ments conducted during the 1989 growing season. In several of the experiments with low disease pressure, seed hydration without the addition of a biocontrol agent was sufficient to increase emergence to the level obtained with bio-priming or treatment with metalaxyl. However, combining these two strategies, i.e., bio-priming, resulted in the most reliable seed protection under all conditions.

Literature Cited

- Ali-Shtayeh, M.S., C.L. Lim-Ho, and M.W. Dick. 1986. An improved method and medium for quantitative estimates of populations of *Pythium* species from soil. *Trans. Br. Mycol. Soc.* 86:39-47.
- American Association of Cereal Chemists. 1979. Cereal laboratory methods. Amer. Assn. Cereal Chem. (AACC), St. Paul.
- Basra, A.S., S. Bedi, and C.P. Malik. 1988. Accelerated germination of maize seeds under chilling stress by osmotic priming and associated changes in embryo phospholipids. *Ann. Bot.* 61:635-639.
- Bennett, M.A. and L. Waters, Jr. 1987. Germination and emergence of high-sugar sweet corn is improved by presowing hydration of seed. *HortScience* 22:236-238.
- Bradford, K.J. 1986. Manipulation of seed water relations via osmotic priming to improve germination under stress conditions. *HortScience* 21:1105-1112.
- Cal, J.P. and R.L. Obendorf. 1972. Imbibitional chilling injury in *Zea mays* L. altered by initial kernel moisture and maternal parent. *Crop Sci.* 12:369-373.
- Callan, N.W., D.E. Mathre, and J.B. Miller. 1990. Bio-priming seed treatment for control of *Pythium ultimum* preemergence damping-off in sh-2 sweet corn. *Plant Dis.* 74:368-372.
- Elad, Y. and I. Chet. 1987. Possible role of competition for nutrients in biocontrol of *Pythium* damping-off by bacteria. *Phytopathology* 77:190-195.
- Elad, Y., I. Chet, and R. Baker. 1987. Increased growth response of plants induced by rhizobacteria antagonistic to soilborne pathogenic fungi. *Plant Soil* 98:325-330.
- El-Meleigi, M.A. 1989. Effect of soil *Pseudomonas* isolates applied to corn, sorghum and wheat seeds on seedling growth and corn yield. *Can. J. Plant Sci.* 69:101-108.
- Hadar, Y., G.E. Harman, A.G. Taylor, and J.M. Norton. 1983. Effects of pregermination of pea and cucumber seeds and of seed treatment with *Enterobacter cloacae* on rots caused by *Pythium*. *Phytopathology* 73:1322-1325.
- Harman, G.E. and A.G. Taylor. 1988. Improved seedling emergence by integration of biological control agents at favorable pH levels with solid matrix priming. *Phytopathology* 78:520-525.
- Harman, G.E., A.G. Taylor, and T.E. Stasz. 1989. Combining effective strains of *Trichoderma harzianum* and solid matrix priming to improve biological seed treatments. *Plant Dis.* 73:631-637.
- Harris, M.J. and D.A. DeMason. 1989. Comparative kernel structure of three endosperm mutants relating to seed viability and seedling vigor. *Bot. Gaz.* 150:50-62.
- Herner, R.C. 1986. Germination under cold soil conditions. *HortScience* 21:1118-1122.
- Howell, C.R. and R.D. Stipanovic. 1980. Suppression of *Pythium ultimum*-induced damping-off of cotton seedlings by *Pseudomonas fluorescens* and its antibiotic, pyoluteorin. *Phytopathology* 70:712-715.
- Kaiser, W.J., R.M. Hannan, and D.M. Weller. 1989. Biological control of seed rot and pre-emergence damping-off of chickpea with fluorescent pseudomonads. *Soil Biol. Biochem.* 21:269-273.
- Loper, J.E. 1988. Role of fluorescent siderophore production in biological control of *Pythium ultimum* by a *Pseudomonas fluorescens* strain. *Phytopathology* 78:166-172.
- Murray, G.A. 1990. Priming sweet corn seed to improve emergence under cool conditions. *HortScience* 25:231.
- Osburn, R.M. and M.N. Schroth. 1988. Effect of osmopriming sugar beet seed on exudation and subsequent damping-off caused by *Pythium ultimum*. *Phytopathology* 78:1246-1250.
- Osburn, R.M., M.N. Schroth, J.G. Hancock, and M. Henderson. 1989. Dynamics of sugar beet seed colonization by *Pythium ultimum* and *Pseudomonas* species: effects on seed rot and damping-off. *Phytopathology* 79:709-716.
- Styer, R.C. and D.J. Cantliffe. 1983. Changes in seed structure and composition during development and their effects on leakage in two endosperm mutants of sweet corn. *J. Amer. Soc. Hort. Sci.* 108:721-728.
- Taylor, A.G., Y. Hadar, J.M. Norton, and G.E. Harman. 1985. Influence of presowing seed treatments of table beets on the susceptibility to damping-off caused by *Pythium*. *J. Amer. Soc. Hort. Sci.* 110:516-519.
- Taylor, A.G., D.E. Klein, and T.H. Whitlow. 1988. SMP: Solid matrix priming of seeds. *Scientia Hort.* 37:1-11.
- Wann, E.V. 1986. Leaching of metabolites during imbibition of sweet corn seed of different endosperm genotypes. *Crop Sci.* 26:731-733.
- Weller, E.D.M. 1988. Biological control of soil-borne plant pathogens in the rhizosphere with bacteria. *Annu. Rev. Phytopathol.* 26:379-407.

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Flower Bud Blast in Easter Lily Is Induced by Ethephon and Inhibited by Silver Thiosulfate

Michael R. Mason¹ and William B. Miller²

Department of Plant Sciences, University of Arizona, Tucson, AZ 85721

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Abstract. Interactions of ethephon and irradiance reduction were investigated in terms of flower bud blasting in Easter lily (*Lilium longiflorum* Thunb. 'Nellie White'). Silver thiosulfate (STS) was investigated as an inhibitor of ethylene-induced bud abortion. Fourteen days of 92% irradiance reduction significantly increased bud abortion when plants were exposed to 2.1 mM ethephon. Bud abortion was 39% and 60% for plants grown in ambient and reduced irradiance, respectively. Silver thiosulfate was applied to plants 2 or 3 weeks after the date of the first visible bud, followed by ethephon treatment 2 days later. Bud abortion was significantly reduced by 1 or 2 mM STS, without phytotoxicity. Pretreatment with 1 or 2 mM STS as early as 4 weeks before ethephon exposure significantly reduced ethephon-induced bud abortion. Silver thiosulfate application could inexpensively reduce flower bud abortion during latter stages of greenhouse forcing of Easter lilies.

Easter lily is an important floriculture crop in the United States. Bud abortion (blasting),

a disorder that causes arrested development and death of floral buds before they reach anthesis, is a production problem with the Easter lily. Since lilies are priced partially by the number of flowers they carry, or "bud count," it is imperative to reduce or eliminate bud abortion for maximum grower profit.

Commercially, bud abortion refers to arrested bud development at an extremely early stage. Evidence of bud abortion is a tiny bump at the base of the inflorescence, usually subtended by a nondeveloped axillary leaf 5 to 20 mm long. Bud blast usually refers to death of larger (≥ 10 mm) buds. Blasted buds are diagnosed by a rapid drying of the tissue at the base of the bud, followed by its death but not its abscission. Technically, flower bud abortion is defined as the cessation of floral bud growth at any stage of development (De Hertogh et al., 1971). Thus, flower bud abortion encompasses flower bud blasting. Although we are only considering flower bud blasting (from the industry standpoint),

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¹Graduate Research Assistant. Presently, Graduate Research Assistant, Dept. of Horticultural Sciences, North Carolina State Univ., Raleigh, NC 27695.

²Assistant Professor of Plant Sciences, to whom reprint requests should be sent. Current address: Dept. of Horticulture, Clemson Univ., Clemson, SC 29634.

Table 1. Ethephon-induced flower bud abortion in 'Nellie White' Easter lilies as influenced by 14 days of 92% irradiance reduction. Irradiance reduction began 2 weeks after the visible bud stage. Ethephon was applied at the termination of irradiance treatments (4 weeks after the visible bud stage). Plants were subsequently held in nonshaded greenhouse conditions.

Ethephon concn (mM)	Irradiance	
	Natural	Reduced
	Flower buds aborted (%)	
0.0	0.0	3.3
2.1	38.6	60.1
4.2	53.7	53.8
Significance ^a		
Ethephon (Eth)	***	
Irradiance (Irr)	*	
Eth × Irr	NS	

^aMeans based on 10 plants per treatment.

NS,*,***Nonsignificant or significant at $\alpha \leq 0.05$ and 0.001, respectively.

Table 2. Ethephon-induced flower bud abortion inhibited by silver thiosulfate (STS) in 'Nellie White' Easter lily. STS was applied 2 weeks after visible bud in 1988 and 3 weeks after visible bud in 1989. Ethephon applications were made 2 days later.

STS concn (mM)	Ethephon (mM)		
	0	2.1	4.2
	Flower buds aborted (%)		
	1987/88		
0	0	74.7	100
1	0	21.5	68.1
2	0	3.8	54.4
	1988/89		
	0 mM	1.4 mM	2.8 mM
0	0	49.0	69.0
1	0	1.3	26.8
2	0	2.9	12.7
Significance ^a			
Ethephon (Eth)	***		
STS	***		
Eth × STS	***		

^aMeans for each experiment based on 10 plants per treatment.

***Significant at $\alpha \leq 0.001$.

we will use the correct technical term, abortion.

Previous studies with Easter lilies and *Hibiscus* have suggested that carbohydrate depletion can result in flower bud abortion or abscission (Force et al., 1988; Mastalerz, 1965), although other work has shown that flower bud carbohydrate level by itself is not the controlling factor in Easter lily bud abortion (Miller and Langhans, 1989). In several other studies that subjected Easter lilies to environmental conditions that presumably reduced plant carbohydrate, no increase in abortion was seen (Einert and Box, 1967; Heins et al., 1982; Weiler, 1978).

Weinbaum and Muraoka (1978) suggest that carbohydrate deprivation increased sensitivity to ethylene (as measured by *Prunus* fruit abscission), while exogenous sucrose fed to cut carnation flowers increased resistance to exogenous ethylene (Mayak and Dilley, 1976).

Here we report on experiments designed to determine Easter lily sensitivity to ethyl-

ene (applied as ethephon) and to examine the effect of greenhouse irradiance on Easter lily response to ethylene. Also, the use of silver thiosulfate (STS) was investigated as an economically feasible treatment to prevent ethylene-induced bud abortion.

'Nellie White' Easter lily bulbs were received 27 Oct. 1987 or 25 Oct. 1988 and vernalized for 6 weeks at 4.5°C. Bulbs were potted one per 15-cm-diameter (1.8-liter) plastic container, and placed into a 26/15C (venting/night) greenhouse. The growth medium consisted of a pasteurized 1 soil : 2 sphagnum peat : 2 perlite (by volume) mixture as amended by Bailey and Miller (1989). Plants were grown according to standard cultural practices for pest and disease control, and fertilized as described by Bailey and Miller (1989).

In a preliminary experiment conducted in Ithaca, N.Y., several low rates of ethephon were applied as 10-ml sprays to plants at a slightly earlier developmental stage than used in our Expt. 1. There was a linear response to ethephon in the range 0–3.5 mM, causing 0% to 87% flower abortion. Based on these results, similar ethephon levels were chosen for the current experiments.

Ethephon solutions were prepared using a commercially available formulation of 2-chloroethylphosphonic acid. Solutions contained one drop of dishwashing detergent per 100 ml solution (1988), or 0.1% Tween-20 (1989). Silver thiosulfate stock solutions were made as described by Reid et al. (1980). Stock solutions consisted of AgNO₃ (0.1 M) and Na₂S₂O₃ (0.1 M) and were stored in dark bottles at room temperature. Dilute STS was prepared on the day of application using a 1:4 molar ratio of silver to thiosulfate. Solutions contained surfactant as described above.

Irradiance reduction and bud blast. To determine if irradiance reduction increased ethylene-induced bud abortion, 10 plants each received the following treatments: full sun or 92% irradiance reduction and 0, 2.1, or 4.2 mM ethephon in a factorial design. Irradiance was reduced by suspending three layers of black mesh shade cloth over and around the bench on which the plants were placed. Irradiance was monitored with a LICOR meter and 190SA quantum sensors (LICOR, Lincoln, Neb.) to determine actual irradiance reduction achieved. Irradiance reduction treatments began 2 weeks after the first bud was visible (visible bud date), and lasted for 14 days. On day 14 (i.e., 4 weeks after the visible bud date), plants were sprayed with 10 ml of ethephon solution on the flower buds and upper 25% of the plant canopy. Control plants received water with a surfactant. All plant were then placed in ambient (nonreduced) greenhouse irradiance and observed daily for bud abortion until anthesis. The number of healthy or aborted flower buds was recorded and percent abortion calculated for each plant. Statistics were conducted on arcsin-transformed data and analyzed (CoHort Software, Berkeley, Calif.) as a randomized complete-block design with one replication of the irradiance treatment.

Irradiance reduction by 92% and ethephon treatments increased bud abortion in 'Nellie White' Easter lilies (Table 1). As ethephon levels increased from 0 mM to 4.2 mM, percentage bud abortion increased in full irradiance, but with reduced irradiance, percent bud abortion increased between 0 and 2.1 mM and then leveled off. At 2.1 mM ethephon, there was more ($P = 0.0462$) bud abortion on plants receiving reduced irradiance than on plants in full irradiance (Table 1). In all cases, the smallest buds in the inflorescence were the ones that aborted.

Silver thiosulfate and bud blast. To determine the effect of STS on ethephon-induced bud abortion in 1988, 10 plants each received 0, 1, or 2 mM STS, and 0, 2.1, or 4.2 mM ethephon in a factorial design. Silver thiosulfate was applied 2 weeks after the visible bud date. Two days after STS treatment, ethephon was applied. In 1989, 10 plants each received 0, 1, or 2 mM STS and 0, 1.4, or 2.8 mM ethephon in a factorial design. Silver thiosulfate was applied 3 weeks after visible bud. Two days later, ethephon sprays were applied and all plants were observed daily for bud abortion until anthesis. Total number of buds per plant and number of aborted buds were recorded. Arcsin-transformed abortion percentages were analyzed.

Silver thiosulfate at 1 or 2 mM greatly reduced ethephon-induced bud abortion during both years (Table 2). In these experiments, the ethephon × STS concentration interaction and main effects were all highly significant. The interaction, indicating that the protective effect of STS depended on the ethephon level used, was due to the discrete distribution of bud size classes in the lily inflorescence. Again, the smallest bud of the inflorescence showed greatest sensitivity to ethephon and aborted first.

Date of application of silver thiosulfate. This experiment was conducted to determine the duration of effectiveness of STS sprays on Easter lilies. Plant were treated with STS at flower bud initiation (FBI), visible bud (VB), and 2 weeks after visible bud (VB + 2 weeks) using 0, 1, or 2 mM STS. The growth stages FBI, VB, and VB + 2 weeks occurred 25 Jan., 21 Feb., and 5 Mar., respectively. At visible bud + 3 weeks (12 Mar.), plants were treated with 0, 1.4, or 2.8 mM ethephon in a factorial design. Fifteen plants were used per treatment. Plants were observed for bud abortion. Arcsin-transformed bud abortion percentages were analyzed, but nontransformed data are presented.

Silver thiosulfate was effective in reducing ethephon-induced bud abortion when applied at VB or later (Table 3). When applied at FBI, STS did not inhibit ethephon-induced flower abortion. At VB or VB + 2, increases in STS concentration reduced ethephon-induced bud abortion. Application of STS 1 week before ethephon exposure, i.e., VB + 2 weeks, gave the greatest protection from ethephon injury, and at 2 mM, essentially eliminated detrimental effect of 2.8 mM ethephon.

These data support previous findings that

Table 3. Length of STS effectiveness against ethephon-induced bud abortion in 'Nellie White' Easter lily. STS was applied at flower bud initiation (FBI), visible bud (VB), or 2 weeks after visible bud (VB + 2). In all cases, ethephon was applied 3 weeks after visible bud.

STS concn (mM)	Developmental stage at which STS was applied								
	FBI			VB			VB + 2 weeks		
	Ethephon (mM)			Ethephon (mM)			Ethephon (mM)		
	0	1.4	2.8	0	1.4	2.8	0	1.4	2.8
0	0.8*	39.7	55.6	0.8	38.9	60.9	0.0	32.8	61.3
1	1.1	39.8	55.9	0.0	13.9	39.4	0.9	3.1	6.3
2	0.0	31.9	59.4	0.0	5.5	23.4	0.8	0.8	0.8
Significance*									
Time	***								
Ethephon	***								
STS	***								
Time × STS	***								
Time × Eth	***								
STS × Eth	***								
Time × Eth × STS	***								

*Means based on 15 plants per treatment.

***Significant at $\alpha \leq 0.0001$.

ethylene is involved in Easter lily flower abortion (Rhoades et al., 1973), and could be a major cause of Easter lily bud abortion in commercial greenhouses. Damage from ethephon was recorded within 7 days of exposure. Although experiments have not been carried out to accurately determine dose-time-temperature responses of Easter lilies to ethylene, the work of Rhoades et al. (1973) indicates as little as 1 ppm ethylene for 12 h causes abortion ("blasting") of buds <50 mm long. These levels are within ranges recorded in commercial greenhouses: ethylene levels of 0.02 to 1.0 $\mu\text{l}\cdot\text{liter}^{-1}$ have been reported in moderately well-sealed polyethylene glasshouses equipped with gas-fired heaters (Hand, 1982).

Irradiance reduction (92%) for 14 days significantly increased bud abortion when plants were treated with 2.1 mM ethephon (Table 1). One effect of irradiance reduction in Easter lilies is a reduction in leaf and flower bud carbohydrate concentrations (Miller and Langhans, 1989). While this experiment clearly shows that irradiance reduction increases sensitivity of Easter lilies to ethephon, additional experiments are needed to discern the physiological mechanism and potential commercial significance.

De Hertogh et al. (1976) described *Lilium longiflorum* flowers as being primary, raised, primary, and secondary (arising from the axil of a primary flower). Because these flowers have different times of initiation and growth rates, they vary widely in size during forcing. As noted above, the smallest buds in an inflorescence were the ones that aborted most

readily. This response may explain the lack of enhanced flower abortion with 4.2 mM ethylene in the 92% irradiance reduction experiment: 4.2 mM ethephon caused abortion of all raised primary and secondary buds but was not enough to cause abortion of the more mature (unraised) primary buds, even if they had been stressed by carbohydrate deficiency. The difference in bud development also may explain the significant interaction of STS and ethephon (Table 2). Ethylene apparently acts first on the smallest buds, as those are the most susceptible, but the protective effect of STS is exerted most readily on the largest buds.

Silver thiosulfate at 1 to 2 mM was shown to be a potent inhibitor of ethephon injury. With higher levels of STS (4 mM), we observed phytotoxicity in the form of 1- to 2-mm-diameter brown spots on the buds and leaves. Silver thiosulfate applied early in crop development was less effective in inhibiting ethephon-induced bud abortion than later applications (Table 3). With the earliest application, less STS may have been absorbed by the plant since leaf surface area was less well developed and buds were less accessible to the spray, leading to increased STS runoff into the growing medium and less uptake due to adsorption onto the growing medium.

Using STS to prevent ethylene-induced bud abortion would be effective and cost efficient. Considering current silver nitrate prices (\$479 per 500 g, Sigma, St. Louis), the silver cost per plant would be \$0.0016 and \$0.0032 for the 1 and 2 mM STS treatments, respectively. Development of a system for

STS treatment of Easter lilies could provide protection against unexpected ethylene contamination in the greenhouse and would appear to be an economically feasible preventative cultural practice.

Literature Cited

- Bailey, D.A. and W.B. Miller. 1989. Whole-plant response of Easter lilies to ancymidol and uniconazole. *J. Amer. Soc. Hort. Sci.* 114:393-396.
- De Hertogh, A.A., A.N. Roberts, N.W. Stuart, R.W. Langhans, R.G. Linderman, R.H. Lawson, H.F. Wilkins, and D.C. Kiplinger. 1971. A guide to terminology for the Easter lily (*Lilium longiflorum* Thunb.). *HortScience* 6:121-123.
- De Hertogh, A.A., H.P. Rasmussen, and N. Blakely. 1976. Morphological changes and factors influencing shoot apex development of *Lilium longiflorum* Thunb. during forcing. *J. Amer. Soc. Hort. Sci.* 101:463-471.
- Einert, A.E. and C.O. Box. 1967. Effect of light intensity on flower bud abortion and plant growth of *Lilium longiflorum*. *Proc. Amer. Soc. Hort. Sci.* 90:427-432.
- Force, A.R., K.A. Lawton, and W.R. Woodson. 1988. Dark-induced abscission of hibiscus flower buds. *HortScience* 23:592-593.
- Hand, D.W. 1982. CO₂ enrichment, the benefits and problems. *Scientia Hort.* 33:14-43.
- Heins, R.D., H.B. Pemberton, and H.F. Wilkins. 1982. The influence of light on lily (*Lilium longiflorum* Thunb.): I. Influence of light intensity on plant development. *J. Amer. Soc. Hort. Sci.* 107:330-335.
- Mastalerz, J.W. 1965. Bud blasting in *Lilium longiflorum*. *Proc. Amer. Soc. Hort. Sci.* 87:502-509.
- Mayak, S. and D.R. Dilley. 1976. Effect of sucrose on response of cut carnation to kinetin, ethylene, and abscisic acid. *J. Amer. Soc. Hort. Sci.* 101:583-585.
- Miller, W.B. and R.W. Langhans. 1989. Carbohydrate changes of Easter lilies during growth in normal and reduced irradiance environments. *J. Amer. Soc. Hort. Sci.* 114:310-315.
- Reid, M.S., J.L. Paul, M.B. Farhoomand, A.M. Kofranek, and G.L. Staby. 1980. Pulse treatments with the silver thiosulfate complex extend the vase life of cut carnations. *J. Amer. Soc. Hort. Sci.* 105:25-27.
- Rhoades, A., J. Troiano, and E. Brennen. 1973. Ethylene gas as a cause of injury to Easter lilies. *Plant Dis. Rpt.* 57:1023-1024.
- Weiler, T.C. 1978. Shade and ancymidol-altered shape of potted *Lilium longiflorum* 'Ace'. *HortScience* 13:462-463.
- Weinbaum, S.A. and T.T. Muraoka. 1978. Chemical thinning of prune: relation of assimilate deprivation to ethylene-mediated fruit abscission. *HortScience* 13:159-160.