侵入阻害剤処理イネいもち病菌およびメラニン欠損変異株のメラニン前駆体による付着器侵入能の回復

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Original Article

Restoration of Appressorial Penetration Ability by Melanin Precursors in *Pyricularia oryzae* Treated with Anti-penetrants and in Melanin-Deficient Mutants

Tsuneaki CHIDA and Hugh D. SISLER*

Kureha Chemical Industry Co., Ltd., Nishiki Research Laboratories, Nishiki-machi, Iwaki 974, Japan
**Department of Botany, University of Maryland, College Park, MD 20742 U.S.A.*

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The capacity of *Pyricularia oryzae* appressoria to penetrate onion epidermal walls was lost in an albino mutant or in wild type strains treated with melanin biosynthesis inhibitors, cerulenin, fthalide and tricyclazole. Melanization and penetration ability of cerulenin treated wild type or untreated albino mutant appressoria were restored with scytalone or 1,8-dihydroxynaphthalene (1,8-DHN). Fthalide or tricyclazole nullified the restoration by scytalone, but not by 1,8-DHN. Penetration ability of wild type appressoria treated with 0.1 μg/ml of fthalide or tricyclazole was restored by 1,8-DHN, but was not well restored in appressoria treated with 1 or 10 μg/ml of these inhibitors unless cerulenin was also present. This investigation indicates that blocking of the melanin biosynthesis pathway by fthalide or tricyclazole leads to two mechanisms of antipenetrant action (1) interference with melanin synthesis (2) accumulation of inhibitory metabolites. The latter mechanism, which may operate concomitantly with former, is nullified in the presence of cerulenin.

INTRODUCTION

Among the compounds known as non-fungicidal rice blast control agents are PCBA (pentachlorobenzyl alcohol), fthalide (4,5,6,7-tetrachlorophthalide), tricyclazole (5-methyl-[1,2,4]-triazolo-[3,4-*b*]-benzothiazole), pyroquilon (1,2,5,6-tetrahydropyrrolo[3,2,1-*i*, *j*]quinolin-4-one) and chlobenthiazone (4-chloro-3-methylbenzothiazol-2(3*H*)-one).[1-4] These compounds are also classified as both antipenetrants and melanin biosynthesis inhibitors (MBI). Thus far, their practical value is limited to the control of rice blast disease caused by the fungus, *Pyricularia oryzae*.

These compounds have little or no effect on hyphal growth of *P. oryzae in vitro*; however, they specifically inhibit the infection process of the pathogen. Antipenetrant activities of PCBA, fthalide and tricyclazole toward *P. oryzae* have been evaluated on both plant epidermal and cellulosic membrane barriers.[1,2,5-7]

P. oryzae as well as various ascomycetous and imperfect fungi form black melanin derived from a pentaketide pathway.[8,9] Mycelial pigmentation by *P. oryzae* is markedly inhibited by tricyclazole concentrations which effectively inhibit appressorial penetration of plant epidermal barriers.[1,2,8]

It was proposed that tricyclazole blocks two reduction steps of the fungal melanin biosynthesis pathway; the conversion of 1,3,6,8-tetrahydroxynaphthalene (1, 3, 6, 8-THN) to scytalone and 1,3,8-trihydroxynaphthalene (1, 3,8-THN) to vermelone,[8,10] and thus causes abnormal accumulation of 2-hydroxyjuglone (2-HJ), flaviolin and other related intermediates and metabolites. An inhibitory effect of tricyclazole was also demonstrated on appressorial

melanization in penetration tests with *P. oryzae*,[11] *Colletotrichum lindemuthianum*[12] and *C. lagenarium*.[13] Inhibitory effects of PCBA, fthalide and pyroquilon on appressorial melanization by *P. oryzae* have also been observed.[1,2] In *C. lagenarium*, albino isolates (melanin deficient mutants)[14] and the cerulenin treated wild type fungus[15] form hyaline appressoria. Cerulenin inhibits condensation of acetyl CoA and malonyl CoA and thus blocks biosynthesis of fatty acids[16] and presumably also polyketide melanin biosynthesis by the same mechanism. Appressorial penetration by the albino mutants[14] or the cerulenin treated wild type fungus was quite poor.[15] Most of the appressoria germinated laterally instead of penetrating the barrier like untreated wild type appressoria. Tricyclazole treatment resulted in a high frequency of lateral germination instead of barrier penetration in both *C. lagenarium*[13] and *C. lindemuthianum*.[12] In albino mutants of *C. lagenarium*, melanization and appressorial penetration ability could be restored by adding the melanin biosynthesis intermediate, scytalone, and in the tricyclazole treated wild type, melanization and penetration ability could be restored by adding the melanin biosynthesis intermediate, vermelone but not scytalone.[13] Thus, the action of melanin biosynthesis inhibitors in *C. lagenarium* leads to the lack of a rigid cell wall due to the deficiency of proper melanin intermediates needed for wall melanization.[13]

On the other hand, the penetration capacity of melanin biosynthesis inhibitor treated appressoria of *P. oryzae* was only partially restored by adding 1,8-dihydroxynaphthalene (1,8-DHN)[11,17,18] or vermelone.[11] It was suggested that viability of appressoria was damaged in the presence of the inhibitors because of accumulation of cytotoxic intermediates and/or metabolites following the blockade of the melanin biosynthetic pathway.[2,11]

The purpose of this study was to determine the relation between inhibition of the melanin biosynthesis pathway and restoration of appressorial penetration ability with intermediates of this pathway, and to examine the proposed action of fthalide and tricyclazole.

MATERIALS AND METHODS

1. *Chemicals*

Fthalide and tricyclazole were supplied by Kureha Chemical Industry Co., Ltd., Tokyo, Japan and Eli Lilly Co., Greenfield, Indiana, U.S.A. respectively. Cerulenin was purchased from Sigma Chemical Co., St. Louis, MO. Scytalone, vermelone and 1,8-DHN were prepared according to Tokousbalides and Sisler.[10] Chemicals were added as acetonic solution; final organic solvent concentrations did not exceed 1.5%. The same amount of solvent was added to untreated samples.

2. *Cultural Methods*

The test fungi used in this study were *Pyricularia oryzae* P-2 (wild type), buff mutant P-2 m-1 derived from P-2,[8] *P. oryzae* strain O-42 (wild type) and albino strain CP 412 derived from strain O-42. The latter two strains were kindly provided by Dr. Barbara Valent and Dr. Forrest Chumley, Du Pont Co. These fungal strains were maintained on rice bran medium.[8] This medium was also used for spore production.

3. *Penetration Tests*

Yellow onion epidermal strips were used to study effects of melanin biosynthesis inhibitors on appressorial penetration by *P. oryzae*. Onion bulb scales were washed with chloroform to remove wax and thoroughly rinsed with tap water and distilled water. Then the inner epidermis was peeled off and cut into 0.8×0.8 cm^2 sections. These sections were floated on 4 ml of distilled water or chemical solution in 60 mm petri dishes. Approximately 500 conidia in about 10 μl distilled water or chemical solution were placed on the strips and these were incubated at 26–27°C. When cerulenin or scytalone were used, they were added to the spore suspension and floating solution at the time of inoculation. In studies using vermelone or 1,8-DHN, solutions of these chemicals were used to replace both the solution of the spore droplet on the epidermal surface and the floating solution 4 hr after the spore droplet had been applied. Solutions were removed 40 hr after inoculation and 30% methanol was applied to prevent further penetration during

Table 1 Effect of fthalide and tricyclazole on appressorial penetration of onion epidermis by *P. oryzae* O-42 (wild type) or CP 412 (albino strain) treated with scytalone.

Strain	Scytalone (μg/ml)	Penetration ratio and percentage[a]						
		Fthalide (μg/ml)				Tricyclazole (μg/ml)		
		0	0.01	0.1	1.0	0.01	0.1	1.0
O-42	0	267/306 (87)	265/316 (84)	6/333 (2)	1/327 (0)	67/327 (20)	1/322 (0)	0/312 (0)
CP 412	0	0/309 (0)	—[b]	—	—	—	—	—
	20	186/312 (60)	2/319 (1)	0/311 (0)	0/310 (0)	0/345 (0)	1/320 (0)	0/313 (0)

[a] Penetration ratio is number of appressorial penetrations / number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.
[b] Not tested.

observation. Appressorial penetration was evaluated by observing with a light microscope whether or not hyphae emerging from the appressoria had passed through the epidermal wall.

RESULTS

1. *Appressoria of P. oryzae CP 412 Albino Mutant*

An albino mutant of *P. oryzae*, CP 412, which was derived from wild type strain, O-42, formed white mycelia during vegetative growth on agar medium and hyaline appressoria on epidermal barriers. The appressoria of this mutant did not penetrate onion epidermal walls (Table 1). Penetration ability was restored in these appressoria to a level of 60% by 20 μg/ml scytalone. This penetration rate was 69% of that of untreated O-42 wild type appressoria. Penetration ability and associated melanization restored by scytalone in albino strain CP 412 was nullified by fthalide and tricyclazole even at a concentration as low as 0.01 μg/ml. On the other hand, penetration by wild type O-42 appressoria was not inhibited by 0.01 μg/ml fthalide but was inhibited 77% by 0.01 μg/ml tricyclazole. Penetration was almost totally prevented by concentrations of 0.1 or 1.0 μg/ml of both inhibitors (Table 1).

When 1,8-DHN was added to the spore droplets of CP 412, the fungus formed melanized appressoria and 27% of these penetrated onion epidermal walls. In the presence of 0.1, 1.0 and 10 μg/ml of tricyclazole, melanization was also restored by 1,8-DHN and penetration was increased from 0 to 15–18% (Table 2).

Table 2 Effect of tricyclazole on appressorial penetration of onion epidermis by *P. oryzae* CP 412 (albino strain) treated with 1,8-DHN.[a]

Penetration ratio and percentage[b]			
Tricyclazole (μg/ml)			
0	0.1	1.0	10
91/337[c] (27)	60/338 (18)	49/331 (15)	52/304 (17)

[a] 1,8-DHN (final concentration, 1.25 μg/ml) was added to spore suspension 4 hr after inoculation.
[b] Penetration ratio is number of appressorial penetrations/number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.
[c] Penetration ratio of control (CP 412 without 1,8-DHN) was 0/308.

2. *Effect of Cerulenin on Appressorial Melanization and Penetration by Wild Type P. oryzae P-2*

Recently, Kubo *et al.*[15] demonstrated that cerulenin interferes with appressorial melanization by *C. lagenarium*. Cerulenin treated spores of this fungus formed hyaline appressoria; consequently, these melanin deficient appressoria germinated laterally like those of albino mutants of the fungus. Our studies of cerulenin in *P. oryzae* P-2 showed that appressorial

Table 3 Effect of fthalide and tricyclazole on appressorial penetration of onion epidermis by cerulenin treated *P. oryzae* P-2 in the presence of scytalone.

Cerulenin (μg/ml)	Scytalone (μg/ml)	Penetration ratio and percentage[a)]									
		Fthalide (μg/ml)								Tricyclazole (μg/ml)	
		0		0.1		1.0		10		0.1	
0	0	281/306	92	196/336	58	0/316	0	0/307	0	0/330	0
0	20	284/326	87	19/338	6	0/377	0	0/324	0	0/362	0
1.25	0	0/312	0	0/312	0	0/322	0	0/324	0	0/359	0
1.25	20	256/319	80	0/325	0	0/318	0	0/319	0	0/321	0

a) Penetration ratio is number of appressorial penetrations / number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.

Table 4 Restoration of penetration ability by vermelone in fthalide treated appressoria of *P. oryzae* P-2 in the presence or absence of cerulenin.

Cerulenin (μg/ml)	Vermelone[a)] (μg/ml)	Penetration ratio and percentage[b)]							
		Fthalide (μg/ml)							
		0		0.1		1.0		10	
0	0	224/320	70	1/324	0	0/307	0	0/314	0
0	1.25	69/346	20	50/305	16	7/305	2	1/325	0
1.25	0	0/333	0	0/302	0	0/301	0	0/314	0
1.25	1.25	126/331	38	67/322	21	22/352	6	19/359	5

a) Vermelone was added to spore suspension 4 hr after inoculation.

b) Penetration ratio is number of appressorial penetrations / number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.

melanization and penetration were completely inhibited by cerulenin at a concentration of 1.25 μg/ml (Table 3). Cerulenin treated appressoria resembled those of the albino mutant CP 412 in regard to the lack of pigmentation and inability to penetrate epidermal barriers. Lateral germination of appressoria was seldom observed in either the cerulenin treated wild type P-2 strain or the untreated albino isolate CP 412. In the presence of 20 μg/ml of scytalone, cerulenin treated *P. oryzae* P-2 produced normal gray-black melanized appressoria which penetrated at a rate of 80%. Both fthalide and tricyclazole at a concentration of 0.1 μg/ml or greater, markedly or completely inhibited the scytalone restored penetration of cerulenin treated P-2 appressoria. Moreover, these compounds completely inhibited the conversion of scytalone to melanin in these appressoria.

3. Restoration of Penetration by Vermelone in Fthalide Treated Appressoria of P. oryzae P-2

Kubo *et al.*[13] and Yamaguchi *et al.*[11] reported that vermelone restored penetration ability of MBI treated appressoria of *C. lagenarium* and *P. oryzae*. In the present study, 1.25 μg/ml of vermelone was quite inhibitory to penetration by untreated P-2 appressoria (Table 4); however, it increased penetration from less than 1% to 16% in P-2 appressoria treated with 0.1 μg/ml fthalide. At higher concentrations of fthalide, restoration of penetration ability by vermelone was poor or absent. Restoration of penetration ability by vermelone at all concentrations of fthalide tested was improved by cerulenin.

4. Effect of Fthalide and Tricyclazole on Appressorial Penetration by P. oryzae P-2 Treated with 1,8-DHN

Although 1.25 μg/ml of 1,8-DHN reduced

Table 5 Restoration of penetration ability by 1,8-DHN in fthalide or tricyclazole treated appressoria of *P. oryzae* P-2 in the presence or absence of cerulenin.

Cerulenin (μg/ml)	1,8-DHN[a] (μg/ml)	Penetration ratio and percentage[b]					
		Fthalide (μg/ml)				Tricyclazole (μg/ml)	
		0[c]	0.1[c]	1.0[c]	10[d]	0.1[c]	1.0[d]
0	0	686/937 (73)	8/935 (1)	0/955 (0)	0/629 (0)	1/966 (0)	0/620 (0)
0	1.25	433/988 (44)	377/989 (38)	7/978 (1)	0/624 (0)	323/953 (34)	15/633 (2)
1.25	0	2/930 (0)	2/962 (0)	0/950 (0)	0/624 (0)	0/930 (0)	0/630 (0)
1.25	1.25	537/994 (54)	273/955 (29)	259/932 (28)	134/635 (21)	338/984 (34)	96/624 (15)

a) 1,8-DHN was added to spore suspension 4 hr after inoculation.
b) Penetration ratio is number of appressorial penetrations / number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.
c) Sum of three experiments.
d) Sum of two experiments.

Table 6 Restoration of penetration ability of appressoria of *P. oryzae* P-2 m-1 (buff strain) by 1,8-DHN in the presence or absence of fthalide or tricyclazole.

Cerulenin (μg/ml)	1,8-DHN[a] (μg/ml)	Penetration ratio and percentage[b,c]					
		Fthalide (μg/ml)				Tricyclazole (μg/ml)	
		0	0.1	1.0	10	0.1	1.0
0	0	1/637 (0)	—[d]	—	—	—	—
0	1.25	217/644 (34)	14/671 (2)	7/625 (1)	4/626 (1)	56/625 (9)	43/679 (6)
1.25	0	0/623 (0)	—	—	—	—	—
1.25	1.25	259/648 (40)	181/653 (28)	156/637 (24)	187/624 (30)	212/679 (31)	223/638 (35)

a) 1,8-DHN was added to spore suspension 4 hr after inoculation.
b) Penetration ratio is number of appressorial penetrations / number of appressoria observed 40 hr after inoculation. Penetration percentage is penetration ratio × 100.
c) Sum of two experiments.
d) Not tested.

penetration by wild type P-2 appressoria from 73 to 44%, this concentration of 1,8-DHN restored appreciable penetration by P-2 appressoria treated with 0.1 μg/ml of fthalide or tricyclazole (Table 5). However, restoration of penetration ability by 1,8-DHN was poor or absent in the presence of 1 or 10 μg/ml of fthalide or 1 μg/ml of tricyclazole unless cerulenin was also present. Appressoria developed gray-black melanin mixed with yellowish-brown pigments when 1,8-DHN was added to fthalide or tricyclazole treated appressoria. When cerulenin was also present, only gray-black pigmentation developed.

5. *Restoration of Penetration by Appressoria of P. oryzae P-2 m-1 Buff Mutant with 1,8-DHN*

Appressoria of P-2 m-1 rarely penetrate epidermal barriers. In the present study it was

shown that 1,8-DHN increased the rate of penetration of P-2 m-1 appressoria from less than 1% to 34% (Table 6). This restoration of penetration ability by 1,8-DHN was largely nullified when 0.1, 1.0 or 10 μg/ml fthalide or 0.1 or 1.0 μg/ml tricyclazole were also present. These inhibitory effects of fthalide or tricyclazole on restoration of penetration ability by 1,8-DHN were almost completely abolished by 1.25 μg/ml cerulenin (Table 6).

DISCUSSION

This study indicates that blocking of the biosynthetic pathway to melanin by fthalide or tricyclazole can lead to two different mechanisms of antipenetrant action in appressoria of *P. oryzae*. The first mechanism is based on interference with melanin biosynthesis. The second, which may in some cases operate concurrently with the first, is evidently due to the accumulation of inhibitory pentaketide metabolites produced by higher concentrations of MBI such as 1 to 10 μg/ml of fthalide or tricyclazole. The latter mechanism is the antipenetrant mechanism that has been suggested by Yamaguchi *et al.*[2] for MBI of the tricyclazole mechanism group.

Since albino mutant AL-3 of *Pyricularia grisea*[19] as well as albino mutant CP 412 and cerulenin treated wild type P-2 *P. oryzae* are blocked in melanin biosynthesis prior to formation of the first cyclized metabolite, the accumulation of inhibitory intermediates is blocked and, therefore, only the first mechanism is presumed to operate in these appressoria. Moreover, the first mechanism apparently accounts almost exclusively for penetration failure of wild type P-2 appressoria treated with 0.1 μg/ml fthalide or tricyclazole or of untreated appressoria of the buff mutant P-2 m-1. The degree of success achieved in restoring penetration ability by 1,8-DHN in these appressoria indicate that accumulation of inhibitory metabolites such as flaviolin or 2-HJ is too low to have much effect on penetration. Woloshuk *et al.*[8] reported that the quantities of polyketide metabolites accumulating in cultures of P-2 treated with 0.1 μg/ml of tricyclazole resembled those accumulating in untreated P-2 m-1 cultures.

Evidence that a second mechanism of antipenetrant action is involved at higher concentrations of fthalide and tricyclazole is the poor or unsuccessful restoration of penetration ability by wild type P-2 appressoria or by buff P-2 m-1 appressoria with 1,8-DHN unless cerulenin is present. As mentioned previously, cerulenin prevents the accumulation of toxic polyketide metabolites by blocking a very early stage of the melanin biosynthetic pathway.

It remains unclear how inhibition by higher concentrations of fthalide or tricyclazole might result in levels of polyketide metabolites that prevent appressorial penetration. A striking increase in flaviolin accumulation was observed as the concentration of tricyclazole was increased in *Verticillium dahliae*[10] and *P. oryzae* cultures.[8] The increased accumulation of flaviolin was attributed, at least in part, to greater inhibition of the 1, 3, 6, 8-THN to scytalone conversion. However, since 2-HJ levels were not reduced in the aforementioned studies as flaviolin levels increased as would be expected if 2-HJ had been derived only from 1,3,8-THN, it seems likely that 2-HJ might also be formed by an alternate pathway. Such a pathway has not been demonstrated in *P. oryzae,* but Wheeler and Stipanovic[20] have recently demonstrated an alternate pathway to 2-HJ in *Wangiella dermatitidis* through flaviolin and 5-hydroxyscytalone. Evidence already exists that MBI such as tricyclazole block reactions in shunt pathways that may be involved in detoxication of products such as 2-HJ and flaviolin.[8,10,20] It appears more likely that an action of fthalide and tricyclazole in these shunt pathways rather than in the main melanin biosynthetic pathway lead to the second mechanism of antipenetrant action.

Inoue *et al.*[21] reported that appressoria of *P. oryzae* exposed to relatively high concentrations of fthalide had melanized but had failed to penetrate when observed after 4 days. In this case, penetration may have been prevented by the accumulation of toxic metabolites (second mechanism) while a slow leakage through the fthalide blocks in the main pathway ultimately allowed production of visible quantities of melanin. We often observed in the present study that 1,8-DHN restored melanization but not penetration when high

concentrations of fthalide or tricyclazole were used. Even in P-2 appressoria treated with a low concentration of fthalide or tricyclazole (0.1 μg/ml) and in untreated albino, P-2 m-1 or cerulenin exposed P-2 appressoria, the restoration of appressorial penetration ability by 1,8-DHN was incomplete. This limited restoration is believed to be due, at least in part, to the toxicity of 1,8-DHN because this metabolite reduces the penetration rate of untreated P-2 appressoria at a concentration as low as 0.62 μg/ml.

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要　　約

侵入阻害剤処理イネいもち病菌およびメラニン欠損変異株のメラニン前駆体による付着器侵入能の回復

千田常明，Hugh D. Sisler

イネいもち病菌の付着器によるタマネギ表皮細胞への侵入能は，アルビノ株や，メラニン生合成阻害剤であるセルレニン，フサライド，トリシクラゾールで処理された野生株では欠損していた．シタロンおよび1,8-ジヒドロキシナフタリン (1,8-DHN) の添加によって，アルビノ株およびセルレニン処理された野生株のメラニン生成と侵入能は回復した．シタロンによる回復効果はフサライドあるいはトリシクラゾールによって打ち消されたが，1,8-DHN による回復効果は妨げられなかった．フサライドあるいはトリシクラゾール 0.1 μg/ml で処理された野生株の侵入能は，1,8-DHN の添加によって回復したが，1,10 μg/ml 処理区ではセルレニンを添加しなければ，1,8-DHN による回復効果は認められなかった．以上の結果から，フサライド，トリシクラゾールによるメラニン生合成経路の阻害は二つの侵入阻害作用，(1) メラニン合成系の阻害，(2) 阻害性物質の蓄積，をもたらすことが示唆される．後者の作用は前者に随伴して起こると推察されるが，その効果はセルレニンによって打ち消された．