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Probenazole-Induced Resistance of Lily Leaves against *Botrytis elliptica*

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ABSTRACT

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The protection effect of probenazole on lily plants against *Botrytis elliptica* was examined in this study. Application of probenazole in the rhizosphere of lily plants at concentrations of 4, 40 or 400 mg per kg of soil at day 7 before inoculation of *B. elliptica* was able to reduce the number of lesions on plants. However, the treatment did not influence the size of lesions. Furthermore, applying this chemical three times at the concentration of 40 mg per kg of soil at days 7, 4, and 1 pre-inoculation more obviously reduced the number of lesions than treating one time with probenazole. Probenazole, at the concentration of 40 mg per kg of soil, protected lily plants from the infection of *B. elliptica* without retarding the growth of plants. *In vitro* assays revealed that probenazole at the concentration of 2 or 20 μg/ml did not inhibit spore germination in distilled water and mycelial growth of *B. elliptica* on V-8 agar. Spore germination and mycelial growth became inhibited only if the concentration of probenazole was raised to 200 μg/ml. The protection of lily plants by probenazole may be attributed to the resistance of host plants induced by the chemical. However, the level of salicylic acid in the lily leaves did not significantly increase after the treatment of probenazole.

Key words: lily, Botrytis leaf blight, gray mold, oryzemate, salicylic acid, induced disease resistance.

INTRODUCTION

Blight or gray mold incited by *Botrytis elliptica* (Berk.) Cook is a serious disease of lily crops. The diseased lily plants have generally reduced floral quality and production (6,23). Frequent fungicide applications are necessary to control the disease since the infection by *B. elliptica* may occur within 24 hr, particularly in predisposed conditions (3). However, resistance of this pathogen to fungicides is common in many parts of the world (14). Therefore, we considered alternative control measures, such as chemical-induced disease resistance (9), to protect lily plants against *B. elliptica*. Induced disease resistance is a plant defense mechanism in response to pathogen attack or induced by rhizobacteria (2,27). Some chemicals also had ability in inducing plant resistance to pathogen attack (9). Our previous study have demonstrated that resistance of lily to *Botrytis elliptica* could be induced by salicylic acid (SA) (1,7).

Probenazole (oryzemate, 3-allyloxy-1,2-benzisothiazole-1,1-dioxide, Meiji Seika Kaish, Ltd.) has effectively controlled rice blast and bacterial leaf blight for over two decades (24,25). The effectiveness of probenazole in controlling blast disease is related to the induction of plant defense (8,10,12,15,19,20,21,22,26). Recent studies (16) have demonstrated that probenazole treatment enhances the resistance of tobacco to tobacco mosaic virus (TMV) and the production of pathogenesis-related proteins of tobacco and Arabidopsis, implying that probenazole- induced disease resistance may be common among plants.

In the light of above reports, we have treated lily plants with probenazole to investigate whether this chemical could prevent the infection by *B. elliptica*. By examining the effect of probenazole on the germination and growth of *B. elliptica*, we presumed that this chemical could induce the disease resistance in lily plants. We have also measured the amount of

SA within lily leaf tissues after treatment of probenazole to explore the pathways of induced resistance in lily.

MATERIALS AND METHODS

Lily planting and fungal culture

Oriental lily hybrid "Star Gazer" was planted in a pot with 1:3 perlite-culture soil (Bas Van Buuren) in a semi-opened canopy. Experiments were performed at room temperature (20 C). The lily plants used in a small-scale field experiment were planted in soil. The seedlings of Easter lily hybrid " Risan No. 1" and the tissue culture seedlings of Oriental lily hybrid " Casablanca" were also used in some tests. The cultural conditions were similar to that for Oriental lily hybrid "Star Gazer". *B. elliptica* B061 was donated by Ting-Fang Hsieh in Taiwan Agricultural Research Institute and cultured on V-8 agar slants (One liter medium contained V-8 juice, 200 ml; $CaCO_3$, 3 g; and 1.8% agar) at 20 C under near UV light (7 cm below the light tube, light intensity ca. 200 lux) for 5 to 7 days. Spore suspension was prepared by gentle vortex of the culture with 0.1% Tween 20. Finally, the spore concentration was calculated with hemacytometer and adjusted to 5×10^4 spores/ml for plant inoculation.

Inoculation of probenazole-treated lily with *B. elliptica*

Probenazole (6% active ingredient [*a. i.*] in granule form, Taiwan San Lee Chemical LTD.) was applied at concentrations of 4, 40, or 400 mg *a. i.* per kg of soil. By estimation, a lily plant was treated with 2, 20, or 200 mg *a. i.* of probenazole. Granules were placed directly in the rhizosphere of lily plants (40 day-old) at day 7 before inoculation of the pathogen. In the same trail, 40 mg *a. i.* per kg of soil was applied three times at days 7, 4, and 1 before inoculating the pathogen. For inoculation, lower surface of lily leaves was sprayed with spore suspension of *B. elliptica* and the plants were incubated in moisture chamber at 20 C. The number and size of lesions were recorded three days after inoculation. In each treatment, five lily plants and five full-spanded and younger leaves of each plant were used. Deionized water instead of probenazole solution was used as a control treatment.

Control of Botrytis leaf blight by probenazole in the field

Probenazole was applied in the rhizosphere of 14-day old lily plants at a concentration of 40 mg *a. i.* per kg of soil in the form of granule (6% *a. i.*) or solution. Lily plants treated with water were used as controls. Thirty lily plants were used in each treatment. The treatment was applied at 7-day intervals for five times. The effect of probenazole on the growth of lily plants, including plant height, number of leaf, number of flower, length and width of leaf was recorded 7 days after final treatment. Meanwhile, the natural infection of *B. elliptica* was examined.

In another trial, lily plants were treated with probenazole at a concentration of 40 mg *a. i.* per kg of soil in the form of granule (6% *a. i.*) or solution for eight times at 7-day intervals. Thirty plants were used for each treatment. Spore suspension of *B. elliptica* was sprayed on the abaxial surface of leaves 7 days after final treatment. Five leaves of each plants were inoculated. Lesions on the leaves were examined five days after inoculation.

Determination of the amount of SA in lily leaves

Lily plants were treated with probenazole at the concentration of 40 mg *a. i.* per kg of soil. The leaves were excised and stored at -80 C at days 7, 4, and 1 prior to the extraction of SA. Four plants were used for each treatment. Total SA in three leaf tissues of each lily plant was then pool-extracted according to a method previously described (1). Next, the amount of SA was determined with a fluorescence spectrophotometer (F-4500, Hitachi). Regression analysis was performed to calculate the concentration of SA per gram of leaf.

Effect of probenazole treatment on spore germination and mycelial growth of *B. elliptica*

Spore suspension of *B. elliptica* (10^5 conidia/ml in 0.2% Tween 20) was mixed with an equal amount of probenazole solution of 4, 40, or 400 μg *a. i.*/ml. Two hundred microliters of spore suspension was applied onto a microscope slide; the slide was kept in a moisture chamber for 16 hr at 20 C. Germination of spores was examined under a microscope and inhibition rates of germination were calculated.

The extent to which probenazole influenced the growth of *B. elliptica* was observed by mixing various amounts of probenazole with the V-8 agar media. Mycelial discs from 3-day culture were then placed at the center of agar plates containing 2, 20, or 200 μg *a. i.*/ml of probenazole. Finally, the diameter of colony was recorded after 3-day incubation at 20 C in darkness.

RESULTS

Effect of probenazole treatment on the protection againt *Botrytis elliptica*

Probenazole at various concentrations, 4, 40 or 400 mg *a. i.* per kg of soil, effectively protected lily plants from *B. elliptica* infection if the chemical was applied at day 7 before inoculation. This protection was reflected primarily in the number of lesions in all treatments. Interestingly, the size of lesion was not significantly affected unless probenazole was applied at a concentration of 400 mg *a. i.* per kg of soil. When probenazole (40 mg *a. i.* per kg of soil) was applied on three consecutive occasions at days 7, 4, and 1 before inoculation, lesion number was reduced more than by a single treatment. Our results also indicated that these treatments did not profoundly affect the size of lesion (Table 1).

Table 1. Effect of probenazole treatment on control of Botrytis leaf blight of Oriental lily hybrid "Star Gazer" [1]

Application of Probenazole[2]		Number of lesion per leaf	Size of lesion (mm/dm)
mg *a.i.*/kg soil	Times and day (s)		
400	One, day 7 before inoculation	30.67 b[3]	3.4 *b*
40	One, day 7 before inoculation	34.22 b	4.3 *a*
4	One, day 7 before inoculation	34.22 b	4.8 a
40	Three, days 7,4,1 before inoculation	19.22 c	3.9 *ab*
0		43.56 a	5.7 *a*

1. Lily plants of 40 day-old were treated with probenazole and inoculated with 5×10^4 conidia/ml of *B. elliptica* at the abaxial surface of leaf. Five full-expanded and younger leaves of each plant were inoculated. Number and size of lesions were recorded at the 3rd day after inoculation. Five plants were used for each treatment.
2. Probenazole granules were applied to the rhizosphere of lily plants.
3. Data in the same column followed by the same letter are not significantly different (P=0.05) according to Duncan's multiple range test.

Contrary to the above findings, similar treatments did not apparently protect the seedlings of Easter lily hybrid "Risan No. 1" and tissue culture seedlings of Oriental lily hybrid "Casablanca" from the disease.

In addition, the field experiment confirmed the protection effect of probenazole when it was applied eight times at 7-day intervals. Regardless of whether in granule or solution form, probenazole again reduced the number of lesions, but did not affect the size of lesion. Comparatively, better protection was observed if a granule rather than a solution form of probenazole was used (Table 2).

Table 2. Field control of Botrytis leaf blight of lily by the treatment of probenazole [1]

Treatment of probenazole [2]	Number of lesion per leaf	Size of lesion (mm/dm)
Granule	15.34 c[3]	1.21 a
Solution	22.85 b	1.21 a
Control	33.82 a	1.44 a

1. Oriental lily hybrid "Star Gazer" of 14 day-old was treated with probenazole and then inoculated with 5×10^4 conidia/ml of *B. elliptica.* Spore suspension was sprayed on the abaxial surface of five full-expanded leaves of each plant. Number and size of the lesions were recorded five days after inoculation. Thirty plants were used for each treatment.
2. Probenazole at the concentration of 40 mg active ingredient per kg of soil in different forms was treated eight times at 7-day intervals.
3. Data in the same column followed by the same letter are not significantly different (P=0.05) according to Duncan's multiple range test.

Effect of probenazole treatment on the growth of lily plants

Lily plants were treated five times with probenazole at a concentration of 40 mg *a. i.* per kg of soil at 7-day intervals. The effect of treatment on plant growth was observed 7 days after the final treatment. Results indicated that probenazole did not affect the height of plant, length and width of leaf, number of leaf and number of flower. Furthermore, the treatment protected the host plants against Botrytis leaf blight. The percentage of natural infection by *B. elliptica* was significantly lower than that of untreated plants (Table 3).

Effect of probenazole treatment on the concentration of SA in leaf tissue

SA was extracted from the leaves of plants which were treated with probenazole at days 7, 4, and 1 before extraction. The amount of SA was estimated to be 20.38, 20.04, and 18.21 μg per gram of leaf (leaf fresh weight), respectively, and slightly exceeded those of the control plant (15.79 μg per gram of leaf). Three consecutive treatments at days 7, 4, and 1 did not cause significant accumulation of SA; the amount of SA was 19.16 μg per gram of leaf (Table 4).

Table 3. Effect of probenazole on the growth of Oriental lily hybrid "Star Gazer" [1]

Characteristic	Control	Form of probenazole [2] Granule	Solution
Height of plant (cm)	40.57	43.10	40.75
Number of flower / plant	0.59	0.97	0.48
Number of leaf / plant	23.55	24.24	21.89
Length of leaf (cm)	6.92	7.12	7.16
Width of leaf (cm)	2.72	2.84	3.09
Infected leaves / plant (%)[3]	50.00 a	26.20 b	27.80 b

1. Lily plants of 14 day-old were treated with probenazole at the concentration of 40 mg active ingredient per kg of soil in different forms. Thirty plants were used for each treatment.
2. Probenazole at the concentration of 40 mg active ingredient per kg of soil was treated five times at 7-day intervals.
3. Natural infection by *B. elliptica*. The percentage of infected leaves in upper ten leaves per plant were recorded. Data followed by the same letter are not significantly different (P=0.05) according to Duncan's multiple range test.

Table 4. Total salicylic acid concentration in leaf tissues of Oriental lily hybrid "Star Gazer" after treatment of probenazole [1]

Application of probenazole [2] (day (s) before extraction)	Salicylic acid concentration (μg/g leaf)
1	20.38 a[3]
4	20.04 ab
7	18.21 b
1, 4, 7	19.16 b
Control	15.79 b

1. Salicylic acid was extracted from three combined leaves of each plant. Four plants were used for each treatment.
2. The rhizosphere of lily plants was treated with probenazole at the concentration of 40 mg active ingredient per kg of soil prior to extraction of salicylic acid. Control was untreated.
3. Data followed by the same letter are not significantly different (P=0.05) according to Duncan's multiple range test.

Effect of probenazole on the inhibition of spore germination and mycelial growth of *B. elliptica*

At lower concentrations of probenazole (2 and 20 μg *a. i.*/ml), spore germination of *B. elliptica* was not significantly reduced unless the concentration of probenazole was increased to 200 μg *a. i.*/ml. The effect of probenazole on mycelial growth of *B. elliptica* closely resembled that on germination of conidia. Always, mycelial growth was inhibited only at a high concentration (200 μg *a. i.*/ml) (Table 5).

Table 5. Effect of probenazole on spore germination and mycelial growth of *Botrytis elliptica*

Concentration of probenazole (μg active ingredient/ml)	Inhibition rate (%) Spore germination [1]	Mycelial growth [2]
2	17.47 a	1.07 a
20	22.53 a	2.67 a
200	97.47 b	16.80 b
Control	0.00 a	0.00 a

1. Spore suspension of *B. elliptica* (10^5 conidia/ml) was mixed with an equal volume of probenazole solution. Germination of conidia was examined and transformed to the inhibition rate.
2. Mycelial disc of *B. elliptica* was placed on the center of V-8 plates with different concentrations of probenazole and incubated at 20 C in darkness. The diameters of colonies were recorded at the 3rd day after inoculation. The inhibition rate was calculated.

DISCUSSION

Probenazole is a commonly used agrochemical capable of inducing resistance of rice plants against blast disease and bacterial leaf blight (9,11,26). In this study we found that probenazole also reduce lesion number caused by *B. elliptica* on lily plants. Even at a low concentration (4 mg *a. i.* per kg of soil), probenazole could effectively protect lily plants against gray mold. Moreover, an enhanced protective effect was also observed when probenazole granules were applied three times weekly in the rhizosphere of lily plants. The reduction of lesion number by probenazole indicated that spore germination, and/or the process of pre-penetration and penetration of *B. elliptica* might be retarded. However, the process of post-penetration might not significantly affected by the treatment of probenazole in our test conditions. In rice blast disease, effect of probenazole on the penetration of fungus and the disease development have been demonstrated (24).

The findings that probenazole did not significantly inhibit the mycelial growth of *B. elliptica* on V-8 agar at concentration of 20 μg *a. i.*/ml and only had inhibition effect at the concentration of 200 μg *a. i.*/ml were similar to the observation on *Botrytis cinerea* (24). Since we did not observe significant inhibition on the lesion size caused by *B. elliptica*, the growth of *B. elliptica* within lily tissues might be not affected by the treatment of probenazole. The effective protection at the concentration of 4 mg probenazole per kg of soil (about 2 mg per plant) implicated that the treatment of probenazole possibly induced the plant response to pathogen attack instead of function by itself. The protective effect of

probenazole may be attributed to the induced resistance of lily plants. The exploration of defense responses of lily will provide further evidence of disease resistance induced by probenazole.

In the preparative field test, probenazole in granule form showed a better efficacy in protecting the plants againt *B. elliptica* than in the solution form. Presumably, the granule form of probenazole remained longer in soil than the solution form. It is also possible that the additive or auxilary chemicals in the granules enhanced absorption of probenazole by lily roots. In addition, the ineffectiveness of probenazole to induce the resistance of lily against *B. elliptica* in the Oriental lily hybrid "Casablanca" and Easter lily hybrid "Risan No. 1" might be explained by different varieties or ages of lily plants.

SA accumulation in plant tissues treated with abiotic inducers was observed in many cases (1,4,5,17). However, the amount of SA did not increase in lily leaves after treatment with probenazole. A lack of accumulation of SA after probenazole treatment was also observed in Arabidopsis and tobacco; under which circumstance, the amount of SA increased only slightly. Nevertheless, the expression of pathogenesis-related proteins in Arabidopsis and tobacco and the resistance of tobacco to TMV were still enhanced (16). Nakashita *et al*. (16) suggested that probenazole may act at a step downstream of SA in the signal transduction pathway of plant defense system or a signal transduction pathway different from the SA pathway may be involved in probenazole-induced disease resistance. Our results on the quantification of SA in lily leaves also supported these hypotheses.

Probenazole is known to be metabolized to 1,2-benzisothiazole-3 (2H)-one 1,1-dioxide (BIT) in rice plants (28), and both compounds, although not adversely influencing fungal growth, can induce resistance of rice plants to blast disease. Moreover, the effect of probenazole is shown stronger than that of BIT in terms of inducing disease resistance (25). Within rice plants, probenazole and BIT may confer different reactions in rice tissues (13,18). Probenazole is able to induce expression of several defense-related genes (13) whereas BIT acts on the GTPase located in the cell membrane of rice and is possibly involved in the activation of G-protein (18). Predictably, more than one signal transduction pathway may be also involved in the probenazole-induced resistance of lily against fungal pathogens.

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摘　要

路幼妍[1]、陳昭瑩[1,2]. 1998. 撲殺熱 (probenazole) 誘導百合系統性抗灰黴病之研究 . 植病會刊 7:134-140. ([1.] 臺北市國立臺灣大學植物病理系. [2.] 聯絡作者：電子郵件 cychen@ccms.ntu.edu.tw；傳真 02-23657735)。

本研究探討施用撲殺熱促進百合抗灰黴病的效果。以撲殺熱 (4、40 及400 毫克 / 公斤土壤) 處理百合根圈，可明顯地減少灰黴病菌 *Botrytis elliptica* 感染百合葉片所造成的病斑數目；但對病斑大小並無顯著的影響。連續於接種前 7、4、1 天處理撲殺熱 (40 毫克 / 公斤土壤) 三次者，較分別於接種前 7、4、1 天處理一次者更能有效地減少病斑數目。小規模田間試驗顯示，施用撲殺熱 (40 毫克/公斤土壤) 並不影響百合的正常生長，且能有效地降低 *B. elliptica* 對百合的感染程度。實驗室試驗結果顯示撲殺熱濃度為 2 或 20 μg / ml 時不會抑制 *B. elliptica* 孢子發芽或菌絲的生長;僅當濃度提高至200 μg/ml時，則有些微的抑制作用，顯示撲殺熱可能經由誘導抗病性的作用而達到保護植物的效果。然而，以撲殺熱處理並不會明顯地造成百合葉片內水楊酸含量的增加。

關鍵詞：百合、灰黴病、撲殺熱、水楊酸、誘導抗病性