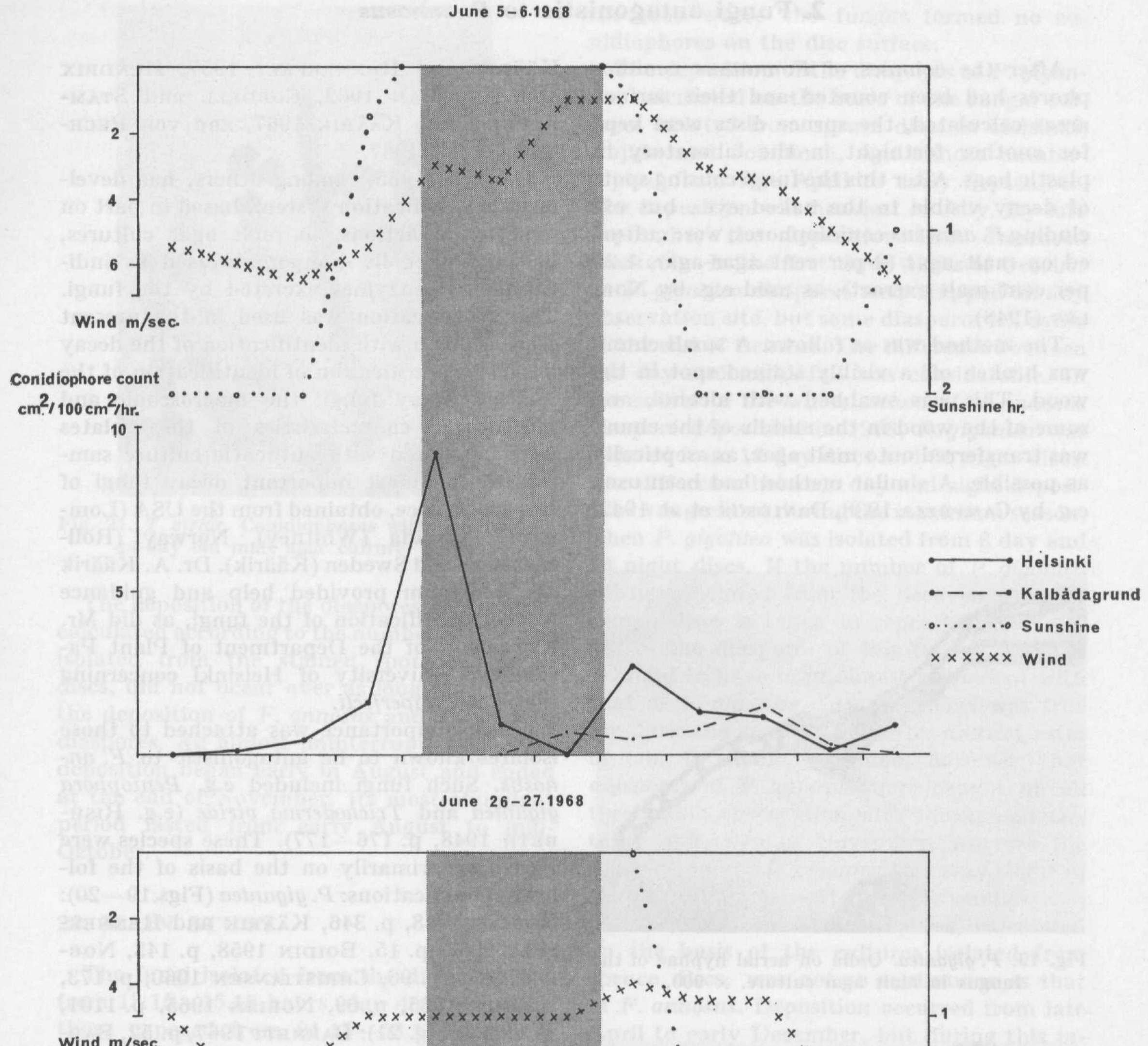

Fig. 18. Diurnal catches of *F. annosus* diaspores on spruce discs (conidiophores sq.cm./100 sq.cm./hour) in a Helsinki forest and over the sea at Kalbådagrund lighthouse. Wind: wind velocity (m/sec.) by recording periods in Helsinki (Malmi). Sunshine: hours of bright sunshine by recording periods in Helsinki (Viikki). The darkened area represents the nocturnal hours.

2. Fungi antagonistic to *F. annosus*

After the colonies of *F. annosus* conidiophores had been counted and their surface areas calculated, the spruce discs were kept for another fortnight in the laboratory in plastic bags. After this the fungi causing spots of decay visible to the naked eye., but excluding *F. annosus* conidiophores, were cultured on malt agar (2 per cent agar-agar, 1.25 per cent malt extract), as used e.g. by NOBLES (1948).

The method was as follows. A small chunk was broken off a visibly stained spot in the wood. This was swabbed with alcohol, and some of the wood in the middle of the chunk was transferred onto malt agar, as aseptically as possible. A similar method had been used e.g. by CAMPBELL 1938, DAVIDSON et al. 1942, KÄÄRIK and RENNERFELT 1957, HENDRIX and KUHLMAN 1962, CORDELL and STAMBAUGH 1966, KÄÄRIK 1967, and von PECHMANN et al. 1967.

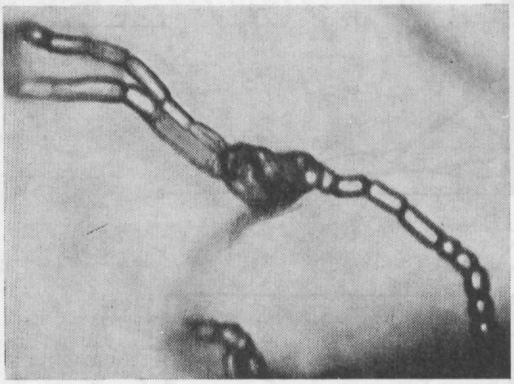

Fig. 19. *P. gigantea.* Oidia on aerial hyphae of the fungus in malt agar culture. × 900.

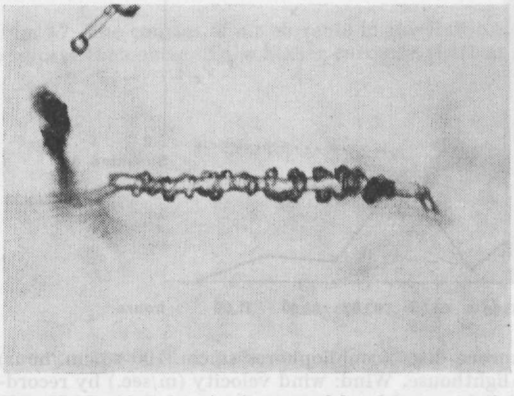

Fig. 20. *P. gigantea.* An incrusted hypha among the aerial hyphae of a month-old malt agar culture. × 700.

KÄÄRIK (1965), among others, has developed a classification system, based in part on oxidation reactions, in malt agar cultures, between phenolic compounds used as indicators and enzymes excreted by the fungi. This classification was used in the present study to help with identification of the decay fungi. For verification of identification of the isolated decay fungi, the macroscopic and microscopic characteristics of the isolates were compared with authentic culture samples of the most important decay fungi of Norway spruce, obtained from the USA (Lombard), Canada (Whitney), Norway (Roll-Hansen), and Sweden (Käärik). Dr. A. Käärik of Stockholm provided help and guidance in the identification of the fungi, as did Mr. A. Salonen of the Department of Plant Pathology, University of Helsinki concerning the *Fungi imperfecti.*

Special importance was attached to those isolates known to be antagonistic to *F. annosus.* Such fungi included e.g. *Peniophora gigantea* and *Trichoderma viride* (e.g. RISHBETH 1948, p. 176—177). These species were identified primarily on the basis of the following publications: *P. gigantea* (Figs.19—20): NOBLES 1948, p. 346, KÄÄRIK and RENNERFELT 1957, p. 15, BOIDIN 1958, p. 143, NOBLES 1958, p. 96, CHRISTIANSEN 1960, p. 173, KÄÄRIK 1965, p. 69, NOBLES 1965, p. 1101, *T. viride* (Fig. 21): BARNETT 1967, p. 52, BARRON 1968, p. 306.

21. PRELIMINARY STUDY

On spruce discs exposed on the South Finnish observation sites (Helsinki, Turku, Lappeenranta and Jyväskylä) of the preliminary study, diaspores of *P. gigantea* were trapped almost throughout the year apart from midwinter. Seasonally, its diaspore deposition practically coincided with that of *F. annosus.* Diaspores of *P. gigantea* fell almost uninterruptedly from early June to mid-November, most heavily from early August to mid-October.

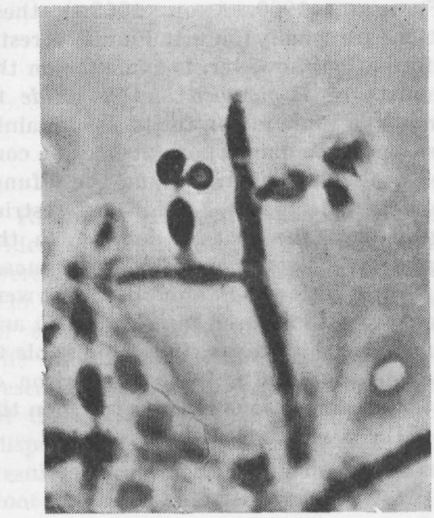

Fig. 21. *T. viride.* Conidiophores with conidia in a 14-day old malt agar culture. × 300.

The deposition of the diaspores of *T. viride*, calculated according to the number of cultures isolated from the stained spots of spruce discs, did not occur over as long a period as the deposition of *F. annosus* and *P. gigantea* diaspores. An almost uninterrupted *T. viride* deposition began early in August and ended at the end of November. Its most abundant period lasted from early August to mid-October.

22. MAIN STUDY

The fungi isolated from the discs exposed from 13.15—15.15 hours (day disc) and from those exposed from 01.15—03.15 hours (in Helsinki, between July 31 and September 26, from 01.15—02.15, night disc) were chosen to represent the fall of diaspores during the day and the night of each 24-hour observation day. A study of the aerial dispersal of all decay fungi, other than *F. annosus*, in Helsinki, Anjala and Jokioinen was based on these isolates. After an incubation period of about 25 days (+ 22° C and 70 per cent), pure cultures of the fungi were made — as noted earlier — from visibly stained spots with no *F. annosus* conidiophores present. Identification was attempted as described on p. 44. A few times *F. annosus* could be isolated from the cultures. This suggests that mycelia of *F. annosus* grew even on those spots of the disc where the fungus formed no conidiophores on the disc surface.

The deposition of the diaspores of *P. gigantea*, calculated on the basis of the fungal cultures isolated from spruce discs in Helsinki, Anjala and Jokioinen, was almost uninterrupted from late April to early September. The deposition was heaviest in July. By late September the deposition had decreased markedly. In the first three weeks of October no *P. gigantea* diaspores were trapped on any observation site, but some diaspores fell again at the end of October. The difference between the day and night fall was considerable. In the course of the whole season of *F. annosus* diaspore deposition in 1968, *P. gigantea* was isolated from 18 day discs and 51 night discs. The difference between day and night deposition was greatest during the maximum season, when *P. gigantea* was isolated from 6 day and 39 night discs. If the number of *P. gigantea* cultures isolated from the decayed spots of spruce discs is taken to represent the total fall of the diaspores of this fungus, the fall is found to have been almost coincident with that of *F. annosus* diaspores. This was true for both the seasonal and the diurnal rates of fall. It should be noted, however, that diaspores of *F. annosus* were caught on all three main observation sites throughout October and even in November, whereas the recorded fall of *P. gigantea* was very slight in October and non-existent in November.

The fall of *T. viride* diaspores, calculated on the basis of the cultures isolated from spruce discs, was not so continuous as that of *F. annosus*. Deposition occurred from late April to early December, but during this interval there were several occasions on which no diaspores of this fungus were trapped. During the season of maximum deposition of *F. annosus* diaspores, diaspores of *T. viride* were trapped least frequently; rather, they were most prevalent during the pre-maximum season. In the maximum season the fungus was caught only twice, both times from day discs. On the whole, there was little difference between the day and night frequencies of this fungus.

According to this evidence, the deposition of *F. annosus* diaspores was simultaneous with that of these fungi antagonistic to it, *P. gigantea* and *T. viride*. A similar coincidence was reported from England e.g. by

Rishbeth (1948, 1950, 1957, 1959) and Meredith (1959, 1960), from Canada e.g. by Reynolds and Craig (1968) and from the USA e.g. by Ross (1968), and Driver and Ginns (1969). Many authors have concluded that these particular antagonists are the natural and effective competitors of *F. annosus. P. gigantea* is probably most capable of competition in stumps (e.g. Rishbeth 1948, 1950, 1961, Reynolds and Craig 1968), and *T. viride* in the soil, e.g. Rishbeth (1948, 1950). Soil conditions for effective antagonism by *T. viride*, according to Rishbeth, are acid character (pH 4.0—6.0), temperature in excess of +15° C, and the presence of undecomposed organic matter on the surface of mineral soil. Except for the temperature, (cf. Franssila 1960, Anon. 1968 c), these conditions are usually found in Finnish forests. No information, however, is available on the antagonism of *P. gigantea* and *T. viride* to *F. annosus* in Finland. On the basis of mainly English and Canadian reports it may be considered probable that in Finland these fungi do, in fact, under natural conditions, restrict the growth of the root-rot fungus. In the present study, however, the methods for measuring the deposition of *F. annosus* spores were different from those used for *P. gigantea* and *T. viride*. For this reason, it is impossible to make a detailed and reliable comparison of the diaspore depositions of these fungi on the basis of the present results.

IV DISCUSSION

Rishbeth (1948, 1951 a), in England, provided evidence that the airborne diaspores were important infection agents of *F. annosus*. The diaspores entered the exposed surfaces of stumps of felled pine trees, and thence the roots. Since Rishbeth's report, lively research has been going on in different parts of the world concerning the production and dispersal of the *F. annosus* diaspores. As a result, ideas about the control of annosus root rot have changed a great deal. In the present study, the aerial diaspores of *F. annosus* were demonstrated in various parts of Finland. Diaspores were also found on needles and leaves, and in the soil.

The dependence of spore production on weather elements has been widely studied. Walkey and Harvey (1968) studied some *Pyrenomycetes* fungi and divided the investigated fungi into groups according to the correlation of spore production and weather elements. The rhythm of the spore production of certain *Pyrenomycetes* fungi and the effects of weather elements on it was studied by Hodgkiss and Harvey (1969). According to them, the spore production of some fungi of the group is positively correlated with precipitation, of others with air humidity, and of one fungus with the number of hours of bright sunshine.

Important carriers of aerial diaspores are air currents (e.g., Gregory 1952 a, b, Gregory and Hirst 1957, Rishbeth 1959, Stambaugh et al. 1962). The influence of wind velocity was also obvious in the present study. The fall of diaspores was studied in the present work using mainly two growth substrates — spruce discs and agar. The statistical analyses undertaken, owing to the disparity of some results obtained on the two substrates, do not always indicate the same level of dependence between weather elements and the recorded catch of diaspores. However, statistically significant correlation is indicated between wind velocity and the catch of *F. annosus* diaspores, whether obtained on the discs or agar. The correlation was negative both at Jokioinen (Table 3) and in Helsinki (Table 5). The results obtained on agar plates in Helsinki, during the entire season of *F. annosus* diaspore deposition, showed as definite a correlation between wind velocity and fall of diaspores (Table 7) as that indicated by the results on spruce discs. In the pre-maximum and maximum seasons, however, diaspore deposition recorded on spruce discs showed more clearly (statistically) a dependence on wind velocity than did the deposition recorded on agar plates.

All the spruce trees from which the discs of the present study were made, were felled in the same forest in Helsinki (Viikki). The fact that, during the entire diaspore deposition season in the main study, some diaspores could always be found on the spruce discs of at least one observation site, may be sufficient evidence that these discs were suitable for the production of conidiophores. The discs were always cut from the same side of the stem, and the maximum distance longitudinally along the stem never exceeded 1 m. All discs exposed simultaneously, therefore, provided practically equivalent growth substrates for fungi.

Sinclair (1964) reported a significant positive correlation between the aerial amount of *F. annosus* spores and air temperature, and a similar correlation between the spore production of *F. annosus* sporophores and the deposition of aerial spores. In the spring, after the temperature on an open site, at a 2-metre height, had exceeded zero for a considerable period of time, it was two to three weeks in Helsinki, Anjala and Jokioinen before a continuous fall of diaspores began. All the significant correlation coefficients between the air temperature recorded on an open site near the observation sites in the forest, at a 2-metre height, and the fall of *F. annosus* diaspores were positive. The decisive importance of temperature for the depposition of diaspores was clearly seen in the post-maximum season in Helsinki. According to the multiple regression analysis (Table 7), the mean temperature of six sporophores one week earlier was the recorded weather element that most reliably explained the fluctuations in the fall of *F. annosus* diaspores during this observation season.

Clear-cutting and subsequent burning-over considerably reduced the aerial distribution of the root-rot fungus through spruce stumps (Kallio 1965). A contributory factor to the reduced spread may have been high temperatures from the burning. However, the situation reported by Ross and Driver (1966) from southern parts of the USA is probably very rare in Finland. They found that the temperature of the surface of the stump, and of a layer extending to a depth of 6 cm from the surface, increased to such an extent (40° C) that the fungal mycelia were probably inactivated. Even in Finland, the freshly cut surfaces of stumps not covered by logging waste, dry up relatively soon after cutting during the summer. After a few days, the substrate for new fungal growth offered by the surface of the stump is different from what it was at the moment of felling. The spruce discs of the present study were always freshly cut, and this may be one of the reasons why the deposition of *F. annosus* spores obtained from them did not always exactly correspond to the infection which takes place when aerial diaspores reach the cut surfaces of stumps under natural conditions.

Findings that have been reported on the dependence of the deposition of *F. annosus* diaspores on precipitation are conflicting (Sinclair 1964, Ross 1969). The present results obtained at Anjala and Helsinki were also conflicting with respect to the correlation between precipitation and spore deposition: at Anjala the significant correlation coefficients were positive, in Helsinki negative. A contributory factor to this circumstance may have been that the observation site in Helsinki was about 10 m above sea level at a distance of some 200 m from the sea shore, whereas that at Anjala was about 40 m above sea level and almost 20 km from the sea. Moreover, air humidity in Helsinki apparently exceeded that at Anjala, and the part played by precipitation in spore production and diaspore deposition may also have been different on the two sites. On the other hand, the correlation between weather elements and diaspore deposition need not be, and probably is not, linear although this was presupposed under the statistical methods used in the present study.

The spore production in each stand, which in average weather conditions largely governs the diaspore deposition in a stand, is affected by several weather elements simultaneously. The individual component effect of each and the aggregate effect of several factors is different in the different seasons of diaspore deposition. Many weather elements are strongly correlated mutually.

Weather elements may vary considerably in Finland from year to year. A comparison with long-term mean values (1931—1960) reveals that at Anjala, Helsinki and Jokioinen, the year 1968 (Anon. 1970) approached the long-term mean values in temperature (Kolkki 1966) and precipitation (Helimäki 1967). Hence the diaspore deposition in 1968 can well serve as a prediction model as far as temperature and precipitation are concerned.

Ingold (1933) found that light was the main factor governing the rhythm of spore liberation among *Ascomycetes*. Subsequently, many authors (e.g. Hirst 1953, Stambaugh et al. 1962, De Groot 1968) found that *F. annosus* diaspores (or hyaline spores in general) are more frequent during the night than the day and, as pointed out e.g. by Hirst (1953), immense changes may suddenly take place in the number of hyaline spores in the air. Hirst reports that, within four hours, their number fell from a quarter of a million per cubic metre air to something like a thousand. He attributed the rapid decrease to air currents which gained strength and diluted spore concentrations after sunrise. Pady and Kramer (1969) studied the periodicity in the liberation of *Bombardia fasciculata* Fr. spores. According to them, this rhythm was mainly endogenous. They came to the conclusion that at high temperatures light may restrict the liberation of spores, whereas in a cool climate the temperature is a liberation-restricting factor. According to De Groot (1968), the profuse occurrence of basidiospores of *Ganoderma applanatum* (Pers.) Pat. and other small spores is associated with the higher relative humidity and lower temperature of the air during the night than during the day.

One reason why the number of viable *F. annosus* diaspores on the surface of needles and leaves of the crown varies so much is, according to RISHBETH (1959), sunlight. In Helsinki and Jokioinen also, highly significant negative correlations were noted between bright sunshine and the deposition of *F. annosus* spores. The amount of bright sunshine may vary considerably in Finland from year to year. The monthly sunshine hours of 1968 can be compared with the monthly mean values of 1957—1967 only for Helsinki and Jokioinen (KOLKKI 1969). According to the comparison, during the season of uninterrupted fall of *F. annosus* diaspores, the number of sunshine hours in Helsinki 1968 was about 5 per cent lower and at Jokioinen about 8 per cent higher than the means for 1957—1967. MCKEE (1969) found that exposure of zoospores of *Phytophthora infestans* to ultraviolet irradiation reduced their ability, in order of increasing sensitivity, to germinate, to infect, and to grow in culture. LEACH (1967) studied some *Fungi imperfecti* and divided them into groups according to the changes caused by ultraviolet irradiation and associated temperature in their production of conidiophores and/or conidia. SCHLÖSSER (1970) noticed that ultraviolet irradiation mostly stimulated conidia formation of some *Ascomycetes* and *Fungi imperfecti* isolated from *Graminae*. If LUNELUND'S data (1945, p. 19) illustrating the amount of ultraviolet irradiation in South Finland in July are compared with the diurnal deposition of *F. annosus* diaspores during the maximum season in Helsinki (Fig. 13, p. 24), a distinct inverse relationship is indicated. The fall of viable diaspores was heaviest during those hours when the amount of ultraviolet irradiation was at its lowest or nil. On the other hand, it is possible that thermal updrafts during the heat of the day may have been the chief cause of the diminished viable diaspores. Measurements made by KULMALA (1970) at Jokioinen during the summer 1968 indicated that the net flux of radiation at the earth's surface on open sites produced vertical air currents upward from the earth's surface. These currents are more pronounced during the day than night. Thus they may contribute to keep the fall of diaspores at its lowest during the day. KULMALA, however, made his measurements at an open site. No information is available regarding vertical air currents that may be produced in a forest by radiation at the earth's surface. It is also not known whether the velocity of the vertical air currents at the earth's surface exceeds the minimal 2 m/sec. needed, according to GREGORY (1952 a), by air currents in order to overcome the force of gravity sufficiently to lift the spores.

The aerial spores of numerous different fungi may infect the same substrate. The fungi compete, and eventually a composite fungal population may arise (MEREDITH 1959, 1960, SHIGO 1967). For example, because of competition by other fungi, the number of aerial *F. annosus* diaspores deposited does not always result in a proportionate infection of stumps by the fungus (RISHBETH 1951 a, DIMITRI 1963, DRIVER and GINNS 1969). Well known among the fungi antagonistic to *F. annosus* are *Peniophora gigantea* (e.g., RISHBETH 1948, 1951 a, 1952, 1959, 1961, 1963, MEREDITH 1959, 1960, BOYCE 1966), and *Trichoderma viride* (e.g. RISHBETH 1948, 1950, 1951 b, BOYCE 1963, NEGRUTSKIJ and SYSEV 1969). These two fungi have been and are being used in many countries to control the root and butt rot fungus. In addition to these two, there are a few other fungi antagonistic to *F. annosus*, such as *Penicillium* spp. (RISHBETH 1948, DIMITRI 1963), *Hypholoma fasciculare* (Huds.) Fr. (RISHBETH 1948, 1951 b), *Streptomyces* spp. (NISSEN 1956), *Scytalidium* spp. (KLINGSTRÖM and BEYER 1965). A few of these were isolated from the spruce discs of the present study. It is difficult, in this connection, to appraise the part played by the antagonists in the development, growth and survival of the conidiophores of *F. annosus* on spruce discs and agar plates. To reduce or eliminate error caused by antagonists, two agar media specially developed to grow the *F. annosus* (KUHLMAN and HENDRIX 1962, KUHLMAN 1966) were used in addition to the spruce discs. The agar plates, however, could be exposed for only relatively short periods, during which the individual colonies could still be distinguished and their numbers counted. Owing to the short time of exposure, diaspores fell on the agar plates only during the season of abundant diaspore deposition (cf. Fig. 14, p. 34).

Most of the *F. annosus* diaspores fell relatively close to their source. In a Finnish stand of large-sized spruce, the total basal area of all trees, as measured at breast height, amounts to some 25—30 sq.m/ha. The population of *F. annosus* and accompanying other microbes usually produce a root swelling in the affected spruce trees. However, this pathological swelling together with the natural root swelling, for instance in a mature spruce stand, hardly makes the basal area measured at stump height any larger than some 50 sq.m./ha. Consequently, the probability of a diaspore falling on a stump surface rather than on the ground in a clear-cut stand with a large diameter breast height, would be about 1: 200. With respect to the distribution of *F. annosus*, what happens to the minimum of 200 diaspores which fall on the ground in the forest?

In the present study, some diaspores were isolated from the forest soil, in which they remain viable for months. The mycelium arising from them has to compete for development and survival in the soil with innumerable associated microbial populations. Thus antagonists, nutritive substances and water, quantity and quality of organic matter, water and air capacity, and many other factors produce an infinite variety of conditions affecting the competitive position of each organism, and this variety of conditions may contribute towards the erratic occurrence of *F. annosus* in the forests.

The wood of stumps or roots apparently provides *F. annosus* with better competitive conditions vis-à-vis many microbes than does the soil. For this reason, damage by the root-rot fungus might be expected to be greater as the number of fellings increases (cf. MIKOLA 1962, MURRAY 1962). Fellings and the, associated mechanized transport of wood, damage the remaining growing stock and also the stumps, causing injuries both above the soil surface and in subterranean roots (NILSSON and HYPPEL 1968, KÄRKKÄINEN 1969). *F. annosus* attacks the injured points underground by means of the viable diaspores in the soil (KUHLMAN 1969). Introduction of year round fellings provides the possibility for a considerable increase in the damage caused by this fungus, since there are freshly cut stumps, and growing stock and roots are being injured even during the season of maximum deposition of *F. annosus* diaspores.

V SUMMARY

An investigation into the aerial distribution of *F. annosus* in Finland was carried out. Prevalence of the fungus in the air was estimated from cultural counts of mycelia produced by diaspores which had fallen onto spruce discs and agar plates. The influence of climate on deposition of diaspores was determined from weather recordings. In a preliminary study from June 7, 1967, to May 29, 1968, aerial diaspores were trapped in various parts of Finland. During this period, they were found only once each at the airfields of Ivalo and Oulu. Elsewhere in Finland (Jyväskylä, Lappeenranta, Turku and Helsinki) *F. annosus* diaspores fell from April to November, and deposition was more frequent than in North Finland.

For the main study, *F. annosus* diaspores collected from spruce stands in Helsinki, Anjala and Jokioinen were recorded at weekly or fortnightly intervals throughout 1968. For this, spruce discs were exposed usually for 2 hour recording periods throughout the 24 hours of a day and night, and agar plates mostly for 5 minute recording periods at 2 hour intervals, also throughout the 24 hours of day and night. Diaspores fell during the 24 hour periods almost continuously at all three observation sites from April to November, but the deposition was most frequent from late May to the end of October. The amounts of deposition varied greatly with the observation sites, seasons of the year, and hour of the day or night. The fall was heaviest at Anjala and slightest at Jokioinen. At both these sites the fall was heaviest in July. Fluctuations in diaspore count were largest in Helsinki. There the fall was heaviest in September, but remained at a remarkably high level throughout the interval from July to October.

The continuous season of *F. annosus* diaspore deposition was divided into three parts to enable an analysis of environmental effects at different levels of the deposition: the pre-maximum (spring), maximum (summer and early autumn) and post-maximum (autumn) seasons. Throughout the season of deposition, more diaspores were trapped on all observation sites at night than during the day. The difference between the night and day catches was greatest during the maximum season, on all observation sites. At Anjala the difference was considerable also in the pre-maximum season. Throughout the season of continuous diaspore deposition, a highly significant positive correlation was found between the fall of *F. annosus* diaspores in forests at Anjala, Helsinki and Jokioinen and the air temperature recorded at a height of 2 metres from the ground over open sites near the forests. Helsinki produced an amount of study material nearly equal to that obtained from Anjala and Jokioinen together. The diaspore fall in the Helsinki forest during the season of continuous deposition was indicated, at a statistical significance level below 0.1 per cent, to be negatively correlated with the wind velocity, with the number of bright sunshine hours, and with the difference between maximum and minimum atmospheric pressures recorded on the open site. According to a multiple regression analysis, wind velocity recorded on the open site best explained the variation in the fall of diaspores in Helsinki during the pre-maximum and maximum seasons. Also, indicated to be a determining factor, but less significantly so, of the fluctuation in the fall of diaspores during this observation season was the mean relative air humidity in the vicinity of the *F. annosus* sporophores in the week preceding the diaspore count. In the post-maximum season the mean temperature of the sporophores recorded one week earlier was the climate variable that best explained the fluctuation in the fall of diaspores. Correlation with wind velocity was second in statistical significance.

Diaspores of *F. annosus* were found in the forest on needles and leaves, and underneath the humus layer in mineral soil. The fall of diaspores decreased as the distance from sporophores increased. On open sites and above the forest, the fall of diaspores was considerably less than in the forest, when the wind was weak. But when a strong wind was blowing the difference was smaller. Viable diaspores were also caught over open sea. They were indicated to have travelled with air currents over distances ranging from 50 to 500 km.

The aerial distribution of two antagonists to *F. annosus*, viz. *Peniophora gigantea* and *Trichoderma viride*, was also studied. It was found that the diaspores of the former fell mainly during the same seasons as those of *F. annosus*. Hence *P. gigantea* may reduce the damage caused by *F. annosus*. The fall of *T. viride* diaspores was not so profuse or so continuous as that of the *P. gigantea* diaspores.

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