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Control of Field Root and Bulb Diseases of Easter Lily

The name "Easter lily" for *Lilium longiflorum* refers to the present use of the species as an ornamental plant in North America. Fifty years ago, according to the then current edition of *Encyclopaedia Britannica* (8): "In all countries [of Western Europe and North America] the chief lily of the market gardener is the White Trumpet, (*Lilium longiflorum*), the bulbs of which are raised in Japan and Bermuda. By forcing some bulbs, growing others in natural heat, and retarding the growth of others by keeping the bulbs in refrigerated chambers, the grower produces these tall White Lilies at all seasons of the year, though the greatest demand comes at Easter and Christmas. . . . The flowers are cut with long stems in the bud stage, packed firmly in very long shallow boxes and dispatched to the market."

During the second world war, when the supply of lily bulbs from Japan was cut off, an area in southern Oregon and northern California was developed to supply lily bulbs for planting in pots and for sale at Easter as flowering plants. To survive, the bulb industry in this region (and in the southeastern states) had to learn how to cope with diseases and pests. By the mid 1950s the industry was in serious trouble. Growers had previously planted lilies in "new ground," but now they were planting in fields in which earlier crops of lilies had been grown. The reappearance of Japanese bulbs on the American market was an imminent threat to the California and Oregon lily growers.

Foliage blight, caused by *Botrytis*, could be held in check by spraying with Bordeaux mixture about 25 times during a season, but there was no equivalent control for soilborne and bulb-borne diseases.

The decline in Easter lily bulb stocks was first represented to the University of California as due to nutritional difficulties, and work on lily nutrition and leaf scorch (9) was undertaken by the Department of Floriculture and the Department of Irrigation and Soils at the University of California at Los Angeles (3). Diseases damaging to the root system were found to be a large part of the problem. This was confirmed by discussions in the field with F. P. McWhorter of the USDA, then stationed at Oregon State University in Corvallis. A program of research on soilborne and bulb-borne diseases was initiated by the University of California's Department of Plant Pathology, first at Los Angeles and later at Riverside, and linked with a program already begun by the extension services in Humboldt and San Mateo counties. Representatives of field growers and forcers combined with University of California personnel and with McWhorter and others in Oregon to find the means of control.

The work in California took the form of laboratory and greenhouse research (J. G. Bald, the late Philip A. Chandler, R. A. Solberg, and others) combined with field trials and extension (A. O. Paulus and J. V. Lenz) and trials in commercial greenhouses (R. H. Sciaroni and R. W. Lateer). Because the work had a practical aim, most of the results were published so growers would have quick, direct access to the information they needed (5,13); relatively little was published in regular scientific periodicals (2,6,7).

Symptoms of Root and Bulb Rot

The full range of symptoms on Easter lilies eventually associated with root, bulb, and stem rot organisms was discovered only after healthy plants were obtained, first by rigorous pesticidal treatment, later by aseptic culture of bulb scales. Plants free from soilborne diseases and pests and growing in nearly pathogen-free soil were different from all Easter lilies grown commercially at that time. The main cultivar then was Croft. Bulbs and stems of healthy Easter lilies are white; the best plants from commercial stocks then had yellow stems and yellow bulbs pitted with minor blemishes and superficial lesions (Fig. 1). Bulb scales from most plants were rotted at the tips and definite lesions were present on the median portions of outer scales. The more resistant cultivar Ace had less obviously damaged scale tips and fewer medial lesions, but the bulbs were yellow.

On a completely healthy mature plant, depleted outer bulb scales form a sheath protecting much of the surface of the underlying white scales from direct contact with the soil. During the 1950s, most of the yellow outer bulb scales invariably failed to mobilize all their contents for translocation to the developing shoot; what remained served as substrate for organisms that had

Fig. 1. Bulb and bulbils from healthy (white) and diseased (yellow) stocks of Croft Easter lily.

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caused the surface yellowing and lesions, helping them colonize the underlying scales. Senescent scales rotted and underlying scales became yellow.

Plants with basal rot (11) were found quite often. The symptoms were large lesions in the basal plate, rotting at the base of adjacent scales, destruction of the basal root system, and sometimes disintegration of the bulb. Symptoms on the roots of most field-grown plants were less extreme, consisting of elongate lesions increasing in size and number and collapse of the greater part of the basal root system. Stem roots growing out above the bulb then supported the plant, but lesions soon appeared on them. The sequence, development, and collapse of the two root systems were accepted as normal. When completely healthy plants were grown in almost noninfested soil, both root systems survived until maturity.

Definite lesions, elongate and at first superficial, appeared on the stems of field-grown plants. In some years and some fields, they remained superficial; in others, many lesions spread around the stems and penetrated deeply, killing or severely damaging the shoots. Sometimes the stem lesion syndrome became serious in both cultivars, Croft and Ace, considerably reducing bulb yields.

Root and Bulb Rot Pathogens

Fusarium oxysporum was dominant among the pathogens appearing in the bulbil plants rigorously treated with pesticides. This might have been partly due to superior resistance against heat and pesticide treatment. Over a period, however, it was the pathogen most frequently isolated from lesions on bulbs, stems, and roots of field-grown Easter lilies.

After plants grown from sterile scales became available, the yellow discoloration of the outer bulb scales was proved to be due to mild, almost nonpathogenic strains of *F. oxysporum*. These strains penetrated the surface of the outer bulb scales and grew between the epidermal cells without going much deeper into the tissues. They induced reddish intercellular deposits of gum that appeared yellow at a macroscopic level.

Many strains of *F. oxysporum* were found on Easter lily, ranging in severity from surface invaders to those causing severe basal rot. In addition to differences in severity, indications of tissue specificity were noted. For example, isolates obtained from stem lesions seemed to cause severer lesions on stems than on roots, and the opposite was true for root lesion isolates (7).

The results of propagating the clonal bulb stocks and the occasional appearance of virulent strains of *Fusarium* led to the deduction that mild strains limited the growth of severe ones, giving them the status of latent infections that might become active at any time. Evidence for the presence of severe strains on bulbs with mild symptoms appeared during the first efforts to propagate healthy plants from treated bulb scales. Of several thousand bulbil plants, only a few expressed definite symptoms of disease. Aboveground, symptoms on individual plants varied from slight loss of color on lower leaves to severe chlorosis and dwarfing. Belowground, symptoms varied from yellow discoloration of bulbs or a few root lesions to typical Fusarium basal rot (2). Later evidence was consistent with the experience that mild symptoms were likely to mask the presence of severe strains of *F. oxysporum*.

A difficulty in accepting the idea that *F. oxysporum* was the main soilborne pathogen of field-grown Easter lilies in northern California was the cool

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temperate climate of that region. Other forms of *F. oxysporum* were adapted to specific hosts in warm temperate and even tropical climates. Initially, the presence on lily of a form species of *F. oxysporum* was understandable because of the subtropical origin of *L. longiflorum* (10) and the likelihood of introduction with its host; but forma *lilii* was serious on lilies grown in a cool climate. Temperatures recorded at the Oregon Bulb Research Station by W. L. Riddle gave a clue to this anomaly. During winter and spring, soil temperatures in the bulb fields were generally below 13 C, that is, below the level at which periderm readily forms a protective layer around lesions and wounds (1). A strain of *Fusarium* that could continue growing in the tissues at such temperatures and could avoid precipitation of gum or polyphenol barriers between the cells should be able to form lesions.

Isolates of the bacterium *Pseudomonas gladioli* pv. *gladioli* were cultured from some lesions on Croft lily bulbs, and other lesions gave *Fusarium* and *Pseudomonas* (Fig. 2). The combination of *Fusarium* and *Pseudomonas* was later isolated from stem lesions. Parallel studies of a disease on another host, scorch disease of rhizomatous iris, also yielded *P. gladioli* pv. *gladioli* from the rotting roots. The iris isolate inoculated to Croft lily was equally pathogenic on bulb scales. In culture, the lily and iris isolates were indistinguishable from those causing scab disease of gladiolus and were closely related to two named species from onion, *P. allii* and *P. alliicola* (renamed *P. gladioli* pv. *alliicola*) (18).

Several symptoms associated with *P. gladioli* pv. *gladioli* from Croft lily were confirmed by inoculation and reisolation of the pathogen. The bacterium produced round, slightly sunken lesions on bulb scales that were about the same size as bacterial scab lesions on gladiolus. On Ace lily, wound inoculation produced smaller and less well defined lesions. Other symptoms were shriveling of lower leaves, associated with damage to vascular bundles leading to those leaves, and twist, a malformation of leaves caused by tiny lesions produced by infection during development and emergence of shoots from the bulb.

Cylindrocarpon radicicola was isolated from a number of lesions on Easter lily, and an isolate from bulbs reinoculated to lily caused minute but clearly visible red lesions (6). Other *C. radicicola* isolates were not pathogenic. More recent studies elsewhere have shown this species to be pathogenic on species of lily other than *L. longiflorum* (17).

Experiments were conducted to compare the pathogenicity of these three organisms (6) singly and in mixtures of one fungus and one bacterium. The clones of the two fungi caused harmless, barely perceptible lesions. The mixture of *Fusarium* plus *Pseudomonas* at first caused lesions like those caused by *Pseudomonas* alone, but instead of being restricted in diameter to about 0.5 cm, lesions continued to grow until whole scales rotted and *Fusarium* sporulated over the surface. *Fusarium* inoculated alone slightly enhanced the damage due to wounding during inoculation but caused no discoloration (Fig. 3).

Cylindrocarpon in a balanced mixture with *Pseudomonas* suppressed the production of lesions; also, the red spots caused by *Cylindrocarpon* failed to appear. Higher proportions of either component in the mixture gave the same result as single inoculations with that component. The control isolate of *Cylindrocarpon*, which could not establish itself in the tissue, had no effect when inoculated as a mixture with *Pseudomonas*, whatever the proportions of fungus and bacterium in the inoculum (6).

The mutual enhancement of pathogenicity in mixtures of *Fusarium* and *Pseudomonas* provided an explanation for the severity of scale tip rot in the susceptible cultivar, Croft. Both *Fusarium* and *Pseudomonas* have been isolated from stem lesions also. Many isolates of *Fusarium* can produce stem lesions unaided (7), but in field-grown Easter lilies, the stem lesion syndrome most likely involves both organisms. Preplanting treatments with both fungicides and bactericides reduced stem lesions and improved root condition. The mutual antagonism between *Pseudomonas* and *Cylindrocarpon* indicates the complexity of interactions between microorganisms during infection and development of lesions and the likelihood of some anomalous results from pesticide treatment.

Wet, cold weather beginning early in the season has generally been associated with severe stem lesions. Reasons for the expansion of stem lesions under these conditions could be lack of defensive tissue reactions against *Fusarium* and encouragement of bacterial movement by water in the intercellular spaces. The temperature relations of the two organisms are consistent with their complementary action. *P. gladioli* pv. *gladioli* is pathogenic below 20 C and survives exposure in tissues to high temperatures as well as *F. oxysporum* does.

Pythium ultimum was isolated from Easter lilies in northern California but in our experience was not usually a serious root rot pathogen in the field. Its distribution in field lilies was occasionally observed when dead tissue of lesions was examined for oospores. These were found more in bulb scale tissue than in root remnants, possibly because dead roots disintegrated so easily. *Pythium* appears to be the pathogen most often causing root rot and accompanying foliar symptoms under forcing conditions (16).

Rhizoctonia solani was found early in our investigations on diseased bulbs and roots. Several isolates tested as possible causes of the yellow discoloration of bulbs failed to produce yellowing on bulbs but were slightly pathogenic on roots. *Rhizoctonia* seemed not to be a damaging pathogen of field-grown Easter lilies but has been described as a pathogen under forcing conditions.

Sclerotinia sclerotiorum was isolated from a basal rot lesion, but only once. It has been recorded elsewhere as a pathogen of Easter lilies.

Environment and Disease

Cultivation of an ornamental outside its natural range of climate is common. Combined with monoculture, this practice increases the incidence of disease and may be a reason why diseases of both foliate and underground plant parts play a critical role in the cultivation of Easter lilies in the Pacific Northwest. *L. longiflorum* is native to the islands of the Ryukyu Archipelago (10). The main island, Okinawa, is between 26 and 27° latitude, in a subtropical region. The California-Oregon border is at 42° latitude, in a cool temperate coastal zone. When such a plant is grown in a range of climates, local conditions may determine which of its pathogens become active. Easter lilies grown under conditions warmer than those in northern California have for a long time been subject to black scale disease, caused by *Colletotrichum* spp. (12). If black scale disease is present on lilies in northern California, we have not recognized it.

Fig. 2. Field-grown Croft lily bulb with yellowing and scale tip rot caused by *Fusarium oxysporum* and *Pseudomonas gladioli* pv. *gladioli*.

Fig. 3. Ace Easter lily inoculated in greenhouse with a clone of *Fusarium oxysporum*.

Propagating Healthy Plants from Bulb Scales

Individual bulb scales may be broken from an Easter lily bulb and kept in moist soil or planting medium until adventitious buds form at the base and swell into bulbils about 0.5 cm in diameter. These may be detached and planted separately, or the whole scale may be planted. During the 1950s, growers attempting to use this method of propagation suffered losses from rotting of the scales. McClellan and Stuart (14) introduced thiram as a preplanting treatment to reduce these losses.

On the same principle, a rigorous treatment was designed to destroy nematodes as well as fungal and bacterial pathogens. Twenty-three Croft Easter lily plants were chosen for health and vigor in a commercial greenhouse and grown to maturity. The preplanting schedule applied to the harvested bulbs before replanting included soaking them first in hot water plus 0.5% formaldehyde for 2 hours at 46 C, then in 1:1,000 phenylmercury triethanol ammonium lactate (Puratized Agricultural Spray) (12) for 24 hours, and dusting them with ferbam. One thousand bulb scales were removed and planted in moist vermiculite. About 6,000 bulbils were produced and 3,500 were detached and propagated individually in 3-in. pots. All but one scale survived to produce at least one bulbil.

The bulbil plants were grown for 5 months and maintained as single plant progenies (clones). Samples of 18 clones were then shipped in pots to northern California and planted in methyl bromide-treated soil. Other samples were sent to commercial greenhouses, where they were grown under forcing conditions similar to those applied to bulbs planted for the Easter trade. In health and productivity, these Easter lilies were far superior to commercial stocks.

There were clear differences between clones in agronomic characters, such as maturity, bulb and stem bulblet production, and flowering (bud count). Clonal differences were taken into account in any further selections for treatment and propagation. As the growers shifted from the disease-susceptible cultivar Croft to the slightly less attractive but more resistant cultivar Ace, selection of clonal stocks continued. Elimination of severe strains of latent virus, by discarding all clones with visible symptoms of virus infection, was part of the selection process.

The reduction of pathogens in Easter lily bulb stocks was carried one step further by test-tube culturing surface-sterilized scales and selecting those yielding sterile plantlets. This was done in sufficient numbers to provide a nucleus of bulbs of selected clones for planting in fumigated field soil in growers' farms. This material was used in inoculation tests for pathogenicity and other studies in the laboratory and the greenhouse and also in field trials. The field trials showed that: 1) soils in which lilies had not been grown before were relatively free from organisms pathogenic on lilies, 2) soils in which lilies had been grown before rapidly infected healthy plants, and 3) fumigation of infected soil with methyl bromide or methyl bromide-chloropicrin killed most of the pathogens carried over from previous crops of lilies. An apparently trivial but important finding was that completely healthy bulbs in pathogen-free soil were white. For the growers, yellow discoloration of bulbs, instead of being universally accepted as normal, became a warning signal that remedial action was needed.

Control

A standard dipping solution. A preplanting dip for the treatment of Easter lily bulbs was originally formulated on the basis of tests with *Fusarium* disease of gladiolus. A suspension of ferbam plus the proprietary material Lysol had been tried against the gladiolus *Fusarium* without much success. Used on lily bulbs, it seemed more promising. As the composition of Lysol was then being changed by the manufacturers, pentachloronitrobenzene (PCNB) was substituted, and the mixture became PCNB-ferbam. The mixture was obviously effective in reducing symptoms on Easter lilies (Fig. 4) and has remained in use ever since. Meanwhile, in Oregon, McWhorter (15) tested PCNB alone as a preplanting dip, with considerable success. The question arose whether dips for lilies should consist of a single material or a combination of materials. A series of field trials was designed to answer this and related questions.

Action of preplanting bulb dips. A mature bulb has 50–100 fingerlike bulb scales, modified leaves, closely folded together and arising from a compressed stalk, the basal plate (Fig. 5). A turgid bulb in moist soil has its scales pressed together, and its center is almost impermeable to direct invasion by water and waterborne microorganisms. During dipping, the bulbs are immersed in a turbulent suspension of pesticide. The outer bulb scales open and close sufficiently to force the liquid in and out between them, leaving a residue of pesticide on all contacted surfaces. Deposits of PCNB-ferbam remain visible between bulb scales after a growing season in the field and presumably are still potent. Infested scale tips and remnants of the basal root system from the previous season are saturated or coated by dipping, particularly with PCNB-ferbam. Once planted and compressed again by the surrounding soil, the bulb has a series of defensive surfaces between the scales. The passage of *Fusarium* or other pathogens from outer infested senescent scales to the surfaces of underlying scales is checked, and discoloration and lesions are thereby reduced.

Emerging roots and shoots are also protected, although the fungicide barriers around the origins of new roots and the scale tips are less well defined. In an experiment with Ace lilies, bulbs were dipped and planted in containers with soil temperature held at 10 C. PCNB-ferbam checked even advanced basal rot lesions and allowed affected bulbs to produce apparently normal plants. Bulbs with similar lesions not treated with PCNB-ferbam rotted in the soil or barely survived to produce weak plants.

Combinations of fungicides and bactericides in bulb dips. Fungicides tested as preplanting bulb dips for Easter lilies were routinely compared with the standard PCNB-ferbam mix. The original recommendation was 2 lb of each component in 100 gal of water. Mainly to accommodate loss of materials from repeated use of dipping suspensions, growers increased the amounts to about 6 lb of 75% PCNB and 3 lb of 76% ferbam.

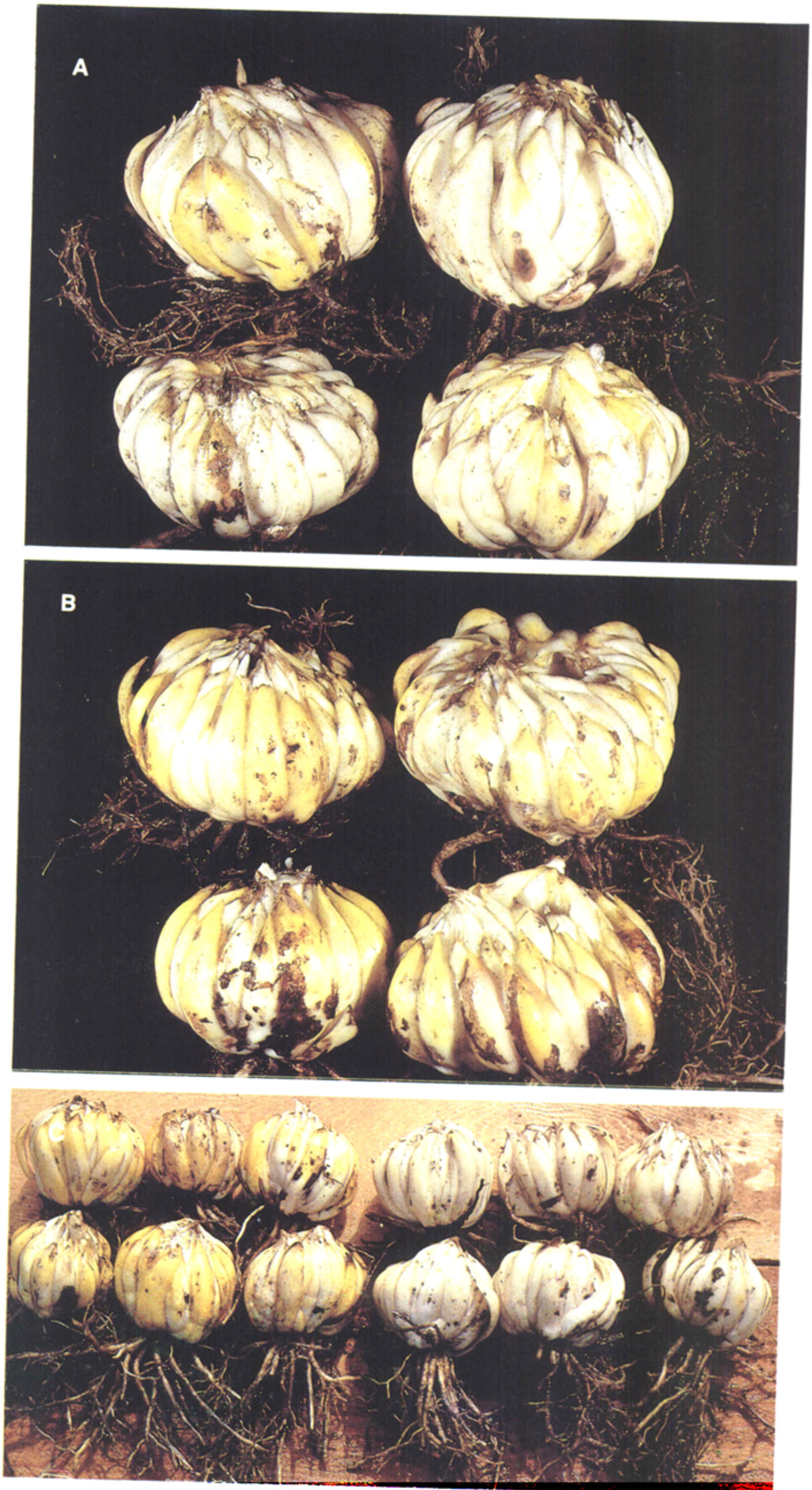

Fig. 4. Effect of preplanting dip on harvested bulbs: (A) Ferbam treatment, (B) PCNB treatment, and (C) PCNB-ferbam treatment (white bulbs) and no treatment (yellow bulbs).

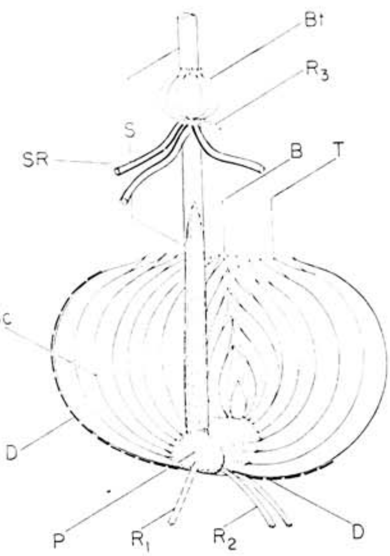

Fig. 5. Longitudinal section through bulb and stem base of a mature Easter lily. B = developing bud of next year's shoot, Bt = stem bulblet, D = dead and depleted outer scale, P = basal plate, R_1 = basal roots of current season's shoot, R_2 = basal roots of next year's shoot, R_3 = first root on stem bulblet, S = current season's shoot (lower part sectioned, upper part surface view), Sc = bulb scales, SR = stem root, and T = scale tips.

Other materials tested were used at rates recommended by the manufacturer. Of those, only benomyl seemed to have qualities for commercial application that might make it a useful addition to or substitute for the standard preplanting dip.

Addition of a bactericide, Agrimycin (streptomycin plus a small proportion of oxytetracycline), to the preplanting dip was tested after the presence of *Pseudomonas* in bulb and stem lesions was recognized. Although the main constituent was not very active against pseudomonads, Agrimycin significantly decreased stem lesions. Its practical value was doubtful, however.

Later, a search was made among nonantibiotic bactericides that had been forgotten when antibiotics were introduced. Thymol was chosen for study because it was found to be lethal to *Pseudomonas*. It was almost insoluble in water, but a saturated solution, less than 1:1,000 w/v, was effective. One gram could be fully dispersed in 1 L of PCNB-ferbam suspension and appeared to add to its efficiency when used on detached scales of Ace lilies. The scales, treated after being infested with *Pseudomonas*, were planted in pots and grown to maturity before records were taken.

Two field trials and a greenhouse experiment with Ace lilies used thymol as a bactericide in various mixtures with PCNB, ferbam, and benomyl. In the first field trial, addition of thymol, particularly to PCNB-ferbam, significantly reduced stem lesions; the lesions, though numerous, were superficial, so thymol did not increase the yield of bulbs. In the greenhouse trial, root condition was improved by the addition of thymol. In the second field trial, superficial and atypical stem lesions appeared equally with all treatments; indications were that most lesions were due to infection directly from the soil.

The data on bulb color, lesions other than those on the stems, and yield showed PCNB-ferbam significantly better than materials used singly. The most effective preplanting bulb dip was PCNB, ferbam, benomyl, and thymol applied together. Addition of benomyl without thymol to PCNB-ferbam slightly improved the yield of bulbs, without altering the total yield, by changing the relative proportions of bulbs to stem bulblets produced (4).

Overall control procedures. Preplanting bulb dips reduced inoculum of pathogens left in the soil and carried over from one Easter lily planting to the next but did not eliminate soil infestation. Continual cropping with lilies was obviously dangerous. The question arose whether, for example, rotation with pasture between crops of Easter lilies, which were reasonably healthy and protected by preplanting dips, would be sufficient to keep soilborne inoculum at a commercially acceptable level. Experience has shown this is possible. The expensive procedure of soil fumigation with methyl bromide-chloropicrin is seldom necessary; fumigation with nematicides is more useful.

Recommendations were prepared for maintaining relatively disease-free stocks of lilies in mother blocks of elite clones, dipped and planted in fumigated soil. Growers adopted the principles of the plan, adapting it to their own particular situations. Instead of propagating bulbs from stem bulblets, as they had done for many years, they planted bulb scales after hot water treatment against nematodes and dipping against fungal pathogens. Deep planting of bulb scales was essential for the production of single bulblets of maximum size. During autumn, the yearling bulblets were dug, treated, and replanted. Bulbs of forcing size were obtained 3 years after scales were planted, and some were ready after 2 years. In addition to raising commercial stocks in this way, growers continued the process of clonal selection and testing of new clones.

Comment

Growing Easter lilies is a small, specialized segment of agriculture. It does not command much research money. Most of the people who studied its problems worked on them part-time. The logical order of investigation was often reversed because a cure of sorts had to be found before diseases were understood. Repeated observations often had to replace experiments and replicated field trials.

Only in retrospect, when there is no longer an opportunity to test results of doubtful validity, do these studies appear to have a consistent scientific rationale. A summary of the work as a whole had to wait until disease problems were at least partly understood and control measures were fitted into a system of agriculture that gave stability to the industry.

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