Growth of Various Powdery Mildew Fungi on the Barley Leaves Infected Preliminarily with the Barley Powdery Mildew Fungus*

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土屋和夫**・平田幸治***: うどんこ病罹病オオムギ葉上
における種々のうどんこ病菌の生育

Abstract

Young colonies of the barley powdery mildew fungus growing on barley leaves were rubbed off with water-drenched absorbent cotton and then the leaves were inoculated secondarily with the powdery mildew fungi collected from wheat and *Agropyron ciliare* Franch. var. *minus* Ohwi and 49 powdery mildew fungi from dicotyledons. The haustoria of the barley powdery mildew fungus, torn off from the hyphae and remaining in the barley epidermal cells, survive for many days. Out of the 51 fungi, 45 grew close to the colonies of the barley fungus on the barley leaves and 30 produced conidia, though the hyphal growth and conidial formation were different in their degree according to the fungi. The powdery mildew fungi from wheat, *Agropyron*, cucumber, *Physalis alkekengi* L. var. *francheti* Hort. form. *bunyardii* Makino, etc. grew nearly as well as on their respective proper host plants at least for the first several days after inoculation. Some dicotyledonous species, such as *Plantago asiatica* L., *Lycium chinense* Mill., *Euonymus japonicus* Thunb., etc., were also proved to be susceptible to some secondarily inoculated fungi. For example, the powdery mildew fungi from cucumber, buckwheat and barley produced conidia on *Lycium*, but neither the cucumber fungus nor barley fungus grew at all on buckwheat. (Received March 1, 1973)

Moseman, Scharen and Greeley (1965)¹⁾ found that when barley leaves bearing young colonies of the barley powdery mildew fungus (*Erysiphe graminis* DC. f. sp. *hordei* Marchal) were inoculated with the wheat powdery mildew fungus (*Erysiphe graminis* DC. f. sp. *tritici* Marchal), some of the conidia produced subsequently on the barley leaves were able to infect wheat plants. They supposed that barley leaves infected preliminarily with the barley fungus would be susceptible to the wheat fungus. Later Naito and Hirata (1969)²⁾ observed that the conidia not only of the barley fungus but also of the wheat fungus and the fungus from *Agropyron ciliare* Franch. var. *minus* Ohwi (*Erysiphe graminis* DC. f. sp. *agropyri* Marchal), which were inoculated around older colonies of the barley fungus growing on barley leaves, germinated occasionally without formation of appressoria and haustoria and that such abnormal germ tubes, coming in contact with hyphae of the barley fungus colonies, fused with the hyphae. Further they observed that hyphae grew out from the germ tubes, probably getting nutrients from the barley fungus, and produced conidia which were testified to be

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infective to wheat or *Agropyron* plants. Thus the colony development of the wheat powdery mildew fungus on barley leaves was induced by either way given in the above mentioned two papers.

While examining the conidial germination of the barley powdery mildew fungus on the barley leaf bearing young colonies of the barley fungus, we noticed the following phenomena. In the neighborhood of young colonies of Race 9* of the barley fungus growing on a barley variety, Golden Melon, conidia of Race 1* which is ordinarily unable to infect the barley variety were found to germinate normally leading to profuse development of colonies. Then the conidia of the wheat fungus and the fungus from the above mentioned *Agropyron* species, in place of those of the barley fungus, were secondarily inoculated on barley leaves and observed to grow as well as the barley fungus at least for several days after inoculation. Interested in these phenomena, we inoculated barley leaves bearing young colonies of the barley fungus with the cucumber fungus (*Sphaerotheca fuliginea* (Schlecht.) Pollacci) and the fungus from *Potentilla togasi* Ohwi (*Sphaerotheca humuli* (DC.) Burr.). These two fungi were observed to grow and produce conidia on the barley leaves. Since then 47 powdery mildew fungi from dicotyledonous species covering 26 families have been employed as the secondary inocula.

This paper reports the results of the secondary inoculation on barley leaves with the above mentioned various powdery mildew fungi and some observations on the growth of the wheat, *Agropyron* and cucumber fungi on the barley leaves: with these three fungi the inoculation experiments were repeated most frequently.

Methods

It is not always easy to distinguish the colonies of the secondarily inoculated fungus from those of the primarily inoculated barley fungus growing near each other on the same barley leaf. But, when the secondary inoculation is carried out while the barley fungus has not yet produced conidia, that is, within four days after the primary inoculation, the colonies of the two fungi found a few days later on the barley leaf are distinguishable by their sizes; the colonies of the secondarily inoculated fungus are smaller than those of the barley fungus. Besides the sizes of the colonies, the shapes of the conidia, germ tubes and haustoria and the pattern of hyphal branching are distinctly different between the fungi from dicotyledons and the barley fungus.

However, the colonies of the barley fungus and those of the secondarily inoculated fungus become difficult to discern clearly as the colonies of the two fungi become older and overlap each other. In order to avoid this difficulty, the secondary inoculation was tried on the barley leaf from whose surface the colonies of the primarily inoculated barley fungus had been rubbed off with water-drenched adsorbent cotton. The haustoria of the barley fungus, cut off from the hyphae and remaining in the epidermal cells, survive for many days. By such a preliminary treatment the secondarily inoculated fungus was also observed to develop on the barley leaf, making haustoria in the epidermal cells containing the haustoria of the barley fungus or adjacent epidermal cells**. The results of the experiments reported in this paper were obtained mostly by such an inoculation method.

* Races determined and reported by Hiura, U. and H. Heta in their papers "Studies on the disease resistance in barley, II. Physiologic races of *Erysiphe graminis hordei* in Japan" and "III. Further studies on the physiologic races of *Erysiphe graminis hordei* in Japan" published in Ber. Ohara Inst. Landw. Forsch. 10: 17-28 (1953) and Ibid.: 135-156 (1955).

** Hyphal fragments connected with haustoria sometimes escape being rubbed off and remain alive on the barley leaf. The colony of the secondarily inoculated fungus which happened to be growing near such a hyphal fragment was observed to grow better, to produce more conidia and to survive longer than the colony which had not such a hyphal fragment nearby.

For microscopical observation the secondarily inoculated barley leaf was fixed with FAA and stained with cotton blue. According to this method the fungus colony is stained differentially blue and can be observed easily.

Results

1. Classification of the secondarily inoculated powdery mildew fungi according to their development on barley leaves

Table 1 classifies the 51 secondarily inoculated powdery mildew fungi into three groups according to their development upon barley leaves found generally on the sixth day after inoculation: (I) those which produced conidia (Fig. 1, A), (II) those which developed hyphae but produced no conidium, and (III) those which developed no hypha. The inoculation experiment was, however, carried out only once for each of many of the tested fungi. Repeated experiments might give some corrections in the table. For all that, 45 fungi out of the 51 grew on the barley leaf and 30 produced conidia. The 45 fungi are those from dicotyledons excepting the wheat fungus and *Agropyron* fungus and include various species belonging to *Erysiphe*, *Sphaerotheca*, *Podosphaera*, *Microsphaera* and *Uncinula*. The conidia produced by the cucumber fungus classified in the group (I) were proved to be infective to cucumber leaves, but those produced by the other fungi in the group were not tested for their pathogenicity.

The fungi in the groups (I) and (II) are arranged according to the extent of hyphal growth, those which developed hyphae most profusely being listed at the top part of each group. Generally speaking the growth of the fungi in both groups was not as good as that of the barley fungus. But the first several fungi in the group (I), namely, *Erysiphe graminis* from wheat and *Agropyron*, *Sphaerotheca fuliginea* from cucumber, *Melothria japonica* Maxim. *Boehmeria nipononivea* Koidzumi, *Erysiphe cichoracearum* from *Physalis alkekengi* L. var. *francheti* Hort. form. *bunyardii* Makino, etc., developed fairly well. In an experiment with the cucumber fungus the hyphal development and conidial formation of the fungus on the barley leaf were compared with those on the cucumber leaf and found not to fall behind at least for six days after inoculation. *Sphaerotheca humuli* from *Geranium nepalense* Sweet var. *thunbergii* Kudo ranked at the top of the group (II) developed hyphae as much as the cucumber fungus but produced no conidiophore during the first six days after inoculation.

The fungi which did not grow on the barley leaf, as listed in the group (III), are only six. *Phyllactinia moricola* (P. Henn.) Homma from mulberry, *Ph. imperialis* Miyabe from *Paulownia tomentosa* Steud. and *Leveillula taurica* (Lév.) Arn. from green pepper belonging to this group are endophytic unlike the other fungi in Table 1. Although very rarely, germ tubes of the former two fungi intruded through stomata of the barley leaf and external hyphae grew considerably long and branched. Judging from the length of the developed hyphae the fungi might have made haustoria in mesophyll cells of the barley leaf and the nutrients absorbed by the haustoria, not the contents of inoculated conidia, might have nourished the hyphae.

As mentioned so far, the barley leaf infected primarily with the barley fungus is susceptible to various powdery mildew fungi from dicotyledons. In order to know if dicotyledons infected primarily with their own fungi are also susceptible to various other fungi, colonies which were growing naturally on leaves of *Plantago asiatica* L., *Euonymus japonicus* Thunb., rose, buckwheat and *Lycium chinense* Mill. were rubbed off and then the leaves were inoculated with various fungi. The results are given in Table 2. As indicated in the table the combinations of plant and fungus in which the secondarily inoculated fungi did not grow at all were rather few. In consideration that various powdery mildew fungi from dicotyledons grow on barley and the barley powdery mildew

Table 1. Seconadarily inoculated powdery mildew fungi classified according to their development on barley leaves

(I) Fungi which produced conidia

Fungus ^{a)}	Original host
<i>E. graminis</i>	<i>Triticum sativum</i> L.
<i>E. graminis</i>	<i>Agropyron ciliare</i> Franch. var. <i>minus</i> Ohwi
<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.
<i>S. fuliginea</i>	<i>Melothria japonica</i> Maxim.
<i>S. fuliginea</i>	<i>Boehmeria nipononivea</i> Koidzumi
<i>E. cichoracearum</i>	<i>Physalis alkekengi</i> L. var. <i>francheti</i> Hort. form. <i>bunyardii</i> Makino
<i>S. pannosa</i>	<i>Rosa</i> sp. cult.
<i>E. polygoni</i>	<i>Schizopepon bryoniaefolius</i> Maxim.
<i>E. polygoni</i>	<i>Pilea mongolica</i> Wedd.
<i>M. russellii</i>	<i>Oxalis corniculata</i> L.
<i>S. humuli</i>	<i>Potentilla togasi</i> Ohwi
<i>S. humuli</i>	<i>Spiraea thunbergii</i> Sieb.
<i>M. alphitoides</i>	<i>Quercus serrata</i> Thunb.
<i>M. alphitoides</i>	<i>Quercus dentata</i> Thunb.
<i>M. alni</i>	<i>Castanea crenata</i> Sieb. et Zucc.
<i>M. mougeotii</i>	<i>Lycium chinense</i> Mill.
<i>M. sp.</i>	<i>Hydrangea macrophylla</i> Ser. var. <i>otaksa</i> Makino
<i>E. cichoracearum</i>	<i>Plantago asiatica</i> L.
<i>Saw. tulasnei</i>	<i>Acer crataegifolium</i> Sieb. et Zucc.
<i>Saw. sp.</i>	<i>Acer nipponicum</i> Hara
<i>E. heraclei</i>	<i>Dystaenia ibukiensis</i> Kitagawa
<i>E. cichoracearum</i>	<i>Solidago virga-aurea</i> L. subsp. <i>asiatica</i> Kitamura
<i>E. cichoracearum</i>	<i>Solidago gigantea</i> Ait. var. <i>leiophylla</i> Fern.
<i>E. cichoracearum</i>	<i>Rudbeckia laciniata</i> L.
<i>E. cichoracearum</i>	<i>Artemisia princeps</i> Pamp.
<i>M. grossulariae</i>	<i>Sambucus racemosa</i> L. subsp. <i>sieboldiana</i> Hara
<i>E. pisi</i>	<i>Pisum sativum</i> L.
<i>O. euonymi-japonicae</i>	<i>Euonymus japonicus</i> Thunb.
<i>M. alni</i>	<i>Benthamidia japonica</i> Hara
<i>U. australiana</i>	<i>Lagerstroemia indica</i> L.

(II) Fungi which developed hyphae but did not produce conidia

Fungus ^{a)}	Original host
<i>S. humuli</i>	<i>Geranium nepalense</i> Sweet var. <i>thunbergii</i> Kudo
<i>M. coryli</i>	<i>Corylus sieboldiana</i> Blume
<i>P. tridactyla</i>	<i>Prunus grayana</i> Maxim.
<i>E. galeopsidis</i>	<i>Chelonopsis moschata</i> Miq.
<i>E. polygoni</i>	<i>Fagopyrum esculentum</i> Moench.
<i>E. galeopsidis</i>	<i>Isodon trichocarpus</i> Kudo
<i>E. aquilegiae</i>	<i>Ranunculus quelpaertensis</i> Nakai
<i>E. pisi</i>	<i>Amphicarpa edgeworthii</i> Benth. var. <i>japonica</i> Oliv.
<i>M. bäumleri</i>	<i>Robinia pseudacacia</i> L.
<i>U. sp.</i>	<i>Fraxinus japonica</i> Blume
<i>U. salicis</i>	<i>Salix futura</i> Seemen
<i>E. cichoracearum</i>	<i>Adenophora triphylla</i> DC. var. <i>japonica</i> Hara
<i>E. cichoracearum</i>	<i>Cirsium nipponicum</i> Makino
<i>S. humuli</i>	<i>Agrimonia pilosa</i> Ledeb. var. <i>japonica</i> Nakai
<i>U. actinidiae</i>	<i>Actinidia polygama</i> Planch.

(III) Fungi which developed no hypha

Fungus ^{a)}	Original host
<i>E. polygoni</i>	<i>Polygonum aviculare</i> L.
<i>C. wrightii</i>	<i>Cyclobalanopsis myrsinaefolia</i> Oerst.
<i>M. viciae-unijugae</i>	<i>Vicia unijuga</i> A. Br.
<i>Ph. moricola</i>	<i>Morus bombycis</i> Koidzumi
<i>Ph. imperialis</i>	<i>Paulownia tomentosa</i> Steud.
<i>L. taurica</i>	<i>Capsicum annuum</i> L. var. <i>grossum</i> Sendt.

a) *E.*, *S.*, *C.*, *P.*, *M.*, *U.*, *Saw.*, *Ph.*, *L.*, and *O.* in this column are abbreviations of *Erysiphe*, *Sphaerotheca*, *Cystotheca*, *Podosphaera*, *Microsphaera*, *Uncinula*, *Sawadaea*, *Phyllactinia*, *Leveillula* and *Oidium*, respectively.

Table 2. Secondarily inoculated powdery mildew fungi and their development on some dicotyledons infected primarily with their own fungi

Preliminary infection		Secondary inoculation			
Host	Fungus ^{a)}	Fungus ^{a)}	Original host	Hyphal growth	Conidial formation
<i>Plantago asiatica</i> L.	<i>E. cichoracearum</i>	<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.	+	+
"	"	<i>E. cichoracearum</i>	<i>Physalis alkekengi</i> L. var. <i>francheti</i> Hort. form. <i>bunyardii</i> Makino	+	+
"	"	<i>E. cichoracearum</i>	<i>Artemisia japonica</i> Thunb.	+	+
"	"	<i>M. grossulariae</i>	<i>Sambucus racemosa</i> L. subsp. <i>sieboldiana</i> Hara	+	+
"	"	<i>M. alphitoides</i>	<i>Quercus serrata</i> Thunb.	+	—
"	"	<i>E. galeopsidis</i>	<i>Isodon trichocarpus</i> Kudo	+	—
"	"	<i>E. polygoni</i>	<i>Fagopyrum esculentum</i> Moench.	+	—
<i>Fagopyrum esculentum</i> Moench.	<i>E. polygoni</i>	<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.	—	—
"	"	<i>E. graminis</i>	<i>Hordeum vulgare</i> L.	—	—
<i>Rosa</i> sp. cult.	<i>S. pannosa</i>	<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.	+	—
"	"	<i>E. polygoni</i>	<i>Fagopyrum esculentum</i> Moench.	—	—
<i>Lycium chinense</i> Mill.	<i>M. mougeotii</i>	<i>E. polygoni</i>	<i>Fagopyrum esculentum</i> Moench.	+	+
"	"	<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.	+	+
"	"	<i>E. cichoracearum</i>	<i>Sonchus oleraceus</i> L.	+	+
"	"	<i>E. cichoracearum</i>	<i>Artemisia princeps</i> Pamp.	+	+
"	"	<i>E. graminis</i>	<i>Hordeum vulgare</i> L.	+	+
"	"	<i>E. graminis</i>	<i>Triticum sativum</i> L.	+	+
"	"	<i>S. humuli</i>	<i>Geranium nepalense</i> Sweet var. <i>thunbergii</i> Kudo	+	—
<i>Euonymus japonicus</i> Thunb.	<i>O. euonymi-japonicae</i>	<i>S. fuliginea</i>	<i>Cucumis sativus</i> L.	+	+
"	"	<i>E. polygoni</i>	<i>Fagopyrum esculentum</i> Moench.	—	—

a) *E.*, *S.*, *M.* and *O.* in this column are abbreviations of *Erysiphe*, *Sphaerotheca*, *Microsphaera* and *Oidium*, respectively.

Fig. 1. Colony development of secondarily inoculated powdery mildew fungi.

- A) Six day old colony of cucumber powdery mildew fungus (*Sphaerotheca fuliginea*) on barley leaf ($\times 30$).
 B) Six day old colony of barley powdery mildew fungus (*Erysiphe graminis hordei*) on *Lycium chinense* ($\times 70$).

fungus grows on a *Lycium* species (Fig. 1, B), the gap between the Gramineae and dicotyedons as host plants of the fungi appears not so wide as we formerly supposed.

2. Some observations on the colony development of the powdery mildew fungi from wheat, *Agropyron* and cucumber inoculated secondarily upon barley leaves

The secondary inoculation experiments were repeated most frequently with the fungi from wheat, *Agropyron ciliare* Franch. var. *minus* Ohwi and cucumber. Some observations on the colony development of these three fungi are described below.

(1) When the *Agropyron* fungus or cucumber fungus was inoculated secondarily onto barley leaves bearing young colonies of the barley fungus, the colonies of the secondary inoculum were found close to those of the barley fungus. Those colonies which began to grow at some distance from the colonies of the barley fungus ceased to grow further within one or two days after inoculation. When the cucumber fungus was inoculated secondarily, its colonies also were distributed near those of the barley fungus. Thus the two fungi developed well on the barley leaves, but they were different in the following point: when the surface of barley leaves reverse to that bearing the colonies of the barley fungus was inoculated with the two fungi, the *Agropyron* fungus developed colonies while no colony of the cucumber fungus was formed.

In order to know more exactly the relative position of the colonies of the secondarily inoculated fungus and those of the primarily inoculated barley fungus, the epidermal cells containing the first haustoria of the cucumber fungus or wheat fungus were checked with the epidermal cells containing the haustoria of the barley fungus. In an experiment more than 90% of the first haustoria of the cucumber fungus were formed in the epidermal cells harboring the haustoria of the barley fungus and in their neighboring epidermal cells. In a case of the secondary inoculation with the wheat fungus, the range in which the first haustoria grew was a little wider than in the case of the cucumber fungus: more than 80% of the first haustoria were formed in the epidermal cells containing the haustoria of the barley fungus, their neighboring epidermal cells and the next neighboring ones.

Regarding the formation of the second and subsequent haustoria of the secondarily inoculated fungus, the epidermal range where these haustoria were formed was a little wider than the range in which the first haustoria were formed. The haustoria of the secondarily inoculated fungus, like the

haustoria of the barley fungus, may render the surrounding barley epidermal cells susceptible to the secondary inoculum.

(2) For the purpose of knowing the effect of the age of the haustorium of the barley fungus upon the colony development of the secondarily inoculated fungus, the barley fungus colonies which passed 12, 14, 16, 18, 20, 22 and 24 hours after inoculation were rubbed off the barley leaf and then the leaf was inoculated with the wheat fungus. (The barley fungus begins to make the first haustorium from the conidial germ tube about 10 hours after inoculation and to extend hyphae about 10 hours later. Therefore the barley fungus colonies rubbed away within 24 hours after inoculation bears only very short hyphae, if any.) When the barley fungus colonies were rubbed away within 14 hours after inoculation, the wheat fungus failed to develop, while it developed when the rubbing-off was done 16 or more hours after inoculation. The first haustorium of the barley fungus died when the colony was rubbed away within 14 hours after inoculation, breaking the connection between the haustorium and germ tube, while the haustorium survived and grew when the colony detachment was done 16 or more hours after inoculation. The first haustorium found within 14 hours after inoculation may be too young to endure being torn off from the germ tube. It seems necessary for the growth of the wheat fungus upon the barley leaf that the haustorium of the barley fungus is alive.

As a subsequent experiment the cucumber fungus was inoculated onto the barley leaf from which 2, 4, 6, 8, 10 and 12 day old colonies of the preliminarily inoculated barley fungus had been rubbed off, and the colony development of the cucumber fungus was compared. The colony development of the cucumber fungus was the best when four day old colonies of the barley fungus were rubbed off. When the detached colonies were older, the colony development of the cucumber fungus was inferior. The colony development of the secondarily inoculated wheat fungus or *Agropyron* fungus on the barley leaf, from which six day old or older colonies of the barley fungus were preliminarily detached, was also not as good as when four day old colonies were detached. But the inferiority in the colony development of the wheat or *Agropyron* fungus was not so conspicuous as in the case of the cucumber fungus. This is another point indicating the difference in the behavior between the cucumber fungus and the wheat or *Agropyron* fungus growing on the barley leaf.

(3) Aizu No. 4, a barley variety, is less susceptible to Race 1 of the barley fungus than to Race 9. Leaves of the variety inoculated primarily with either one of the races were inoculated with the cucumber fungus five days after the primary inoculation. On the barley leaves inoculated primarily with Race 9 the cucumber fungus developed well and produced conidia on the fifth day after inoculation. On the other hand, in the case of the primary inoculation with Race 1, the cucumber fungus stopped growing by the fifth day after inoculation. Similar results were obtained when Aizu No. 4 was inoculated primarily with the above mentioned races of the barley fungus and then with the wheat fungus. So far as these experiments are concerned, the nutrient absorption by the haustorium of the secondarily inoculated fungus seems to be influenced by the degree of compatibility between the barley variety and the primarily inoculated race of the barley fungus. Successful inoculation may be a prerequisite to comparatively rich development of the secondary inoculum.

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和文摘要

うどんこ病罹病オオムギ葉上における
種々のうどんこ病菌の生育

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オオムギうどんこ病菌の若い菌叢を、水に濡らした脱脂綿でこすりとったオオムギの葉に、コムギ、カモジグサのうどんこ病菌、キュウリ、カラムシなど 49 種の双子葉植物のうどんこ病菌を接種して発育を調べた（菌叢をこすり取ると、菌糸からちぎれて吸器が表皮細胞内に残るが、この吸器は長期間生存する）。その結果 51 のうどんこ病菌の中で 30 は分生胞子を形成し、15 は分生胞子を形成しなかったが菌糸を伸ばした。ただし、これらの菌の発育は、こすりとったオオムギ菌の菌叢のすぐ近くだけでみられた。発育程度はうどんこ病菌により様々であったが、コムギ、カモジグサ、キュウリ、ハウズキなどの菌の発育は最もよく、菌糸の伸長、分生胞子の形成状況は、少なくとも接種後 6 日目までは、それぞれの本来の寄主植物上における場合に比べて劣らないと思われる程であった。オオムギ葉上で全然または殆んど発育しなかったものは、ミチヤナギ、シラカシ、キリなどの 6 菌だけである。自然に発生しているうどんこ病菌の菌叢をこすりとったオオバコ、クコ、マサキ、バラ、ソバの葉に、種々のうどんこ病菌を接種した場合にも、発育程度は様々であるが、発育することが多かった。たとえば、オオバコの葉にキュウリ、ハウズキ、ニワトコの菌が、クコの葉にキュウリ、ソバ、オオムギの菌が発育して分生胞子を形成した。しかしソバの葉にはキュウリの菌もオオムギの菌も発育しなかった。