The Influence of Temperature on the Sporangial Germination of Phytophthora colocasiae

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By

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I. Introduction

Leaf blight of Taro (*Colocasia* spp.) is severe in warm, moist, and cloudy weather[6,35]. *Phytophthora colocasiae* is the causal organism of the disease. The fungus was first described by Raciborski in Java in 1900[25]. Since that time the disease was reported from Hawaii[21-28], Formosa[8,26], China[30], India[2,5,12,13,24,31], Burma[16,27,28], Ceylon[20], Malay[29,32-35], Philippines[6], New Guinea[1,17], Fiji[15,18,19], Java[25], and others. Parris[21] wrote, in Hawaii, that a conservative estimate for the average loss of Taro from the disease is 25 percent. Another report, in Burma, said that the fungus was responsible to a rather serious foot rot of piper bettle, destroying some 50 percent of the veins in one locality[16].

The sporangia of the genus *Phytophthora* may germinate by the liberation of zoospores (indirect germination) or by the production of a germ tube (direct germination). Temperature plays an important role in determining sporangial germination of some species of the genus; studies showing this effect have been made on *P. infestans*[4,7,14], *P. phaseoli*[9], and *P. capsici*[10]. These species germinate directly at high temperature, and indirectly at low temperature. Melhus'[14] study with *P. infestans* demonstrated that the minimum temperature for sporangial germination is 2 to 3°C., optimum temperature lies between 10 and 13°C., 24°C. is the maximum for indirect germination, 30°C. is the maximum for direct germination, and direct germination approaches zero at 30°C. Uppal[36] showed that sporangia of *P. colocasiae* formed zoospores at 11 to 12°C. Furthermore direct germination of sporangia was shown to occur at 30 to 31°C.

In preliminary observations the direct germination of the fungus occured at low temperature, and indirect germination at high temperature when the sporangia were obtained from cultures growing at 24°C. The ratio of the two types of the germination is influenced by different growth temperatures, and age of culture. These observations are contrary to expectation: not only do they differ from Uppal's work with *P. colocasiae* but also do not conform to what is known of other *Phytophthora* species.

This paper reports the influence of temperature on direct and indirect germination of sporangia of *P. colocasiae* which were obtained from cultures growing at different temperatures, and were obtained from different age of cultures.***

II. Materials and Methods

The fungus *P. colocasiae* on *Colocasia* sp. was obtained from the pure culture which was isolated on 17th of April in 1963. V-8 juice agar media which consists of 100 ml. of V-8

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*** *Each test was repeated three times.*

juice, 2.0 g. of $CaCO_3$, 15 g. of agar, and 900 ml. of water was used through the tests. Tests were made at nine levels of temperature at the same time. The levels of temperature are as follows: 5°, 8°, 12°, 16°, 20°, 24°, 28°, 31°, and 34°C.

1. The influence of temperature on vegetative growth. Twenty-seven plates of 10 percent V-8 juice agar media, three for each level of temperature, were prepared. From the 10-day-old culture, the fungus was transfered to these plates with a cork borer (5 mm. in diameter). These plates were placed into nine incubators which kept different temperature. Diameters of colonies were measured every three days.

2. The influence of temperature on sporulation. Five ml. of sterilized water was poured into each plates containing 7-day-old culture, which was incubated at the different temperatures, and sporangia on the media were removed from sporangiophores and dispersed into the water with a fine brush. The sporangia suspension from the each culture was transfered onto a Haemacytometer slide and the sporangia were counted.

3. The influence of temperature on sporangial germination. Sporangial suspension for germination was prepared as follows: a) Sterilized water was poured onto a culture. Sporangiophores with sporangia on the culture were rubbed with a fine brush and the sporangia were suspended in the water. b) The sporangial suspension was diluted as follows:

Growth temperature (°C.)	Age of culture (days)	Poured water per dish (ml.)	Original spore suspension (ml.)	Added water for dilution (ml.)	Number of spores per ml.
16	10	25	25	0	2,000
	16	25	25	0	3,000
20	10	20	6	24	3,500
	16	20	4	26	2,700
24	10	20	6	24	3,100
	16	20	4	26	2,500
28	10	30	30	0	2,500
	16	30	30	0	2,100

c)* The diluted spore suspension was divided into small tubes (5 cm. in hight, 2 cm. in diameter) as each tube contains two ml. of the suspension. The tubes were kept in the incubators.

Ten hours after incubation, germinated sporangia were counted under a microscope. Three hundred of sporangia were counted from each tubes. The count was done to investigate; 1) number of spores that germinated indirectly, as shown by the empty sporangia, 2) the number that germinated directly, and 3) the number that did not germinated at all.

III. Results

1. The influence of temperature on vegetative growth. The fungus grows between 12° and 31°C. As the Table 1. shows no growth was observed at 8° and 34°C. Eight degree is below the minimum and 34°C. is above the maximum temperature. The optimum temperature for growth of the fungus is 28°C. (Table 1 & Figure 1).

2. The influence of temperature on sporulation. Sporulation is influenced by the temperature. The temperature range of sporulation is very narrow. It is between 16° and 28°C. Optimum

* These processes, from a) to c), were done within three minutes in order to avoiding germination before the tests.

Table 1. The growth of *P. colocasiae* at the various levels of temperature

Temperature (°C)	Days after transfer			
	3	6	9	12
5	0*	0	0	0
8	0	0	0	0
12	0	1	2	3
16	9	21	31	39
20	23	36	47	62
24	25	40	57	74
28	28	47	68	86
31	23	45	64	74
34	0	0	0	0

* Milimeter in diameter of culture. Average of three plates.

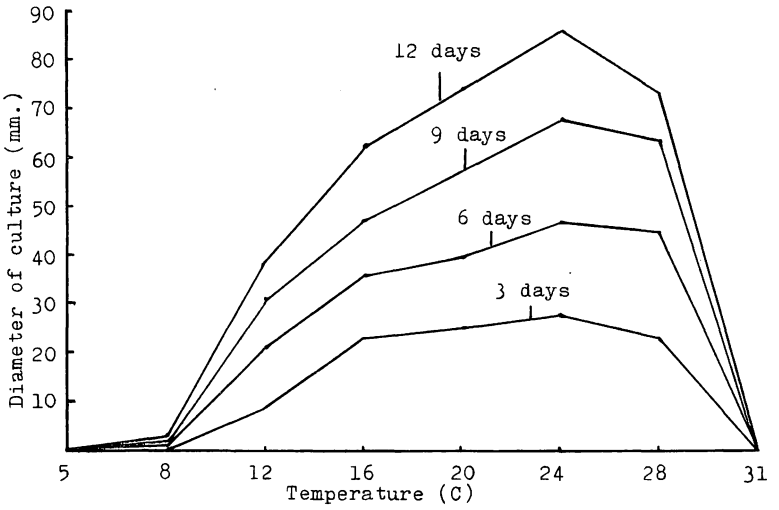

Fig. 1. The vegetative growth of *P. colocasiae* at the various levels of temperature.

temperature for sporulation is 24°C. (Table 2).

3. The influence of temperature on sporangial germination. Temperature between 16° and 28°C. is favorable for both direct and indirect germination of *P. colocasiae*. A few germination was observed at 5° and 34°C. Most sporangia germinated in 8 or 9 hours. Indirect germination is rapid. It begins in about 15 minutes. It is mostly completed in three or four hours, especially at its optimum temperature, while the direct germination occurs slowly.

The graphic representation of the influence of temperature on the sporangial germination at 10 hours after incubation is shown in Figures 2 to 9. A few indirect and direct germination occured at 34° and 5°C. showing that 34°C. is very near the maximum, and 5°C. is close to minimum for both germination. Optimum temperature of indirect germination is 24°C. The percent of the indirect germination decreases rapidly as the temperature increases from 28° to 31°C. while the germination decreases gradually as the temperature decreases from 20° to 5°C. Optimum temperature of direct germination is 16°C.

Table 2. The sporulation of *P. colocasiae* at the different temperature

	Growth temperature					
	12	16	20	24	28	31
Number of sporangia (per ml.)	0	75,600	123,300	218,900	7,200	0

1) The germination of sporangia which were obtained from the cultures growing at different temperatures. The ratio of direct and indirect germination is variable in different growth temperature of the culture taken.

Sporangia grown at 16°C.: The ratio of direct germination of sporangia obtained from the culture growing at 16°C. is the highest at higher germination temperature among all the sporangia growing at different growth temperatures. (Table 3 & Figure 2). They are: 22 percent at 20°C. of germination temperature, 20 percent at 24°C., and 22 percent at 28°C. The ratio of direct germination (12%) at 16°C. of germination temperature is lower than that of indirect germination (30%).

Sporangia grown at 20°C.: The ratio of both germination of sporangia obtained from the culture growing at 20°C. is very low. (Table 3 & Figure 3).

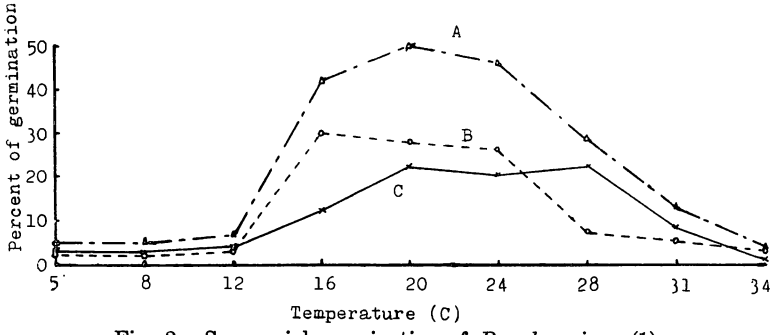

Fig. 2. Sporangial germination of *P. colocasiae*. (1)
The culture was grown at 16°C. for 10 days.
A=total germination, B=indirect germination
C=direct germination

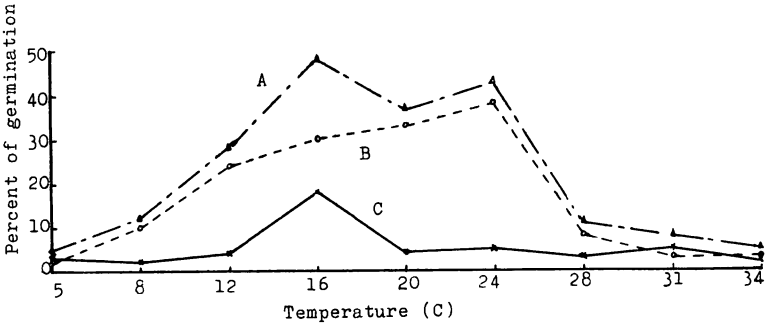

Fig. 3. Sporangial germination of *P. colocasiae*. (2)
The culture was grown at 20°C. for 10 days.
A=total germination, B=indirect germination
C=direct germination

Table 3. Direct and indirect germination of sporangia of *P. colocasiae* obtained from the cultures growing at different temperature (10-day-old cultures).

Growing temperature (°C)	Temperature for germination																							
	5			8			12			16			20			24			28			31			34		
	D*	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T
16	3%	2	5	3	2	5	4	3	7	12	30	42	22	28	50	20	26	46	22	7	29	8	5	13	1	3	4
20	3	2	5	2	10	12	4	24	28	18	30	48	4	33	37	5	38	43	3	8	11	5	3	8	2	3	5
24	4	13	17	7	21	28	12	24	36	33	20	53	12	70	82	13	75	88	11	40	51	12	8	20	9	12	21
28	3	2	5	2	6	8	7	13	20	19	22	41	13	66	79	10	71	81	3	66	69	1	3	4	1	3	4

* D=Direct germination, I=Indirect germination, T=Total germination

Table 4. Direct and indirect germination of sporangia of *P. colocasiae* obtained from the different age of culture

Growing temperature (°C)	Age (days)	Temperature for germination																								
		5			8			12			16			20			24			28			31			34		
		D*	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T	D	I	T
16	10	3%	2	5	3	2	5	4	3	7	12	30	42	22	28	50	20	26	46	22	7	29	8	5	13	1	3	4
	16	4	4	8	11	10	21	13	16	29	24	19	43	26	36	62	28	35	63	32	7	39	12	3	15	4	1	5
20	10	3	2	5	2	10	12	4	24	28	18	30	48	4	33	37	5	38	43	3	8	11	5	3	8	2	3	5
	16	6	2	8	18	14	32	27	28	55	31	36	67	25	52	77	25	55	80	9	22	31	10	4	14	8	4	12
24	10	4	13	17	7	21	28	12	24	36	33	20	53	12	70	82	13	75	88	11	40	51	12	8	20	9	12	21
	16	9	6	15	19	14	33	21	23	44	36	22	58	34	45	79	28	42	70	29	47	76	18	19	37	16	15	31
28	10	3	2	5	2	6	8	7	13	20	19	22	41	13	66	79	10	71	81	3	66	69	1	3	4	1	3	4
	16	11	2	13	12	5	17	11	4	15	31	6	37	57	12	69	55	20	75	58	16	74	13	7	20	7	4	11

* D=Direct germination, I=Indirect germination, T=Total germination

Sporangia grown at 24°C.: Indirect germination of sporangia obtained from the culture growing at 24°C. is the highest among the sporangia from all the cultures growing at the different temperature. Especially the indirect germination is remarkable at 20° to 24°C. of germination temperature. They are: Seventy percent at 20°C., and 75 percent at 24°C. The direct germination of sporangia obtained from the culture growing at 24°C. (33%) is the highest at 16°C. of germination temperature among the sporangia obtained from all the cultures growing at the different temperature. It is higher than that of indirect germination (20%) at the same germination temperature. (Table 3 & Figure 4).

Sporangia grown at 28°C.: Indirect germination of the sporangia obtained from the culture growing at 28°C. is high. It is followed to that of 24°C. The indirect germination of the sporangia at 28°C. of germination temperature (66%) is higher than that of 24°C.

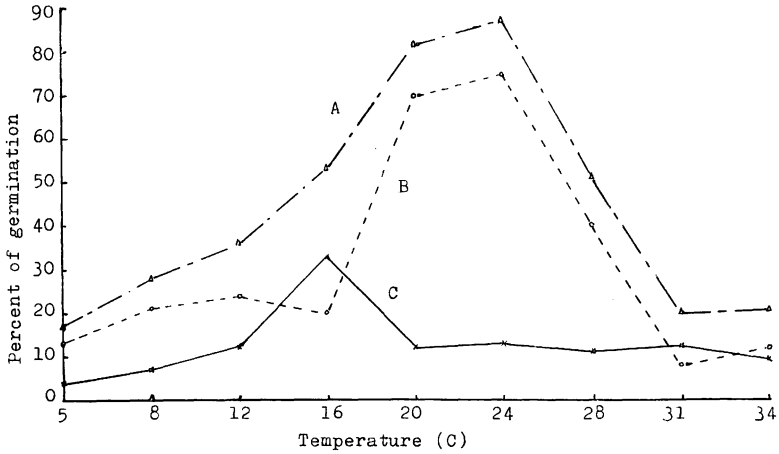

Fig. 4. Sporangial germination of *P. colocasiae*. (3)
The culture was grown at 24°C. for 10 days.
A=total germination, B=indirect germination
C=direct germination

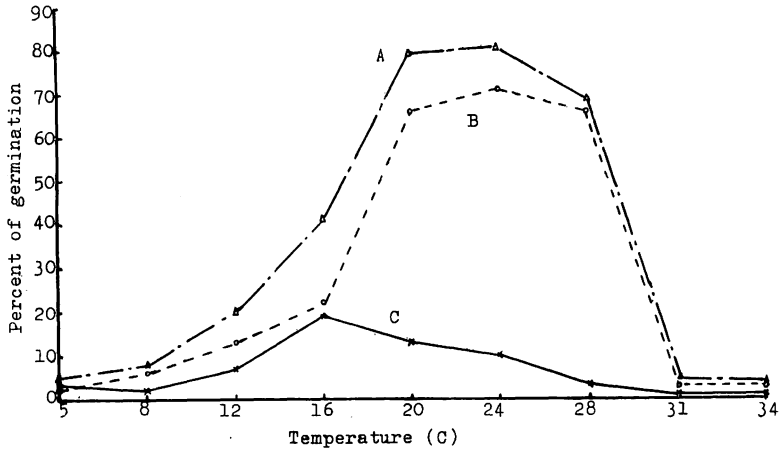

Fig. 5. Sporangial germination of *P. colocasiae*. (4)
The culture was grown at 28°C. for 10 days.
A=total germination, B=indirect germination
C=direct germination

culture (40%). Direct germination of the sporangia at 16°C. of germination temperature (19%) is the highest among all the germination temperature. (Table 3 & Figure 5).

2) The influence of culture age on sporangial germination. The ratio of direct germination of sporangia increases as the culture becomes old. (Table 4 & Figures 6 to 9). This phenomenon is notable on the sporangia obtained from the culture growing at 28°C. It is higher than indirect germination at any germination temperature. The indirect germination of sporangia obtained from the culture growing at 24° and 28°C. decreases as the culture becomes old, while that of sporangia grown at 16° and 20°C. increases.

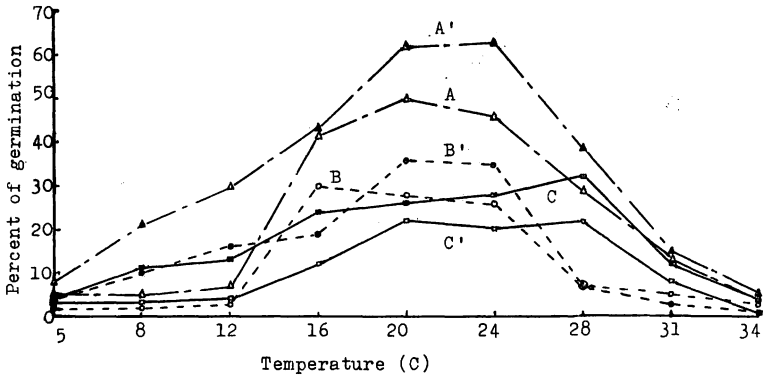

Fig. 6. Sporangial germination of *P. colocasiae*. (5) The cultures were grown at 16°C. for 10 days (A, B, C) and 16 days (A′, B′, C′). A=total germination of sporangia obtained from 10-day-old culture, B=indirect germination-10-day-old culture, C=direct germination-10-day-old culture, A′=total germination-16-day-old culture, B′=indirect germination-16-day-old culture, C′=direct germination-16-day-old culture.

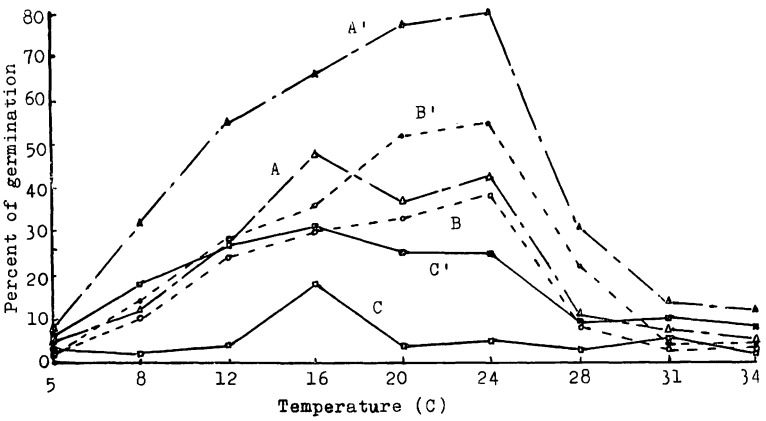

Fig. 7. Sporangial germination of *P. colocasiae*. (6) The cultures were grown at 20°C. for 10 days (A, B, C) and 16 days (A′, B′, C′). A=total germination of sporangia obtained from 10-day-old culture, B=indirect germination-10-day-old culture, C=direct germination-10-day-old culture, A′=total germination-16-day-old culture, B′=direct germination-16-day-old culture, C′=direct germination-16-day-old culture.

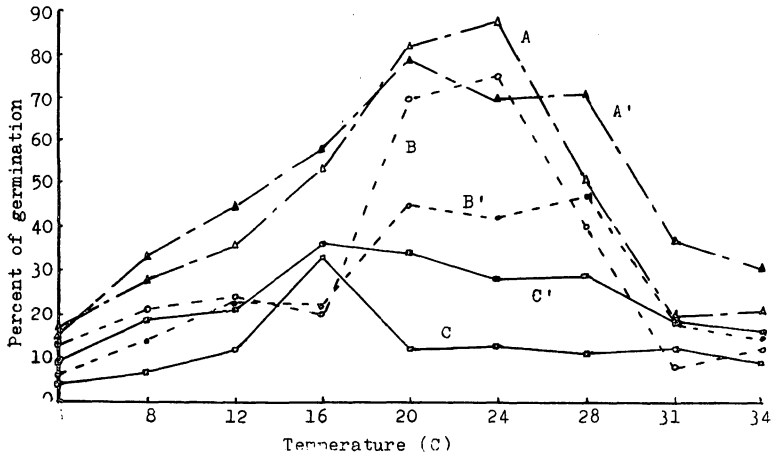

Fig. 8. Sporangial germination of *P. colocasiae*. (7) The cultures were grown at 24°C. for 10 days (A, B, C) and 16 days (A′, B′, C′). A=total germination of sporangia obtained from 10-day-old culture, B=indirect germination-10-day-old culture, C=direct germination-10-day-old culture, A′=total germination-16-day-old culture, B′=indirect germination-16-day-old culture, C′=direct germination-16-day-old culture.

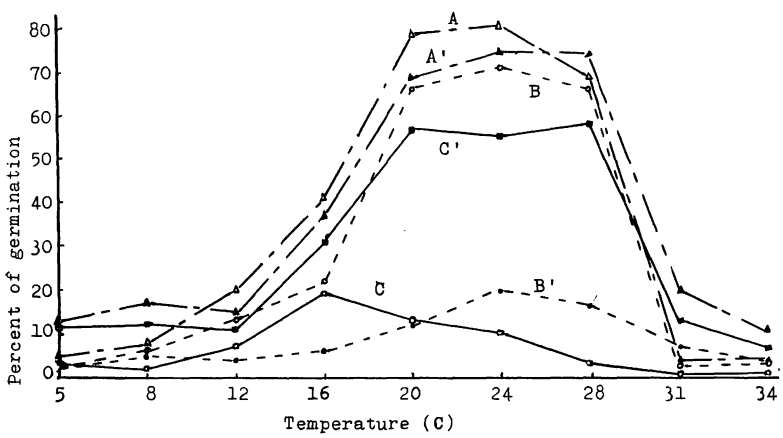

Fig. 9. Sporangial germination of *P. colocasiae*. (8) The cultures were grown at 28°C. for 10 days (A, B, C) and 16 days (A′, B′, C′). A=total germination of sporangia obtained from 10-day-old culture, B=indirect germination-10-day-old culture, C=direct germination-10-day-old culture, A′=total germination-16-day-old culture, B′=indirect germination-16-day-old culture, C′=direct germination-16-day-old culture.

IV. Discussion

Leonian[11] studied the growth of *Phytophthora colocasiae* on various media, comparing with the other species of the genus *Phytophthora*. Although most of his tests were done at 20°C., he found different growth of the fungus only on Maltextract agar media in the different temperatures in one test. He reported the diameter of the fungus colonies at the 6-day-old cultures were 12 mm. at 12°C., 45 mm. at 20°C., and 68 mm. at 30°C. His report indicates that the optimum temperature for growth of the fungus lies between 20° and 30°C.

In the writer's tests, the optimum temperature for the growth of the fungus is 28°C. and the range of the growth temperature lies between 12° and 31°C. The both tests show the growth of the fungus rapid at rather high temperature. And its optimum temperature for vegetative growth is 28°C. on this study.

Leonian also studied the sporulation of the fungus on the media contained various sugar, and found that sporulation is better on Dextrose and Levulose. But he did not studied in various level of temperature. As the results of the writer's tests show, the temperature range of sporulation is very narrow and the optimum temperature (20° to 24°C.) is lower than that of vegetative growth.

Influence of temperature on sporangial germination of genus *Phytophthora* was studied by Melhus[14] using *P. infestans*. He found that: 1) the minimum temperature on sporangial germination is near 2° or 3°C., 2) optimum temperature lies between 10° and 13°C., 3) 24°C. is very near the maximum for indirect germination, 4) 30°C. is near the maximum for direct germination, 5) direct germination begins at or near the optimum for indirect germination, gradually increases up to or nearly to the maximum for indirect germination, and approaches zero at 30°C. Uppal[86] showed that sporangia of *P. colocasiae* formed zoospores at 11° to 12°C. Furthermore that direct germination of sporangia was shown to occur at 30° to 31°C.

According to the writer's studies, *P. colocasiae* is quite different from *P. infestans* which had been studied by Melhus in the sporangial germination. These studies also differ from the Uppals' study on the *P. colocasiae*. Favorable temperature for sporangial germination of *P. colocasiae* is high, and range is wide. It lies between 16° and 28°C. The maximum temperature for germination is 34°C., and minimum temperature is 5°C. Optimum temperature for direct germination is rather low (16°C.). Optimum temperature for indirect germination is high (24° to 28°C.). The percent of indirect germination decreases rapidly as the temperature increases from the optimum temperature, while the germination decreases gradually as the temperature decreases.

The ratio of direct and indirect germination is variable in different growth temperature of the culture taken. Direct germination of sporangia taken from the culture growing at 16°C. is the highest at higher treatment temperature for germination among all the sporangia growing at different growth temperature. The both germinations of the sporangia taken from the culture growing at 20°C. is very low. Indirect germination of sporangia obtained from the culture growing at 24°C. is the highest among the sporangia obtained from all the cultures growing at different temperature. Especially the ratio of the indirect germination at 20° to 24°C. of germination temperature is remarkable. At 16°C. of germination temperature, the ratio of direct germination of sporangia obtained from the culture growing at 24°C. is the highest among the sporangia obtained from all the cultures growing at different temperature. It is higher than indirect germination at the same germination temperature. Indirect germination of sporangia, obtained from the culture growing at 28°C., is as high as that of sporangia from 24°C. culture. At the 28°C. of germination temperature it is higher than that of 24°C. culture. The optimum temperature on direct germination of the sporangia taken from 28°C. culture is 16°C.

The direct germination of sporangia increases as the culture becomes old. The ratio of indirect germination of sporangia obtained from the culture growing at 24° and 28°C. decreases

as the culture becomes old, while that of sporangia obtained from the culture growing at 16° and 20°C. increases.

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温度が，*Phytophthora colocasiae* の胞子嚢の発芽におよぼす影響（摘要）

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1. この論文は，温度が，*Phytophthora colocasiae* の胞子嚢の発芽におよぼす影響を主とし，その生育や胞子嚢形成におよぼす影響をも含めた研究をまとめたものである。

2. この菌の菌糸体は，12～31°C. で生育し，28°C. でもっとも伸長する。

3. 胞子嚢を形成する温度の範囲はせまく，16～28°C. である。最適温度は 24°C. である。

4. この菌の胞子嚢の発芽は，*Phytophthora* 属のほかの種類に比較してやや高温でおこなわれ，その好適温度は 16～28°C. の範囲にあり，最低温度は 5°C.，最高温度は 24°C. 附近にある。

5. この菌の胞子嚢の発芽には，直接発芽（発芽管を出す）と間接発芽（游走子を出す）があり，間接発芽は発芽開始が早く，15 分間で発芽はじめて，3～4 時間で大部分が発芽する。それに反し，直接発芽はおそい。両発芽とも 8～9 時間でほとんど完成する。

6. 直接発芽は，間接発芽に比較して，その発芽率は低い。また，その最適温度は低く，16°C. である。

7. 間接発芽の最適温度は，やや高く，24°C. である。

8. 直接，間接発芽率は，その菌が生育した温度の影響をうける。16°C. で生育した菌の胞子嚢は，高い発芽温度において，ほかの温度で生育した菌よりも高い直接発芽率を示す。すなわち，20°C. で 22%，24°C. で 20%，28°C. で 22% である。また，間接発芽率は，16°C. の発芽温度において高く（30%），ほかの温度で生育した菌とは異なった結果があらわれている。

9. 20°C. で生育した菌の胞子嚢の発芽率は，全般に低い。

10. 24°C. で生育した菌の胞子嚢の間接発芽率は，ほかの温度で生育した菌と比較してもっとも高い。特に，発芽温度 20～24°C. での間接発芽率は，注目に値する。すなわち，20°C. で 70%，24°C. で 75% である。発芽温度 16°C. における直接発芽（33%）は，間接発芽（20%）よりも高

い発芽率を示す。

11. 28°C. で生育した菌の胞子嚢の間接発芽率も，24°C. で生育した菌についで高く，発芽温度28°C. において（66%）は，24°C. で生育した菌（40%）よりも高くなっている。発芽温度 16°C. での直発芽率は，ほかの発芽温度に比較してもっとも高く，19% である。

12. この菌の生育期間が長くなることによって，直接発芽率が高くなる。その現象は，特に 28°C. で生育した菌にいちじるしくあらわれる。すなわち，20°C. で 57%，24°C. で 55%，28°C. で 58% である。それは，若い菌とは逆に，間接発芽率（20°C. で 12%，24°C. で 20%，28°C. で 16%）よりも高くなっている。