STUDIES IN THE GENUS COLLETOTRICHUM—III

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In earlier communications (Ramakrishnan, 1941)[1,2] the parasitism of *Colletotrichum indicum* and the occurrence of saltations in *C. capsici* Syd. have been dealt with. During the course of further investigations it was observed that a close resemblance existed between these two species and some other isolates belonging to this genus. The results of these investigations embodying the studies of certain aspects of the physiology of *C. indicum* and the comparison of the isolates from *Capsicuum annum* (*C. capsici*), *Curcuma longa* Syd. (*C. curcumæ* Syd.), *Aristolochia bracteata* Retz. and *Cicer arietinum* (*C. capsici*) are recorded in this paper.

Materials and Methods

The isolate of *C. indicum* Dast. obtained from specimens sent by Prof. Dastur in 1938 was used. *C. capsici* was isolated from diseased specimens of *Capsicum annuum* from the Agricultural Research Station, Taliparamba (Malabar). Sundararaman (1930) and Thomas (1941) have recorded the occurrence of *Colletotrichum* on *Aristolochia bracteata* in Coimbatore. The fungus was isolated from fresh leaf-spots on this host. Fresh specimens of diseased leaves of *Curcuma longa* were obtained from Bhavani (Coimbatore District) through the courtesy of Sri. A. Rathnavelu, the Agricultural Demonstrator, Bhavani, and the fungus *C. curcumæ* was obtained from these. *Cicer arietinum* was affected by a blight at Pollachi (Coimbatore). This was found to be due to *Colletotrichum* and this isolate was also included in the comparative studies. Sundararaman (1926) has recorded *Colletotrichum* (*Vermicularia*) on *Cicer arietinum.*

The cultures of the isolates were initiated from single spores and maintained on either oat agar or french bean agar. Petri-dish cultures were grown inside an incubator at 32° C. unless otherwise stated. The dry weights of the fungus growths and the reaction of the fungus to different sources of nitrogen and carbon were determined following the method described by Ramakrishnan (1941.)[3] For all inoculation experiments on cotton *G. herbaceum* strain H_1 was employed.

A. Physiology of C. indicum.

Temperature relations.—The isolate grows well on agar media at the laboratory temperature (27° to 30° C.). The relative growth and sporulation at other temperatures also were studied. The fungus was inoculated into Petri-dishes containing oat agar and french bean agar and the dishes were transferred to controlled temperature chambers where the temperatures were maintained at 5°, 10°, 15°, 20°, 32°, 37° and 44° C. respectively. Closer intervals could not be utilised. The results were as follows:—

TABLE I

Temperature	*Oat agar*		*French bean agar*	
	Diameter in mm. in 7 days	Nature of growth	Diameter in mm. in 7 days	Nature of growth
5° C.		No growth.		
10° C.	Slight development		Not measurable.	
15° C.	31·3	Dark growth, black stromata in the centre, very few acervuli.	26·0	Dark, thin growth few acervuli.
20° C.	63·5	Olive-black growth, grey aerial mycelium, fair production of acervuli.	28·5	Black centre, lighter outside, numerous acervuli.
32° C.	80·0	Aerial mycelium pale olive grey, numerous buff pink acervuli.	73·7	White and grey aerial growth, numerous black stromata and pink acervuli.
37° C.	62·3	Acervuli fewer.	54·25	Less of aerial growth and fewer acervuli.
44° C.		No growth.		

The best growth occurs in the neighbourhood of 32° C. among the temperatures under trial. Sporulation is evident between 15° and 37° C. and the maximum acervular development is at about 32° C. There was no development at 5° C. but the fungus remained quiescent. When the dish was transferred from 5° C. to the laboratory temperature after one week, the fungus began to grow again and covered the dish in 8 days. The dishes kept at 44° C. did not exhibit any growth and even after removal to the laboratory temperature a week later there was no revival of the fungus. Continuous exposure to 44° C. for a week had evidently killed the fungus. Ling and Yang (1941) have found that the Chinese isolate of *C. indicum* grew best at 28° C. This temperature, however, was not included in the experiments conducted here and therefore it cannot be said that the optimum temperature for the local isolate is different. But the same authors have

also found that even in the Chinese isolate the highest germination of spores and the maximum length of germ tubes are at 32° C.

The dry weights of fungus mats grown in liquid cultures at different temperatures were also recorded. The results are given below.

TABLE II

Temperature	Dry weight in milligrammes of fungus mat (17 days' old)
10° C.	43·9
15° C.	243·0
20° C.	245·6
26°5 C.	265·3
32° C.	315·2
37° C.	155·2

These results show that liquid cultures follow a similar trend as the dish cultures.

Temperature is known to influence the spore size in some fungi (Johann, 1913, Ramakrishnan, 1941, 3). Measurements of spores from the cultures kept at different temperatures were taken and the mean length and frequency distribution are given below.

TABLE III

Class in μ	Frequency distribution at						
	15° C.		20° C.		32° C.		37° C.
	Oat agar.	F. bean agar.	Oat agar.	F. bean agar.	Oat agar.	F. bean agar.	Oat agar.
16—20	3	3	9	3	16	11	19
21—25	95	102	111	103	111	95	99
26—30	96	86	77	88	68	91	81
31—35	6	9	3	4	5	3	1
Mean length in μ	26·1	26·0	25·5	25·6	25·2	25·6	25·2

The spore length has been remarkably constant at all temperatures in this isolate.

The optimum temperature for infection of cotton was determined. Cotton seeds soaked for one hour in a spore suspension in distilled water were sown in pots containing sterilized soil. Twenty seeds were sown in each treatment. The pots were kept in chambers with air temperatures at 15°, 20°, 30° and 35° C. respectively. Control pots containing sterilised soil sown with uninfected healthy seeds were also kept. The pots were kept under observation for one week and the following results were obtained.

TABLE IV

Temperature	Inoculated		Control	
	No. germinated	No. of seedlings infected	No. germinated	No. of seedlings dead
15° C.	5	1	6	—
20° C.	11	8	12	—
30° C.	14	14	16	—
35° C.	13	4	16	—

Among the temperatures included in the experiment mortality is high at 30° C.

Carbon and nitrogen sources on growth and sporulation.—Different sources of carbon and nitrogen are known to influence the growth and sporulation of *Colletotrichum* in different ways. To ascertain whether this isolate also behaves in a similar manner it was grown on media having a basic composition (Ramakrishnan, 1941, 3) to which equivalent weights of different carbohydrates or nitrogenous substances were added.

Carbohydrates.—The fungus was grown on solid and liquid media. The average diameter of the growth after 7 days and the average dry weight of the fungus mat in liquid media after 17 days were determined.

TABLE V

Statement showing the diameter of growth or dry weight in different carbon sources

Carbon source	Agar media		Liquid media		
	Diameter in mm. 7 days	Remarks	pH at start	pH after 17 days	Weight of dry mat in mg.
Sucrose ..	68·3	Numerous black and light vinaceous fawn acervuli with spore smasses.	4·4	6·8	266·7
Glucose ..	68·5	Black sclerotioid bodies and big light vinaceous fawn spore-bearing acervuli.	4·3	7·3	223·3
Maltose ..	80·3	Black sclerotioid bodies, acervuli less than in sucrose.	4·4	7·3	270·9
Lactose ..	71·0	Thin growth, black sclerotioid bodies formed, few acervuli.	4·4	6·0	107·6
Starch (soluble)	74·5	Thin white growth with a number of drab masses. Acervuli more than in lactose.	4·6	7·2	188·4

Maltose and sucrose induce good growth but sporulation is best in sucrose.

TABLE VI

Statement showing the growth of the fungus and spore length on different sources of nitrogen

Source of Nitrogen	Diameter of growth in 8 days mm.	Spore length in microns		REMARKS
		Range	Mean	
Peptone ..	60·8	20–36	27·7	Smoke grey growth, numerous pale vinaceous acervuli all over the growth.
Asparagin ..	43·5	20–32	25·8	Pale smoke grey aerial growth margin regular, numerous acervuli and black stromatoid bodies all over the growth.
Potassium nitrate ..	45·5	20–36	27·4	Pale smoke grey aerial growth, numerous black stromatoid bodies acervuli scattered in growth.
Ammonium sulphate ..	19·7	42–28	24·2	Thick growth, margin crenate, and ridged, pale olive grey aerial growth, very few acervuli.
Urea ..	32·5	16–32	23·3	Mealy, pale greyish vinaceous growth, acervuli more than in ammonium sulphate, spore vacuolated.
Potassium nitrate ..	—	No growth.		

Peptone serves as a good source of nitrogen. The growth is slow and sporulation less when ammonium sulphate or urea are used.

Staling.—The uniform rate of growth of the fungus for 10 to 12 days on agar media, does not suggest any accumulation of staling products in the early stages of its growth. But in liquid cultures maintained for over three weeks there is evidence of the development of staling products, as no further increases in weight of fungus were obtained. In order to clear this point the fungus was grown on filtrates from cultures 25 days old. The filtrate was mixed with fresh Richards solution in the proportion of 1 : 1 and autoclaved before use. The control consisted of Richards solution mixed with an equivalent volume of distilled water before autoclaving. The two sets of media were inoculated from the same culture with equal quantities of inoculum. After fifteen days' growth the fungus mat was removed and the dry weight determined. The weights were as follows:—

TABBLE VII

Medium used	Average dry weight of fungus mat in mgm.
Filtrate from culture of *C. indicum* + Richards solution ..	50·8
Richards solution + Distilled water ..	169·7

From the above it is evident that staling products accumulate in cultures over three weeks old and these inhibit the growth of the organism. The presence of these substances was further demonstrated by allowing fresh seedlings of cotton (H_1 strain) to stand with their roots and hypocotyl immersed in the filtrate (filtered through coarse filter-paper) of cultures 25 days old. The controls were kept with the roots immersed in Richard's solution adjusted to the same pH as the filtrate. In 12 hours the seedlings kept in the filtrate wilted while the controls were quite turgid (Plate III, Fig. 4). Ling and Yang (1944) state that they were not able to demonstrate the production of toxic substances. This may be due to the fact that the toxic staling products had not developed in the filtrate from 10-day-old cultures used by them. Under Coimbatore conditions it was observed that the formation of staling products or their accumulation in sufficient quantity becomes evident only in old cultures. Further these authors have been studying an isolate of the fungus prevalent in China. It is quite probable that the Chinese strain and the Indian strain do not behave alike. This view is supported by the observation that the Chinese strain infects two varieties of *G. hirsutum, viz.*, Trice and Delfos—while all the isolates studied in Coimbatore including the strain, kindly supplied by Dastur from Nagpur have not been found to be pathogenic on *G. hirsutum* but only on *G. herbaceum* and *G. arboreum*. This fungus has been under observation in South India for over twenty years and all through this period there has been no record of its occurrence on any strain of *G. hirsutum* though Combodia cotton (*G. hirsutum*) is cultivated over a large area in Coimbatore. Thus neither in nature nor by artificial infection was the fungus found to infect *G. hirsutum*. Dastur (1934) who described the fungus from Nagpur has recorded it only on *G. arboreum*. Consequently it is presumed that the Chinese strain behaves differently from the Indian strain of the fungus in some of its physiological reactions.

Saltation.—A number of saltants were developed by this isolate on Richards agar and oat agar in the form of sectors or islands (Plate III, Fig. 3). The saltants exhibited differences in the colour and texture of the growths and in the intensity of sporulation. Non-spore-forming saltants were also formed.

B. Comparative study of C. indicum *with* C. capsici, C. curcumæ *and isolates from gram* (Cicer arietinum) and Aristolichia bracteata.

A comparison of the external morphology of the different isolates under study revealed a very close resemblance to one another. The appearance of the acervuli on the respective hosts was similar. Very often they exhibited

formation in concentric rings. Normally they are black with a well developed stroma which projects outside the host tissue. On the stroma are developed long dark septate setæ mixed with hyaline one-celled conidiophores. Falcate (crescent-shaped) unicellular, hyaline conidia are formed on these conidiophores. When large numbers of spores are formed the spore mass on the acervulus assumes a deep to light pink colour.

The size of the acervulus exhibits a wide variation in the same host, the range of variation being from 45 to 295 μ. The range of variation exhibited by setæ of any one isolate is very great. The size of the setæ in agar cultures also varies within wide limits.

The conidia of all the isolates of the same age were of the same shape. Measurements were taken of 200 conidia of each. The range of variations and the average measurements agree very closely. The following table represents the measurements of the spores of these isolates as compared to the original measurements obtained by different authors.

TABLE VIII

Species or isolate	Size of spore given by original authors		Size of spores found on host tissue Author's measurements	
	Length μ	Breadth μ	Length μ	Breadth μ
C. indicum ..	15–25 (Dastur)	1·8–4·3	24·60 (18–31)	3·1
C. capsiei ..	17–28 (Butler)	3–4	25·3 (19–31)	3·2
C. curcumae ..	18–29 (Sundararaman)	3–5	25·4 (17–31)	3·1
C. on *Aristolochia* ..	..	..	24·4 (20–30)	3·2
C. on gram. ..	21–34 (Sundararaman)	3–6	24·5 (22–28)	3·1

(Figures within brackets represent the range of measurements.)

From the above table it can be seen that there is no difference in the spore size between the isolates. On the other hand, there is very close agreement.

On agar media the first generation of the isolates exhibits a medium proportion of pale grey to pale olive grey aerial mycelium and numerous acervuli with pink spore masses. When the same isolate is carried through a number of generations the aerial mycelium diminishes in quantity. Slight differences are noticed between the isolates in the colour developed during the later generations but these fall within the normal variability of the same isolate or may be due to the formation of saltants.

In order to determine the host range of these isolates inoculation experiments were conducted on *G. herbaceum, Capsicum annuum, Cicer arietinum* and *Aristolochia bracteata.* Fifteen inoculations were made in each case on the respective plants and the results recorded after seven days are noted below.

TABLE IX

Statement showing the number of positive infections at the end of seven days

Isolate	Cotton seedlings	*Capsicum* fruits	*Aristolochia* leaves	Gram seedlings
C. indicum ..	15	4	13	15
C. capsici. ..	—	11	14	15
C. curcumae ..	—	10	12	13
C. from *Aristolochia* ..	9	6	14	14
C. from gram ..	8	8	10	14

The controls remained healthy in all cases. The isolates from *Capsicum* and *Curcuma longa* do not affect cotton. All the isolates have infected varying numbers of the other hosts.

Sansome (1938) has described how Reddick was able to improve the parasitism of *Phytophthora infestans.* He found " that the variety of potato President is resistant to *P. infestans.* But after two passages through President by artificial infection the degree of virulence of *P. infestans* is increased so that the lesions formed on President are as large as those formed on a susceptible variety, Green mountain. This higher virulence is kept up even after twenty passages through the susceptible variety." A modified method was adopted to improve the virulence of the isolates of *Colletotrichum.* They were grown on sterilised cotton seeds (strain H_1) of *G. herbaceum* and after five passages through cotton seed, the cultures were used to inoculate cotton seedlings. The results were very interesting.

TABLE X

Statement showing the incidence of infection of cotton seedlings

Isolate	No. of seedlings inoculated	Total number infected on							
		3rd day	4th day	5th day	6th day	7th day	8th day	9th day	10th day
Cotton ..	15	4	15	—	—	—	—	—	—
Capsicum ..	15	—	7	11	13	14	15	—	—
Aristolochia ..	15	—	1	4	6	10	15	—	—
Curcuma ..	15	—	—	—	5	6	6	8	8
Cicer ..	15	—	7	10	14	15	—	—	—
Control ..	15	all healthy.							

The results indicate that all the isolates can be gradually 'educated' to become pathogenic on cotton seedlings which were not being infected originally, by growing the organisms on sterilised cotton seeds for a number of generations. All of them do not become equally virulent and there is a difference in the speed of infection (Plate III, Fig. 7).

Another experiment was conducted in which the cotton isolate was grown on sterilised cotton seed or *Capsicum* fruits for seven generations and then used for virulence tests on cotton seedlings. The following results were obtained.

TABLE XI

Statement showing the virulence of the cotton isolate after passage through cotton or Capsicum

Medium	No. of seedlings inoculated	No. of seedlings infected on									
		3rd day	4th day	5th day	6th day	7th day	8th day	9th day	10th day	11th day	12th day
Cotton seed ..	20	12	20	—	—	—	—	—	—	—	—
Capsicum fruits	20	—	—	—	1	2	4	8	12	15	20
Control ..	20	all healthy									

The results show that the infective capacity of the cotton isolate becomes attenuated when grown on *Capsicum* fruits for a number of generations (Plate III, Fig. 8). When grown on agar media, however, the virulence is maintained for a much longer period.

DISCUSSION

It is evident from the studies described above that the taxonomy of the isolates of *Colletotrichum* under study at present classified as three or more different species, is in need of revision. It is seen that these isolates produce saltants very readily on agar media and such changes are bound to take place in nature also. The factors that have guided the erection of these species shall be reviewed and their validity examined.

The chief characteristics that are taken into consideration in defining species are the morphological characters, the dimension of the reproductive bodies, the acervuli and conidia and the pathogenicity of the isolate. These shall be examined one after another to assess the amount of reliability that can be placed on them.

The morphological characters of the isolates under study resemble one another very closely. If they were not properly labelled it will be difficult to distinguish one isolate from another. Ling and Lin (1944) state that "in comparison with a number of species of *Colletotrichum* such as *C. circinnans*

C. indicum, C. truncatum and *Glomerella glycines, C. capsici* differs from them in no essential way."

The dimensions of the acervulus fluctuate very much in the same isolate and consequently its size is not of much taxonomic value. Butler (1918) has recorded the size of the acervulus of *C. capsici* as 75–120 μ. The acervuli of the same species on the fruits of *Capsicum* collected locally have exhibited a fluctuation of 63 to 295 μ and on agar media the maximum reached was 315 μ. Ling and Lin (1944) state that the size of the acervulus of *C. capsici* on one host varied from 74–187 μ while on another host the variation was from 97–288 μ. A structure which exhibits such wide variation cannot be relied upon for specific differentiation.

The setæ formed on the acervuli have been known to be definitely influenced by the environment and substratum to a large extent. Sometimes their formation itself is suppressed. Ikata (1937) and Ramakrishnan (1941) have indicated that the setæ cannot be considered to be of any consequence for the purpose of specific differentiation. The shape and size of the conidium form important taxonomic characters. In the genus *Colletotrichum* the shape of the spore is useful in distinguishing certain species from others. The spores are either oblong, spindle-shaped, or falcate with tapering or blunt ends in different species, being more or less constant in the same species. The size is however influenced by the substrate and varies within limits. Yet its significance in specific differentiation cannot be ignored. Judged by these standards it is seen that all the isolates under study have similar mean dimensions of conidia and cannot be distinguished from each other either by the shape or size of the conidium.

An undue emphasis has been laid on the pathogenicity of the isolates of this genus in differentiating species. *C. capsici* was first recorded on *Capsicum.* Butler and Bisby (1931) have given a long list of plants serving as hosts for this species. They are: *Capsicum* spp., *Solanum nigrum, S. xanthocarpum, Datura fastuosa, Hibiscus esculuntus, Canvalia ensiformis,* fruit of *Vigna catjang, Dolichos lab lab, Solanum melongena, Citrus* sp. and *Carica papaya.* Ramakrishnan (1941) has observed the fungus on *Carthamus tinctorius.* Ling and Lin (1944) have noticed the fungus on fruits of *Lycopersicum esculentum* causing a fruit rot in China. A wide host range is thus established for this species. *C. curcumæ* was described as causing leaf-spot of *Curcuma longa,* to which host it owes its specific name. Sundararaman (1925, 1926) carried out a number of cross-inoculations with this isolate and considered that the fungi on *Capsicum* and *Curcuma longa* belong to the same species.

Sundararaman (1922) has however erected a new species *C. zingiberi* (*Vermicularia zingiberi*) causing leaf-spot of *Zingiber officinale.* His decision was arrived at owing to (*a*) " the difference in the measurements of sporodochia between the *Colletotrichum* (*Vermicularia*) on ginger, turmeric, and chillies; (*b*) the character of the chalmydospores; and (*c*) the negative results in the cross-inoculations on chillies and turmeric." In the paper describing this species the measurements recorded of the acervuli (sporodochia) are 50 to 140 μ for *C. zingiberi* and 35 to 160 μ for *C. curcumæ.* The former comes within the range of the latter and does not exhibit any difference. Appressoria (chlamydospores) are formed in all the isolates under study in the paper and no difference in their formation could be made out. It is questionable whether much importance can be attached to negative results of inoculation. In the absence of a thorough knowledge of the optimum environmental conditions necessary to produce successful infections there is every likelihood of failures of infection. The spore measurements were however found to agree with those of *C. capsici.*

Dastur (1934) has erected a provisional new species of *C. indicum* causing seedling blight of cotton. The only difference he found in this isolate when compared with *C. capsici* was in its pathogenicity. He found that the isolate from cotton did not infect *Capsicum* nor *C. capsici* cotton seedlings. But the infection experiments carried out at Coimbatore with the two fungi have shown that both the isolates can parasitize the two hosts.

It can be seen from the above that the occurrence of the fungi on different hosts and the variation in the pathogenicity of the isolates had prompted the creation of new species of *Colletotrichum.* Species of this genus are not obligate parasites but facultative saprophytes capable of leading a saprophytic existence in nature. Specific differentiation on differences of pathogenicity alone is not a reliable guide with such organisms. The substratum on which the fungus grows for a protracted period has been shown to influence the infective capacity of the isolates of this genus. Therefore the creation of new species on the variation of the pathogenic capabilities alone of the organisms cannot be approved. More reliance has to be placed on stable characters.

It is therefore concluded that all the isolates studied above should be included in one species. According to the rules of botanical nomenclature the name *C. capsici* has to be adopted being the earliest. *C. curcumæ* and *C. indicum* have to be merged into this species. The reasons for creating the species of *C. zingiberi* (Sundararaman, 1922) are not tenable and this fungus has also to be brought under *C. capsici* which it resembles very much.

The author himself has stated that "there is a good deal of similarity among the ginger, chillies, and turmeric *Vermicularias* in point of spore measurements." These must be considered only as strains or races of *C. capsici.* This species has a wide host range, and it produces saltants freely and the different races met with in nature might have arisen in a similar manner. Being associated with a particular host for some period the infective capacity of the race on the particular host becomes pronounced. This accounts for the variability in the pathogenicity of the races.

I am grateful to K. M. Thomas, Esq., Government Mycologist, for all the help rendered in carrying out this investigation.

Summary

Studies on the physiology of *C. indicum* Dast. were made. The fungus grows best in the neighbourhood of 32° C. The size of the conidium is not affected by temperature. Maltose and sucrose form the best sources of carbohydrates among those tried. Peptone serves as a good source of nitrogen. Staling products are formed in cultures over three weeks old. Filtrates of old cultures inhibit the growth of the fungus. Seedlings of cotton kept in these filtrates wilt in twelve hours.

A comparative study of *C. indicum, C. capsici, C. curcumæ* and isolates from gram (*Cicer arietinum*) and *Aristolochia bracteata* was made. It was found that by growing the isolate on the tissues of a particular host for a number of generations its pathogenicity on that host is improved. Thus the various isolates under study were able to infect cotton seedlings when they were grown on sterilised cotton seeds for five generations. The taxonomic position of these isolates is discussed and it is concluded that all of them belong to one species, *C. capsici* Syd.

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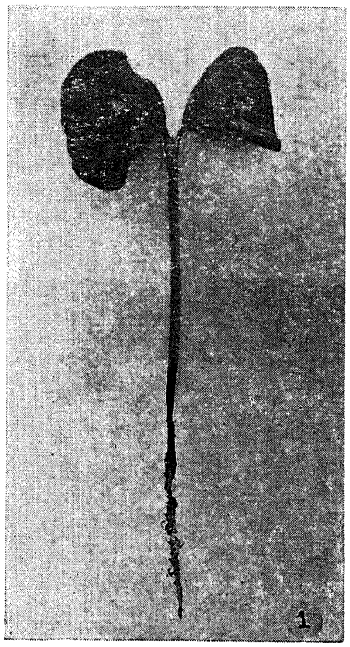
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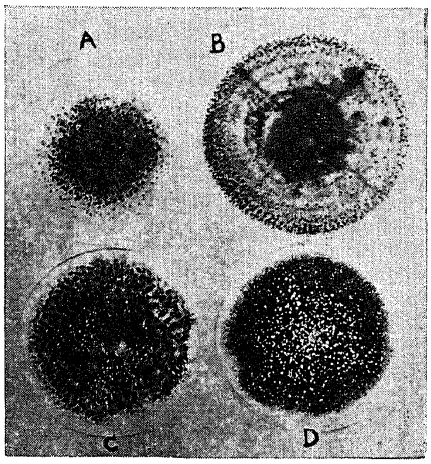
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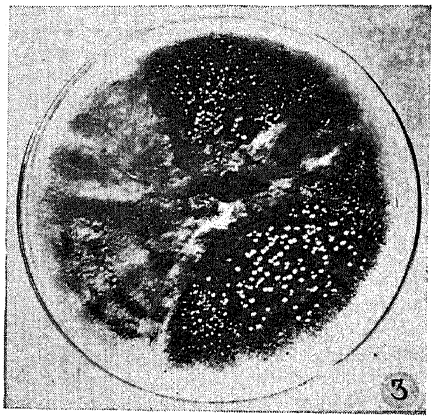
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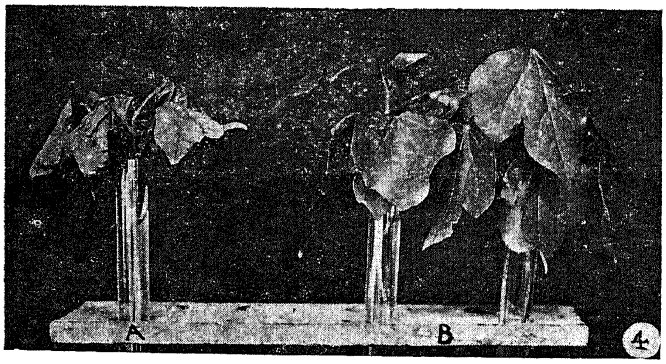
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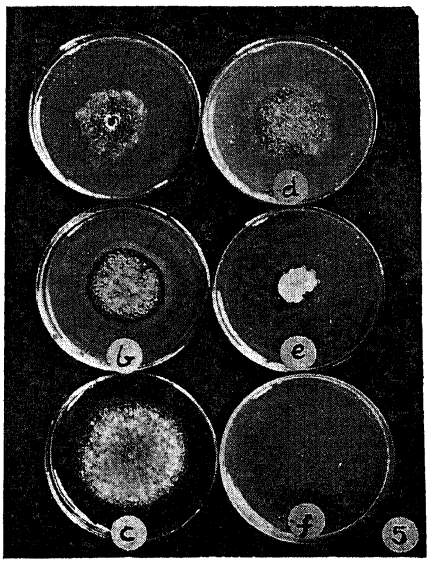
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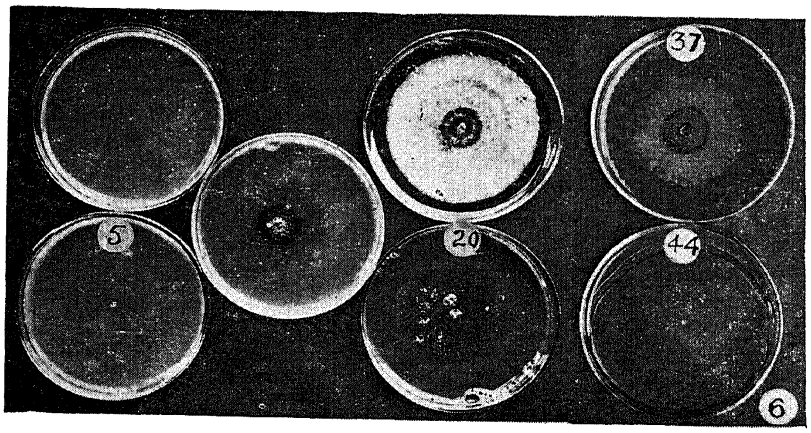
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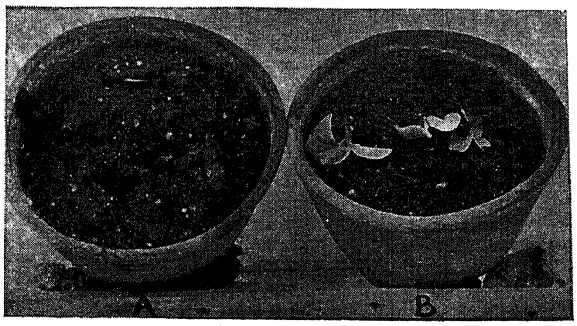
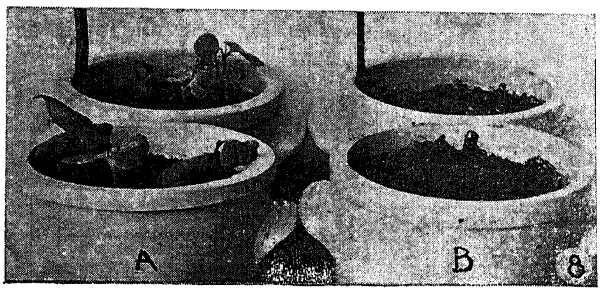

A
B


A
B
8

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Explanation of Plate

1. Cotton seedling affected by *Colletotrichum.*
2. Growth of *Colletotrichum* (Cotton strain) on
   (*a*) Lactose. (*b*) Maltose.
   (*c*) Glucose. (*d*) Sucrose.
3. Saltants of *Colletotrichum* (cotton) on Richards agar.
4. Effect of filtrate on cotton seedlings.
   (*a*) Filtrate. (*b*) Richards solution (control).
5. Nitrogen sources and growth of *Colletotrichum* (cotton).
   (*a*) Urea. (*b*) Asparagin. (*c*) Peptone. (*d*) Potassium nitrate.
   (*e*) Ammonium sulphate. (*f*) Potassium nitrite.
6. Effect of temperature on growth.

10° C.	15° C.	32	37
5° C.		20	44° C.

7. Cotton seedlings infected by (*a*) *C. capsici* (*Capsicum* strain); (*b*) *C. capsici* (*Aristolochia* strain) grown on cotton seeds.
8. Cotton seedlings infected by *Colletotrichum* (cotton strain): (*a*) after 7 passages through *Capsicum*; (*b*) grown on cotton seeds.