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Comparison of the epidemiology of Metopolophium dirhodum and Sitobion avenae on winter wheat

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Abstract

The epidemiology of *Metopolophium dirhodum* and its natural enemies on winter wheat was studied from 1975 to 1979 inclusive. Alate *M. dirhodum* colonize wheat from the middle of May onwards. Immigration occurs until mid-June. Population growth rates of *M. dirhodum* can be as high as or occasionally even higer than those of *Sitobion avenae*. In *M. dirhodum* alatae are formed in a high proportion throughout the epidemic whereas in *S. avenae* the % of alatae becomes high at the end. In both species most of these alatae seem to emigrate. Both species have a similar potential to become a pest.

Additional keywords: Entomophthora, cereal aphids.

Introduction

The English grain aphid, *Sitobion avenae* F., has commanded the most attention from research workers since the serious cereal aphid outbreaks in Europe of 1968. This is because it feeds on the ears of cereals and hence it was thought to cause more damage than *Metopolophium dirhodum* Wlk. (Vereijken, 1979). Recent studies, however, on damage effects of cereal aphids (George, 1974; Rabbinge and Mantel, 1981; Rabbinge et al., 1980; Wratten, 1975, 1978) indicate that the rose-grain aphid, *Metopolophium dirhodum*, is also important in reducing yield in cereals. In 1979 it was the most numerous aphid on cereals in Western Europe and therefore should be included in warning schemes, such as EPIPRE in the Netherlands (Zadoks et al., 1981).

The aim of this paper is to describe the fluctuation in the population density of *M. dirhodum,* comparing it with *S. avenae* where relevant, with a view to develop forecasting methods. This will be done using field results collected from cereal fields near Wageningen from 1975 to 1979.

M. dirhodum overwinters in the egg stage on *Rosa* spp., in contrast to *S. avenae* which overwinters in the egg stage or viviparously on Gramineae. The eggs of *M. dirhodum* hatch in March and April and give rise to apterous fundatrices. Casual observations of roses in Wageningen revealed the presence of eggs every winter except for 1974/5, and it is interesting to note that during the five years of observation the summer population level of *M. dirhodum* was lowest in 1975.

The proportion of alate emigrants in the second generation is variable whereas the third generation is totally alate. These alatae migrate to grasses and cereals mostly during May (Hille Ris Lambers, 1947), and settle on the leaves, in contrast to *S. avenae* which moves to the ears soon after they settle in the crop. Population levels build up and as the crop ripens alatae are produced and these migrate to other grasses, in July and August. In the autumn gynoparae and males, that have developed on grasses, migrate to *Rosa* spp. In regions with mild winters some *M. dirhodum,* as with *S. avenae,* overwinter viviparously on grasses and cereals (Dean, 1974, 1978).

While *M. dirhodum* hibernates in the egg stage on roses, frequently in high numbers, *S. avenae* occurs in extremely low densities but on a very large area of Gramineae and so far the resulting fundatrices were nog recorded (Müller, 1977).

Methods

The epidemiology of *M. dirhodum* and *S. avenae* was studied in wheat fields from 1975-9 inclusive. For 1975-7 the same fields as those described by Rabbinge et al. (1979) were sampled, while in 1978 a 1 ha field (cv. Caribo) was used and in 1979 a 0.5 ha field (cv. Arminda) was sampled twice per week. Initially the numbers of aphids on 600-1000 tillers were counted but the number of tillers examined was reduced as the aphid population density increased. The tillers were sampled at random from subplots of 10 × 10 m divided over the centre of the field. The number of tillers counted was varied to maintain an accuracy level of $\sigma_{\bar{x}} < 0.1\bar{x}$ for the most numerous aphid (Rabbinge et al., 1979). At the start of the season the $\sigma_{\bar{x}}$ were larger than 0.1 of $\bar{x}$ (for *M. dirhodum* in 1976, 0.25 and in 1979, 0.22).

Aphids were identified to instar and morph; L_1, L_2, L_3, L_4 apteriform, L_4 alatiform, adult apterae and alatae. Predators, such as coccinellids, syrphids and chrysopids, were recorded during the counts, as were the numbers of mummified and diseased aphids. Mummified aphids were taken back to the laboratory and reared for the identification of the parasites and hyperparasites and for the determination of the degree of hyperparasitism.

Results

Immigration. M. dirhodum first appeared in cereal crops in the last two weeks of May and the first week of June. In 1977, 1978 and 1979 *M. dirhodum* arrived earlier or was found to be more numerous at the first census than *S. avenae.* After the initial input of aphids the daily relative population growth rates of *M. dirhodum* were usually as high as, if not higher than those of *S. avenae* (Table 1). The average over the whole period was more or less similar for both species. Exceptionally high relative growth rates for *M. dirhodum* of over 0.4 occurred (population doubling time 1.7 days) while for S. avenae the peak value was 0.34 (doubling time 2 days). These two aspects of its biology, its early colonization of cereals and its potential high daily relative population growth rate, could make *M. dirhodum* as important a pest as *S. avenae.*

Population increase. Population levels rose during June and July and usually peaked around the milky ripe stage of cereals, i.e. prior to the hardening off of the grain (Zadoks scale 80, doughy ripe) (Fig. 1). This knowledge may be of some as-

Table 1. Relative population growth rates per day [$(\ln N_{t_2} - \ln N_{t_1}) \cdot (t_2 - t_1)^{-1}$, N_{t_1} is number of aphids at time t_1, N_{t_2} is number of aphids at time t_2] of *M. dirhodum* and *S. avenae* in 1976-1979 during the period of population growth.

1976			1977			1978			1979		
date	*M. dirhodum*	*S. avenae*	date	*M. dirhodum*	*S. avenae*	date	*M. dirhodum*	*S. avenae*	date	*M. dirhodum*	*S. avenae*
25/5- 1/6		0.11	2/6- 9/6	0.17	0.15	19/5-27/5	0.14		22/5-29/5	0.10	
1/6- 8/6	0.06	0.08	9/6-16/6	0.23	0.20	27/5- 2/6	0.34		29/5- 5/6	0.25	
8/6-15/6	0,42	0.31	16/6-21/6	0.37	0.31	2/6- 9/6	0.22	0.27	5/6-12/6	0.08	
15/6-22/6	0.09	0.20	21/6-28/6	0.04	0.08	9/6-13/6	−0.003	0.19	12/6-19/6	0.10	
22/6-25/6	0.41	0.24	28/6- 1/7	0.04	0.06	13/6-20/6	0.11	0.21	19/6-26/6	0.14	0.21
25/6-29/6		0.02				20/6-27/6	0.07	0.11	26/6- 3/7	0.02	0.34
						27/6-30/6	0.03	0.05	3/7-11/7	0.12	0.26
						30/6- 4/7		0.02	11/7-17/7	0.08	0.07
									17/7-20/7	0.13	0.09
Over total period	0.19	0.16	Over total period	0.17	0.17	Over total period	0.14	0.16	Over total period	0.11	0.17

Tabel 1. Relatieve groeisnelheden per dag [$(\ln N_{t_2} - \ln N_{t_1}) \cdot (t_2 - t_1)^{-1}$, N_{t_1} is aantal bladluizen op tijdstip t_1, N_{t_2} is aantal bladluizen op tijdstip t_2] van M. dirhodum en S. avenae van 1976-1979 gedurende de periode van populatiegroei.

Fig. 1. Total number of aphids in 1976, '78, '79 at crop stages according to the Zadoks' scale. A = *Metopolophium dirhodum*, B = *Sitobion avenae*.

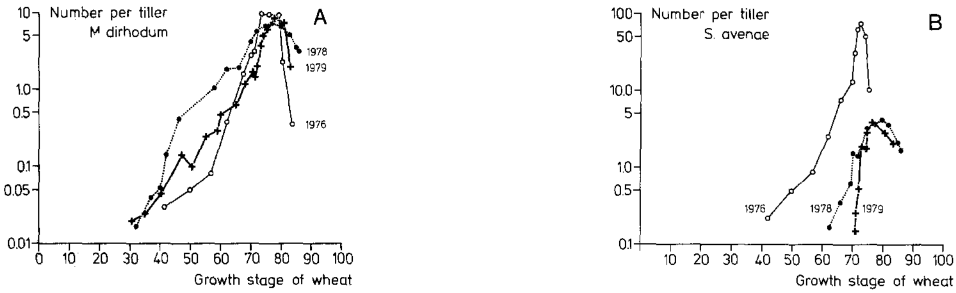

Fig. 1. Totaal aantal luizen in 1976, '78, '79 tijdens ontwikkelingsstadia van het gewas volgens de Zadoks-schaal.

sistance to forecasting. Sometimes, as in 1979, the major invasion of aphids and the population build-up were very late but this coincided with late maturing of the crops that year, because of the cool wet summer. Crop development was also retarded in 1978. The highest peak density during the study was reached in 1977 (45.5 *M. dirhodum* tiller^{-1} = 34 000 m^{-2}) although it must be pointed out that 1979 was the most serious year in Western Europe as far as *M. dirhodum* is concerned. In Wageningen, in 1979, the peak density was only 10.2 aphids tiller^{-1} = 4733 m^{-2}, (464 tillers m^{-2}), while in 1975 the lowest density was recorded (0.2 tiller^{-1} = 50 m^{-2}, 259 tillers m^{-2}). The peak densities of *M. dirhodum* in 1976 and 1978 were only slightly lower than in 1979. In Norfolk, England, during the same period, peak densities of *M. dirhodum* were generally lower than in Wageningen. For 1976 to 1978 they were 0.68, 1.28 and 3.12 tiller^{-1} (Carter, McLean and Watt, unpubl.) whereas in 1979 the peak density was much higher, nearly 60 tiller^{-1}, and *M. dirhodum* was more common than *S. avenae* (A.F.G. Dixon, pers. comm.).

The number of L_1 per adult (Table 2), used as an index of reproductive activity, shows no consistent trend in the course of time for either species. *M. dirhodum* usually has a higher reproductive activity than *S. avenae,* Watt (1979) however, found that *S. avenae* on the ears of wheat had a higher reproductive rate than *M. dirhodum* on the leaves. The number of L_1 per adult does not correlate with changes in the daily relative population growth rates (Table 1) nor are the ratios significantly higher in years with higher peaks.

Population decline. As the populations of *M. dirhodum* increased the proportions of L_4 alatiform increased but many L_4 apteriform were present until the end of the season, except in 1976 when the number of L_4 apteriform exceeded L_4 alatiform throughout the season (Table 3). The highest proportions in L_4 alatiform were found in 1977, the year with the highest peak density. Once the L_4 alatiform had moulted to the adult stage they generally left the crop. This is shown by comparison of the number of L_4 alatiform with the number of alate adults and the number of L_4 apteriform with the number of adult apterae, 3-4 days later and also at the peak

Table 2. Number of L1 per adult of *S. avenae* (S.a) and *M. dirhodum* (M.d) during a period that more than one aphid per tiller was present and when both species were found.
+ = adults, apterae + alatae; – = adults, only apterae

1976					1977					1978					1979				
date	S.a.		M.d.		date	S.a.		M.d.		date	S.a.		M.d.		date	S.a.		M.d.	
	+	–	+	–		+	–	+	–		+	–	+	–		+	–	+	–
					13-6	2.5	9.9	5.2	5.7	20-6	5.2	6.1	6.3	7.0	11-7	4.7	4.9	4.0	5.9
15-6	4.0	12.0	8.5	12.1	16-6	1.3	7.9	2.6	2.8	23-6	6.5	8.0	5.9	7.4	13-7	3.5	5.0	6.8	8.5
18-6	4.3	7.3	8.6	10.5	21-6	3.2	5.3	6.0	6.7	27-6	4.3	5.6	5.8	9.1	17-7	4.3	6.3	2.8	5.9
22-6	4.8	6.6	4.2	4.8	24-6	2.3	3.0	7.2	9.2	30-6	5.5	5.7	9.0	12.0	20-7	3.1	5.9	3.5	6.4
25-6	6.2	7.6	8.6	10.0	28-6	2.8	3.3	6.4	9.1	4-7	6.0	7.0	9.4	13.3	24-7	2.1	3.5	4.9	12.7
29-6	1.6	2.1	3.4	4.3	1-7	3.7	3.7	8.5	16.3	7-7	7.6	8.1	7.5	9.8	27-7	2.1	3.4	1.4	2.7
2-7	1.2	3.6	4.0	5.8	5-7	5.0	6.2	5.5	13.6	11-7	5.6	7.2	5.3	6.7	31-7	2.2	4.5	1.9	2.0
					8.7	2.2	3.0	7.2	13.2	14-7	5.5	14.0	8.9	14.5					
Average	3.7	6.5	6.2	7.9		2.9	5.3	6.1	9.6		5.8	7.7	7.3	10.0		3.1	4.8	3.6	6.3

Tabel 2. Aantal L1 per volwassen luis [S. avenae, (S.a) en M. dirhodum (M.d)] gedurende de periode dat meer dan een luis per halm aanwezig was.

Table 3. Number of L4 alatiform and apteriform per tiller and ratio L4 al/L4 al + L4 apt. in *S. avenae* and *M. dirhodum* during 1976-1979. – No aphid found.

Date	*S. avenae*			*M. dirhodum*			Date	*S. avenae*			*M. dirhodum*		
	number		ratio	number		ratio		number		ratio	number		ratio
	L4al.	L4apt.		L4al.	L4apt.			L4al.	L4apt.		L4al.	L4apt.	
1976							**1977**						
18/6	0.17	0.73	0.19	0.02	0.12	0.14	16/6	—	—	—	0.05	0.20	0.05
22/6	0.38	2.38	0.14	0.03	0.39	0.07	21/6	0.07	0.17	0.29	0.61	1.63	0.27
25/6	4.04	2.78	0.59	0.23	0.67	0.26	24/6	0.79	1.25	0.39	3.32	0.72	0.82
29/6	6.76	1.54	0.81	0.24	0.64	0.27	28/6	1.28	1.53	0.46	3.86	0.04	0.99
2/7	5.96	0.76	0.89	0.24	0.86	0.22	1/7	0.44	0.50	0.47	6.82	0.16	0.98
6/7	0.47	0.07	0.87	0.13	0.22	0.37							
9/7	0.17	0.01	0.94	0.03	0.01	—							
Total number per tiller at peak 67						10	Total number per tiller at peak 14						45
1978							**1979**						
9/6	—	0.015	—	0.03	0.13	0.18	22/6	—	—	—	0.01	0.06	—
13/6	0.0024	0.04	—	0.08	0.10	0.44	26/6	0.00	—.	—	0.03	0.08	0.28
16/6	—	0.09	—	—	—	—	29/6	0.00	0.01	—	0.09	0.02	0.81
20/6	0.01	0.09	0.10	0.51	0.19	0.73	3/7	0.03	0.01.	0.71	0.13	0.05	0.71
23/6	0.04	0.09	0.31	0,76	0.19	0.80	6/7	0.00	0.03	—	0.19	0.09	0.68
27/6	0.13	0.14	0.48	0.84	0.14	0.86	11/7	0.19	0.09	0.67	0.47	0.10	0.82
30/6	0.17	0.25	0.44	0.49	0.16	0.75	13/7	0.35	0.13	0.73	0.58	0.23	0.68
4/7	0.37	0.21	0.64	0.56	0.15	0.79	17/7	0.52	0.14	0.79	1.39	0.36	0.79
7/7	0.31	0.13	0.70	0.51	0.15	0.77	20/7	0.67	0.16	0.81	2.23	0.17	0.93
11/7	0.25	0.03	0.89	0.39	0.18	0.68	24/7	0.81	0.15	0.84	1.53	0.08	0.95
14/7	—	—.	—	0.28	0.15	0.65	27/7	0.83	0.11	0.94	0.84	0.09	0.90
							31/7	0.30	0.10	0.74	0.17	0.01	0.93
							3/8	0.35	0.03	0.92	0.05	—	—
Total number per tiller at peak 4						7	Total number per tiller at peak 4						10

Tabel 3. Aantallen per halm en verhouding L4 alatiform/L4 alatiform + L4 apteriform bij S. avenae en M. dirhodum in 1976-1979.

Table 4. Maximum number of L4 compared with number of adults of next counting day or maximum number of adults.

		Number per tiller			
		1976	1977	1978	1979
M. dirhodum	L4 Alatiform maximum	0.2	6.8	0.8	2.2
	Alatae 3 or 4 days later	0.2	0.6	0.1	0.3
	Alatae maximum	0.2	1.3	0.2	0.5
	L4 Apteriform maximum	0.9	1.6	0.2	0.4
	Apterae 3 or 4 days later	0.4	2.1	0.4	0.4
	Apterae maximum	0.8	2.5	0.4	0.4
S. avenae	L4 Alatiform maximum	6.8	1.3	0.4	0.8
	Alatae 3 or 4 days later	3.1	0.1	0.01	0.1
	Alatae maximum	3.1	0.2	0.1	0.1
	L4 Apteriform maximum	2.8	1.5	0.2	0.2
	Apterae 3 or 4 days later	4.3	1.2	0.2	0.1
	Apterae maximum	4.3	1.2	0.3	0.2

Tabel 4. Maximum aantal L4 (alatiform en apteriform) vergeleken met maximum aantal volwassen bladluizen en aantal op volgende teldag.

(Table 4). The numbers of apterae were always in the same order for both species but the numbers of alatae were always much lower than those expected from the numbers of L_4 alatiform, for both species. In 1976 this effect was masked by the low number of L_4 alatiform found. Almost immediate emigration from the crop after moulting seems to be the general rule for both species.

Natural enemies. Predators, parasites and *Entomophthora* spp. occurred each year but their relative contribution to the aphid population decline was not clear. Predators were generally uncommon, except in 1976 when syrphids were very numerous (Rabbinge et al., 1979). In 1977 and 1979 *Entomophthora* spp. played an important part in the aphid decline (Table 5), while parasites were uncommon in all years. In 1976, 1978 and 1979 this was possibly due to the high percentage hyperparasitism.

Discussion

The *M. dirhodum: S. avenae* ratio changes from year to year. In 1975 and 1976 *S. avenae* was more numerous, at Wageningen, but in 1977 the ratio was reversed and *M. dirhodum* was more common from 1977 to 1979. Part of the explanation might be offered by their different overwintering strategies.

In 1975 when *M. dirhodum* was rare, no eggs had been found on roses near Wageningen during the preceding winter. This was probably caused by the extremely cool (av. temp. October 1974, 7.4 °C) and wet autumn of 1974 which inhibited migration

Table 5. Maximum percentage mummified L4 and adult *M.dirhodum* during growth phase of aphid population, percentage of *M. dirhodum* killed by *Entomophthora* spp. at peak number of aphids and peak number of mummies and aphids killed by *Entomophthora* spp. per tiller.

Year	Total number L4 + adults per tiller	Mummies (%)	Peak number of aphids per tiller	Killed by Entomophthora (%)	Peak number of aphids mummified	Entomophthora
1976	1.9	9	10.0	0	0.2	0.4
1977	7.5	7	49.6	8	0.5	26.9
1978	1.5	3	7.4	0	0.1	1.0
1979	0.9	3	10.2	28	0.0	2.9

Tabel 5. Maximum percentage gemummificeerde L4 en volwassen M. dirhodum gedurende de groeifase van de populatie, percentage gedood door Entomophthora spp. tijdens de bladluistop en maximum aantal mummies en door Entomophthora spp. gedode bladluizen per halm.

from grass to roses. In most years however winter-eggs and fundatrices in spring are rather abundant on roses. The above observation might provoke the idea of using a census of alatae on roses in spring to predict the timing and size of migration into cereals and the subsequent population build-up, as is done with the black bean aphid, *Aphis fabae* (Way and Cammell, 1974).

Though timing and size of immigration into cereals will probably be related to the appearance and abundance of alatae on roses, the population build-up is affected by environmental conditions and is only partly related to immigration. This is shown by English field results of 1979 when the density of *M. dirhodum* did not exceed 1 tiller^{-1}until the watery-ripe stage (71 on the Zadoks scale) and reached 60 tiller^{-1} afterwards (A.F.G. Dixon, pers. comm.). Rabbinge et al. (1979) showed that cool summers as that of 1979 slow down crop development relatively more than the aphid development and reproduction and can result in late aphid outbursts.

Moreover, a forecasting system based on sampling roses will not exclude a census in wheat-fields as *S. avenae* is a serious pest and has to be monitored in crops.

Little relation seems to exist between the growth rates of the two aphid species. In Table 1 low growth rates for *M. dirhodum* coincide with high growth rates for *S. avenae.* In a few cases high growth rates for *M. dirhodum* seem more connected with high rates for *S. avenae*. This may mean that conditions favourable for *M. dirhodum* are also favourable for *A. avenae* but that *M. dirhodum* is more vulnerable to adverse conditions. The relative growth rates taken over the whole period differ only slightly.

A cause of the rapid explosion of *M. dirhodum* can be its higher reproduction as expressed by the higher number of L_1 per adult (Table 2).

As in *S. avenae* the course of the epidemic of *M. dirhodum* is largely determined by the behaviour of the alatae. Rabbinge et al. (1979) postulated that alatae of *S. avenae* will leave the crop. This hypothesis is supported by the results in Table 4 and seems to hold for *M. dirhodum* as well. Nevertheless some alatae of both species can be observed reproducing in the field at a rather late stage of crop development but these are a minority. It is remarkable that only few of the enormous number of alatae produced by the wheat crop enter wheat crop again.

In both species the developmental stage of the crop seems to set a limit to further population growth. Fig. 1 shows that after doughy ripe (80 on scale) no increase occurs. In some years notably 1976, 1977 the population collapsed earlier because of heavy attacks of Syrphid larvae and *Entomophthora* spp. respectively. The timing of collapse for the two species did not coincide exactly. In 1976 *S. avenae* decreased earlier than *M. dirhodum* while in 1977 the reverse occurred.

The results indicate that *M. dirhodum* is as potentially important as a pest as *S. avenae*. Forecasting of its outbreaks will be more difficult because of its greater potential for increase. The danger for such outbreaks decreases with the development of the crop towards doughy ripe, as with *S. avenae.*

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Samenvatting

Vergelijking van de epidemiologie van Metopolophium dirhodum en Sitobion avenae op wintertarwe

De epidemiologie van *Metopolophium dirhodum* werd bestudeerd van 1975-1979 en vergeleken met die van *Sitobion avenae*. Beide soorten migreren naar tarwe in de loop van mei. De relatieve populatie groeisnelheid van *M. dirhodum* bleek tijdelijk zeer hoog te zijn (verdubbelingstijd 1,7 dag tegenover 2,0 voor *S. avenae*). Over de gehele periode van de epidemie is er weinig verschil in dagelijkse relatieve groeisnelheid van de populatie.

Bij de ineenstorting, die altijd begint voor het deegrijpstadium van de tarwe, is van belang het ontstaan van gevleugelde bladluizen. Deze verlaten merendeels het gewas. Het belang van de natuurlijke vijanden voor de afname van de populatie is niet altijd duidelijk maar is soms groot en veroorzaakt dan een vroege ineenstorting van de plaag.

M. dirhodum heeft even grote mogelijkheden de plaagstatus te bereiken als *S. avenae* maar door zijn soms tijdelijk groter vermeerderingsvermogen zal het voorspellen moeilijker zijn.

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Book review

E. Punithalingam, 1979. Graminicolous Ascochyta species. Mycological Papers No. 142, Commonwealth Mycological Institute, Kew, Surrey, England. 214 pp., 109 text figures and 17 photographic plates. Price £ 12.

This publication is the first of a series of monographs concerning the coelomycetous genus *Ascochyta*. The species occurring on gramineous hosts are considered first because of their economical importance.

Short introductory chapters go into the history of the genus, including the genus and species concepts, and particular attention is paid to the processes of conidiation. The genus concept of *Ascochyta* is rather broad and the genus comprises species formerly described in the genera *Ascochyta, Ascochytula, Ascochytella, Pseudodiplodia, Diplodina, Diplodinula, Macrodiplodina, Stagonosporopsis* and *Apiocarpella.* The subdivision in sections proposed by Melnik (Opredelitel' gribov roda Ascochyta Lib., Izvo Nauka, Leningrad, 1971) is justly avoided but the old Saccardian sections Euascochyta (species with hyaline conidia) and *Ascochytella* (species with faintly coloured conidia) are adopted and supplemented by a third section: *Apiocarpella* (species with unequally two-celled conidia).

In the delimitation of *Ascochyta* from other genera, especially from *Phoma,* the conidiogenous process is regarded as one of the most important characters and is described from light microscopy of *Ascochyta* species in pure culture. The author distinguishes between temporary conidiogenous cells, which are short-lived, holoblastic, form only one conidium and are found in immature pycnidia, and permanent conidiogenous cells, which are phialidic and occur in mature pycnidia. The latter are considered to be annellidic by Boerema & Bollen (1975) on the basis of detailed electron-microscopical studies and this interpretation is not sufficiently disproved by Punithalingam's light-microscopical observations. In addition, Boerema & Bollen's well documented interpretation of the distoseptation of the two-celled conidium of *Ascochyta* is regarded as a disputable hypothesis by Punithalingam. The electron micrograph that shows this distoseptation (Plate 2; reproduced from Brewer & Boerema, 1965) is used to illustrate that the conidial septum is not always median in relation to the conidium. However, the author apparently did not notice that the 'unequally septate conidia' in this micrograph were cut at an oblique angle.

The species are distinguished by morphological characters and by teleomorphs where possible. Host specificity is not used except that species on gramineous host plants are generally regarded as restricted to members of this host family. The major part of this book consists of the dichotomous keys and descriptions of the taxa. The general key leads to the sections and is