2.5 pounds of lime to 100 gallons of water) or zinc oxide (2 pounds to 100 gallons) may be used. For severe cases in Florida, twice the indicated dosage of zinc sulfate and lime is recommended. Sprays should be applied soon after new growth appears.

Iron deficiency occasionally occurs in California, primarily in trees on calcareous soils. It is characterized by yellowing of the major portion of the leaf, with the veins remaining green. Little change is caused in fruit size or shape or in leaf size. Soil applications of sulfur and similar acidifying materials have generally been only moderately successful. Reduction in water applications to trees in the problem soils has usually resulted in a lessening of the chlorosis.

Copper deficiency has been reported in Florida on young avocado trees. Symptoms include development of S-shaped shoots and lateral branches, premature defoliation, a multiple-bud condition, and dieback. This trouble is usually corrected by soil or spray applications of copper sulfate.

The presence of excess chlorides in soil or irrigation water is the primary cause of tipburn of leaves in California. Tipburn causes a considerable reduction of green-leaf area, with consequent weakening of the tree. The dead areas are also commonly invaded by fungi such as Botryosphaeria ribis, which then spread to the fruit. Control of tipburn is difficult unless water with a lower chloride content is available to use in leaching the soil.

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Ethylene From Diseased Plants

C. E. Williamson, A. W. Dimock

A number of symptoms of some fungus, bacterial, and virus diseases of plants are similar to those that develop on plants exposed to ethylene gas, the colorless, inflammable C₂H₄. Those common symptoms include epinasty, or downward bending of leaves; yellowing; excessive overgrowths; retardation of growth; and premature dropping of leaves, flowers, and fruits. The development of such symptoms suggests the possibility that the diseased plant tissue may produce ethylene.

The role of ethylene gas in inducing various physiological responses in plants has been the subject of investigation for more than 50 years. The earliest recorded observation was made in Germany in 1864 on the toxic effects of illuminating gas on trees. The identification in 1901 of ethylene as the cause of the observed physiological effects of illuminating gas led to the accumulation of a large volume of information on the morphological, anatomical, and biochemical responses of plants to ethylene.

The citrus industry in California established the practice of degreening lemons with the products of incomplete combustion from kerosene stoves or the exhaust gases of internal combustion engines. In 1924, ethylene was identified as the constituent responsible for the loss of the green color.

Our present-day concept of fruit
ripening, especially the sharp rise in respiratory rate with ripening—termed the climacteric—was developed in England from studies of apples in storage. The fundamental effect of ethylene is to initiate the climacteric rise in respiration. Emanations from ripening fruit will stimulate the onset of the climacteric in green fruit. The active emanation from ripening apples was identified by chemical analysis as ethylene in 1934. Subsequently, in all cases of physiologically active emanations investigated chemically, the active substance evolved has been shown to be ethylene. That is now so well established that the demonstration of a physiologically active emanation by any of the bioassay methods is a strong indication that ethylene is present in the gases evolved. In fact, F. E. Denny and Lawrence P. Miller, of the Boyce Thompson Institute, wrote in 1935: "... Any evidence that some other chemical is the principal factor must be accompanied by proof that ethylene was not present as an impurity in amounts sufficient to give a concentration of at least 1 part of ethylene in 20 million of air." For chemical identification, at least 25 to 100 parts per million by volume of ethylene is necessary. Where only small quantities of plant material are available or the amount of ethylene is extremely small, the chemical methods are useless. Bioassay methods thus become of paramount importance.

The response of various plant parts has been used to demonstrate the production of physiologically active emanations by plant tissues, especially by ripening fruit. Inhibition of sprouting of potato, inhibition of seed germination, and epinasty of sunflower, potato, and tomato leaves have all been used to detect ethylene. However, the triple response of etiolated pea seedlings, defined as a decrease in rate of growth in length and a swelling and horizontal placing of the region growing while exposed to ethylene, is the only bioassay method that readily yields quantitative results. The triple response has been demonstrated repeatedly to have distinctive qualitative and quantitative characteristics for different concentrations of gas. Etiolated Alaska pea seedlings are extremely sensitive and will respond to as little as 0.025 to 0.05 part ethylene per million of air. The triple response of etiolated pea seedlings has had widespread use since 1944.

Many species of fungi growing in culture on an artificial medium of one sort or another have been tested for the production of an active emanation. Rhizopus nigricans, baker’s yeast, Diploporthe citri, Diplodia natalensis, Alternaria citri, Penicillium italicum, Sclerotinia sclerotiorum, Aspergillus niger, Oospora species, Alternaria species, Diplacarpus rosae, Cryptostictis caudata, Mycosphaerella ligulicola, Alternaria zinniae, and Histoplasma capsulatum (a pathogen affecting man) failed to give a positive response by bioassay methods. Penicillium digitatum, on the other hand, has been shown repeatedly to produce ethylene in abundance from a culture medium. Blastomyces dermatitidis and B. brasiliensis, causal agents of blastomycosis, a lung disease of man, also produce ethylene from a synthetic medium.

The earliest report of an active emanation from healthy tissues is credited to a Captain Seife, who observed that the gases from oranges packed in the hold of a ship were apt to cause premature ripening of bananas. His observations were verified in the laboratory by H. H. Cousins, who in 1910 reported: "It was shown, however, by direct trial that the emanations from oranges stored in a chamber were found to have the effect of bringing about a premature ripening of bananas if these gases were passed through a chamber laden with this fruit."

Similar observations made by the United Fruit Company before 1917 showed that some bananas ripened
more rapidly than the bulk of a shipment and this ripening tended to occur in pockets. The ripe pocket often acted as a starting point for the ripening of an entire bin of bananas. The ripe pocket was not caused by heat or carbon dioxide accumulation, although there seemed to be a direct correlation between respiration rate and accelerated ripening. A United Fruit Company chemist in 1923 reported the presence of an unknown gas in the respiration products of ripe bananas which caused accelerated ripening of green bananas.

In 1932 the volatile substances from ripe apples and pears were observed to inhibit the normal sprout development of potatoes. Healthy immature apple fruits were demonstrated in 1935 to produce ethylene in small amounts. When immature fruits were placed in closed containers, the accumulated volatile substances induced the climacteric, but similar fruits ventilated by a continuous stream of pure air did not ripen. Apparently a threshold value for the stimulating dose exists below which no effect is produced.

Denny and Miller reported a long list of plant tissues that produced an active emanation, as indicated by epinasty of potato leaves. The list included a wide variety of fruits and vegetables and the flowers, leaves, stems, seeds, and roots of other plants. Elmer Hansen, working with pears in storage in 1942, studied the relationship between ethylene production and respiration and observed that ethylene production was either greatly retarded or inhibited under anaerobic conditions, although little difference in the amount of carbon dioxide produced under aerobic and anaerobic conditions was obtained. Ethylene produced by Comice pears increased steadily from 0.11 milliliter per kilogram per 24 hours at 0°C to 0.19 at 10°C, to 0.44 at 20°C, then dropped to 0.33 at 30°C, and ceased at 40°C.

Investigators had observed as early as 1936 that the volatile combustible matter produced by orange fruits increased rapidly when the fruits became infected with Penicillium digitatum. Because the amount of combustible volatiles produced by P. digitatum growing on agar was very small, the rapid increase in amount of volatile combustible matter that occurs with the onset of fungal attack was assumed to be due to injury to the fruit and not to byproducts of the fungus. Similarly other workers found that when Golden Delicious apples in the postclimacteric state became infected with Penicillium and Botrytis, a rapid rise in the amount of volatile compounds occurred. No tests were made to determine the presence of ethylene in these cases.

The emanations of citrus fruits infected with Penicillium digitatum, Diaporthe citri, Alternaria citri, or Diplodia natalensis have been found to induce epinasty of the test plant leaves more quickly than the emanations of sound fruits. It was found also that the emanations of lemons infected with green mold, Penicillium digitatum, caused a rapid yellowing of green lemons and a shedding of the stem ends. The effects seemed to be due to ethylene. The emanations over a 24-hour period from a single lemon infected with P. digitatum contain approximately 0.064 milliliter of ethylene.

Recognition of the facts that diseased tissues produce considerably more ethylene than do healthy tissues and that a number of symptoms of common plant diseases are strikingly similar to the responses of healthy plants to exposure to ethylene gas led to the hypothesis that the symptoms of certain plant diseases may be caused by increased ethylene production. The rapid yellow coloration and early abscission of leaves infected by certain pathogens certainly suggest the action of a substance such as ethylene.

Two diseases characterized by such symptoms are the black spot of rose and the shot hole of cherry, caused by Diplolarion rosae and Coccomyces hielalis, respectively. An investigation was undertaken by C. E. Williamson...
to determine whether diseased tissues produced increased amounts of ethylene and, if so, to correlate the symptoms of the disease with the quantity of ethylene produced.

Different amounts of ethylene were indeed found to be produced by the different diseases, the amount apparently depending upon the pathogen involved. Large amounts of ethylene were produced by rose leaves infected with *Diplocarpon rosae*, cherry leaves infected with *Coccomyces hiemalis*, and chrysanthemum flowers infected with *Mycosphaerella ligulicola*. Somewhat less ethylene was produced by chrysanthemum flowers infected with *Botrytis cinerea* and rose leaves infected with *Cryptosporella umbrina*. A still smaller quantity, though significantly larger than that produced by healthy tissue, was produced by rose leaves infected with *Sphaceloma rosarum* and carnation foliage infected with *Alternaria dianthi*.

In the other diseases studied, the infected tissue produced little more ethylene than did the comparable healthy tissue. Bean leaves infected with the halo blight bacterium, *Pseudomonas phaseolicola*, did not produce ethylene in a detectable quantity. In the black spot disease of rose ethylene production is at a maximum while the infected leaf is green, decreases as the leaf becomes yellow, and ceases when the leaf becomes brown. In those experiments, healthy leaves generally produced small quantities of ethylene, the amount depending to some extent upon the species of plant.

Plants infected with certain viruses were found by A. Frank Ross and Williamson to produce different amounts of ethylene. Large amounts of ethylene were produced by *Physalis floridana* plants infected with potato virus Y, provided the temperature of the greenhouse was such as to permit the development of local lesions and consequent necrosis or death of the tissues involved. Other viruses that produce local lesions on inoculated leaves were employed. They included tobacco mosaic virus (*Marmor tabaci*) on *Nicotiana glutinosa*, *Datura stramonium*, and *Phaseolus vulgaris* var. Scotia; alfalfa mosaic virus (*Marmor medicaginis*) on *Phaseolus vulgaris* var. Scotia; tobacco ring spot virus (*Annulus tabaci*) on *Nicotiana tabacum* var. Turkish; and potato virus X (*Annulus dubius*) on *Gomphrena globosa* and *Nicotiana tabacum* var. Turkish.

Except for tobacco mosaic virus in leaves of Scotia bean and potato virus X in Turkish tobacco leaves, the diseased leaves produced greater amounts of ethylene than did corresponding healthy leaves. Those two failures apparently were not due to peculiarities of the plants, as healthy controls produced detectable amounts of ethylene and leaves of these same plants infected with other viruses produced large amounts of ethylene. In general, the amount of ethylene produced was roughly proportional to the extent of necrosis.

Leaves of Better Times rose infested with the two-spotted spider mite, *Tetranychus bimaculatus*, produced considerably more ethylene than comparable healthy leaves. Leaves of *Physalis floridana* and of *Nicotiana tabacum* with necrotic lesions induced by copper sulfate also produced ethylene, but in slightly smaller amounts than did comparable leaves with lesions induced by viruses. Healthy leaves shredded with a sharp knife just before testing generally produced more ethylene than did uninjured leaves, but the increased quantity varied with the species of plant. These results indicate that ethylene is a product of injured or dying cells rather than the cause of the necrosis that occurs.

The fungus diseases investigated appear to belong in three categories. With some diseases, such as those caused by the obligate parasites, relatively little ethylene is produced; with certain others, such as black spot of rose and shot hole of cherry, caused by facultative saprophytes, relatively large amounts of ethylene are produced. Between those extremes is a
large group of diseases with which intermediate quantities of ethylene are produced. Observations of diseases in this category indicate that in some cases slow yellowing and eventual abscission may occur. In each of the five diseases of roses that were studied, there was a positive correlation between the degree of yellowing and defoliation and the amount of ethylene produced. Only with black spot was there rapid defoliation and production of large amounts of ethylene. The anthracnose and the brown canker diseases may result in some yellowing and possibly abscission and production of a moderate amount of ethylene. With the rust and the powdery mildew diseases there was little or no yellowing or abscission and only negligible amounts of ethylene were produced. It appears, then, that the large amount of ethylene produced with certain diseases is the cause of the rapid yellowing and early abscission of infected leaves.

Flowers as well as foliage may be affected by ethylene from diseased tissues. In experiments reported by Dimock and Baker in 1950, it was shown that flower drop ("shelling") of snapdragons and calceolarias and closing of the blooms ("sleepiness") of carnations could be caused by the enclosure of diseased tissues with normal healthy snapdragon, calceolaria, or carnation flowers. In these tests, chrysanthemum flowers infected with the chrysanthemum ray blight fungus, *Mycosphaerella ligulicola*, or with *Botrytis cinerea* were used as ethylene sources.

In other experiments, conducted by C. W. Fischer, Jr., and J. R. Keller in 1951, brominated activated charcoal enclosed in sealed containers with flowers was highly effective both in controlling growth of molds and in preventing ethylene damage to the blossoms. In those tests, chrysanthemum flowers infected with *M. ligulicola* and carnation blooms infected with *B. cinerea* were used as sources of ethylene. The brominated activated charcoal was not effective unless it was in close proximity to the blooms, but not touching them.

Since healthy cells normally produce a small amount of ethylene, there would seem to be a minimum threshold concentration which must be exceeded if the toxic effects of ethylene are to occur. Investigations at Cornell University of storage of flowers have demonstrated that if certain ethylene-sensitive healthy flowers are stored in airtight containers enough ethylene is produced to cause self-injury. With most healthy tissues, ethylene production is slow, and, unless confined, dissipation into the atmosphere is sufficiently rapid to prevent accumulation of ethylene within plant tissues in toxic quantities.

Stimulated ethylene production appears to be associated with aging, diseased, or dying cells. In such cells the normal respiratory cycle may be partially disrupted to produce ethylene in abnormal quantities. Necrosis or death of cells does not seem to be the entire answer, although in experiments where phytotoxic chemicals were used there was a positive correlation between the degree of necrosis and the quantity of ethylene produced. Where injury to the surface layer of plant cells occurs, as by feeding of spider mites, a large number of cells are affected but necrosis is not readily evident.

The observed relationship between temperature and ethylene production, and the decrease in ethylene production to near-zero under anaerobic conditions have direct application to storage of cut flowers. Recent work at Cornell University on low-temperature storage of flowers demonstrated that for most flowers the length of the storage period and the quality of the flower after removal from storage was directly related to temperature and to type of storage pack. The best results were obtained with temperatures near 0°C (32°F).
and with a nearly airtight pack or container.

For prepackaged flowers or for flowers stored in water in a moderately tight cold room, the potential damage that can be done if ethylene-producing diseased material is included is serious. Observations have indicated that once a blossom is injured by ethylene it immediately becomes more liable to attack by Botrytis. Thus a chain-reaction type of response is initiated that will lead to more ethylene production and thus to more injury.

The observed effects of ethylene produced by diseased plant tissues emphasize the desirability of either near-perfect control or complete elimination of plant disease. If adequate disease control is maintained in field or greenhouse and in the storage room, one of the important factors in successful long-term storage of cut flowers is reduced to negligible proportions.

G. E. Williamson, assistant professor of plant pathology in Cornell University, is a native of Indiana. His work with diseases of ornamental plants began at Cornell in 1937. His studies on ethylene effects began with the demonstration of stimulated ethylene production by rose leaves affected with black spot. He is a graduate of Wabash College and Cornell University.

A. W. Dimock, professor of plant pathology in Cornell University, has specialized in diseases affecting ornamental crops for many years. His interest in ethylene effects was a natural consequence of his close association with Dr. Williamson during his studies on ethylene production by diseased plant tissues and with Dr. C. W. Fischer, Jr., during his studies on effects of ethylene on cut flowers in storage.

For further reference:
C. E. Williamson: Ethylene, a Metabolic Product of Diseased or Injured Plants, Phytopathology, volume 40, pages 205-208, 1950.

Apricot and Almond Brown Rot

E. E. Wilson

Probably nowhere else in the world are stone fruits grown in such variety and number as in the three States that border the Pacific Ocean. There are grown the edible varieties of peaches, nectarines, apricots, the three types of cherries, plums, prunes, and almonds. There, too, are produced the numerous other species of stone fruits that are utilized as rootstocks for the edible sorts. The orchards in the region are composed not of a few trees of miscellaneous kinds grown in the back yards of scattered farm homes but many trees of the same kind in contiguous blocks extending over hundreds of acres. One entire locality may be given over to cherries, peaches, or prunes; another may be planted only to apricots and peaches; and another to almonds and peaches.

The foundation stocks of all these stone fruits were introduced into the region. Some came from the Orient and others from Europe; some were introduced first into eastern United States and later brought west; others came directly from their foreign home. With the establishment of the fruit industry in the Pacific coast region came disease problems: The frequent shipments of nursery stock and other propagative material provided ample opportunity for introduction of diseases. Once introduced, the diseases found large numbers of hosts to affect. Typical of the maladies occurring on stone-fruit trees in this region are the