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THE DISTRIBUTION PATTERN OF HIRNEOLA AURICULA-JUDAE IN THE NETHERLANDS

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(With three Text-figures and two Tables)

The distribution pattern of *Hirneola auricula-judae* in the Netherlands is discussed. At first this pattern was thought to be mainly determined by the average daily minimum temperatures in winter; high population densities correlating with high winter temperatures. The curve which best fits the data is so steep, that it would mean the virtual exclusion of *Hirneola auricula-judae* from regions with winter temperatures only a few degrees lower than in the Netherlands. Nevertheless the species is reported as not uncommon in the northern U.S.A. and southern Canada, as well as in Central Europe. From the literature it appears that '*H. auricula-judae*' in North America is not conspecific with the taxon so named in Europe, but specimens from Central Europe were found to be morphologically inseparable from specimens from Western Europe. Revaluation of the data on the distribution of the species in the Netherlands in relation to plant geographical districts showed that coexistent with the positive correlation of high population density with high winter temperatures is another one with alcaline soils. The corrected gradient of the correlation between population density and winter temperatures is less steep than originally calculated and consequently the relatively high population density in Central Europe is no longer inconsistent with the distribution pattern of the species in the Netherlands.

PRELIMINARY STUDY AND FIRST WORKING HYPOTHESIS

A few years ago a preliminary study of the distribution of *Hirneola auricula-judae* in the Netherlands was made within the framework of the survey of the distribution of one hundred macromycetes in Europe by a committee of the European Mycological Congress (van der Laan, 1970). Purpose of the study was not only to record the distribution, but also to find the principal factors responsible for its pattern. *Hirneola auricula-judae* was chosen because it may be found all year round and can be easily identified. The results were recorded in a topographical grid of 5×5 km squares. Only collections of which specimens had been deposited in the Rijksherbarium, Leiden, were accepted as records. The majority was the result of accidental finds of numerous mycologists. They were supplemented by special searches of the author trying to fill gaps in the knowledge thus obtained. No attempt was made to search any area systematically square by square.

The preliminary results indicated that *H. auricula-judae* may be found almost anywhere in the Netherlands, but that its population density varies within wide limits. Population density in this study is measured by the number of squares in which *H. auricula-judae* has been found, expressed as a percentage of the total number

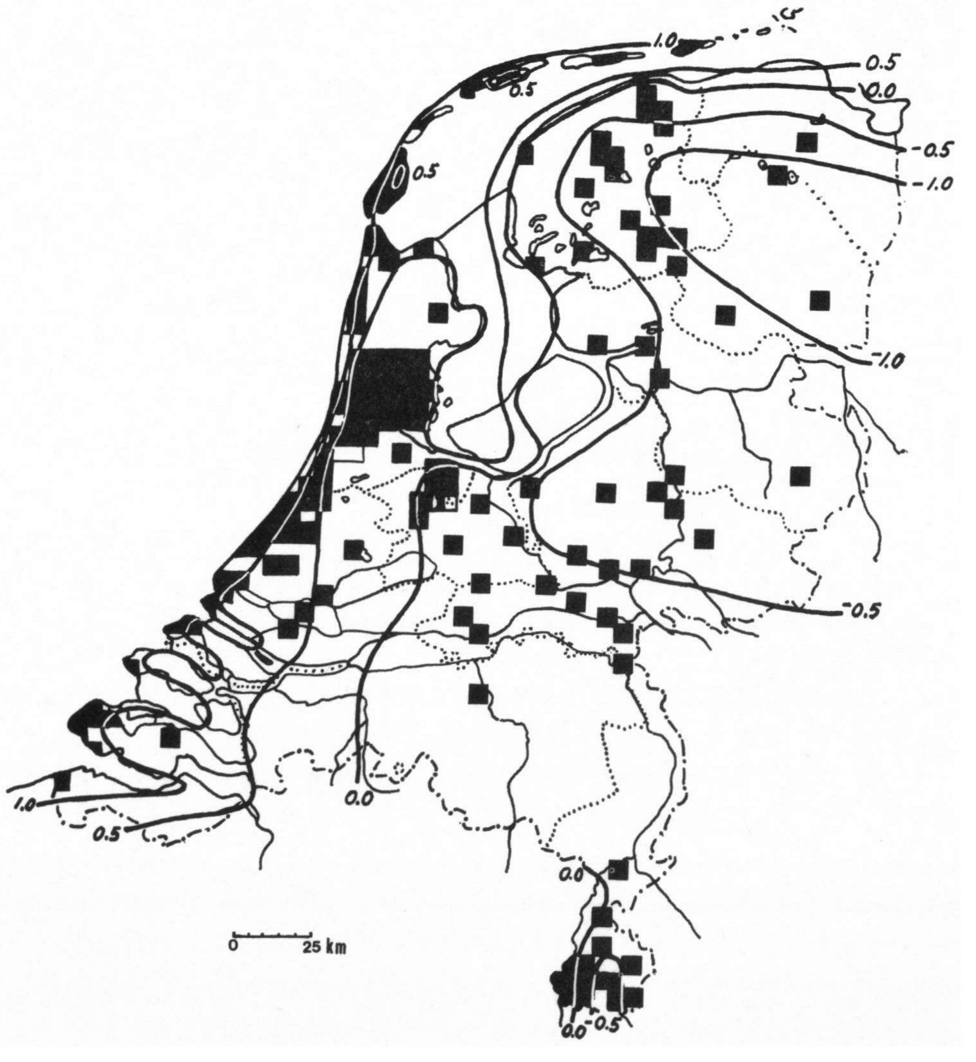

Fig. 1. Distribution of *H. auricula-judae* in the Netherlands related to division into zones of equal average daily minimum temperature in winter; black squares indicating squares of 5 × 5 km in which *H. auricula-judae* has been collected; fat lines indicating isotherms in °C.

of squares in a certain area. It was found to be at a maximum (of 30) along the coast. Further inland a gradual drop of the population density to less than one was found in the east and south. A notable exception was found in the extreme south-east, where the population density was almost equal to that in the coastal regions.

The preliminary study did not suggest a connection with soil conditions but, as shown later, this proved to be an erroneous conclusion. To a certain extent there seemed to be a correlation with the population density of *Sambucus nigra*, which in the Netherlands like elsewhere in Europe is the principal substrate of *H. auricula-judae*. In areas where the latter is abundant also *Sambucus nigra* is frequently found. The reverse, however, is not necessarily true.

Observations in the field showed that the fructifications are sensitive to low temperatures, especially below freezing point. As a rule the species is found only in relatively sheltered places. Experiments showed that sporulation is discontinued when the fruit-bodies are exposed to a temperature of 0 °C, but resumed when the temperature is again raised by a few degrees. However, sporulation of a (moist) specimen that had been exposed to —13 °C was not resumed after thawing.

The connection between chances of survival and occurence of low temperatures seemed to be fully confirmed by the excellent correlation which was found to exist between average daily minimum temperatures in winter (December–February) and population density of *H. auricula-judae*. The country was divided into zones between isotherms at 0.5 °C intervals, which were drawn up especially for this purpose by Dr. J. P. M. Woudenberg of the Royal Netherlands Meteorological Institute. They are based on observations at 35 weather stations during a period of 17 years (Fig. 1). They only provide a broad picture, because the number of stations is too small to allow conclusions on local conditions. The population density of each temperature zone was calculated, and the results were plotted in the manner shown in Figure 2. It was possible to draw a closely fitting exponential curve.

At the conclusion of the preliminary study it seemed to be justified to accept a working hypothesis, based on the following:

(1) Winter temperatures are the principal factor determining the distribution pattern in the Netherlands.
(2) Low temperatures correlate with low population densities.
(3) The population density gradient is very steep.

ADDITIONAL DATA CONFIRMING HYPOTHESIS

The working hypothesis seemed to be fully confirmed when in the course of the next few years the number of localities where *H. auricula-judae* had been found had increased from 80 to the present number of 175. (Figs. 1 and 2.) A reduction of the minimum temperature in winter of 1 °C corresponds with a reduction of the population density by 70%.

Again most of the finds were made by chance but an exeption must be made for the results from the collections of Mr. J. A. Witte, who within a period of a few months succeeded in locating the species in every square from which it was not recorded before on the island of Texel and in an area of 25×25 km around his place of residence, Wormer, in the province of North Holland. These data have been included in the present work, but it should be noted that they were not obtained in the same manner as the others. For that reason, any calculation or conclusion based on all of the distribution data has been checked after excluding these 32 squares. Fortunately, their influence is rather limited, because 28 of them are situated in one temperature zone (+0.5–0) in which the population density amounts to only 8 if Mr. Witte's data are excluded, instead of the 20 shown in Figure 2.

The fact that Mr. Witte collected in the extremely mild winter of 1974–5 undoubtedly contributed to his success, for there was hardly any frost that winter. Moreover several of the preceding winters had had temperatures well above average. An important question is whether it would be possible to duplicate Mr. Witte's results in most of the other parts of the country. If so, our distribution pattern would be accidental and meaningless. The answer is that, while this may be possible in zones with a very high population density, it is extremely unlikely to happen in zones where the population density is medium or low. At about the same time when Mr. Witte made his survey, the author investigated the Achterhoek in the eastern part of the country, from where *H. auricula-judae* had not previously been reported. The search of this area produced only one locality where the species was found. *Hirneola auricula-judae* was also found several times in a region in the province of South Holland, similar to the one in which Mr. Witte had worked, but there was no indication of its simultaneous presence in every square of this area.[1]

The sensitivity of *H. auricula-judae* to low temperatures is confirmed by the results of the work of Tryel (1971: 413), who reports that the mycelium of the species is killed by exposure to a temperature of —22°C for a period of 5 weeks.

The existence of a relation between distribution and temperature conditions also follows in a general way from the data presented by Lowy (1952: 659), which show that *H. auricula-judae* is limited to a range between latitudes 22° and 55° N.

The North American form

Extrapolation of the graph shown in Figure 2 leads to the conclusion that *H. auricula-judae* should be extremely rare in regions where minimum temperatures in winter are but a few degrees below those prevailing in the eastern part of the Netherlands. Lowy's data on Europe are very scanty, but his map clearly shows that the species is found all over the U.S.A. and southern Canada, including areas that have much more severe winters than the Netherlands. In some of these areas *H. auricula-judae* is even considered to be common (Graham, 1944: 77).

[1] Mr. Witte (personal communication, 1976) confirmed these experiences in failing to find a single specimen when searching for *H. auricula-judae* in the north-western part of the province of North Brabant, from which region the species had been reported but once.

Duncan & Macdonald (1967: 817) have shown that there are sufficient reasons to consider *H. auricula-judae* of Western Europe and the similar taxon in North America to be two 'evolutionary units' or even distinct species. In the first place there is an important difference in substrates. In the southern, midwestern and eastern states of the U.S.A. *Hirneola auricula-judae* is found on deciduous trees, but not on *Sambucus nigra* which does not exist in North America. In the northern and western states of the U.S.A. and in Canada the species is exclusively found on coniferous trees (ibid: 807). Collections from deciduous trees were found to be completely, and collections from coniferous trees virtually intersterile with collections from Western Europe, including some from Austria (ibid: 808). Spore dimensions of the North American and West European material were found to be significantly different (Table I). The authors do not mention any macroscopical characters by which the two species might be distinguished.

This is in accordance with the experience of the present author. Ten collections from coniferous trees collected by the late Dr. M. A. Donk in the U.S.A. and Canada and one from Newfoundland, obtained by courtesy of Dr. F. Tjallingii, were compared with an equal number of collections from Sambucus nigra in the Netherlands. Although one is immediately struck by the dense pilosity of the upper surface and the pronounced venulose folds of the American material, in the Netherlands' collections too one frequently finds specimens showing folds of the same height (1–3 mm) and width (1–2 mm) and having a pilose upper surface as well.

Duncan & Macdonald measured 125 spores per collection to a tenth of a μm, calculated the arithmetical mean, and determined the range of means at the 5 % level of confidence. For the present study as a rule only 20 spores per collection were measured, rounded off to whole μm. Instead of calculating the arithmetical mean, the median value was determined for each collection, and for a group of collections the range of such medians. This considerably simpler method appears to give just as good results as the far more time consuming one of Duncan & Macdonald (Table I).

All specimens that had been air-dried after collecting, readily sporulated upon resuscitation under moist conditions. An exception was found with the material from North America available to the author, which probably was too old to resume sporulation, and in this the spores had to be scraped from the hymenium. In four of these collections no spores could be found at all. In the others an average of only 12 spores per collection was measured. The different conditions of the material studied, should account for the difference in length between the spores measured by Duncan & Macdonald and those measured by the present author.

The forms of *H. auricula-judae* in Western Europe and North America are so different from each other that the presence of this species in areas of North America, where winter temperatures are very much lower than in the Netherlands, does not have to be considered inconsistent with the correlation between population density and temperature established for the latter country.

Raitviir (1971: 93–94) reports that also in the extreme eastern part of Siberia *H. auricula judae* is found on deciduous and on coniferous trees. He mentions the

Table I

Spore dimensions (in μm)

Region	Substrate	Author	Length		Breadth	
			Average or Median	Range	Average or Median	Range
W. Europe	Sambucus	Duncan/Macdonald	20.2 (a)	18.2–22.2	6.6 (a)	6.0–7.2
Netherlands	Sambucus	van der Laan	20 (m)	19–21	7 (m)	7–8
N. America	coniferous	Duncan/Macdonald	15.0 (a)	13.0–17.0	5.2 (a)	4.6–5.8
N. America	coniferous	van der Laan	14 (m)	13–14(–15)	5 (m)	5–6
N. America	deciduous	Duncan/Macdonald	13.8 (a)	12.6–15.0	5.3 (a)	4.7–5.9
E. Siberia	coniferous deciduous	Raitviir		13–15		5–6
C. Europe	deciduous	Michael-Hennig		11–15		4–7
C. Europe	deciduous	Pilát		13–15		5–6
C. Europe	deciduous	Schroeter		11–15		5–7
C. Europe	deciduous	Velenovsky		12–15		
C. Europe	deciduous	van der Laan	20 (m)	19–21	7 (m)	7–(8)

a = arithmetical mean; the range is calculated on basis of the 5% level of confidence
m = median of all collections, range of medians of individual collections is indicated in the next column

conspicuous pilosity of the form growing on coniferous wood, which he named forma *abietis*. One set of spore dimensions is given (Table I), which agrees well with Duncan & Macdonald's figures for North American collections. In European Russia *H. auricula-judae* is found in the Baltic states, the Ukraine and the Caucasus on deciduous trees only, principally *Sambucus* and *Quercus* (Raitviir, 1967: 34). Unfortunately, data on spore dimensions of collections from these areas are not available. The species has not been reported from western Siberia.

Central European data

The map showing the distribution of *H. auricula-judae* in (part of) Europe, based on the survey of a committee of the European Mycological Congress (Lange, 1974: 55) reflects considerable differences in the approach of the work by the participating countries. For that reason, a quantitative comparison of data, as attempted for the Netherlands, is out of the question.

A part of the picture seems to corroborate the working hypothesis arrived at in the Netherlands. The species is absent in Norway and Sweden, hence its northern limit is rather close to the Netherlands, as was to be expected from the steep gradient of the curve in Figure 2. The relatively high population density in England and the much lower one in Scotland, as well as the fact that in Scotland and in Denmark the species is predominantly found along the coast, are in accordance with the findings in the Netherlands. This may also apply to the relatively low population density in the northern part of West Germany and the higher one in the southern parts of that country (see also Bresinsky & Dichtel, 1971: 101).

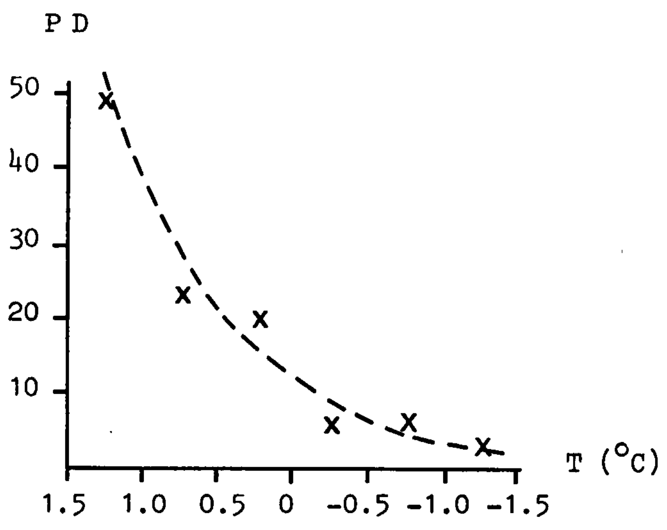

Fig. 2. Population density (PD) and average daily minimum temperature in winter (T); broken line indicating exponential curve of best fit.

The data presented for Central Europe, on the other hand, appear to be completely inconsistent with our working hypothesis. In Czechoslovakia, for instance, winter temperatures are about 5 °C below those in the Netherlands. Extrapolation of the (exponential) curve of Figure 2 gives at that temperature a population density of *H. auricula-judae* of less than one hundredth of that of the Netherlands. Application of the 'round dot mapping method' employed by Lange (1974: 12) to the finds in the Netherlands as recorded in Figure 1 results in about 50 'dots' for this country. (The European survey map shows but a fraction of this number, because it presents the distribution data as known before the present study had been started.) The surface area of Czechoslovakia is about 4 times that of the Netherlands. Therefore, by application of our working hypothesis one could expect $(4:100) \times 50 = 2$ dots in Czechoslovakia. The map shows a total of 86! The situation in East Germany is similar, and unexpectedly high population densities are also found in Hungary, Poland, and Rumania.

Could it be that *H. auricula-judae* found in Central Europe, like the one of North America, is different from the Western European form? Against this supposition is the fact that in Central Europe the species is usually found on Sambucus nigra but never on coniferous trees. On the other hand, Pilát (1957: 140) and Velenovský (1920: 794) in Czechoslovakia as well as Hennig (1960: 281) and Schroeter (1888: 386) in East Germany give spore dimensions in the range of $11-15 \times 4-7$ µm (Table I).

By courtesy of Dr. F. Kotlaba four fresh collections of *H. auricula-judae* from central Bohemia, two from southern Slovakia and three from East Germany (Baltic coast) were studied. Of six of them the substrate was *Sambucus nigra*; the others were found on *Acer* and *Morus*. Macroscopically they did not seem to be different from material found in Western Europe. Of each collection the spores of two fruit-bodies have been measured. As shown in Table I there is no difference between spore dimensions of the Western- and Central European material as far as studied by me. For the time being I am not yet prepared to incorporate into my considerations the smaller dimensions as given by Pilàt, Velenovský, Hennig, and Schroeter.

As no support has been found for the assumption that the *H. auricula-judae* from Central Europe is not conspecific with that from Western Europe, the working hypothesis had to be modified, for instance by taking into account other factors which might determine the distribution pattern.

Soil composition and distribution

An indication of where to look for other influences on the distribution pattern of *H. auricula-judae* was the fact that large differences of population density exist within the temperature zones into which the Netherlands has been divided. In some parts of the country the species has hardly been located at all, and such almost blank areas seem to range over more than one temperature zone. This is especially noticeable in the province North Brabant and the northern part of the province Limburg in the south of the country, and also in the eastern parts of the provinces Gelderland

and Overijssel in the east of the country. At first it was thought that these gaps were a consequence of lack of interest on the part of the mycologists working in those areas, but after special attention had been given to the problem it became a certainty that H. auricula-judae is extremely rare in those parts of the country.

The plant geographical districts which van Soest (1929) distinguished in the Netherlands have proved their value in the study of distribution of higher plants. It seemed worthwhile to investigate whether or not they also might throw some light on the distribution of *H. auricula-judae*. It should be understood that van Soest's division is based on the distribution pattern of several plants and plant associations as well as on soil conditions. It is only meant to give a broad picture, hence boundaries are almost straight lines. The districts are shown in Figure 3, together with the distribution data of *H. auricula-judae*. The population density of each district is shown in the second column of Table II.

The most conspicuous figures are the far above average ones of the Marl district (Krijt) in the south-east, of the Dunes district along the coast in the south-west, and of the Shallows district (Wadden) that comprises the northern part of the sand dunes on the mainland and the islands in the north. The data on the population density of the small Shallows district, however, are very much influenced by Mr. Witte's collecting. Without the latter its population density amounts to only 36. The Marl district and the Dunes district are characterized by a highly calcareous soil. In the Marl district Cretaceous rocks are close to the surface, in the Dunes district the lime content is derived from shell fragments. The Shallows district is heterogeneous, containing sand dunes with a relatively low lime content and clays that are partly calcareous.

At the other end of the scale are the Campine, the Subcentreuropean and the Guelders districts with very low population densities of *H. auricula-judae*. In all these districts acid sandy soils are abundant. The Drentian district has similar soils, but a somewhat higher population density.

Intermediate between these extremes are the small Loess district (adjacent to the Marl district, but with a less alkaline soil), and the large Haff and Fluviatile districts together covering about half of the country. Also the population density of the Haff district shown in Table II has strongly been influenced by Mr. Witte's survey which was carried out almost exclusively within this district. The population density of the Haff district drops to 9 if Mr. Witte's results are left out. Both Haff and Fluviatile districts are characterized by being largely 'man-made'. Nearly all of the former and 20% of the latter is reclaimed land, situated below sea level. The remaining 80% of the Fluviatile district would be flooded frequently if the rivers had not been embanked. Both are intensively used for agricultural purposes. Neither highly calcareous nor acid soils are found in these districts. The Haff district consists of a very heterogeneous mixture of marine clays (calcareous as well as non-calcareous) and clayey peat soils. River clays and sands with a varying lime content and calcareous marine clay constitute the Fluviatile district. Large parts of the last mentioned clay area, in the south-west of the country, were inundated at the end of World War

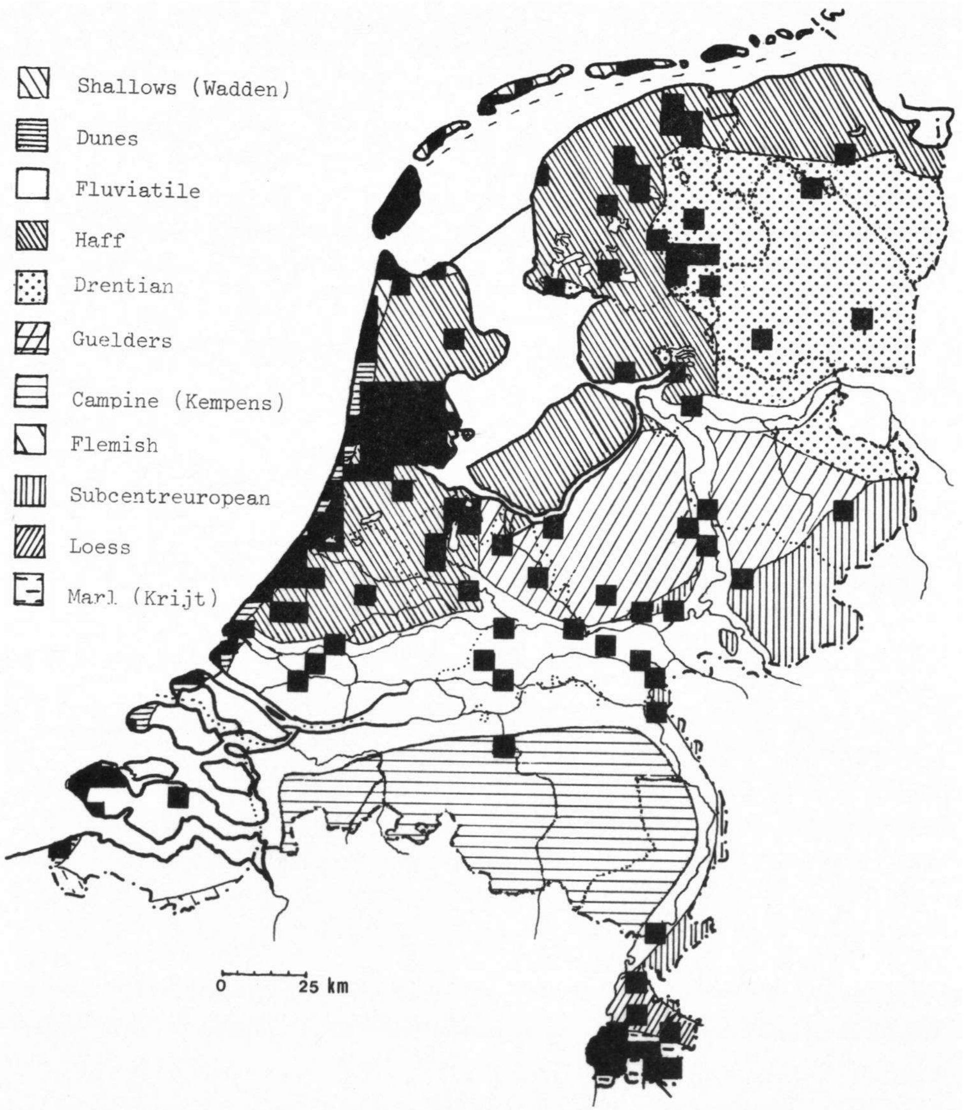

Fig. 3. Distribution of *H. auricula-judae* in the Netherlands related to division into plant geographical districts; black squares indicating squares of 5 × 5 km in which *H. auricula-judae* has been collected.

II or flooded in 1953 by salt water, which might explain the paucity of records of *H. auricula-judae* from this region. The population density in the remainder of the Fluviatile district amounts to 6.

It appears from the above that the population density of *H. auricula-judae* is considerably higher on calcareous or alkaline soils than on neutral or acid ones.

Distribution pattern as a result of soil conditions and temperature

It is difficult to differentiate between the influences of soil condition and of temperature on the distribution pattern. Most of the districts with alkaline soil are situated in the zones with high temperature and those with acid soil are found in the zones with low temperature. One may even ask whether the correlation between population density and temperature is perhaps merely accidental. Clear indication that this is not the case is found when the districts are divided into temperature zones and the population density is calculated for each zone of each district. The results are shown in Table II. To separate the influences of temperature and soil conditions the population density corresponding to temperature zones within each district has been adjusted by dividing by the overall population density for that district. The overall population density corresponding to temperature zones for the whole country, after adjustment in this manner, is shown in the last line of Table II. It is calculated by dividing the numer of squares in which *H. auricula-judae* has been found within a zone by the sum of the products of the overall population density of each district and the total number of squares of that district in that zone.[2]

It can be shown that a highly significant positive correlation exists between temperature and adjusted population density. The estimated upper tail-probability is 0.016. The latter has been found by comparing the calculated correlation coefficient with the corresponding ones when the columns of Table II are independently permutated at random (500 times).

Repetition of the calculations without making use of Mr. Witte's data yields a result which is not very different from the above.

2 The adjusted overall population density is calculated by the formula

$$\frac{\sum_{i=1}^{11} P_{ij}}{\sum_{i=1}^{11} PD^{*}_{i} T_{ij}} \quad \text{where } j = 1, 2, \ldots 6.$$

Here i refers to the different plant geographical districts and j refers to the different temperature zones. P_{ij} is the number of squares in which *H. auricula-judae* has been found in district i and temperature zone j. T_{ij} is the total number of squares in district i and temperature zone j. PD^{*}_{i} is the overall population density for district i, indicated in the third column of Table II.

Table II
Population densities in plant geographical districts and temperature zones

Temperature zone (°C)	Combined			+1.0			+1.0–+0.5			+0.5–0			0—0.5			—0.5—1.0			—1.0		
Plant geographical district	T*	P*	PD*	T	P	PD	T	P	PD	T	P	PD	T	P	PD	T	P	PD	T	P	PD
Shallows-Wadden	18½	10½	57	4	4	100	13	5½	42	1½	1	67									
Dunes	26	18½	71	18½	14	76	7½	4½	60												
Fluviatile	322½	15½	5	17	2½	15	73	2	3	49½	–	–	147	8	5	36	3	8			
Haff	371	71½	19	1½	–	–	29½	15½	52	140	39½	28	133	10	8	67	6½	10			
Drents	221	12½	6				1½	1½	100	2	1	50	1	–	–	82	6	7	134½	4	3
Gelders	139½	6	4							½	–	–	38½	3½	9	100½	2½	2			
Campine-Kempens	173½	1	1							19	–	–	154½	1	1						
Flemish	5½	–	–	½	–	–	2½	–	–	2½	–	–									
Subcentreuropean	71½	2	3										16½	½	3	55	1½	3			
Loess	14½	3	21							3	–	–	10	3	30	1½	–	–			
Marl-Krijt	16	12	75							3½	3	86	6½	5½	85	6	3½	58			
Total country	1379½	152½	11	41½	20½	49	127	29	23	221½	44½	20	507	31½	6	348	23	7	134½	4	3
Adjusted overall population densities				1.24			1.32			1.32			0.74			0.77			0.53		

T = Total number of squares in area P = Number of squares in which *H. auricula-judae* has been found PD = Population density
* Refers to combined (or overall) values

Obviously it is not feasible to construct a smooth curve from a plot of the adjusted population density values against the temperatures. The densities may be compared, however, with the results found originally and shown in Figure 2, after adjusting the latter by dividing by the overall population density for the whole country. The adjusted population densities of the zones shown in the same sequence as in Table II are as follows: 4.48, 2.08, 1.82, 0.56, 0.60, 0.27. A cursory comparison of these results with those shown in the last line of Table II reveals that the gradient of the population density due to temperature conditions is now much smaller than the one arrived at before. Consequently the calculated population density of *H. auricula-judae* in Czechoslovakia, found by extrapolation of the findings in the Netherlands will now be much higher. (By a factor 10, roughly estimated.) This fact, together with the discovery of the importance of soil composition, appear to be sufficient to remove the inconsistency which seemed to exist between the distribution data published for Central Europe and the experience gained in the Netherlands.

It appears that further study may be based on a new working hypothesis, which may be worded as follows:

The distribution pattern of *Hirneola auricula-judae* in the Netherlands is mainly formed by the following factors:

(i) the availability of *Sambucus nigra*,
(ii) average daily minimum temperatures in winter, and
(iii) composition of the soil.

High temperatures and alkaline soils correlate with high population densities.

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The most important contribution to this study, however, was undoubtedly made by the numerous mycologists, most of them amateurs, who took the trouble te record (with proof !) the presence of the subject of this study. Without their spontaneous cooperation the work could not even have been started.

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